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Farmland ponds as unique aquatic islands for plant diversity

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“It's incredible how many things you find while looking for something else”

Content

Abstract

Wetlands are among the world's most vulnerable ecosystems, and in the Mediterranean region, farmland ponds are particularly exposed to the influence of surrounding agricultural land use while still supporting unique biodiversity. These small waterbodies are widely recognized as "island-like" systems; however, key functional differences exist among them. Ponds host not only strictly aquatic plants but also adjacent terrestrial species, and living at the land–water interface, these species interact with aquatic environments and, as for the aquatic species, they can be influenced by water physical and chemical properties. With this work we aimed to: i) provide an accessible collection of pond vegetation data with water physico-chemical measurements, serving as a resource for investigating the links between plant communities and their environmental settings; ii) analyze how the extent of agricultural land use and various factors at multiple spatial scales influence the diversity and structure of plant communities; iii) examine beta diversity patterns to identify levels of biological isolation among ponds and explore the relevance of island biogeography concepts to ponds within agricultural landscapes. We studied 115 ponds located in landscapes with varying agricultural land-use extents, surveying aquatic and riparian communities and water parameters. This thesis has enabled the creation of a dataset covering plant diversity and abundance, community composition, habitat types, and water chemistry parameters for ponds in Italy. Furthermore, this work has shown that plant richness decreased with increasing agricultural land use and that pond-specific features, possibly related to pond management, are more important than landscape-scale features in shaping plant diversity. It has also revealed the presence of high beta diversity among ponds, primarily driven by species turnover, making them resemble traditional island systems. Despite this, unique local processes and distinct dynamics distinguish them from true islands.

Riassunto

Le zone umide sono tra gli ecosistemi più vulnerabili al mondo e, nella regione mediterranea, i laghetti agricoli sono particolarmente esposti all'influenza della

gestione agricola circostante, pur sostenendo una biodiversità unica. Questi piccoli corpi idrici sono ampiamente riconosciuti come sistemi "simili a isole"; tuttavia, esistono differenze funzionali chiave tra essi. I laghetti ospitano non solo piante strettamente acquatiche, ma anche specie terrestri adiacenti che, vivendo all'interfaccia tra terra e acqua, interagiscono con l'ambiente acquatico e, come le specie acquatiche, possono essere influenzate dalle proprietà fisico-chimiche dell'acqua. In questo studio abbiamo avuto come obiettivi: i) fornire una raccolta accessibile di dati sulla vegetazione degli stagni con misurazioni fisico-chimiche dell'acqua, come risorsa per indagare i legami tra comunità vegetali e condizioni ambientali; ii) analizzare come l'estensione dell'uso agricolo del suolo e vari fattori a molteplici scale spaziali influenzano la diversità e la struttura delle specie vegetali; iii) esaminare i pattern di beta diversità per identificare i livelli di isolamento biologico tra gli stagni ed esplorare la rilevanza dei concetti di biogeografia insulare per gli stagni in paesaggi agricoli. Sono stati studiati 115 laghetti ubicati in paesaggi con diversa estensione dell'uso agricolo del territorio, analizzando le comunità acquatiche e ripariali e i parametri idrici. Questa tesi ha permesso la creazione di un dataset che copre la diversità e l'abbondanza delle piante, la composizione delle comunità, i tipi di habitat e i parametri chimico-fisici dell'acqua per gli stagni in Italia. Inoltre, questo lavoro ha mostrato che la ricchezza delle piante diminuisce con l'aumento dell'uso agricolo del suolo e che le caratteristiche specifiche degli stagni, probabilmente legate alla loro gestione, hanno un ruolo più significativo rispetto a quelle a scala paesaggistica nel determinare la diversità delle piante. È stata anche rilevata un'alta diversità beta tra gli stagni, principalmente dovuta alla sostituzione di specie, che li fa assomigliare ai tradizionali sistemi insulari. Nonostante ciò, processi locali unici e dinamiche distinte li distinguono dalle vere isole.

Author contributions for published and submitted chapters

Chapter 1

SC and RB collected the data in the field with contributions from CA, EF, TF, and FM. SC, CA, RB, and SM designed the sampling plan. SC and RB identified vascular plant species with contributions from FM and TF. TF identified Charophyceae species. AdV performed the chemical analysis in the laboratory. SC and RB assembled the dataset with contribution from LS. FC performed the semi-automatic habitat EUNIS classification. SC did the analysis. SC led the writing with contributions from GB. SC prepared the figures. CA and GB supervised the research. All authors critically revised the manuscript and approved the final version.

Chapter 2

SC, CA, RB, EF, and TF conceived the research idea. SC, CA, RB, and SM designed the sampling plan. SC collected the data in the field with contributions from CA, EF, TF, LdS, FM, and EP. SC identified vascular plant species. TF identified Charophyceae species. SC led the writing with contributions from CA, GB, EF, and SM. SC and SM performed the statistical analysis. SC prepared the figures. CA, GB, EF, and SM supervised the research. All authors critically revised the manuscript and approved the final version.

Chapter 3

SC, CA, and GB conceived the research idea. SC, CA, RB, and SM designed the sampling plan. SC and RB collected the data in the field with contributions from CA, EF, TF, and FM. SC and RB identified vascular plant species with contributions from FM and TF. TF identified Charophyceae species. ADV performed the chemical analysis in the laboratory. SC led the writing with contributions from CA, GB, and AB. SC performed the statistical analysis with contributions from AB. SC prepared the figures. CA and GB supervised the research. All authors critically revised the manuscript and approved the final version.

General introduction

Ponds: definitions, threats, and conservation value

Wetlands, including artificial water bodies, are important ecosystems that support a wide range of organisms such as freshwater macrophytes, amphibians, insects, and birds (Simaika et al., 2016; Zamora-Marín et al., 2021). However, these ecosystems are also highly vulnerable and rank among the most threatened on Earth (Dudgeon et al., 2006). Aquatic flora in particular is experiencing marked declines due to anthropogenic pressures such as urbanization, habitat transformation and loss, pollution, eutrophication, and the spread of invasive species (Bolpagni et al., 2020; Du Toit et al., 2021). Ponds are among the most widespread and abundant types of water bodies, especially in landscapes shaped by human activity. Despite their ubiquity, there is still no universally accepted definition of what constitutes a pond. Among other definitions, the Ramsar Convention on Wetlands defines ponds as wetlands under 8 hectares in size. By contrast, the Ponds Conservation Trust characterizes them as permanent or seasonal water bodies ranging from as little as 1 m^2 to 2 ha (Collinson et al., 1995). These definitional differences reflect differences in management contexts, conservation priorities, and regional traditions (Biggs et al., 2005). However, there is broad consensus in distinguishing ponds from larger freshwater systems such as lakes by their relatively small size, limited volume, and shallower depth, which typically allows light to penetrate to the bottom, enabling the growth of submerged vegetation throughout (Biggs et al., 2005; Williams et al., 2004).

Despite their small size compared to lakes or other freshwater systems, ponds play a crucial role in biodiversity conservation. These small water bodies provide habitat and resources for both aquatic and terrestrial taxa (Bubíková & Hrivnák, 2018a; Fehlinger et al., 2023; Svitok et al., 2025) leading to the occurrence of unique or rare species which are often absent from larger aquatic systems (Oertli et al., 2005). Their small size, diverse microhabitats, and frequent isolation from larger water bodies create conditions that favor the maintenance of distinctive communities. Moreover, ponds can act as refugia in intensively used landscapes, buffering species against regional declines and serving as stepping stones that facilitate species dispersal (Biggs et al., 2017). This role is particularly important in farmland contexts. Farmland ponds, although smaller than lakes, offer valuable habitats for plant and animal species of conservation concern in agricultural landscapes (Angiolini et al., 2019; Bolpagni et al., 2019; Williams et al., 2004). Their importance is underscored by the unique biodiversity they sustain, especially in the Mediterranean region (Novikmec et al., 2016; Viciani et al., 2022), where they are considered biodiversity "hotspots" (Fuentes-Rodríguez et al., 2013). Nevertheless, Mediterranean wetlands within agricultural areas are experiencing biodiversity loss driven by intensified farming practices and the abandonment of traditional pond management (Casas et al., 2012). In agricultural landscapes, many permanent ponds have an artificial origin. They are often constructed for irrigation, livestock watering, aquaculture, or flood control. Although these ponds were not originally designed for conservation purposes, they nevertheless provide important ecosystem services. These include carbon sequestration through sediment accumulation and macrophyte growth, water purification by trapping nutrients and pollutants, groundwater recharge, and even local climate mitigation (Du Toit et al., 2021; Meerhoff & De Los Ángeles González-Sagrario, 2021; Pedersen et al., 2019). Their role in intercepting agricultural runoff is especially valuable, reducing nutrient loads and mitigating eutrophication downstream.

Adaptations and diversity of aquatic plants

Ponds host wetland plants. These plants are classified in: i) emergent species rooted in sediment with vegetative parts above the water; ii) aquatic plants, or hydrophytes, which consist of rooted submerged species with leaves entirely submersed; iii) rooted floating and iv) free-floating species (Ervin, 2023).

Hydrophytes are more influenced by water conditions than emergent species which are, for instance, more tolerant to drought (Bertuzzi et al., 2019; Boschilia et al., 2016). Moreover, submerged species are particularly sensitive to underwater conditions such as light availability and oxygen concentration (Luhtala et al., 2016), while floating forms, especially free-floating ones, benefit from the exposure to light but rely heavily on nutrient availability in the water column (Henry-Silva et al., 2008). Additionally, dispersal ability helps emphasizing the species-isolation relationship, a key topic in the application of biogeographical theories, especially in island-like systems like ponds, since such mechanism is one of the key elements determining the spatial dynamics of plant populations and the structure of plant communities (Lososová et al., 2023).

Farmland ponds as "island-like" systems

Ponds, as freshwater habitats embedded within terrestrial landscapes, are often considered as "island-like" systems (Figure 1) due to their isolation, spatial fragmentation, and limited size, characteristics typical of insular environments (Itescu, 2019). While these island-like systems share some biological patterns with true islands, where isolation is a key distinguishing factor, important differences remain (Lomolino et al., 2017). According to the classical Theory of Island Biogeography (MacArthur & Wilson, 1967), species richness tends to increase with island size and decrease with distance from the mainland. Additionally, nearby islands often have more similar species compositions, as defined by Nekola & White (1999). However, in island-like systems such as farmland ponds, the concept of distance from the mainland is difficult to define due to their patchy distribution (Ramette & Tiedje, 2007). Consequently, these systems may not completely conform to the classical biogeographical theory or the distance decay of similarity concept, which predicts that species similarity declines with geographic distance (MacArthur & Wilson, 1967; Nekola & White, 1999). Furthermore, farmland ponds typically have an artificial origin and are established for agricultural purposes. In these man-made systems, disturbance plays a significant role in species colonization, a factor that has been largely overlooked in traditional island biogeography theories (Villa et al., 1992).

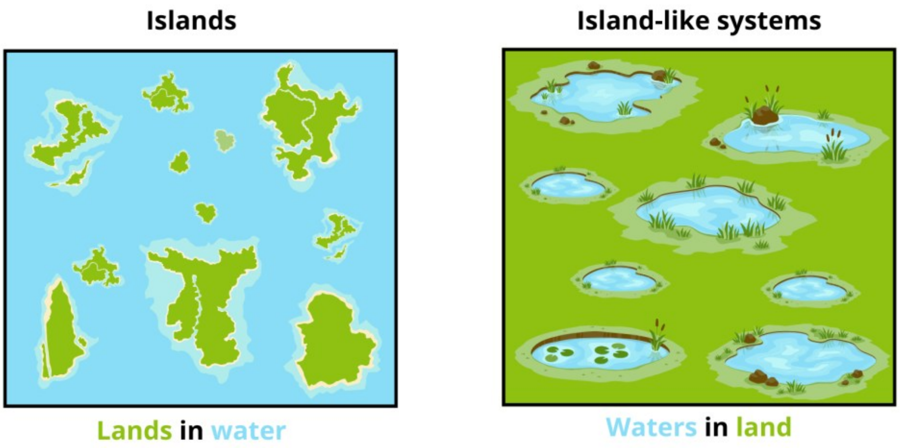

Figure 1: Graphical representation of islands and ponds as "island-like" systems.

Species similarity, commonly measured as beta diversity, is a useful metric for understanding the ecological processes that shape plant community formation (Baselga, 2010). Compared to other water body types, ponds show high heterogeneity in conditions, resulting in higher beta diversity in plant communities and unique species assemblages, including red-listed species (Svitok et al., 2025).

For this reason, examining beta diversity in ponds, along with its two components, turnover (species replacement between communities at different sites) and nestedness (when the species assemblage of a site is a subset of a richer site's assemblage), provides insights into community composition in island-like systems and highlights similarities with true islands. Island-like systems tend to show different beta diversity patterns when compared to true islands, notably with nestedness being more pronounced in true islands than in island-like systems (Matthews et al., 2015; Watling & Donnelly, 2006). Ponds are patchily distributed aquatic "islands" connected within a network, known as "pondscape". Pondscapes represent the surrounding landscape matrix where groups of ponds occur (Bartrons et al., 2024) and they include not only the individual ponds themselves but also the hydrological, ecological, and functional connections among them, such as temporary streams, wet meadows, riparian zones, and surrounding terrestrial habitats that influence species dispersal. Within pondscapes, species disperse and migrate among patches, with ponds acting simultaneously as both sources and sinks for species. This makes dispersal and spatial heterogeneity key factors shaping community structure (Mendez-Castro et al., 2021). The connectivity of ponds within these pondscapes is essential for maintaining metapopulation dynamics, facilitating species movement, and supporting biodiversity at the landscape scale (Biggs et al., 2005; Briggs et al., 2019). In intensively managed agricultural landscapes, fragmented by roads, fields, and other human infrastructures, pondscapes play a critical role in preserving ecological connectivity.

Drivers of farmland pond community composition

Freshwater habitats are highly vulnerable to pollution and habitat degradation due to their close connections with surrounding land and frequent location within urbanized or agricultural areas (Reid et al., 2019). The decline in freshwater populations is largely driven by human activities such as water usage, alteration of natural flow regimes, and nutrient runoff from land (Dudgeon et al., 2006). Nonetheless, research focusing on the impact of human pressures on communities is disproportionately greater for terrestrial ecosystems than for freshwater ones, particularly regarding plant communities (Keck et al., 2025).

Numerous studies have explored the ecological factors influencing macrophyte diversity, revealing that local environmental variables, such as pond size and trophic conditions, greatly explain patterns of beta diversity in ponds (Fernández-Aláez et al., 2020; Heino & Tolonen, 2017). Specifically, Fernández-Aláez et al. (2020) observed a decline in macrophyte species richness with increasing total phosphorus levels in ponds. Similarly, García-Girón et al. (2019) identified physical and chemical factors including water depth, pond area, pH, and total nitrogen as significant drivers of both species richness and beta diversity. Furthermore, pH and conductivity were shown to have a greater influence on diversity in high-elevation ponds, whereas trophic status becomes more prominent in shaping diversity in lowland ponds (Hinden et al., 2005). Ponds not only sustain diverse communities of strictly aquatic plants but also support adjacent terrestrial species (Scheff et al., 2022), which in turn enhance animal biodiversity (Forio et al., 2020). These species residing at the land-water interface interact with the aquatic environment and are influenced by its characteristics (Wang et al., 2021). However, targeted research exploring the relationship between riparian vegetation and water quality remains limited.

Community composition is shaped by multiple interacting filters, notably local environmental filtering, such as pond physical characteristics (e.g., area, depth) and water quality, which shape beta diversity components and determine the composition of aquatic plant assemblages (Hrivnák et al., 2013; Lauridsen et al., 2015; Lischeid et al., 2018). Environmental conditions affect species selecting only the one having specific traits suited to those conditions. Moreover, species' dispersal abilities and biotic interactions ultimately determine which species successfully establish in a community (Grime, 2006; Keddy, 1992; Ottaviani et al., 2020). In a prior study, Joye et al. (2006) modeled the distribution of pond macrophytes considering environmental factors related to water quality, pond morphometry, and catchment characteristics. Other studies integrate local environmental factors into species distribution models, often aiming to predict the spread of invasive species (Thomas et al., 2021; Zarkami et al., 2021). However, these approaches likewise tend to focus on individual species and overlook the complexity at the community level.

General aims

This doctoral thesis entitled “Farmland ponds as unique aquatic islands” has three main objectives, namely to: i) provide an accessible dataset of pond vegetation data and water physico-chemical parameters, as a tool for studies on the relationships between plant communities and environmental conditions; ii) evaluate the effects of agricultural land-use extent and other factors at different spatial scales on the species richness and composition of plant communities; iii) assess patterns of beta diversity indicating biological isolation among ponds and test the applicability of island biogeography principles to farmland ponds.

CHAPTER 1

Dive into the Italian PONDY dataset: Pond vegetation data and water physico-chemical parameters

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Dive into the Italian PONDY dataset: Pond vegetation data and water physico-chemical parameters*

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Data paper

*All authors of the published article agreed to use it as a chapter of this PhD thesis.

Summary

Ponds are widespread yet highly vulnerable freshwater habitats that support diverse aquatic and terrestrial plant communities influenced by land use and water characteristics. The PONDY (Pond vegetation data and water physico-chemical parameters) dataset integrates vegetation and water physico-chemical data that have been collected to understand the responses of vegetation to environmental parameters. The dataset comprises 575 plots, of which 232 are aquatic and 343 are terrestrial, derived from 115 ponds across continental and insular areas of Italy. The dataset includes 743 vascular plant taxa and 5 macroalgae encompassing 364 genera and 89 families. Terrestrial plots host 690 taxa belonging to 87 families, while aquatic plots host 117 taxa belonging to 36 families. The dataset includes 10 taxa belonging to the Italian Red List and 39 alien species. Moreover, 11% of the aquatic plots have

been classified in a Habitats Directive 92/43/EEC habitat type, while 48% have been classified in a EUNIS habitat type. The dataset contains, for each plot, measurements of physico-chemical water variables such as dissolved oxygen, water depth, and temperature, pH, turbidity, conductivity, and nutrient concentration. The PONDY dataset provides comprehensive information on plant diversity and abundance, community composition, habitat types, and water chemistry in Italian ponds, serving as a key resource for studying plant–environment relationships, developing predictive models, and supporting freshwater conservation efforts.

1. Introduction

Ponds offer vital resources and living spaces for a wide range of both aquatic and terrestrial organisms (Fehlinger et al., 2022). These small permanent aquatic systems, regardless of their origin (artificial or natural), provide habitats to plants, amphibians, insects, and birds (Bubíková & Hrivnák, 2018a; Simaika et al., 2016; Zamora-Marín et al., 2021) and often rare species that are not found in larger water bodies (Bolpagni et al., 2019; Oertli et al., 2002). Despite their ecological importance, they are among the most vulnerable and endangered habitats in the world (Dudgeon et al., 2006). In particular, aquatic vegetation is undergoing significant declines driven by human activities, including urban expansion, habitat fragmentation and destruction, pollution, eutrophication, and the spread of invasive species (Akasaka et al., 2010; Bolpagni, 2020, 2021; Bolpagni et al., 2020; Du Toit et al., 2021; Fernández-Aláez et al., 2020). Ponds represent one of the most common and widespread freshwater habitats, especially in human-modified landscapes. Despite their small size, ponds are essential for biodiversity conservation (Biggs et al., 2017) since they tend to host significantly higher numbers of species, including more unique and rarer species, than other types of water bodies (Oertli et al., 2002).

Pond vegetation is typically composed of wetland plants, including emergent species that are rooted in the sediment but extend their vegetative parts above the water, and aquatic plants, which include submerged species with entirely underwater leaves, along with rooted floating and free-floating types (Ervin, 2023). Beyond hosting a rich diversity of strictly aquatic flora, ponds also provide suitable conditions for surrounding semi-terrestrial terrestrial plant species, namely riparian vegetation (Scheff et al., 2022). These plants occupying the transition zone between land and water interact closely with aquatic habitats and, as wetland and aquatic species, are shaped both by land use and water characteristics (Wang et al. 2021; Musisi et al., 2025). Pond identity is relevant in defining the plant species richness and community composition (Cannucci et al., 2025) given the interplay of multiple filtering processes, particularly local environmental filters such as physical aspects of ponds (e.g., area, depth) and physico-chemical properties of water, which influence the diversity patterns of plant species (Hrivnák et al., 2013). Plant diversity metrics can change in relation to the type of water body which can contribute uniquely and significantly to plant diversity (Bubíková & Hrivnák 2018b; Grasel et al., 2021). The observation of the ecological patterns occurring in ponds is essential to summarize the vegetation-environment relationships. Many studies on ponds have investigated the responses of plant communities to environmental drivers (Fernández-Aláez et al., 2020; Gallego et al., 2015; Sieben et al., 2021), leading to different outcomes on the most relevant drivers of plant species composition.

Accessible datasets are key tools for providing an overview of species and habitat distribution, and they support biodiversity conservation actions by highlighting the occurrence of species of conservation protection interest or alien species (Santoianni et al., 2025). Given the strong relationship between plant communities and environmental characteristics, we present the PONDY dataset: Pond vegetation data and water physico-chemical parameters. PONDY combines vegetation data of ponds with water physico-chemical parameters, thus aiming to serve as a tool to evaluate the ecological status of water bodies and the analyses of how environmental conditions, related to water quality, affect species presence, abundance, and cover.

2. Study area and methodology

The study area (Fig. 1) encompasses 115 permanent farmland ponds distributed across continental (Fig. 1 a, b) and insular (Fig. 1 c) areas of Italy. We selected permanent ponds ranging from 70 m^2 to 3 ha. In each area (Supplementary material to chapter 1, Fig. S1 a), we chose three zones, namely pondscapes (interconnected pond networks in a landscape) based on the extent of agricultural land use (Supplementary material to chapter 1, Fig S1 b). The percentage of agricultural land around each area was calculated within a 10 km radius using Corine Land Cover maps (Istituto Superiore Protezione Ricerca Ambientale, 2018). Three pondscapes, based on agricultural land-use extent, were established: low (<30% agricultural land-use extent), intermediate (30–60% agricultural land-use extent), and high (>60% agricultural land-use extent). Ponds were identified within each pondscape (Supplementary material to chapter 1, Fig. S2) by extracting water bodies classified under the “Water Bodies” category (5.1.2) from the Corine Land Cover map (ISPRA, 2018) using QGIS (QGIS Development Team, 2023). In each pondscape, the 10 km buffer zone was divided into a 500 m × 500 m grid, which was overlaid on the extracted water bodies. From this grid, we randomly selected one pond per grid cell, using QGIS's *Random Selection tool within subsets*. To overcome potential accessibility issues, the selection process was repeated three times, ensuring a minimum distance of 1 km in a straight line between selected ponds. Within each area, between 10 and 15 ponds were randomly selected (Supplementary material to chapter 1, Fig. S1 c). For each pond, using the QGIS *Random Points Along Lines* plugin, we generated three points along the pond perimeter, setting a minimum distance of 15 m between points. In the field, in proximity of these points we positioned the plots and at each point we surveyed one aquatic plot measuring 2 m × 2 m, along with one terrestrial plot of the same size located 1 m away from the aquatic plot, (Supplementary material to chapter 1, Fig. S1 d), thus obtaining a total of 6 plots (3 aquatic and 3 terrestrial plots) for each pond. With this type of sampling design, some aquatic plots resulted empty (no species recorded); these latter plots were therefore removed from the dataset due to absence of vegetation.

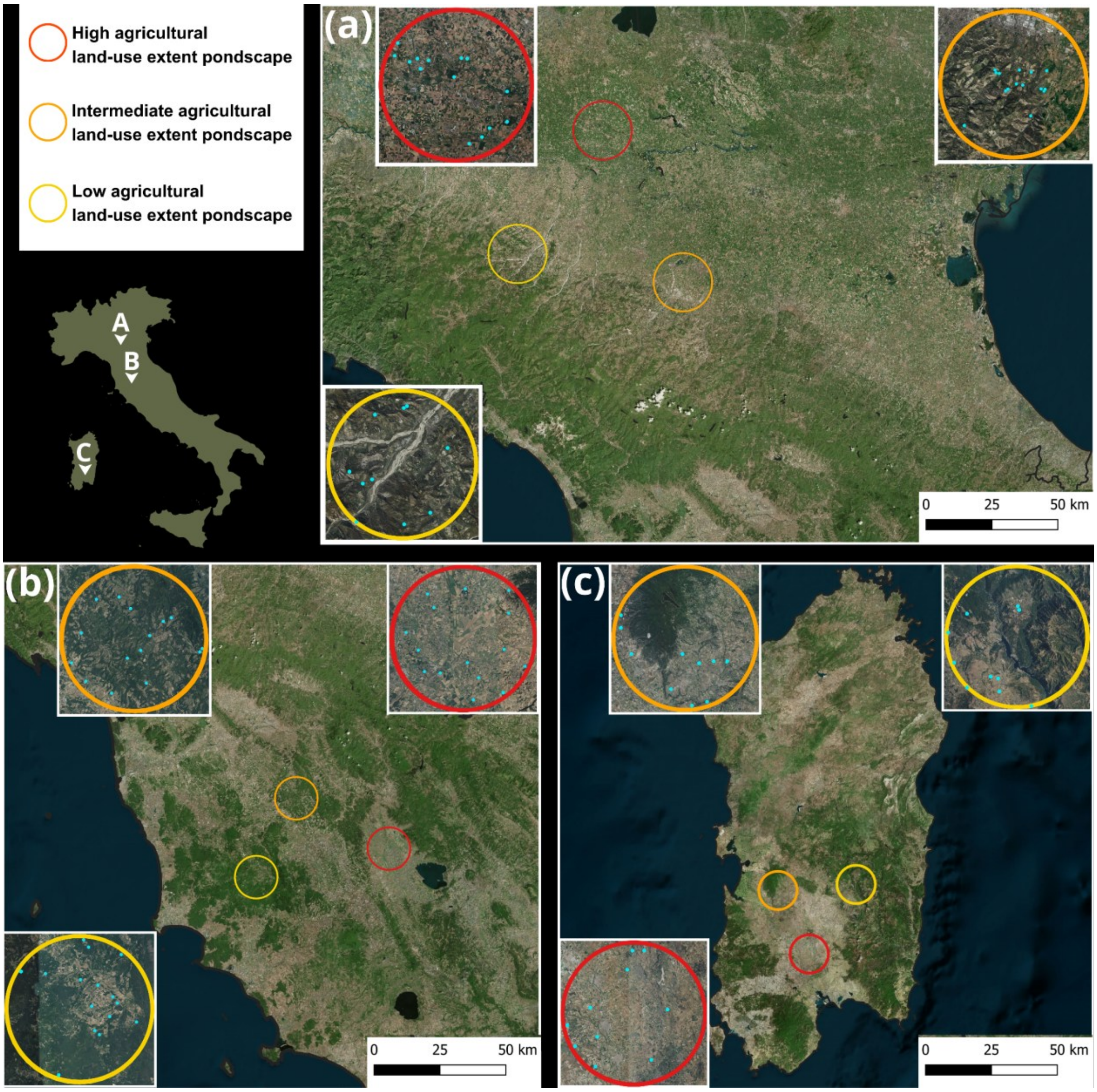

Figure 1. Distribution of the sampled ponds across pondscapes (high, intermediate and low) and the continental (a, b), and insular (c) areas of Italy.

3. Data collection

All ponds were sampled during the peak of the growing season. Specifically, ponds in the continental areas of Italy were surveyed between June and August 2020, 2021, and 2023, those in insular Italy in late April 2024. In each plot, we recorded all the occurring species, including vascular plants and macroalgae of the Characeae family. Vascular plant species nomenclature follows the Portal to the Flora of Italy (2025). Nomenclature of Characeae follows Bazzichelli & Abdelahad (2009). In the field, together with vegetation data, we also collected physico-chemical water parameters to obtain data influencing aquatic and riparian species. Multiparametric probe (Aquaread 2000-d) was used to record several parameters at the center of each aquatic plot, between 8:00 a.m. and 3:00 p.m., including water temperature (°C), depth (m), dissolved oxygen (expressed in percentage, %), pH, turbidity (NTU – Nephelometric Turbidity Unit), and electrical conductivity (µS/cm). Within each plot, a water sample was collected and immediately filtered through a 0.7 µm glass fiber filter (GF/F, Whatman) for subsequent laboratory analyses. In the laboratory, soluble reactive phosphorus (as phosphate ion, PO_4^{3-}; µg/L) was measured spectrophotometrically following the method by Valderrama (1977). The remaining water was filtered using a 0.2 µm nylon membrane, and concentrations of dissolved nitrate (NO_3^-; mg/L) and ammonium (NH_4^+; mg/L) were quantified via ion chromatography (883 Basic IC plus, Metrohm, Herisau, Switzerland). Given the higher relevance of aquatic vegetation for conservation assessment, compared to agricultural lands we classified aquatic plots to i) Annex I of 92/43/EEC Habitats Directive and ii) EUNIS habitat types (v2025-10-03; Chytrý et al., 2020). For these classifications, we used an expert-base approach and the code implemented by Bruelheide et al. (2021) in R 4.5.0 (R Core Team, 2025), respectively.

4. Structure of the dataset

4.1 Species and vegetation

The dataset includes 575 georeferenced vegetation plots (232 aquatic and 343 terrestrial) including 743 vascular plant taxa and 5 macroalgae. The species richness of plots varies between one to 40, with 443 (64.2%) plots having less than 10 species and 121 (17.5%) plots having 20 or more taxa (Fig. 2 A). The average species richness in aquatic and terrestrial plots is 2 and 16, respectively. A total of 748 taxa belonging to 364 genera and 89 families were identified. 690 taxa of 87 families were recorded in terrestrial plots and 117 taxa of 36 families were recorded in aquatic plots. Asteraceae is the largest family in terrestrial plots, with 101 species, followed by Poaceae (93 species), and Fabaceae (84 species, Fig. 2 B), while Ranunculaceae is the largest family in aquatic plots, with 11 taxa, followed by Potamogetonaceae (10 taxa), and Cyperaceae (9 taxa, Fig. 2 C). *Trifolium* is the most represented genus in the terrestrial plots, with 21 species (Fig. 2 D), while in aquatic plots *Ranunculus* is the genus having the highest number of species (9 species; Fig. 2 E). The most frequent species in the terrestrial plots is *Daucus carota* (occurring in 17% of plots) followed by *Phragmites australis* and *Rubus ulmifolius* (Fig. 2 F). *Typha angustifolia*, *Chara vulgaris*, and *Potamogeton natans* are the most frequent taxa in the aquatic plots (all occurring in at least 30% of plots; Fig. 2 G).

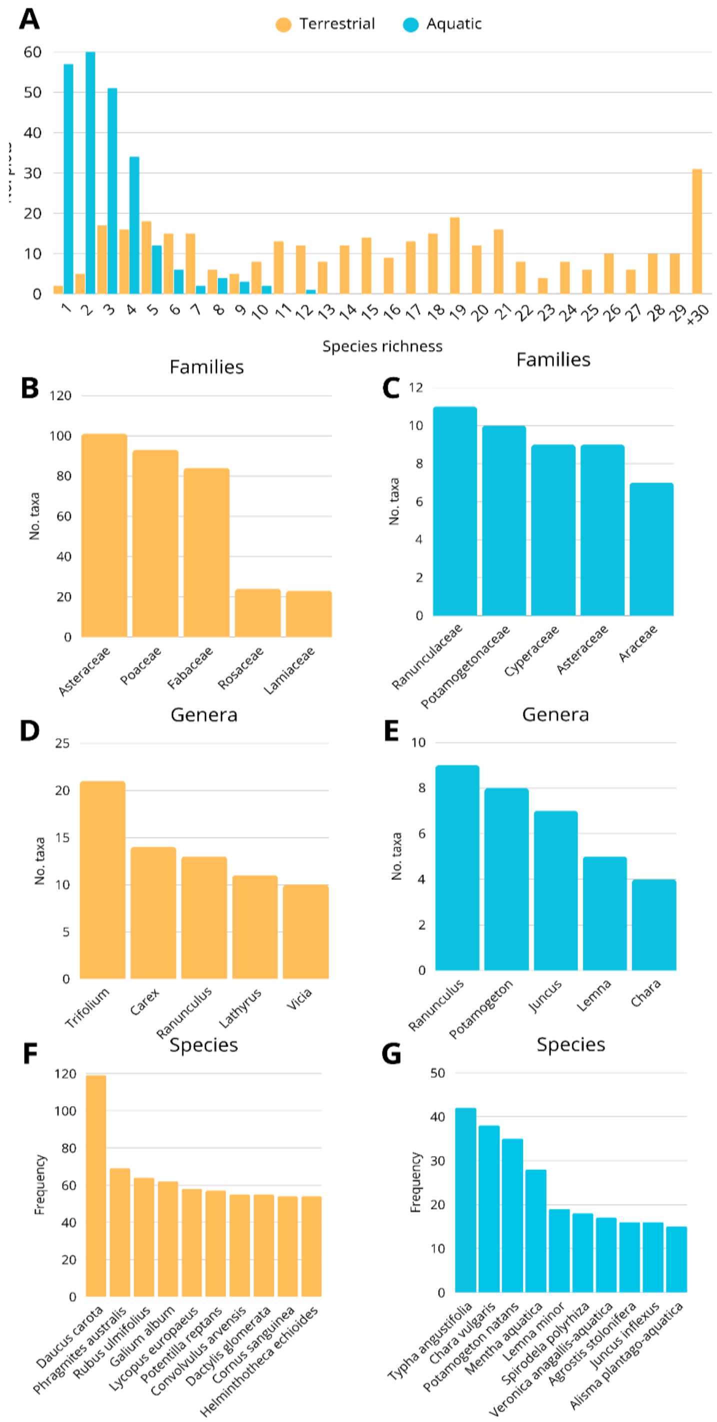

Figure 2. Graphics showing species richness per plot (A), the five most frequent families in terrestrial plots (B), the five most frequent families in aquatic plots (C), the five most abundant genera in terrestrial plots (D), the five most abundant genera in

aquatic plots (E), the ten most frequent taxa in the terrestrial plots (F), and the ten most frequent taxa in the aquatic plots (G).

The dominant life forms are Hemicryptophytes (39%) and Therophytes (37%) in terrestrial plots and Hemicryptophytes (35%) and Hydrophytes (20%) in aquatic plots. Chamaephytes are the less frequent life form in both plot types (Supplementary material to chapter 1, Fig. S3). Moreover, the dataset contains a total of 10 threatened taxa of the Italian Red List (Table 1), mostly linked to the aquatic environment, highlighting the critical conservation status of plant species ecologically connected with freshwater ecosystems. More precisely, these species are mostly threatened by modification of the natural system and to agriculture and aquaculture (Orsenigo et al., 2021).

Table 1. The threatened taxa, their categories from the Italian Red List and major threats (Orsenigo et al., 2020). Major threats: 1 = Residential and commercial development; 2 = Agriculture and aquaculture; 4 = Transportation and service corridors; 5 = Biological resource use; 6 = Human intrusions and disturbance; 7 = Natural system modifications; 8 = Invasive and other problematic species, genes and diseases; 9 = Pollution; and 11 = Climate change and severe weather.

Species	**Status**	**Major threats**
Baldellia ranunculoides	Endangered (EN)	1, 2, 7, 8, 9, 11
Butomus umbellatus	Vulnerable (VU)	7, 8, 9, 11
Carex microcarpa	Near Threatened (NT)	1, 2, 7
Hottonia palustris	Endangered (EN)	2, 5, 6, 7, 8
Leucojum aestivum subsp. *aestivum*	Vulnerable (VU)	5, 7
Plagius flosculosus	Endangered (EN)	1, 2, 4, 7, 8
Ranunculus cordiger subsp. *diffusus*	Endangered (EN)	2, 7
Ranunculus ophioglossifolius	Vulnerable (VU)	2, 4, 6, 7, 9

Thelypteris palustris	Vulnerable (VU)	7, 8, 9
Zannichellia palustris	Near Threatened (NT)	1, 2, 4, 7, 8, 9, 11

The dataset contains a total of 39 alien species, mostly found in terrestrial plots, 33 of which are categorised as invasive in Italy (Table 2).

Table 2. The alien species and their associated status (Portal to the Flora of Italy, 2025) in Italy, as well as their distribution in aquatic or terrestrial plots. Plant species were ordered alphabetically.

Species	Neophyte/ Archaeophyte	Status	Plot
Acalypha virginica	Neophyte	Invasive	Terrestrial
Acer negundo	Neophyte	Invasive	Terrestrial
Amaranthus blitoides	Neophyte	Invasive	Terrestrial
Amaranthus cruentus	Neophyte	Invasive	Terrestrial
Amaranthus retroflexus	Neophyte	Invasive	Terrestrial
Amorpha fruticosa	Neophyte	Invasive	Terrestrial
Arundo donax	Archaeophyte	Invasive	Terrestrial
Avena strigosa	Neophyte	Casual	Terrestrial
Bidens connata	Neophyte	Invasive	Terrestrial
Bidens frondosa	Neophyte	Invasive	Aquatic
Cyperus strigosus	Neophyte	Invasive	Terrestrial
Erigeron annuus	Neophyte	Invasive	Terrestrial

Erigeron bonariensis	Neophyte	Invasive	Terrestrial
Erigeron canadensis	Neophyte	Invasive	Terrestrial
Erigeron sumatrensis	Neophyte	Invasive	Terrestrial
Eucalyptus camaldulensis	Neophyte	Invasive	Terrestrial
Euphorbia humifusa	Neophyte	Naturalized	Terrestrial
Galinsoga parviflora	Neophyte	Invasive	Terrestrial
Hesperocyparis arizonica	Neophyte	Naturalized	Terrestrial
Humulus japonicus	Neophyte	Invasive	Terrestrial
Lemna aequinoctialis	Neophyte	Naturalized	Aquatic
Lemna minuta	Neophyte	Invasive	Aquatic
Lindernia dubia	Neophyte	Invasive	Aquatic
Ludwigia hexapetala	Neophyte	Invasive	Aquatic
Oenothera stucchii	Neophyte	Invasive	Terrestrial
Oxalis pes-caprae	Neophyte	Invasive	Terrestrial
Panicum capillare	Neophyte	Invasive	Terrestrial
Panicum dichotomiflorum	Neophyte	Invasive	Terrestrial
Parthenocissus quinquefolia	Neophyte	Invasive	Terrestrial
Paspalum distichum	Neophyte	Invasive	Aquatic
Sicyos angulatus	Neophyte	Invasive	Terrestrial
Solidago gigantea	Neophyte	Invasive	Terrestrial

Sorghum halepense	Archaeophyte	Invasive	Terrestrial
Symphyotrichum lanceolatum	Neophyte	Invasive	Terrestrial
Symphyotrichum squamatum	Neophyte	Invasive	Aquatic
Trifolium alexandrinum	Neophyte	Naturalized	Terrestrial
Verbena bonariensis	Neophyte	Naturalized	Terrestrial
Veronica persica	Neophyte	Invasive	Terrestrial
Xanthium spinosum	Neophyte	Invasive	Terrestrial

4.2 Habitat types

Overall, we classified 64 aquatic plots (11%) under a Habitats Directive 92/43/EEC habitat type and 275 plots (48%; based on Supplementary material to chapter 1: Table S1) under a EUNIS habitat type (Table 3). More precisely, we assigned 21 plots to 92/43/EEC habitat type 3140 (Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp.) and 43 plots to habitat 3150 (Natural eutrophic lakes with *Magnopotamion* or *Hydrocharition*-type vegetation). The conservation status of both habitats is considered unfavorable in Italy (ISPRA 2021). In particular, habitat 3140 is classified as having unfavorable conservation status in the Alpine and Continental biogeographical regions, while habitat 3150 in the Mediterranean region (ISPRA 2021). The rest of the plots (N = 511) could not be assigned to any 92/43/EEC habitat type. Moreover, 116 plots (based on Supplementary material to chapter 1: Table S1) have been classified to macrohabitat type “P” (Inland waters) and related sublevels of EUNIS classification, while 159 plots (based on Supplementary material to chapter 1: Table S1) to macrohabitat type “Q” (Wetlands) and related sublevels.

Table 3. Classification of the vegetation plots according to EUNIS habitat types. Only habitats occurring in more than 3% of plots classified in the given habitat are reported. The complete table is provided in Supplementary material to chapter 1 (Table S1).

EUNIS	**No. plots**	**Percentage**

Fresh-water small pleustophyte vegetation (P3b)	32	5.6
Fresh-water submerged vegetation (P3d)	18	3.1
Fresh-water nymphaeid vegetation (P3e)	24	4.2
Stonewort vegetation (P3h)	39	6.8
Tall-helophyte bed (Q51)	96	16.7
Helophyte beds (Qb)	36	6.3

4.3 Physico-chemical water parameters

The dataset includes key parameters describing physical aspects, water chemistry and trophic indicators (Fig. 3). The summary of the physico-chemical water parameters recorded in the study ponds, including mean, standard deviation (SD), minimum (Min), and maximum (Max) values is reported in Supplementary material to chapter 1 (Table S2).

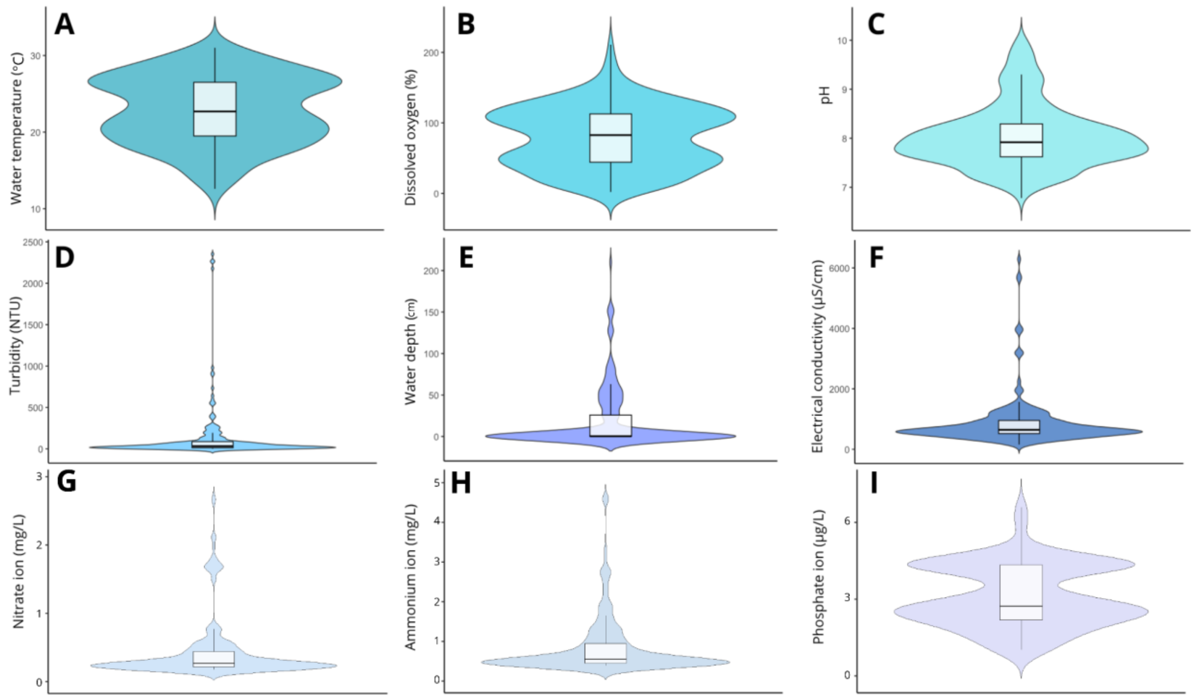

Figure 3. Violin plots of physico-chemical water parameters measured for each aquatic plot. Water temperature (A), dissolved oxygen (B), pH (C), turbidity (D), water

depth (E), electrical conductivity (F), nitrate ion (G), ammonium ion (H), and phosphate ion (I).

Conclusions

The information present in the PONDY dataset strengthens the knowledge of pond plant diversity along insular and continental Italy. This dataset, which provides comprehensive data on plant species, community composition, habitat types, and physico-chemical water parameters, is important for understanding the plant diversity hosted in these freshwater systems and studying their relationship with physico-chemical water parameters. This dataset is the base for future studies on the relationships between plant communities and environmental conditions and can be used for developing predictive models for species distribution based on chemical parameters. Furthermore, in the future, the dataset might be expanded with functional traits data to provide an assessment of functional composition of plant communities in relation to water chemistry. Additionally, it can be used to define conservation status of lentic systems by assessing conservation indices, similarly to the ECELS index used in Catalonia (Sala et al., 2004), based on water characteristics, land use, and vegetation status aspects.

CHAPTER 2

Mediterranean farmland ponds as unique habitats for plant diversity across different pondscapes

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POND BIODIVERSITY AND FUNCTIONS

Mediterranean farmland ponds as unique habitats for plant diversity across different pondscapes

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Summary

Wetlands are among the world's most vulnerable ecosystems. Particularly in the Mediterranean region, farmland ponds are strongly influenced by the agricultural land use in their surroundings, though supporting unique biodiversity. This study aimed to highlight the patterns of farmland pond plant diversity across different pondscapes - networks of interconnected ponds within a landscape - and different spatial scales, from local (pond-scale) to landscape level (pondscape-scale), with the aim of informing conservation planning. We surveyed plant communities across 45 farmland ponds located in three pondscapes of Tuscany in central Italy, with different agricultural land-use extents. We tested species richness and composition differences using multivariate permutational analysis of variance. Species richness and plant community composition varied with the extent of agricultural land-use in the pondscape. Pondscapes with the highest agricultural land-use extent had lower aquatic plant species richness, with dominance of species adapted to anthropogenic disturbance. In contrast, the pondscape with the lowest agricultural land-use extent hosted a richer aquatic biodiversity, particularly of helophytes. We found that pond-specific features,

possibly related to pond management, play a more significant role than landscape-scale features in shaping plant diversity. This underscores the importance of acting on individual ponds in addition to whole pondscapes for plant conservation purposes.

1. Introduction

Wetlands, including artificial water bodies, are important ecosystems providing habitats for a wide range of organisms, like freshwater macrophytes, amphibians, insects, and birds (Simaika et al., 2016; Zamora-Marín et al., 2021). Besides, wetlands are ecologically highly vulnerable, resulting among the most threatened ecosystems on Earth (Dudgeon et al., 2006). In particular, aquatic flora is declining due to anthropogenic pressures such as urbanization, habitat transformation and loss, increasing pollution, eutrophication, and the spread of alien species (Bolpagni et al., 2020; Du Toit et al., 2021). Among wetlands, ponds are a common type of water body, particularly in human-modified landscapes. Groups of ponds and their interconnected networks within a landscape, known as pondscapes (Bartrons et al., 2024), are highly relevant for biodiversity conservation (Oertli et al., 2002; Biggs et al., 2017). They play a crucial role in enabling the movement of plants and animals across the landscape. Especially in artificial agricultural environments where physical barriers, such as roads and cultivated fields, are more prevalent than in natural settings, the connections between ponds serve as stepping-stone habitats for species movement (Briggs et al., 2019). In agricultural pondscapes, permanent ponds usually have an artificial origin and are created for various purposes, including water storage for field irrigation and livestock watering. These artificial water bodies provide multiple ecosystem services such as water purification and pollutant removal (Du Toit et al., 2021; Meerhoff & De Los Ángeles González-Sagrario, 2021; Pedersen et al., 2019). Despite their relatively small size compared to lakes and other freshwater systems, farmland ponds play an important role for biodiversity conservation, offering suitable habitats for animal and plant species of conservation interest within agriculturally dominated landscapes (Williams et al., 2004; Angiolini et al., 2019; Bolpagni et al., 2019). The significance of these small water bodies is further underscored by the unique biodiversity they support, particularly in the Mediterranean region (Novikmec et al., 2016; Viciani et al., 2022), where they are recognized as biodiversity "hotspots" (Fuentes-Rodríguez et al., 2013).

Mediterranean wetlands within agricultural landscapes are facing biodiversity loss due to intensified farming practices in their surroundings and to the abandonment of traditional pond management (Casas et al., 2012). Land use influences aquatic ecosystems through various processes operating across multiple spatial scales, spanning from local (pond-scale) to landscape scales (pondscape-scale; (Buck et al., 2004; Declerck et al., 2006). Many studies have demonstrated that human activities contribute to the decline of macrophyte diversity (Akasaka et al., 2010). In particular, intensive agricultural practices often lead to the simplification of aquatic ecosystems, primarily due to the removal of riparian vegetation (Meerhoff & De Los Ángeles González-Sagrario, 2021). Moreover, pond area is recognized as one of the main predictors influencing plant species richness (Bolpagni et al., 2020). Additionally, pond slope has a role in shaping aquatic plant communities as ponds with steep slopes do not support helophyte communities (Kolada et al., 2024). Therefore, both local and landscape-scale practices affect the plant diversity of ponds.

Understanding patterns of plant species richness and composition in farmland ponds requires considering the role of spatial scales, to assess the impact of land-use practices on plant diversity and develop effective strategies for pond conservation. Accordingly, in this study we aim (i) to assess the patterns of plant diversity in three different pondscapes, with different percentages of agricultural land-use extent, and (ii) to identify the spatial scale from local (pond-scale) to landscape (pondscape-scale) having the highest importance for plant diversity conservation in farmland ponds. We hypothesised that the overall species richness decreases as the extent of agricultural land-use in the pondscape increases. Additionally, we expected that species composition of plant communities mirrors the agricultural land-use setting of the pondscape.

2. Materials and methods

2.1 Study area and selection of ponds

We selected three circular study areas (pondscapes) with a 10 km radius in Tuscany, central Italy (Supplementary material to chapter 2, Fig. S1). These pondscapes differ in the percentages of agricultural land-use extent (hereafter “ALE”). The ALE was quantified for each of the three 10 km radius pondscape using Corine Land Cover maps (ISPRA, 2018) and calculated within the QGIS environment (QGIS Development Team, 2023). We classified pondscapes based on ALE as follows: i) “Low ALE” (less than 30% of agricultural land use), ii) “Intermediate ALE” (agricultural land use between 31% and 60%), and iii) “High ALE” (more than 61% of agricultural land use). The “High ALE” pondscape is an area with a prevalence of intensive cultivation such as cereals, fruits, and vegetables, as well as livestock farming of cattle and pigs (Lastrucci et al., 2010; Supplementary material to chapter 2, Fig. S2a). The “Intermediate ALE” pondscape is an area characterised by the interplay of forests and croplands, predominantly consisting of large extensions of vineyards, and olive groves (Regione Toscana, 2015a; Santoro et al., 2020; Supplementary material to chapter 2, Fig. S2b). The “Low ALE” pondscape is an area with a low percentage of agricultural lands and a high percentage of woods, especially broadleaf trees, and traditionally managed croplands and pastures, some of which being abandoned (Regione Toscana, 2015b; Supplementary material to chapter 2, Fig. S2c). The mean elevation of these areas is 350 m a.s.l., ranging from 250 m a.s.l. to 570 m a.s.l.

The bioclimate is transitional between Temperate and Mediterranean (Pesaresi et al., 2017). The mean annual temperature recorded between 1991 and 2020 was 14.7°C, with a range of 6.4°C in the coldest month (January) and 24.4°C in the hottest month (August). The mean annual precipitation is 823 mm, varying between the driest month of July (29 mm) and the rainiest month of November (125 mm, https://www.lamma.toscana.it/clima-e-energia/climatologia/clima-siena). The climatic data refer to the city of Siena, which is situated at a similar elevation and in the proximity of the three study areas.

2.2 Sampling design

We sampled 15 ponds selected within each pondscape by extracting water bodies classified under the “Water Bodies” category (5.1.2) of the Corine Land Cover map (ISPRA, 2018) using QGIS. We identified ponds based on the size provided by Ponds Conservation Trust, namely considering a surface area between 1 m^2 and 2 ha (Collinson et al., 1995; Biggs et al., 2005). Within each pondscapes, we overlaid a 10 km radius circle divided in a 500 m $\times$ 500 m grid, onto the extracted water bodies. Ponds were then randomly selected, ensuring that only one pond per grid cell was chosen, using the QGIS tool *Random selection within subsets*. To account for potential inaccessibility, we repeated the selection process three times, maintaining a minimum straight-line distance of 1 km between selected ponds. The selected ponds range in size from 84 m^2 to 1.7 ha (mean = 0.25 ha, SD = 0.36 ha). Plant community data were collected between June and August 2023. In each pondscape (Fig. 1a), we implemented the following sampling design: for each pond (Fig. 1b), three points were randomly placed in QGIS along the perimeter, ensuring a minimum distance of 15 m between them (Fig. 1c). In the field, at each selected point, two paired plots (transect) of 4 m^2 were positioned, one in the water (in-water plot), starting from the pond shore, and one on land, positioned 1 m from the shore (out-water plot). This design resulted in a total of 6 square vegetation plots per pond (Fig. 1d). The 1-meter buffer zone from the shore was set based on preliminary surveys which highlighted variations in the water level during the growing season constantly lower than this threshold. In this way we excluded transitional vegetation, namely that which remains submerged during certain periods of the year. Thus, the surveys in non-aquatic plots exclusively captured vegetation that remained always emergent.

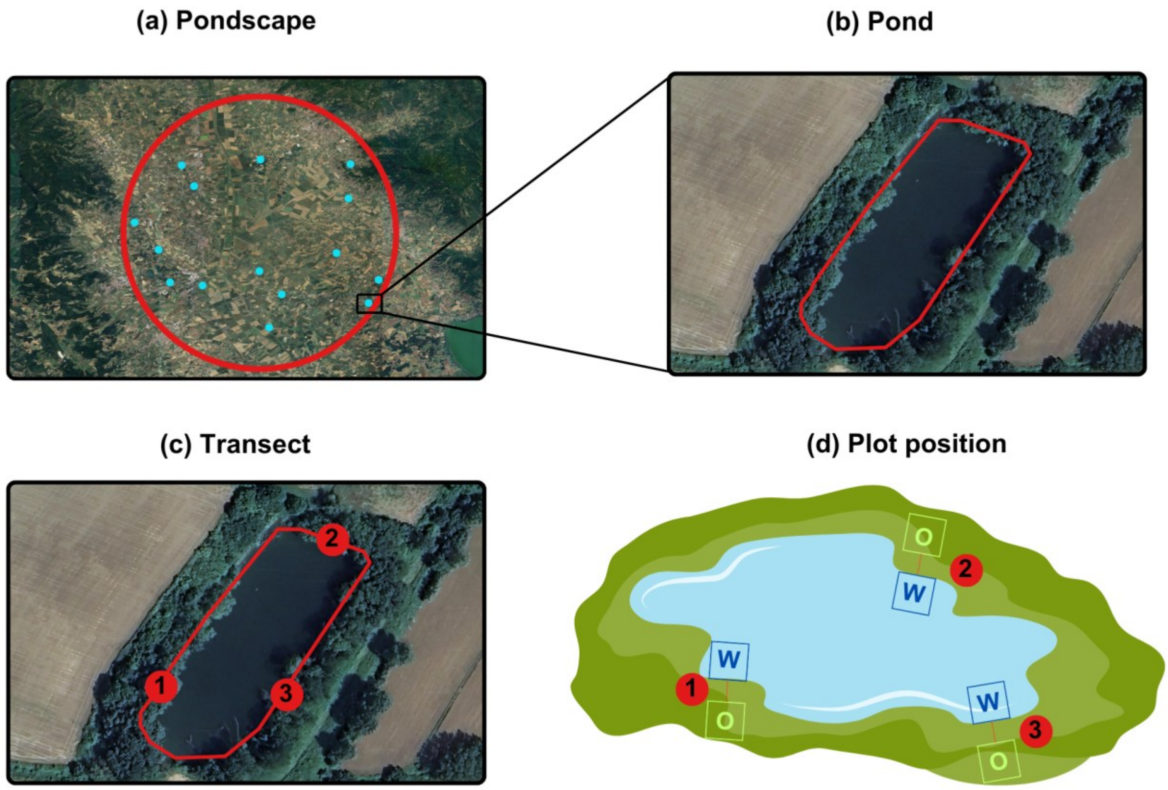

Figure 1: Spatialisation of the sampling design through the selection of the a) pondscapes b) the selection of the pond, c) localisation of the transect along the pond perimeter, and d) localisation of the plots (2 m $\times$ 2 m) within the pond. O = out-water plot; W = in-water plot.

2.3 Data collection

We surveyed a total of 270 (2 positions $\times$ 3 transects $\times$ 15 ponds $\times$ 3 pondscapes) vegetation plots. In each plot, we recorded all vascular plants and algae of the Charophyceae class and we visually estimated the percentage cover of each species using the following intervals: 0.1%, 1% to 10% at 1% intervals, and 10% to 100% at 5% intervals. Vascular plant species nomenclature follows the Portal to the Flora of Italy (2024). Charophyceae nomenclature follows Bazzichelli & Abdelahad (2009). To gain a deeper ecological understanding of the plant communities in the three pondscapes and to characterise their conservation status, we classified plant species into wetlands indicator species (WIS) and synanthropic species (SYN). Species have been classified according to Chytrý et al. (2024). Specifically, we considered WIS those reported as wetland and aquatic species with an Ellenberg moisture value higher than 7, while SYN were those reported as synanthropic species. We included in the latter group also non-native species (Portal to the Flora of Italy 2024).

2.4 Environmental variables

To account for the different morphological characteristics of the three pondscapes and to quantify their topographic heterogeneity, we calculated the Terrain Ruggedness Index (TRI). The TRI expresses the amount of elevation difference between adjacent cells of a digital elevation model (DEM). Rugged terrains are generally linked to less intensive agricultural practices in agricultural landscapes (Fanfarillo et al., 2017). Incorporating TRI enabled us to control for this relationship, allowing for a more accurate assessment of the effects of other variables. The TRI was calculated for each plot through the *Ruggedness index* function in QGIS using a DEM with a cell size of 10 m × 10 m (Regione Toscana, 2024). By overlaying the plot layer with the TRI using the tool *intersection*, we extracted the TRI value for each plot.

Given the differences in size and bank slope among the ponds, we measured the following eco-morphological variables: 1) pond area, calculated in the GIS environment, and 2) bank slope, visually estimated in the field using four intervals of values (<25%, 26-50%, 51-75%, and >76%).

2.5 Statistical analysis

For each plot, we calculated species richness and analyzed species composition regarding all species (ALL), wetland indicator species (WIS), and synanthropic species (SYN).

We tested significant differences in species richness and composition regarding ALL species, WIS, and SYN by multivariate permutational analysis of variance (PERMANOVA; (Anderson, 2001), using the PERMANOVA routine in the software PRIMER 6 and the package PERMANOVA+ (Gorley & Clarke, 2008). Specifically, we tested the following factors included in the PERMANOVA design: i) “Pondscape” (fixed factor with three levels: High ALE, Intermediate ALE, and Low ALE) as a large scale factor (pondscape-scale) affecting plant diversity, proxy of all factors acting at the landscape scale (e.g. isolation, agricultural pressure); ii) “Pond” (random factor nested in Pondscape, with 45 levels) as a local scale factor (pond-scale), proxy for pond-specific environmental factors, such as morphology, hydrology, water chemistry, and management characteristics influencing plant diversity; iii) “Transect” (random factor nested in Pond, with 135 levels) as a within pond scale factor, proxy of the factors acting across the pond; iv) “Plot position” (fixed factor with two levels: W = in-water, O = out-water) to account for the aquatic-terrestrial gradient; v) the interaction “Pondscape × Plot position”, and vi) the interaction “Pond × Plot position”. The test on species richness was performed on a Euclidean distance matrix calculated on untransformed species richness values, with 999 random permutations, while the test on species composition was performed on a Bray–Curtis distance matrix on square-root transformed abundance data, with 999 random permutations (Anderson & Ter Braak, 2003). We included TRI as a covariable in the PERMANOVA model to account for the portion of variance potentially explained by terrain ruggedness. The effect of the TRI on species richness and composition was never significant, as reported in Table S1 and Table S2 in the Supplementary material to chapter 2; this allowed us to perform the analyses without this covariable. After PERMANOVA on species richness and composition, we calculated the percentage of variance of species richness and composition expressed by each factor, to identify the most influential one in shaping plant diversity.

When the “Pondscape” factor or its interaction with the “Plot position” was significant, a pairwise t-test was performed to test the significant differences between the three pondscapes ALE within the in-water plots and within the out-water plots (Wei et al., 2012).

To identify the species associated with each of the three pondscapes and the aquatic-terrestrial gradient (inside-outside water), an Indicator Species Analysis (INSPAN) was carried out using the function *multipatt* in the indicspecies package (Cáceres & Legendre, 2009) of R (version 2024.09.0; R Core Team, 2023).

To visualise the patterns of species composition in relation to ALE, we performed a non-metric multidimensional scaling ordination (NMDS). The NMDS analysis was carried out in R using the *metaMDS* function in the vegan package (Oksanen et al., 2022), with Bray–Curtis distances computed using the *vegdist* function and results displayed using the *ordispider* function highlighting the centroids of the three pondscapes.

3. Results

Overall, we recorded a total of 224 taxa for the High ALE pondscape, 278 taxa for the Intermediate ALE pondscape, and 282 taxa for the Low ALE pondscape. Species are reported in Table S3 in the Supplementary material to chapter 2.

The out-water plots were mainly composed of therophytes and hemicryptophytes, and in some cases woody shrub species, such as *Rubus caesius* L. and *Rubus ulmifolius* Schott. The in-water plots hosted many waterlogged and submerged aquatic vascular species (*Potamogeton crispus* L., *Potamogeton natans* L., *Potamogeton nodosus* Poir., *Myriophyllum spicatum* L.), along with some species belonging to the Characeae (algae), including *Chara* spp. and *Nitella tenuissima* (Desvaux) Kützing. Among the helophytes, *Phragmites australis* (Cav.) Trin. ex Steud., *Typha angustifolia* L., *Typha latifolia* L. and species belonging to *Juncus* and *Schoenoplectus* genera occurred.

The mean values of the eco-morphological variables are provided in Table S4 in the Supplementary material to chapter 2. Ponds belonging to the High ALE pondscape presented higher values of pond bank slope (>76% in 5 ponds) while more gentle slopes occurred in ponds of the Low ALE pondscape (<25% in 9 ponds).

Pondscape, Pond, and Plot position significantly affected the species richness of the groups of species (Tab. 1). A significant effect of the interaction between Pond (nested in Pondscape) and Plot position on species richness also occurred. By contrast, the effect of Transect on species richness and the interaction between Pondscape and Plot position were not significant (Tab. 1).

Table 1: PERMANOVA results for species richness of all the species and groups of species. ALL = all species, WIS = Wetland Indicator Species, SYN = Synanthropic species. Nested factors are reported within brackets. Df = degrees of freedom; MS = mean sum of squares; Pseudo-F = F value by permutation; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Species richness

		ALL		WIS		SYN	
Factors	df	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F
Pondscape	2	243.7	3.97*	43.2	3.44*	43.2	3.44*
Pond (Pondscape)	42	61.3	2.66***	12.5	5.94***	12.5	5.94***
Transect (Pond (Pondscape))	90	22.9	0.97	2.1	1.30	2.1	1.30
Plot position	1	23745	584.41***	233.3	43.36***	233.3	43.36***
Pondscape × Plot position	2	26.0	0.64	5.1	0.94	5.1	0.94
Pond (Pondscape) × Plot position	42	40.6	1.72**	5.4	3.34***	5.4	3.34***
Residuals	90	23.5	-	1.6	-	1.6	-
Total	269	-	-	-	-	-	-

The differences in species richness between the three pondscapes are reported in Fig. 2 and in Table S5 of the Supplementary material to chapter 2. Plots located in Low ALE and Intermediate ALE pondscapes had a higher number of WIS and a lower number of SYN species compared to the High ALE pondscape (Fig. 2a).

Although we did not find any significant interaction between Pondscape and Plot position, we found differences in species richness between all the pondscapes for each level of plot position (Tab. S5; Fig. 2b,c). Specifically, a generally lower number of overall species and WIS occurred in the in-water plots of the High ALE pondscape compared to those in the Intermediate ALE and Low ALE pondscapes, highlighting a decrease in aquatic species in the former (Fig. 2b). In the out-water plots a lower number of overall species occurred in the High ALE pondscape, while a higher number of SYN species were present in the High ALE pondscape compared to in the Low ALE pondscapes (Fig. 2c).

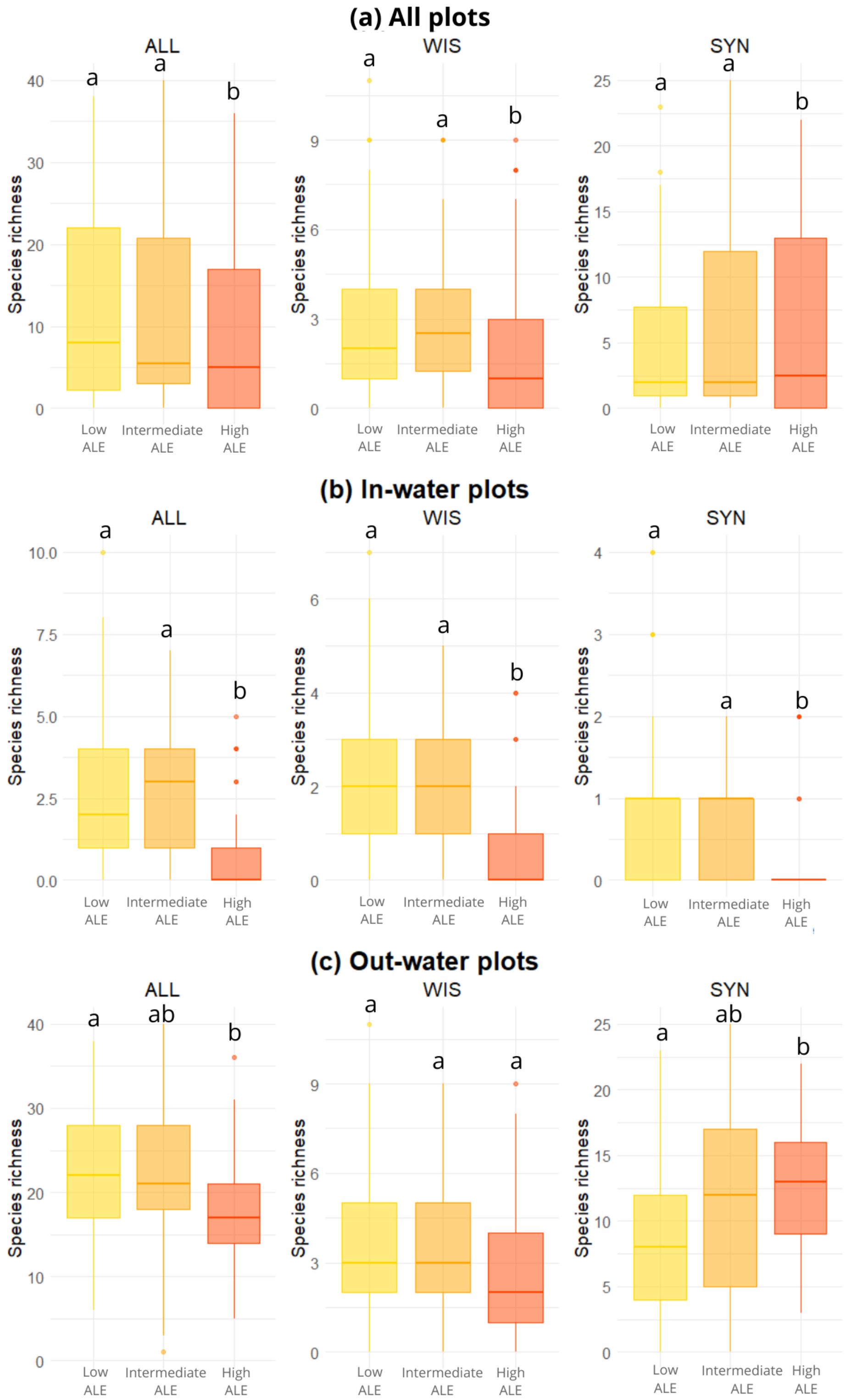

Figure 2: Boxplots of species richness of all the species and groups of species, of (a) all plots and (b) within the two plots positioned in-water, (c) out-water, according to pondscape ALE (Low ALE, Intermediate ALE, High ALE). ALL = all species, WIS = Wetlands Indicator Species, SYN = Synanthropic species. Single dots represent outliers. The median is represented by the thick horizontal strip. Different letters indicate statistically significant differences at $p < 0.05$.

The values of estimated percentage of variance of species richness explained by factors are shown in Fig. S3 of the Supplementary material to chapter 2. The total variance (expressed as %) was mainly driven by Plot position (41%, 21%, and 21% of variance expressed respectively for ALL species, WIS, and SYN) and Pond (10%, 22%, and 22% of variance expressed respectively for ALL species, WIS, and SYN). These two factors were followed by the Pondscape emerging as the third most influencing factor in explaining species richness variation (6%, 10%, and, 10% respectively for ALL species, WIS, and SYN). Transect explained the lowest percentage of expressed variance (3%, 8%, and 8% respectively for ALL species, WIS, and SYN).

The composition of all groups of species (ALL, WIS, and SYN) significantly differed among the Pondscape, the Pond, and the Plot position. The interactions between Pondscape and Plot position ("Pondscape × Plot position") and Pond and Plot position ("Pond (Pondscape) × Plot position"), significantly affected the species composition of all the groups of species (Tab. 2). Moreover, species composition varied among the Transects, except for SYN species.

Table 2: PERMANOVA results for species composition of all the species and groups of species. ALL = all species; WIS = Wetlands Indicator Species; SYN = Synanthropic species. Nested factors are reported within brackets. Df = degrees of freedom; MS = mean sum of squares; Pseudo-F = F value by permutation; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

		Species composition					
		ALL		WIS		SYN	
Factors	df	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F
Pondscape	2	18930	2.71***	18535	3.03***	7696.3	1.50*
Pond (Pondscape)	42	16914	3.71***	6126	3.88***	5101.4	3.48***
Transect (Pond (Pondscape))	90	1882.2	1.08**	1578.7	1.13**	1465.5	1.05

Plot position	1	1268800000	22.09***	41233	9.86***	1.2796	33.88***
Pondscape × Plot position	2	16914	2.94***	10917	2.61**	12103	3.20**
Pond (Pondscape) × Plot position	42	5743.9	3.29***	4189.1	3.01***	3777	2.71***
Residuals	90	1744.1	-	1388.6	-	1393.4	-
Total	269	-	-	-	-	-	-

More specifically, as reported in Table S6 of the Supplementary material to chapter 2, we found statistically significant differences between the Low ALE and High ALE pondscapes, as well as between the Intermediate ALE and High ALE pondscapes. However, we did not find significant differences between the Low ALE and Intermediate ALE pondscapes in terms of species composition. We found similar results when analysing Pondscape in relation to Plot position. Within the in-water plots, we observed significant changes in species composition between the Low ALE and High ALE pondscapes, as well as between the Intermediate ALE and High ALE pondscapes. Conversely, we did not find significant differences in species composition between the Low ALE and Intermediate ALE pondscapes. We found significant differences in species composition among all the pairs of pondscapes within the out-water plots, except for SYN species composition between the Low ALE and Intermediate ALE pondscapes.

The total variance, expressed as %, of species composition was mainly driven by the Plot position (17%, 11%, and 21% of variance expressed respectively for ALL species, WIS, and SYN) and Pond (17%, 19%, and 17% of variance expressed respectively for ALL species, WIS, and SYN) followed by Pondscape (7%, 8%, and 4% of variance expressed respectively for ALL species, WIS, and SYN; Fig. S4 of the Supplementary material to chapter 2). Transect explained the lowest percentage of expressed variance (5%, 7%, and 4% respectively for ALL species, WIS, and SYN).

The results of the indicator species analysis showed a prevalence in the High ALE pondscape of SYN and ruderal species, such as, *Convolvulus arvensis* L., *Lactuca sativa* L. subsp. *serriola* (L.) Galasso, Banfi, Bartolucci & Ardenghi, and *Torilis arvensis* (Huds.) Link subsp. *arvensis*, along with alien species like *Symphyotrichum squamatum* (Spreng.) G.L.Nesom in the out-water plots. Conversely, the Intermediate ALE pondscape featured a mix of SYN and shrub species, such as *Medicago lupulina* L. and *Spartium junceum* L. The Low ALE pondscape was characterised by a greater abundance of woody species like *Quercus cerris* L. and *Ulmus minor* Mill. subsp. *minor* (Table 3).

The in-water plots of the High ALE pondscape were characterized by nutrient-requiring species like *Zannichellia palustris* L. and *Chara globularis* Thuiller. In contrast, the in-water plots of the Intermediate ALE and Low ALE pondscapes were characterized by WIS like *M. spicatum*, *P. nodosus*, *Juncus subnodulosus* Schrank, *Schoenoplectus lacustris* (L.) Palla, and *Schoenoplectus tabernaemontani* (C.C.Gmel.) Palla and by some WIS also classified as SYN such as *Lemna minor* L., *T. angustifolia*, and *T. latifolia*.

Table 3: Results of the indicator species analysis for the entire plant communities between plots positions, according to the pondscape agricultural land-use extent (ALE). Only the 10 species with the highest indicator values are shown. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. ▲ = WIS (Wetland Indicator Species; ■ = SYN (Synanthropic species). The full species list is available in the Supplementary material to chapter 2 (Tab. S7).

	Low ALE		**Intermediate ALE**		**High ALE**	
	Species	**IndVal**	**Species**	**IndVal**	**Species**	**IndVal**
All plots	*Carex flacca* subsp. *flacca*	0.458**	*Rubia peregrina*	0.434**	*Torilis arvensis* subsp. *arvensis* ■	0.450**

Lotus dorycnium	0.414**	*Mentha aquatica* subsp. *aquatica* ▲ ■	0.373*	*Avena sterilis* subsp. *sterilis* ■	0.437 **
Prunus spinosa subsp*. spinosa*	0.411*	*Carex pendula* ▲ ■	0.358**	*Acer campestre*	0.391**
Xeranthemum cylindraceum	0.393**	*Medicago lupulina* ■	0.339**	*Lactuca sativa* subsp*.* *serriola* ■	0.375**
Quercus cerris	0.374**	*Laurus nobilis*	0.298**	*Convolvulus arvensis* ■	0.373**
Ulmus minor subsp. *minor*	0.298*	*Medicago minima*	0.297**	*Symphyotrichum squamatum* ■	0.349**
Lotus hirsutus	0.297**	*Clematis vitalba* ■	0.284**	*Galium aparine* ■	0.315**
Juncus subnodulosus ▲	0.296**	*Eupatorium cannabinum* subsp. *cannabinum* ▲ ■	0.279**	*Lysimachia arvensis* ■	0.296**

	Linum trigynum	0.293**	*Spartium junceum*	0.261**	*Equisetum ramosissimum* ▲ ■	0.293*
	Agrimonia eupatoria subsp. *eupatoria*	0.290*	*Fallopia convolvulus* ■	0.236**	*Epilobium tetragonum* ▲ ■	0.292**
In-water plots	*Typha latifolia* ▲ ■	0.404**	*Veronica anagallis-aquatica* subsp. *anagallis-aquatica* ▲	0.293*	*Zannichellia palustris* ▲	0.250*
	Juncus subnodulosus ▲	0.368**	*Potamogeton nodosus* ▲	0.288*	*Chara globularis* ▲	0.246*
	Typha angustifolia ▲ ■	0.309*	*Chara gymnophylla* ▲	0.258*		
	Lemna minor ▲ ■	0.276*	*Myriophyllum spicatum* ▲	0.258*		
	Schoenoplectus lacustris ▲	0.258 *	*Nymphaea* × *marliacea* ▲ ■	0.258*		
	Schoenoplectus tabernaemontani ▲	0.258*				

	Carex flacca subsp. *flacca*	0.648**	*Rubia peregrina*	0.613**	*Torilis arvensis* subsp. *arvensis* ■	0.636**
	Lotus dorycnium	0.586**	*Medicago lupulina* ■	0.479**	*Avena sterilis* subsp. *sterilis* ■	0.619**
	Prunus spinosa subsp. *spinosa*	0.581**	*Laurus nobilis*	0.422**	*Acer campestre*	0.553**
	Xeranthemum cylindraceum	0.556**	*Medicago minima*	0.420**	*Lactuca sativa* subsp. *serriola* ■	0.530**
Out-water plots	*Quercus cerris*	0.529**	*Clematis vitalba* ■	0.401**	*Convolvulus arvensis* ■	0.527**
	Lotus hirsutus	0.419**	*Eupatorium cannabinum* subsp. *cannabinum* ▲ ■	0.394**	*Symphyotrichum squamatum* ■	0.494**
	Juniperus communis	0.419**	*Bromus hordeaceus* subsp. *hordeaceus*	0.380**	*Galium aparine* ■	0.445**
	Linum trigynum	0.415**	*Carex pendula* ▲ ■	0.373**	*Bidens frondosa* ■	0.424**

Agrimonia eupatoria	0.410**	*Spartium junceum*	0.369**	*Lysimachia arvensis* ■	0.418**
Knautia integrifolia	0.391**	*Crepis capillaris* ■	0.366**	*Equisetum ramosissimum* ▲ ■	0.414**

The difference in species composition between the three pondscapes, as visualized in the NMDS, is reported in Figure S5 of the Supplementary material to chapter 2. A clear separation in species composition between the three pondscapes is observed in the in-water (Supplementary material to chapter 2, Fig. S5b) and out-water plots (Supplementary material to chapter 2, Fig. S5c) while a greater overlap between the pondscapes occurs when considering all the plots (Supplementary material to chapter 2, Fig. S5a).

4. Discussion

Our study revealed that Mediterranean farmland ponds within pondscapes with varying agricultural land-use extent (ALE) exhibit significant variations in plant species richness and composition. Pondscape factor was not the only factor affecting plant species richness and composition variation. Plant diversity was also influenced by local factors (pond-scale), such as pond shape, hydrological dynamics, water quality, and management practices. For this reason, differences in species richness and composition were observed between aquatic and terrestrial plots, as well as among ponds within the same pondscape. Conversely, we found differences between transects of the same pond only for species composition meaning that the heterogeneity within the pond affects the composition of communities but not their overall species richness. Moreover, the pondscape factor was not the most important factor affecting plant species richness and composition. The water-land gradient occurring in each pond along with pond-specific characteristics, contributed to the higher variation in plant diversity, emphasizing that a higher variation in plant diversity occurs at the scale of individual ponds rather than across the entire pondscape.

Effects of agricultural land-use extent on the species richness and composition of plant communities

In accordance with our first hypothesis, we found a decline in species richness with increasing ALE in the pondscape. Declerck et al. (2006) found that intensive livestock land use alters the physicochemical conditions of pond water through nutrient runoff, leading to eutrophication and a consequent reduction in plant species richness. This finding confirms that anthropogenic land uses have a negative impact on the plant diversity of small water bodies (Bolpagni et al., 2019; 2020). Additionally, as expected, species composition of plant communities was affected by the ALE in the pondscape, with synanthropic species being more abundant in the ponds of the High ALE pondscape, while wetland indicator species showing an opposite trend. This trend is particularly evident in the out-water plots. In the High ALE pondscape, synanthropic species such as *Lysimachia arvensis* (L.) U.Manns & Anderb. and *T. arvensis* subsp. *arvensis* and many alien species — mostly invasive in our study area — such as *Bidens frondosa* L., *Erigeron sumatrensis* Retz., and *S. squamatum*, were present. Alien taxa tend to be abundant in ponds of High ALE pondscape, having a lower level of naturalness with respect to the other two pondscapes. Pondscapes like High ALE pondscape are heavily impacted by agriculture and have a scarcity of forest habitats, which act as a barrier to invasion (Bolpagni & Piotti, 2016; Houlahan et al., 2006). On the contrary, in the Low ALE pondscape, species of forest understory, such as *Clematis vitalba* L., *Eupatorium cannabinum* L. subsp. *cannabinum*, and *Rubia peregrina* L., replaced species typical of anthropogenic and disturbed habitats. Moreover, woody species like *Quercus cerris* and *Ulmus minor* subsp. *minor* dominated, suggesting a high degree of naturalness and ecological succession resulting from abandoned fields and transition to forest. The in-water plots of the High ALE pondscape were characterised by the presence of *Z. palustris* and *C. globularis*, both indicators of eutrophic conditions due to agricultural runoff (Pełechaty et al., 2004; Poikane et al., 2018). Conversely, the in-water plots of the Low ALE pondscape showed the presence of the rare Characeae species *N. tenuissima* and helophyte species *Baldellia ranunculoides* (L.) Parl., both not previously recorded in southern Tuscany (Peruzzi et al., 2024; Ravera et al., 2024). These two are indicator species of specific habitats. *N. tenuissima* is an indicator species of the Habitats Directive 92/43/EEC “Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp.”

(code 3140; Biondi et al., 2009) and grows in natural conditions and not disturbed environments characterized by shallow waters, absence of turbidity and pH near to neutrality (Blaženčić et al., 2018; Caffrey & Monahan, 1994). *B. ranunculoides* is a diagnostic species of EUNIS habitat "Oligotrophic-water vegetation" (code P3f; Chytrý et al., 2020) and is characteristic of unpolluted waters. Its sensitivity to elevated nutrients levels, primarily caused by intense agriculture, has contributed to its considerable decline (Chytrý et al., 2024). In ponds within Intermediate ALE and Low ALE pondscapes, the gently sloping margins supported helophyte species of the genera *Carex*, *Juncus*, *Schoenoplectus*, and *Typha.* Furthermore, in ponds within Intermediate ALE and Low ALE pondscapes, the gradual transition to deeper water promoted the presence of submerged macrophytes such as *M. spicatum* and *Potamogeton* spp. Biomass of submerged macrophytes is strongly influenced by slope with a strong decrease of biomass with strong inclined slopes (Kolada et al., 2024).

Effect of factors at different spatial scales on the species richness and composition of plant communities

The landscape factor — namely what we called pondscape — did not result to be the most important factor affecting plant species richness and composition variation. Plot position along the water-land gradient was the factor contributing the most to the variation in plant diversity. Aquatic and terrestrial plant communities have a different ecology and therefore a different species composition. Moreover, this result highlights that very different ecological conditions can occur within a very small spatial scale. Permanent waters sustain aquatic plant diversity and support unique and rare plant communities (Davies et al., 2008), fostering the growth of species with specific adaptations (Den Hartog & Segal, 1964). Furthermore, the percentage of variance in species richness and composition explained by factors showed that the greatest variance in plant diversity was associated with ponds within different pondscapes. This finding suggests that the higher variation in species richness and species composition can occur at pond-scale, not at pondscape-scale. This result is in agreement with previous findings for badlands and winter arable fields (Fanfarillo et al., 2023; Maccherini et al., 2011) highlighting that local gradients exert a stronger influence on plant communities than broader landscape gradients (Bolpagni & Piotti, 2016; Fernández-Aláez et al., 2020). This outcome also emphasizes the uniqueness of

Mediterranean ponds and underscores their role as examples of the ecological phenomenon of patchiness. Often described as wet isolated patches in a dry matrix, these ponds are shaped by processes characteristic of patchily distributed habitats. Species disperse and migrate between patches, creating networks interconnected through physical and biological processes (Biggs et al., 2017). Accordingly, the landscape context remains an important factor of diversity conservation (Sawatzky et al., 2019). However, a distinctive feature of pondscape is the heterogeneity of the plant and animal communities hosted within individual ponds. In the same pondscape, single ponds are subjected to specific natural variations such as hydroperiods and direct agricultural management (Jeffries, 2008) resulting in significant biodiversity differences among ponds. Accordingly, variations at small (local) scales give rise to diverse plant communities. For this reason, from a biodiversity conservation perspective, it is important to preserve several small environments and not only a few large environments (Parker, 2012), mirroring the micro-reserves for plant conservation established in Spain (Laguna et al., 2004, 2016).

5. Conclusions

The central finding of this study is the significant contribution of each farmland pond to overall plant diversity. Though not originally created for conservation purposes, Mediterranean farmland ponds play a crucial role in maintaining biodiversity, especially those located in pondscapes with lower levels of agricultural land use. These small water bodies, despite experiencing varying agricultural land-use extents in their surroundings, host plant species of conservation interest, highlighting the importance of their preservation. Pond-scale hosts a higher variation in species richness and composition compared to the wider spatial scales. We suggest that rather than exclusively focusing on the protection of entire pondscapes, a more effective approach may be to prioritize the conservation of individual ponds. Moderate human activity around these ponds can be to some extent beneficial, as it helps prevent natural degradation through drying out or filling-in processes. Our findings underscore the significance of Mediterranean farmland ponds as unique ecosystems and emphasize the need for targeted conservation efforts at pond level to protect freshwater plant diversity.

CHAPTER 3

Islands in the field: differences in ecological patterns of farmlands ponds and true islands

Summary

Ponds are largely recognized as "island-like" systems, yet important ecological differences exist compared to true islands. While some similarities between islands and island-like systems have been identified, other aspects remain understudied, highlighting the need for further studies to clarify their true resemblance. This study aims to: (i) quantify farmland pond beta diversity of macrophytes by partitioning it into replacement and richness difference components, and identify key conservation sites via local contribution to beta diversity (LCBD); (ii) assess the relative influence of environmental and spatial factors on macrophyte communities to evaluate deterministic processes; and (iii) examine pond interconnections by linking plant life forms to their species contribution to beta diversity and dispersal abilities. We surveyed macrophytes and water parameters in 115 ponds across insular and continental areas of Italy, spanning landscapes with different agricultural land-use extents. We partitioned beta diversity and calculated local and species contributions to beta diversity. We assessed the effects and the relative contribution of climatic, water physico-chemical, and spatial predictors on species composition using Redundancy Analysis and variation partitioning. T-test was used to test differences in species contribution to beta diversity values and dispersal distances between life-form groups. We found high beta diversity, supporting the view of ponds as isolated habitats, mainly driven by species turnover. Environmental factors, particularly climate and water physico-chemistry, had stronger effects than spatial variables on community composition, indicating that local environmental heterogeneity drives species sorting even at small spatial scales. Water-dependent species emerged as the main

contributors to beta diversity, reflecting their sensitivity to site-specific conditions. Overall, ponds are unique habitats partially resembling islands. Their high beta diversity aligns with traditional island systems, but the influence of local factors highlight distinct ecological dynamics compared to true islands.

1. Introduction

Ponds, as freshwater habitats within a terrestrial matrix, are considered “island-like” systems due to their isolation, spatial fragmentation, and limited size, features typical of insular environments (Itescu, 2019). One of the main characteristics of insular systems is the isolation, which can be summarized as the extent of physical disconnection between systems, that is strongly dependent by the nature of the habitat surrounding the systems, namely the matrix (Stamps et al., 1987, Watson, 2002). In true islands, the system-matrix diversity is described by the contrast between the terrestrial systems and the aquatic matrix, and island isolation is defined as the meters of water that separate two islands (physical isolation). For island-like systems, for instance, the matrix can be described by different abiotic conditions between the system and the matrix (physiological isolation) or by the different elevation levels between the system and the matrix (geographical isolation; Itescu, 2019). This suggests that the concept of isolation, for island-like systems, cannot be oversimplified in the physical distance between one system and others or between one system and the mainland.

This latter is another key element in defining insular systems and it is strongly related to the theory of island biogeography (MacArthur and Wilson, 1967). According to this theory, species richness decreases with distance of islands from the mainland. This theory, together with the concept of distance decay of similarity by Nekola and White (1999), predicts greater species similarity among two sites as geographic distance on the two sites decreases. This concept resulted to be true for island-like systems. As reported by Arnott (2009), community composition similarity in island-like systems, such as lakes and ponds, is spatially structured, meaning that the spatial proximity positively influences species similarity. This outcome suggests that the proximity among sites favor the dispersal rates, leading to an increase in the similarity among the sites. More precisely, species similarity between sites in true islands is more commonly dominated by the nestedness (species assemblage of a site as a subset of the species assemblage of a richer site) component, compared to beta diversity of island-like systems (Watling and Donnelly, 2006; Matthews et al., 2015).

Beta diversity (species composition site-to-site variability; Baselga, 2010) can be determined by diverse mechanisms spanning from purely stochastic processes (such as the ecological drift or the dispersal limitation) to deterministic ones (such as environmental filtering), as well as by the interaction between stochastic and deterministic process (Chase, 2010). In true islands, especially small ones, environmental heterogeneity resulted to be more important than ecological drift in positively influencing the beta diversity of tree communities (Liu et al., 2018), while for island-like systems, especially ponds, the processes responsible of aquatic protists community assemblage are more history-sites dependent (Chase, 2003).

In light of the above, it is evident that island-like systems do not fully function as true islands. More precisely, depending on the taxa (Tepedino and Stanton, 1976; Frank and Lounibos, 1987; Shepherd and Brantley, 2005), species dispersal ability (Lososová, et al., 2023), system size (Bond, et al. 1988), or ecological scale and context (Haila, 1990), these systems may experience different degrees of "insularity" and, therefore, some aspects conform to true islands while others do not. The comparison of patterns and processes between islands and other fragmented habitats has been the object of many studies (Simberloff and Abele, 1976; Harris, 1984; Laurance, 2008; 2009; Holt, 2009). Thus some similarities between islands and island-like systems have been identified and described, other aspects are still undetected and far from being differentiated, indicating the need of other studies to define the real ecological similarity between island and island-like systems.

For this reason, our work aims to: analyze the ecological processes leading to the plant community diversity and assemblage in farmland ponds, highlighting the similarity in the processes between true islands and these aquatic island-like systems. More precisely we: i) define the farmland ponds beta diversity value, by decomposing it in its two components replacement (species turnover) and richness difference (species gain and loss) and identify key sites of conservation interest by analyzing local contribution to beta diversity (LCBD), ii) define and balance the roles of environmental and spatial factors in shaping macrophyte communities of farmland ponds, assessing the influence of deterministic processes on aquatic species composition in these island-like systems, and iii) investigate the degree of interconnection between farmland ponds by putting different plant life forms in relation with their beta diversity contributions (SCBD) and dispersal abilities.

2. Methods

2.1 Study sites and sampling design

The study sites and sampling design follow the one reported in “Study area and methodology” paragraph of chapter 1. Moreover, the study areas occur along a bioclimatic gradient spanning from mediterranean to temperate continental through the temperate sub-mediterranean (Pesaresi et al., 2017). Average monthly minimum temperatures across the study area range from -0.5 °C to 7.9 °C, average monthly maximum temperatures from 30.7 °C to 32.3 °C, and average annual precipitation ranges from 453 mm to 823 mm (Supplementary material to chapter 3, Tab. S1).

2.2 Plant community data and environmental data

Vegetation data and physico-chemical water data were collected as reported in the “Data collection” paragraph of chapter 1. Moreover, together with vegetation and physico-chemical water data, to better understand the ecological characteristics of plant communities, we grouped species into two major life forms: non-emergent hydrophytes (NEHY) and wetland emergent rooted plants (WERP). Both life form groups are composed of species reported either as wetland or aquatic species (Chytrý et al., 2024), including Charophyte species. Specifically, we considered NEHY submerged and floating species and WERP emergent species. Values of the dispersal distance were assigned to the species following the classification of Lososová et al. (2023) and avoiding human-assisted dispersal (anthropochory). More precisely, classes 1-2 of dispersal distance indicate local/non-specific dispersal mode, classes 3-4-5 indicate anemochory and myrmecochory dispersal modes, and class 6 indicates all other zoochory dispersal modes (dyszoochory, endozoochory, and epizoochory). Dispersal distance values for species dispersed via hydrochory are not provided; therefore, a total of 18 species (16% of total species) were not assigned to any dispersal class. Furthermore, we considered some climatic data, to account for the different climatic conditions of the three regions. Specifically we selected mean annual air temperature (°C), annual precipitation amount (mm), and potential evapotranspiration (kg m^{-2}) as the relevant climatic factors from CHELSA (Karger et al., 2017). These climatic factors have previously been found to be reliable predictors of freshwater macrophyte diversity (Tapia Grimaldo et al., 2017).

2.3 Data analysis

We performed all analyses in R (version 2024.09.0; R Core Team, 2024), using vegetation plot data averaged at the pond level. Plot data were aggregated per pond to focus on diversity patterns between ponds, in line with our aim to assess the applicability of island biogeography theory to these systems.

The total β-diversity across the region was calculated as the total variance of the community data matrix (a cover-based matrix), which ranges from 0 to a maximum of 1 (Legendre and De Cáceres, 2013), using the *beta.div.comp* function from the R package adespatial (Dray et al., 2023), and was subsequently partitioned into its two components, replacement and richness difference (Legendre, 2014) .

To better understand the contribution of a specific site to the total beta diversity, we computed the Local Contribution to Beta Diversity (LCBD; Legendre & De Cáceres, 2013) for each pond and tested for significance by 999 random permutations. High and low LCBD values indicate unique sites in terms of species composition (Pozzobom et al., 2020). To define the contribution of single species to the total beta diversity, Species Contribution to Beta Diversity (SCBD) were computed for each species. LCBD and SCBD values were computed using *beta.div* function in the R package adespatial (Dray et al., 2023).

Given the island-like feature of ponds and the distance decay similarity we considered the spatial factor in the analysis. Specifically, to assess the impact of spatial autocorrelation we used distance-based Moran's eigenvector maps (db-MEM) as spatial predictors, following the spatial eigenfunction analysis approach (Borcard et al., 2004; Griffith & Peres-Neto, 2006). First, we created a Euclidean distance matrix based on the geographic coordinates of the plots. This matrix was then truncated using a threshold distance, determined by the maximum connection distance in a minimum spanning tree; we used the *spantree* function in vegan R package (Oksanen et al., 2022). Next, we performed a Principal Coordinate Analysis (PCoA), using the *pcoa* function in ape R package (Paradis et al., 2004). From the observation of the eigenvalues, the first axis was significant and accounted for over 70% of the variance, capturing the spatial patterns within the study area (Supplementary material to chapter 3, Table S2); thus, it was selected to represent the spatial component in the models.

Preliminarily, we checked for collinearity among predictors (climatic, water physico-chemical, and spatial variables). This was done using a correlation matrix based on Spearman's correlation coefficient. Correlation matrix was created through *rcorr* function in HmiscR package (Harrell, 2021; Supplementary material to chapter 3, Fig. S2). We defined a subset of environmental variables by excluding those with strong correlations ($\rho > 0.60$). When two variables were strongly correlated, we kept those more ecologically meaningful for aquatic plants. The following variables have been used as predictors in the models: percentage of dissolved oxygen, nitrate ion, ammonium ion, annual precipitation amount, annual range of monthly potential evapotranspiration, and the spatial variable (Supplementary material to chapter 3, Table S3).

We performed a Redundancy Analysis (RDA) considering the spatially nested design, using *rda* function, to assess the effect of climatic, water physico-chemical, and spatial variables on species composition, using the vegan R package (Oksanen et al., 2022). We further applied variation partitioning (using the *varpart* function from vegan package) to disentangle the unique and shared contributions of climate, water physico-chemical components, and space on species composition.

To test whether SCBD values and dispersal distances significantly differ between the two major life form groups, we performed a Welch's *t*-test (unequal variances *t*-test), using the *t.test* function of R base package (R Core Team, 2024).

3. Results

The total beta diversity in the study area was 0.47 and was largely explained by species replacement (0.40, 81.2%).

The significant RDA models accounted for 2.9% of the total variance (adj. $R^2 = 0.029$, $p < 0.05$) with dissolved oxygen, annual precipitation amount, nitrate ion, and the spatial variable being significant drivers of macrophyte composition (Tab. 1). Axis 1 was significant and represented an environmental gradient strongly associated with dissolved oxygen and the spatial factor while Axis 2 was primarily influenced by annual precipitation (Tab. 1). Eighty sites significantly contributed to beta diversity, showing significant LCBD values but with no specific spatial or environmental patterns (Supplementary material to chapter 3, Fig. S3).

Table 1: Results of the redundancy analysis (RDA) showing the direction (RDA1 and RDA2 scores), explained variance, and F-statistic for each environmental and spatial variable. Significant variables (p < 0.05) are reported in bold. DO = dissolved oxygen, NO_3 = nitrate ion, NH_4 = ammonium ion, bio_12 = annual precipitation amount, epot = potential evapotranspiration, Axis 1 = spatial variable.

Factors	RDA1	RDA2	Variance (%)	F-statistic
DO	**0.49**	**0.24**	**4.68**	**1.81**
NO_3	**0.06**	**-0.55**	**3.94**	**1.53**
NH_4	0.01	0.01	0.62	0.24
bio_12	**0.39**	**1.26**	**4.24**	**1.64**
epot	-0.29	-0.49	2.52	0.98
Axis 1	**-3.37**	**-0.16**	**6.81**	**2.64**

Spatial structure (Axis 1) explains a substantial portion of the variance in species composition (Tab. 1). However, variance partitioning (Fig. 1) reveals that the fraction exclusively attributable to space is lower than that explained by environmental variables when the total variance is decomposed into unique components. Moreover, the shared fraction of variance between space and environment is negligible and not significant.

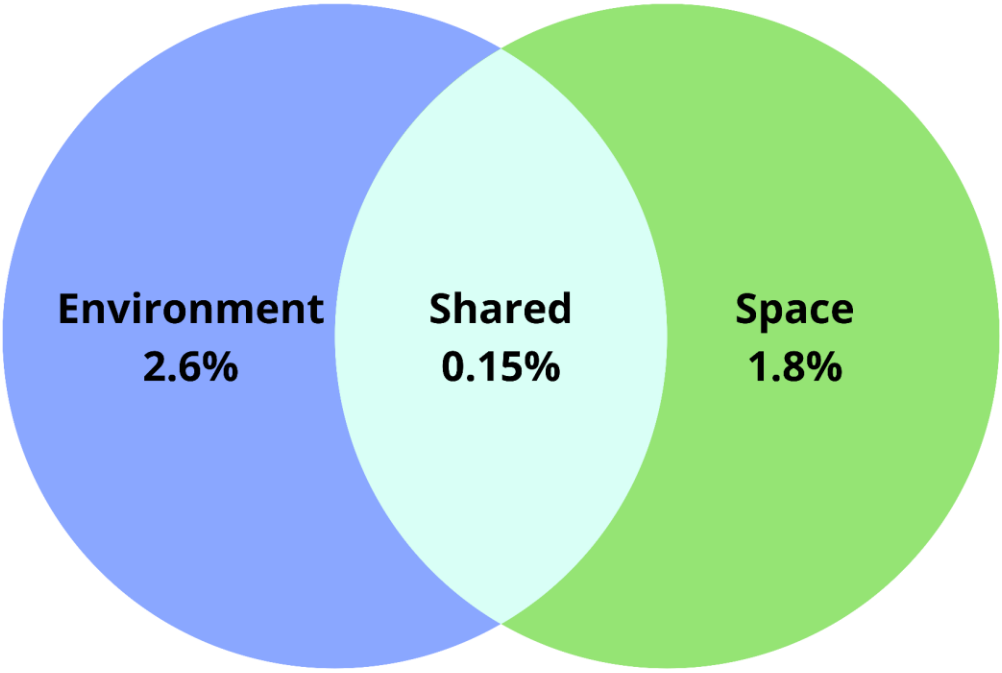

Figure 1: Venn diagram showing the relative contribution of the environmental (climatic and water physico-chemical variables) and spatial variables to the total variation in species composition. * = $p < 0.05$. Residuals= 0.96.

Submerged species such as *Chara vulgaris*, *Potamogeton pusillus*, and *Zannichellia palustris*, were associated with higher levels of dissolved oxygen (Supplementary material to chapter 3, Fig. S4). By contrast, floating and emergent species such as *Spirodela polyrhiza*, *Lemna minor*, *Salvinia natans*, and *Phragmites australis* were associated with oxygen-poor water; moreover, the distribution of the first three species (free-floating *taxa*) was strongly influenced by spatial structure (Supplementary material to chapter 3, Fig. S4). *Typha angustifolia* was mainly linked to high nutrient (NO_3) concentration Supplementary material to chapter 3, Fig. S4).

The species with the highest contribution to beta diversity (SCBD) were *Typha angustifolia*, *Chara vulgaris*, and *Mentha aquatica* which were also among the most frequent ones (Tab. 2). Overall, 8 of the 15 species contributing most to beta diversity belong to the NEHY group.

Table 2: Shortened table of Species Contribution to Beta Diversity (SCBD) and species frequencies (number of plot occurrences). Only the first fifteen species are reported and the species are ordered according to decreasing SCBD values. NEHY = non-emergent hydrophytes, WERP = wetland emergent rooted plants. The complete table is reported in Supplementary material to chapter 3 (Tab. S4).

Species	SCBD	Frequency	Life forms
Typha angustifolia	0.06	23	WERP
Chara vulgaris	0.06	19	NEHY
Mentha aquatica	0.04	17	WERP
Potamogeton natans	0.04	16	NEHY
Phragmites australis	0.03	9	WERP
Juncus inflexus	0.02	9	WERP
Lemna minuta	0.02	7	NEHY
Agrostis stolonifera	0.02	10	WERP
Spirodela polyrhiza	0.02	9	NEHY
Veronica anagallis-aquatica	0.02	9	WERP
Lemna aequinoctialis	0.02	2	NEHY
Lemna minor	0.02	11	NEHY
Ranunculus peltatus	0.02	6	NEHY
Eleocharis palustris	0.02	11	WERP
Lemna gibba	0.02	6	NEHY

Non-emergent hydrophytes exhibited significantly higher SCBD values compared to wetland emergent rooted plants (Welch's t-test, $p < 0.05$), contributing more to overall beta diversity (Fig. 2) and resulted as the life form group having the highest dispersal distance (Supplementary material to chapter 3, Tab. S5, Fig. S5).

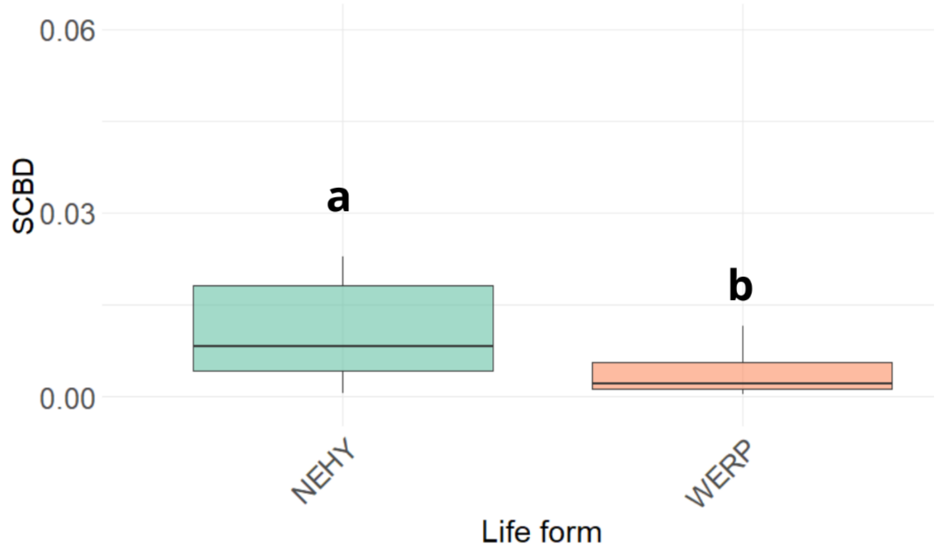

Figure 2: Differences in SCBD (species contribution to beta diversity) between two major life forms groups. Different letters indicate significant differences between the groups (Welch's t-test, $p < 0.05$). NEHY = non-emergent hydrophytes, WERP = wetland emergent rooted plants.

4. Discussion

In this study, we evaluated if ponds work as island-like systems following biogeographical theory. We found moderately high beta diversity between ponds, a pattern that suggests a degree of isolation of these systems, with replacement emerging as the dominant component, highlighting a differentiation in terms of the magnitude of environmental filtering in ponds compared to true islands. Moreover, we found that both environmental (climatic and water physico-chemical) and spatial factors shape aquatic plant community composition, with environmental factors exerting a stronger influence than spatial ones. This highlights the differences in species assemblages across ponds due to the environmental diversity of ponds even at short spatial distances. Furthermore, we found significant differences in the aquatic plant composition, life forms, and dispersal strategies, highlighting the variation in the effects of pond specific features on macrophytes, with water-dependent species being the most sensitive ones and, therefore, contributing more to differences among plant compositions (Fig. 3).

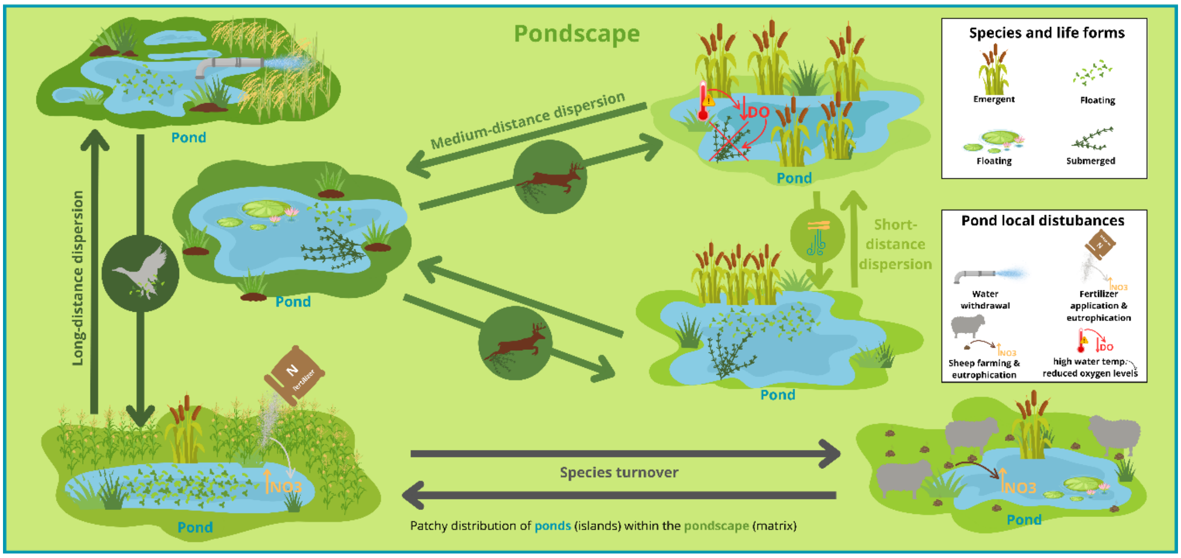

Figure 3: Graphical summary of the main findings of this study, illustrating the relationships between environmental, spatial, and land-use factors, macrophyte community composition, and beta diversity patterns across pondscapes.

Turnover-dominated beta diversity patterns along an isolation–connectivity continuum

We found moderately high beta diversity among ponds indicative of an isolated behavior of these systems. Wetlands are not entirely isolated systems, but they rather exist along an isolation–connectivity continuum (Leibowitz, 2003). Within this framework, ponds can be considered transitional islands, where spatial isolation promotes species turnover, resulting in distinct communities even among ponds within the same network (pondscape). Therefore, unlike true islands, nestedness was not the primary component of beta diversity; on the contrary, we found that species turnover emerged as the main component and this pattern is consistent with previous findings in macrophyte communities (Alahuhta et al., 2017; Bertuzzi et al., 2019; Boschilia et al., 2016; Viana et al., 2016). The predominance of turnover suggests that species replacement is the phenomenon mostly affecting species composition change among ponds. Turnover is the consequence of environmental sorting (Baselga, 2010) and it is typically associated with processes mediated by local environmental factors, such as habitat structure, connectivity, surface area, vegetation shading, hydroperiod, and water/sediment quality (Alahuhta, 2015; Alahuhta & Heino, 2013; Bolpagni et al., 2020; Capers et al., 2010).

Additionally, due to the high variation in plant communities among ponds, we identified numerous sites that significantly contributed more than others to beta diversity and thus hold unique species composition. However, these contributions did not follow clear spatial or land-use patterns. This outcome is a consequence of the high turnover among ponds and highlights the unicity and relevance of many ponds emphasizing the importance of focus on site-specific measures rather than following a particular gradient for conservation purposes (Parker, 2012).

Influence of deterministic processes on aquatic species composition: balancing environmental and spatial effects

Macrophyte species composition was influenced by both environmental (climatic and water physico-chemical) and spatial factors. Oxygen-poor waters were dominated by floating-leaved and emergent species (e.g. *Phragmites australis*, *Lemna minor*, *Salvinia natans,* and *Spirodela polyrhiza*) while submerged macrophytes (e.g. *Chara vulgaris*, *Potamogeton pusillus,* and *Zannichellia palustris*) were associated with oxygen rich waters. Oxygen availability is critical for plant cellular respiration. Under oxygen-poor conditions, emergent and floating-leaved species have an advantage over submerged species because they can access atmospheric oxygen (Ervin, 2023). *Lemna minor*, *Salvinia natans*, and *Spirodela polyrhiza* also showed strong spatial structuring, suggesting that they tend to occur in geographically near sites. These species are capable of significantly modulating the quality of the sites they colonize, for example by triggering deoxygenation of the water column and thus inducing a strong, progressive similarity between them. Thus, low oxygen levels in relation to these species may be as much a consequence of their presence than a cause of it. Moreover, all three are floating species, which likely reflects the observed correlation between spatial patterns and turbidity. Moreover, emergent wetland plants such as *Typha angustifolia* are commonly found in nutrient-rich, oxygen-poor waters, as elevated nutrient levels tend to favor tall, highly competitive species (Bornette & Puijalon, 2011). Floating macrophytes, though sensitive to certain environmental factors such as water depth, are generally better adapted to turbid conditions than submerged species, which typically require clearer waters due to their higher sensitivity to reduced light availability or algal competition (Middelboe & Markager, 1997). This suggests that turbidity acts as a spatially structured environmental filter, influencing non-randomly species distribution.

From these outcomes, it emerges that both environmental (climatic and water physico-chemical) and spatial factors affect the assemblage and dynamics of pond plant communities. However, environmental variables explain a larger portion of the variance in species composition, highlighting the predominance of site-specific dynamics and processes, mainly affected by pond management, in shaping pond communities. In fragmented and isolated ecosystems local environmental gradients are important elements affecting biodiversity (Snoeks et al., 2025). This outcome highlights that despite ponds exhibit island-like dynamics and although ponds within the same network (pondscape) share some environmental condition, the species composition of ponds is only partially spatially structured, meaning that they do not totally follow the distance decay of similarity concept (Nekola and White, 1999). Moreover, the modest amount of explained variance expressed by environmental and spatial factors suggests that these variables, expressing deterministic processes, do not capture a big percentage of macrophyte diversity, meaning that additional variables and site-specific dynamics likely contribute to species composition patterns in ponds. Historical land use, unmeasured biotic and abiotic interactions, hydrological regimes, human disturbance and pond management, are some of the other factors possibly affecting macrophytes species composition (Bornette and Puijalon, 2011; Dawson et al., 2017; Fernández-Aláez et al., 2020; Scheffer et al., 2006). Moreover, this outcome suggests that casual and non predictable events would have a stronger influence on the plant species composition of farmland ponds. This aligns with other studies on different taxa, which have found stochastic processes to exert a stronger influence than deterministic ones in productive ponds (Chase 2003; Chase 2010). Thus, even for macrophytes, given the productive context of the farmland ponds in this study, stochastic processes, such as priority effects, where arrival order determines competitive dominance, and demographic drift would play influential roles in shaping species diversity.

Environmental control overrides distance in structuring beta diversity dominated by non-emergent hydrophytes

Species with a medium to high degree of occurrence strongly contribute to beta diversity. This result aligns with the findings of Gavioli et al. (2022), who reported a positive correlation between species contribution to beta diversity values and the number of sites occupied. This further suggests that frequent species, while widespread, are not ubiquitous and exhibit a differentiated distribution (absent in some sites and present in many others) leading them to occur only in a subset of sites with specific environmental characteristics, such as low water depth or oxygen poor waters. Among the species with the highest contribution to beta diversity values, both non-emergent hydrophytes (*Chara vulgaris* and *Potamogeton natans*) and wetland emergent rooted plants (*Typha angustifolia* and *Phragmites australis*) occurred. Nevertheless, we found significant differences in the species contribution to beta diversity values with non-emergent hydrophytes having higher values compared to wetland emergent rooted plants. Moreover, we found that wetland emergent rooted plants present extremely low values of dispersal distance while high values belong to non-emergent hydrophytes species. These two outcomes highlight that non-emergent species contribute the most to beta diversity, even though they also exhibit the greatest dispersal ability. Such widely dispersing species tend to be more uniformly distributed, which would reduce their contribution to beta diversity. However, this apparent contradiction can be explained by the fact that non-emergent species, despite their successful dispersal ability, are also more sensitive to specific environmental conditions leading to the possible failure of establishment in ponds that do not meet their habitat requirements, consequently leading to higher species turnover across different sites (Alahuhta et al., 2017; Wang et al., 2021). By contrast, emergent species show lower compositional turnover among sites, as they often tolerate a wider range of conditions and exhibit high adaptability (Lawniczak et al., 2010). This highlights that species dispersal mechanisms and the geographic distance between ponds are not exclusively drivers of species replacement (Jesus et al., 2025), since pond environmental conditions shape species distributions in distinct ways. This result not only highlights that species occurrence depends on local environmental conditions but it also suggests, one more time, the relevance of priority effects, meaning that despite the dispersal ability of a species both deterministic and stochastic processes can affect its capacity to establish in a pond.

5. Conclusions

Insularity is a broad concept which can take on different forms depending on the discontinuity and fragmentation of an environment. We found that ponds, peculiar freshwater habitats located within a terrestrial matrix acting as a barrier for dispersion, partially align to the biogeographic island theory. In some respects, ponds can be compared to islands because of their high beta diversity across sites. However, beta diversity here is mainly driven by species turnover (replacement of species between ponds) rather than by the nested community patterns typical of oceanic islands. Moreover, ponds are shaped by unique dynamics and processes, both predictable and casual, which modify and affect them in specific ways, despite spatial proximity. Ponds represent particular ecological, transitional "islands" that do not fully conform to the classical rules and principles typically associated with island systems particularly due to their small size and strong influence of anthropogenic pressures.

General discussion

This work emphasizes the dynamics related to plant species assemblage in farmland ponds. It primarily offers an accessible dataset, PONDY, which, as other datasets (Santoianni et al. 2025), plays a crucial role in mapping species and habitat distributions while supporting conservation efforts by identifying protected or invasive species. Given the tight links between plant communities and environmental factors, PONDY integrates pond vegetation data with water physico-chemical parameters to assess water body ecological status and analyze how water quality influences species presence, abundance, and cover. Moreover, this thesis provides insights essential for assessing the conservation value of these ecosystems. These wet islands host rare taxa and species conservation concerns. The thesis also reveals that Mediterranean farmland ponds, occurring in different pondscapes, exhibit significant variations in plant species richness and composition. This result indicates that the landscape (pondscape) influences species assemblages, even though it is not the primary factor driving variation in plant species richness and composition. Instead, the plot position along with the water-land gradient accounted for the largest share of variation in plant diversity. This outcome emphasizes that highly diverse ecological conditions can exist within very small spatial scales. Permanent water bodies sustain aquatic plant diversity and harbor unique and rare plant communities (Davies et al., 2008), promoting the establishment of species with specific ecological adaptations (Den Hartog & Segal, 1964). Although landscape context remains an important component for conserving biodiversity (Sawatzky et al., 2019), the proportion of variation in species richness and composition explained by the examined factors indicates that the greatest variation in plant diversity occurs among ponds within different pondscapes. This finding suggests that differences in species richness and composition are more present at the pond scale rather than at the pondscape scale. Therefore, even within the same pondscape, individual ponds experience specific natural variations (such as differing hydroperiods and varying degrees of direct agricultural management, Jeffries, 2009) which lead to substantial differences in biodiversity among ponds. This outcome emphasises the uniqueness of Mediterranean farmland ponds indicating their behaviour as wet isolated patches in a dry matrix and, therefore, influence of processes characteristic of patchily distributed habitats on these systems. The second main finding of this thesis supports the idea of ponds as isolated systems. Indeed the high beta diversity occurring among ponds support the hypothesis that they function as isolated habitats. However, since in pondscapes species disperse and migrate between patches (ponds), creating interconnected networks thanks to physical and biological processes (Biggs et al., 2017), farmland ponds should not be viewed as entirely isolated systems, but rather as existing along an isolation–connectivity continuum (Leibowitz, 2003). The high component of turnover in the beta diversity among ponds, highlights the presence of connections among ponds in the same pondscape which are mostly driven by environmental sorting (Baselga, 2010) which is typically associated with processes generated by local environmental factors, such as habitat structure, connectivity, surface area, vegetation shading, hydroperiod, and water/sediment quality (Alahuhta, 2015; Alahuhta & Heino, 2013; Bolpagni et al., 2020; Capers et al., 2010). This aspect, together with the little contribution of space in defining the species assemblage in the ponds, reflect the predominance of site-specific dynamics and processes, in affecting pond communities. In fragmented and isolated ecosystems local environmental gradients are important elements affecting biodiversity (Snoeks et al., 2025). For these reasons, although ponds exhibit island-like dynamics, they do not totally conform to the principle of biogeography theory. Accordingly, in this work, environmental factors have an independent effect on macrophyte composition, compared to space. The significant influence of local environmental factors on aquatic plant community composition is further highlighted by the greater contribution of non-emergent species to beta diversity, compared to wetland emergent rooted plants. Although non-emergent species have superior dispersal capabilities compared to emergent species, they tend to exhibit higher compositional turnover among sites due to their greater sensitivity to environmental conditions. By contrast, emergent species generally show lower compositional turnover across sites as they can tolerate a wider range of conditions and possess higher adaptability (Lawniczak et al., 2010).

General conclusions

Though heavily modified, Mediterranean farmland ponds play a vital role in sustaining biodiversity, particularly those situated in pondscapes with lower agricultural land use, where appropriate management is applied. For example, maintaining riparian vegetation, controlling nutrient inputs, and preserving natural shoreline complexity can greatly enhance the habitat quality of ponds. These small water bodies support plant species of conservation concern, underscoring the importance of their protection. Moreover, given the importance of pond-specific aspects in plant diversity, for conservation purposes it would be more effective to prioritize the protection of individual ponds rather than focusing solely on conserving entire pondscapes. Moreover, understanding the effects of local characteristics of individual ponds (e.g., size, depth, slope, vegetation structure) in affecting the biodiversity of these systems is crucial. These pond-specific factors contribute to the isolated behavior of ponds although inserted in an interconnected network (pondscape). Research on farmland ponds and pondscape highlights the potential and conservation of these small water bodies to act as keystone environments within managed landscape. Moreover, based on this evidence, a future step to deepen the study of plant communities in farmland ponds would be to incorporate species traits. This approach goes beyond identifying which species are present and instead focuses on understanding how species adapt and what functional roles the community performs within the environment. Including traits would clarify even better the ecological mechanisms shaping community structure and dynamics of these water habitats.

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Supplementary material to chapter 1

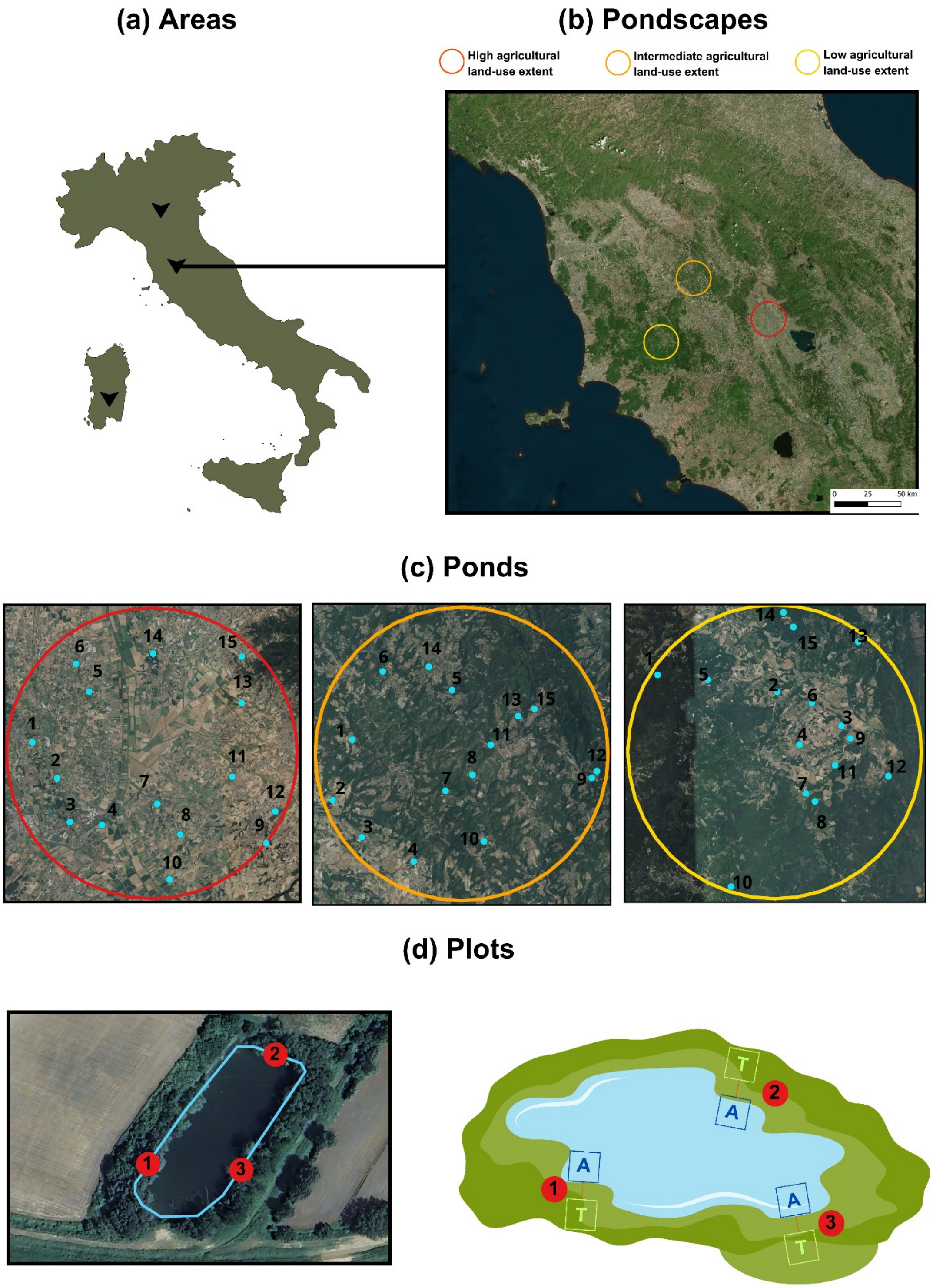

Figure S1. Spatial representation of the sampling design followed, spanning (a) the regions, (b) the selection of pondscapes, (c) the selection of ponds, and (d) the localisation of vegetation plots (2 m × 2 m) within each pond. A = aquatic plot, T = terrestrial plot.

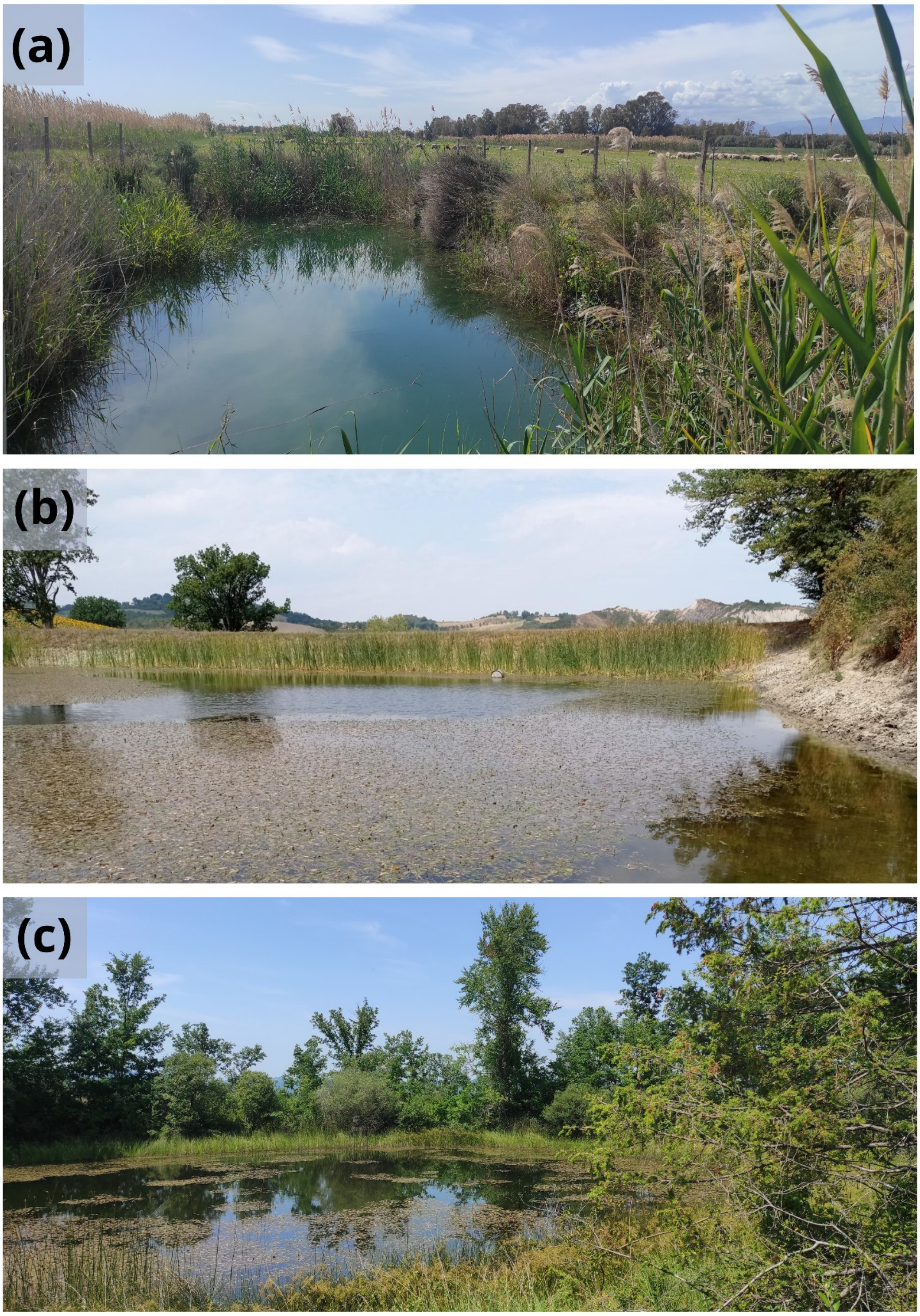

Figure S2: Examples of ponds pertaining the three pondscapes: (a) High agricultural land-use extent pondscape (Monastir, Sud Sardegna, Italy); (b) Low agricultural land-use extent pondscape (Montieri, Grosseto, Italy); and (c) Intermediate agricultural land-use extent pondscape (San Venanzio, Modena, Italy). Photo credits: (a, b) S. Cannucci; (c) R. Bolpagni.

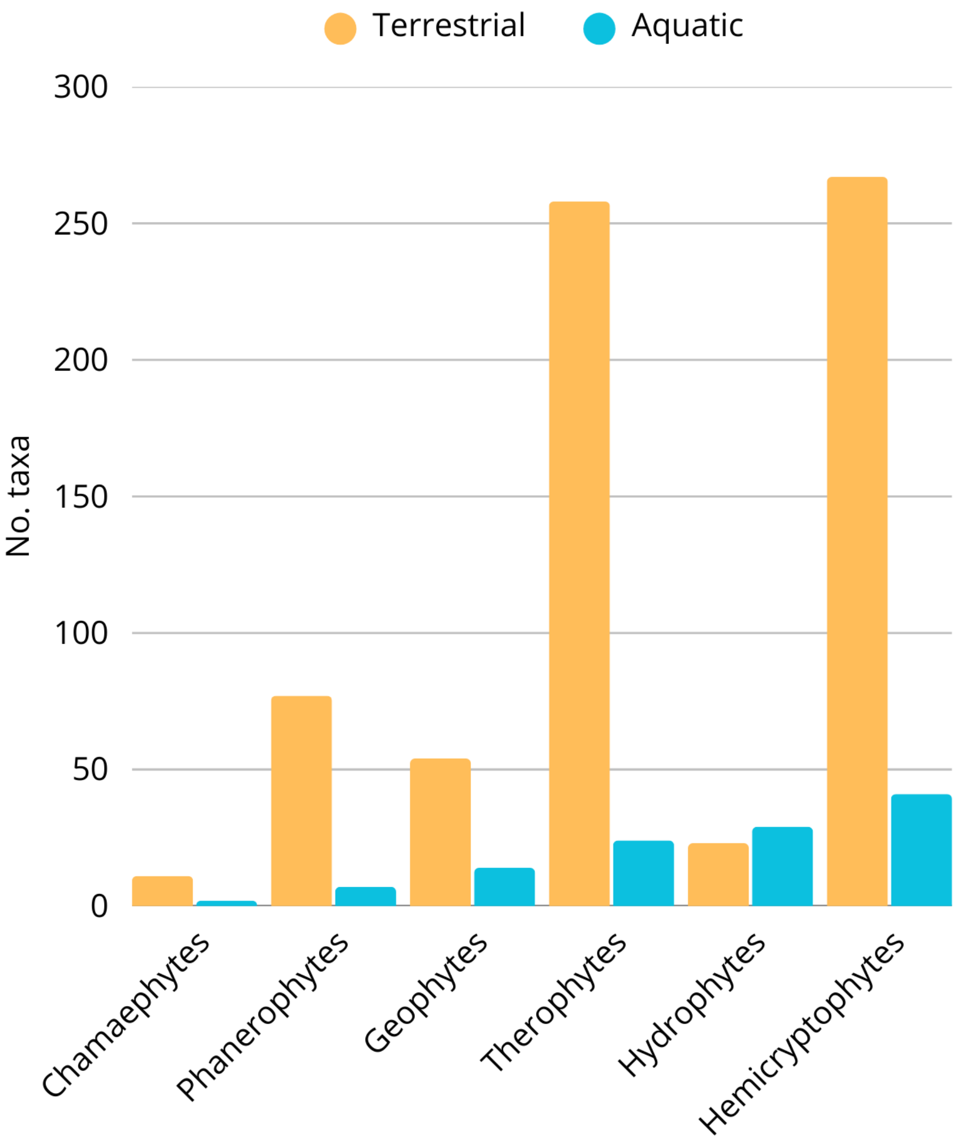

Figure S3. Number of different life forms for both the terrestrial and aquatic plots.

Table S1. Classification of the vegetation plots according to EUNIS habitat types.

EUNIS	No. plots	Percentage
Inland waters (P)	1	0.2
Brackish-water vegetation (P3a)	2	0.5
Fresh-water small pleustophyte vegetation (P3b)	32	5.6
Fresh-water submerged vegetation (P3d)	18	3.1
Fresh-water nymphaeid vegetation (P3e)	24	4.2
Stonewort vegetation (P3h)	39	6.8
Tall-helophyte bed (Q51)	96	16.7
Small-helophyte bed (Q52)	4	0.5
Tall-sedge bed (Q53)	8	1.6
Periodically exposed shore with stable, eutrophic sediments with pioneer or ephemeral vegetation (Q61)	10	1.7
Periodically exposed shore with stable, mesotrophic sediments with pioneer or ephemeral vegetation (Q62)	4	0.7
Periodically exposed saline shore with pioneer or ephemeral vegetation (Q63)	1	0.2
Helophyte beds (Qb)	36	6.3

Table S2: Summary statistics of environmental parameters measured across the plots of the studied ponds.

	Mean	SD	Min	Max
Water depth (m)	18.9	36.2	0	210
Water temperature (C°)	22.9	4.4	12.6	31
pH	8.0	0.6	6.78	10.1
Dissolved oxygen (%)	79.4	43.4	2	211
Electrical conductivity (uS/cm)	864.1	811.8	157	6292
Turbidity (NTU)	125.7	321.8	0	2352
Phosphate ion (ug/L)	51.8	147.2	0	1233.2
Nitrate ion (mg/L)	1.0	3.2	0	29.29
Ammonium ion (mg/L)	1.4	5.8	0	50.31

Supplementary material to chapter 2

Table S1: Results of PERMANOVA test on species richness considering Terrain Ruggedness Index (TRI). Nested factors are in brackets. ALL = all species, WIS = Wetlands Indicator Species, SYN = Synanthropic species. With brackets are reported the nested factors. Df = degrees of freedom; MS = mean sum of squares; Pseudo-F = F value by permutation; * = *p* <

0.05; ** = $p < 0.01$; *** = $p < 0.001$.

Species richness							
		ALL		WIS		SYN	
Factors	df	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F
TRI	1	93.31	1.6175	7.5414	0.65487	7.5414	0.65487
Pondscape	2	197.08	3.2002*	41.663	3.3189*	41.663	3.3189*
Pond (Pondscape)	42	61.885	2.8033***	12.633	6.2183***	12.633	6.2183***
Transect (Pond (Pondscape))	87	22.076	1.1706	2.0316	1.5131	2.0316	1.5131
Plot position	1	23745	565.12***	233.34	39.189***	233.34	39.189***
TRI × Pondscape	2	61.553	2.7883	2.1237	1.0453	2.1237	1.0453
TRI × Pond (Pondscape)	0	-	No test	-	No test	-	No test
TRI × Transect (Pond (Pondscape))	0	-	No test	-	No test	-	No test
TRI × Plot position	1	23.374	0.60182	3.5241	0.65696	3.5241	0.65696
TRI × (Pondscape × Plot position)	2	69.312	3.6755**	1.0875	0.80999	1.0875	0.80999
TRI × Pond (Pondscape) × Plot position	38	27.088	1.4364	1.5037	1.1199	1.5037	1.1199
Pondscape × Plot position	2	16.471	0.4015	3.6651	0.63147	3.6651	0.63147
Pond (Pondscape) × Plot position	42	41.194	2.1844**	5.8382	4.3482***	5.8382	4.3482***
Residuals	49	18.858	-	1.3427	-	1.3427	-
Total	269	-	-	-	-	-	-

Table S2: Results of PERMANOVA test performed in PRIMER 6 software, on species composition considering Terrain Ruggedness Index (TRI). With brackets are reported the nested factors. ALL = all species, WIS = Wetlands Indicator Species, SYN = Synanthropic species. With brackets are reported the nested factors. Df = degrees of freedom; MS = mean sum of squares; Pseudo-F = F value by permutation; * = *p* < 0.05; ** = *p* < 0.01; *** = *p* < 0.001.

Species composition							
		ALL		**WIS**		**SYN**	
Factors	df	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F
TRI	1	9.339.2	1.4684	5792.2	1.2797	4774.3	1.03
Pondscape	2	17558	2.5624***	17721	3.0361***	7944.6	1.5947**
Pond (Pondscape)	42	6890.3	3.7068***	6125.7	3.9013***	5008.7	3.4177***
Transect (Pond (Pondscape))	87	1858.8	1.0677	1567.3	1.1281*	1465.5	1.0579
Plot position	1	126880	21.91***	41029	9.7051***	12790	33.519***
TRI × Pondscape	2	2554.3	1.3742	1834.1	1.169	1510.2	1.0305
TRI × Pond (Pondscape)	0	-	No test	-	No test	-	No test
TRI × Transect (Pond (Pondscape))	0	-	No test	-	No test	-	No test
TRI × Plot position	1	8127.8	1.544	3470.1	1.0877	5135.5	1.4694
TRI × (Pondscape × Plot position)	2	2562.1	1.4717*	2256.2	1.6241*	1690.6	1.2203
TRI × Pond (Pondscape) × Plot position	38	1683.8	0.96714	1332	0.95877	1391.8	1.0046
Pondscape × Plot position	2	15485	2.7411***	11120	2.7886**	10864	2.9158***
Pond (Pondscape) × Plot position	42	5679.2	3.2621***	4153.9	2.99***	3743.6	2.7023***
Residuals	49	1741	-	1389.2	-	1385.4	-
Total	269	-	-	-	-	-	-

Table S3: Species list ◪ = species of the Low ALE pondscape, ◈ = species of Intermediate ALE pondscape, ◉ = species of the High ALE pondscape, ▲ = WIS (Wetland Indicator Species; ■ = SYN (Synanthropic species). Species plant names follow the Portal to the Flora of Italy (2024); Characeae nomenclature follows Bazzichelli and Abdelahad (2009). Only species identified at the specific level are reported.

Species name
Acer campestre L. ◪ ◈ ◉
Acer negundo L. ◉ ■
Achillea ageratum L. ◪
Achillea millefolium L. subsp. *millefolium* ◪ ◉ ■
Aegonychon purpurocaeruleum (L.) Holub ◪ ◈
Agrimonia eupatoria L. subsp. *eupatoria* ◪ ◈ ◉
Agrostis stolonifera L. subsp. *stolonifera* ◪ ◈ ◉ ■
Ajuga genevensis L. ◈ ■
Alisma lanceolatum With. ◉ ▲ ■
Alisma plantago-aquatica L. ◪ ◈ ▲ ■
Alnus glutinosa (L.) Gaertn. ◪ ◈ ▲ ■
Althaea cannabina L. ◉
Ammi majus L. ◪ ■
Anethum foeniculum L. ◈ ■
Anethum piperitum Ucria ◈
Anisantha diandra (Roth) Tutin ex Tzvelev ◈ ■
Anisantha madritensis (L.) Nevski subsp. *madritensis* ■
Anisantha sterilis (L.) Nevski ◪ ◈ ◉ ■
Anisantha tectorum (L.) Nevski ◈ ■
Anthemis arvensis L. subsp. *arvensis* ◪ ◉ ■
Anthemis cotula L. ◉ ■
Anthoxanthum odoratum L. ◉
Aristolochia rotunda L. subsp. *rotunda* ◪ ◈ ◉
Artemisia vulgaris L. ◪ ◈ ◉ ■
Arundo donax L. ◪ ■
Asparagus acutifolius L. ◈
Asplenium onopteris L. ◪ ◈
Asplenium trichomanes L. subsp. *trichomanes* ◈ ■
Astragalus monspessulanus L. subsp. *monspessulanus* ◪ ◈
Atriplex prostrata Boucher ex DC. ◉ ■
Avena barbata Pott ex Link ◈ ◉ ■
Avena fatua L. subsp. *fatua* ◪ ■
Avena sterilis L. subsp. *sterilis* ◪ ◈ ◉ ■
Avena strigosa Schreb. ◈ ■
Baldellia ranunculoides (L.) Parl. ◪ ▲
Bellardia viscosa (L.) Fisch. & C.A.Mey. ◪ ■
Betonica officinalis L. ◪ ■
Bidens frondosa L. ◪ ◈ ◉ ▲ ■
Bidens tripartita L. subsp. *tripartita* ◈ ▲ ■
Blackstonia perfoliata (L.) Huds. subsp. *perfoliata* ◪ ◈

Brachypodium distachyon (L.) P.Beauv. ◪
Brachypodium rupestre (Host) Roem. & Schult. ◪ ◈ ◉
Brachypodium sylvaticum (Huds.) P.Beauv. subsp. *sylvaticum* ◪ ◈ ◉ ■
Briza maxima (L.) Tzvelev ◪
Bromopsis erecta (Huds.) Fourr. ◪ ◈
Bromus arvensis L. subsp. *arvensis* ◪ ■
Bromus commutatus Schrad. subsp. *commutatus* ◉ ■
Bromus hordeaceus L. subsp. *hordeaceus* ◪ ◈ ◉ ■
Bryonia dioica Jacq. ◉ ■
Bupleurum baldense Turra ◈
Campanula rapunculus L. ◪ ◈ ◉
Campanula trachelium L. subsp. *trachelium* ◈ ■
Capsella bursa-pastoris (L.) Medik. subsp. *bursa-pastoris* ◉ ■
Cardamine hirsuta L. ◉ ■
Carduus nutans L. subsp. *nutans* ◪ ■
Carduus pycnocephalus L. subsp. *pycnocephalus* ◪ ◈ ◉ ■
Carex distans L. ◈ ▲
Carex divulsa Stokes ◈▲
Carex flacca Schreb. subsp. *flacca* ◪ ◈ ◉ ▲
Carex hirta L. ◈ ◉ ▲ ■
Carex otrubae Podp. ◪ ◈ ◉ ▲
Carex pendula Huds. ◪ ◈ ◉▲ ■
Carex spicata Huds. subsp. *spicata* ◈ ▲ ■
Carpinus betulus L. ◪
Castanea sativa Mill. ◈
Catapodium rigidum (L.) C.E.Hubb. subsp. *rigidum* ◪ ◈ ■
Centaurea jacea L. subsp. *gaudinii* (Boiss. & Reut.) Gremli ◪
Centaurium erythraea Rafn subsp. *erythraea* ◪ ◈ ◉ ■
Centaurium pulchellum (Sw.) Druce subsp. *pulchellum* ◪ ◈ ■
Cerastium glomeratum Thuill. ◈ ◉ ■
Cervaria rivini Gaertn. ◪
Chaerophyllum temulum L. ◪ ◈ ◉
Chara globularis Thuill. ◈ ◉ ▲
Chara gymnophylla A.Braun ◈ ▲
Chara vulgaris L. ◪ ◈ ◉ ▲
Chenopodium album L. subsp. *album* ◉ ■
Cichorium intybus L. ◪ ◈ ■
Circaea lutetiana L. subsp. *lutetiana* ◈ ■
Cirsium arvense (L.) Scop. ◪ ◈ ◉ ■
Cirsium creticum (Lam.) d'Urv. subsp. *triumfettii* (Lacaita) K.Werner ◪
Cirsium vulgare (Savi) Ten. ◈ ◉ ■
Cistus creticus L. subsp. *eriocephalus* (Viv.) Greuter & Burdet ◪
Clematis vitalba L. ◪ ◈ ◉ ■
Clinopodium nepeta (L.) Kuntze subsp. *nepeta* ◪ ◈
Clinopodium vulgare L. subsp. *vulgare* ◪ ◈ ■
Convolvulus arvensis L. ◪ ◈ ◉ ■
Convolvulus sepium L. ◉ ■
Coriaria myrtifolia L. ◈
Cornus mas L. ◪

Cornus sanguinea L. subsp. *hungarica* (Kárpáti) Soó ◪ ◈ ◉ ▲
Cota altissima (L.) J.Gay ◈ ■
Cota tinctoria (L.) J.Gay subsp. *tinctoria* ◪ ◈ ◉ ■
Crataegus monogyna Jacq. ◪ ◈ ◉
Crepis capillaris (L.) Wallr. ◪ ◈ ◉ ■
Crepis setosa Haller f. ◉ ■
Crepis zacintha (L.) Loisel. ◉ ■
Cruciata glabra (L.) C.Bauhin ex Opiz ◪ ◉
Cruciata leavipes Opiz ◪ ◈ ◉ ■
Cynanchica pyrenaica (L.) P.Caputo & Del Guacchio subsp. *cynanchica* (L.) P.Caputo & Del Guacchio ◪
Cynodon dactylon (L.) Pers. ◪ ◈ ◉ ■
Cynosurus cristatus L. ◪
Cynosurus echinatus L. ◪ ◈ ◉
Cyperus longus L. ◈ ◉ ▲
Cytisophyllum sessilifolium (L.) O.Lang ◪
Cytisus scoparius (L.) Link subsp. *scoparius* ◪ ◈ ◉ ■
Dactylis glomerata L. subsp. *glomerata* ◪ ◈ ◉ ■
Daucus carota L. subsp. *carota* ◪ ◈ ◉ ■
Dianthus carthusianorum L. subsp. *carthusianorum* ◉
Digitalis ferruginea L. ◈
Dioscorea communis (L.) Caddick & Wilkin ◪ ◈ ◉
Dipsacus fullonum L. subsp. *fullonum* ◪ ◈
Dittrichia viscosa (L.) Greuter subsp. v*iscosa* ◪ ◈ ◉ ■
Echinochloa crus-galli (L.) P.Beauv. subsp. *crus-galli* ◉ ▲ ■
Echium vulgare L. subsp. *vulgare* ◈ ■
Eleocharis palustris (L.) Roem. & Schult. subsp. *palustris* ◪ ◈ ◉ ▲
Elymus repens (L.) Gould subsp. *repens* ◉ ■
Emerus major Mill. subsp. *major* ◪ ◈
Epilobium hirsutum L. ◉ ▲ ■
Epilobium tetragonum L. subsp. *tetragonum* ◪ ◈ ◉ ■
Epipactis palustris (L.) Crantz ◪ ▲
Equisetum arvense L. ◈ ◉ ▲ ■
Equisetum ramosissimum Desf. ◈ ◉ ▲ ■
Equisetum telmateia Ehrh. ◪ ◈ ◉ ▲ ■
Erigeron annuus (L.) Desf. subsp. *annuus* ◪ ◈ ■
Erigeron bonariensis L. ◈ ◉ ■
Erigeron canadensis L. ◪ ◈ ◉ ■
Erigeron sumatrensis Retz. ◪ ◉ ■
Ervilia hirsuta (L.) Opiz ◈
Ervum gracile DC. ◪ ◈ ◉
Ervum tetraspermum L. ◪ ◈ ■
Euonymus europaeus L. ◪ ◈
Eupatorium cannabinum L. subsp. *cannabinum* ◈ ▲ ■
Euphorbia cyparissias L. ◪
Euphorbia exigua L. subsp. *exigua* ◪ ■
Euphorbia platyphyllos L. ◉ ■
Fallopia convolvulus (L.) Á.Löve ◈ ■
Festuca heterophylla Lam. ◪

Festuca incurva (Gouan) Gutermann ◉
Festuca myuros L. subsp. *myuros* ◉ ■
Filago germanica (L.) Huds. ◉
Filago pyramidata L. ◈ ■
Filipendula ulmaria (L.) Maxim. ◪
Fragaria viridis Weston subsp. *viridis* ◪ ◈
Fraxinus angustifolia Vahl subsp. *oxycarpa* (M.Bieb. ex Willd.) Franco & Rocha Afonso ◈ ▲
Fraxinus ornus L. subsp. *ornus* ◪ ◈ ◉
Galatella linosyris (L.) Rchb.f. subsp. *linosyris* ◪
Galega officinalis L. ◈ ◉ ■
Galium album Mill. subsp. *album* ◪ ◈ ◉ ■
Galium aparine L. ◪ ◉ ■
Galium mollugo L. ◈
Gastridium ventricosum (Gouan) Schinz & Thell. ◪ ■
Gaudinia fragilis (L.) P.Beauv. ◪ ◈ ◉
Genista januensis Viv. subsp. *januensis* ◪
Genista pilosa L. ◪
Genista tinctoria L. ◪
Geranium colombinum L. ◪ ◈ ■
Geranium dissectum L. ◪ ◈ ◉ ■
Geranium purpureum Vill. ◈ ■
Geranium sanguineum L. ◪ ◈
Geum urbanum L. ◪ ◈ ■
Glebionis segetum (L.) Fourr. ◉ ■
Globularia bisnagarica L. ◪
Gratiola officinalis L. ◉
Hedera helix L. subsp. *helix* ◪ ◈ ◉
Helianthemum nummularium (L.) Mill. subsp. *nummularium* ◪
Helichrysum italicum (Roth) G.Don subsp. *italicum* ◪
Helleborus viridis L. subsp. *bocconei* (Ten.) Peruzzi ◈
Helminthotheca echioides (L.) Holub ◪ ◈ ◉ ■
Helosciadium nodiflorum (L.) W.D.J.Koch subsp. *nodiflorum* ◈ ◉ ▲
Hesperocyparis arizonica (Greene) Bartel ◪ ■
Hippocrepis comosa L. subsp. *comosa* ◪
Holcus lanatus L. subsp. *lanatus*
Holcus mollis L. subsp. *mollis* ◉ ■
Hordeum murinum L. subsp. *leporinum* (Link) Arcang. ◉ ■
Hypericum perforatum L. subsp. *perforatum* ◪ ◈ ◉ ■
Hypochaeris achyrophorus L. ◪
Hypochaeris glabra L. ◪ ◈ ◉
Hypochaeris radicata L. ◪ ◈ ◉
Iris germanica L. ◈ ■
Jacobaea erratica (Bertol.) Fourr. ◪ ◈
Jacobaea erucifolia (L.) G.Gaertn., B.Mey. & Scherb. subsp. *erucifolia* ◈ ◉
Jasione montana L. ◪ ◈ ◉
Juglans regia L. ◉ ■
Juncus articulatus L. subsp. *articulatus* ◪ ◈ ◉ ▲
Juncus bufonius L. ◪ ◉ ▲
Juncus effusus L. subsp. *effusus* ◪ ◉ ▲

Juncus inflexus L. subsp. *inflexus* ◪ ◈ ◉ ▲
Juncus subnodulosus Schrank ◪ ◈ ▲
Juniperus communis L. ◪ ◈
Kickxia elatine (L.) Dumort. subsp. *elatine* ◈ ◉ ■
Knautia arvensis (L.) Coult. ◪ ◈
Knautia integrifolia (L.) Bertol. subsp. *integrifolia* ◪ ◉
Lactuca saligna L. ◈ ◉ ■
Lactuca sativa L. subsp. *serriola* (L.) Galasso, Banfi, Bartolucci & Ardenghi ◪ ◈ ◉ ■
Lactuca viminea (L.) J.Presl & C.Presl subsp. *viminea* ◉ ■
Lamium maculatum L. ◉ ■
Lathyrus annuus L. ◈ ■
Lathyrus aphaca L. subsp. *aphaca* ◪ ◈ ■
Lathyrus cicera L. ◈ ■
Lathyrus hirsutus L. ◪ ■
Lathyrus latifolius L. ◪ ◈
Lathyrus linifolius (Reichard) Bässler ◪
Lathyrus niger (L.) Bernh. ◪
Lathyrus pratensis L. subsp. *pratensis* ◈
Lathyrus sylvestris L. subsp. *sylvestris* ◪ ◈
Laurus nobilis L. ◈ ▲
Lemna minor L. ◪ ◈ ◉ ▲ ■
Leucanthemum ircutianum DC. subsp. *ircutianum* ◪ ◈
Leucanthemum pachyphyllum Marchi & Illum. ◪
Leucanthemum pallens (J.Gay ex Perreym.) DC. ◪ ◈
Leucanthemum vulgare (Vaill.) Lam. subsp. *vulgare* ◪
Ligustrum vulgare L. ◪ ◈ ◉
Limniris pseudacorus (L.) Fuss ◈ ▲
Linaria vulgaris Mill. subsp. *vulgaris* ◈ ■
Linum tenuifolium L. ◪
Linum trigynum L. ◪ ◈
Linum usitatissimum L. subsp. *usitatissimum* ◪ ◈ ■
Lolium arundinaceum (Schreb.) Darbysh. subsp. *arundinaceum* ◪ ◈ ◉
Lolium multiflorum Lam. ◈ ◉ ■
Lolium perenne L. ◈ ◉ ■
Lolium pratense (Huds.) Darbysh. ◉
Lolium rigidum Gaudin subsp. *rigidum* ◈ ■
Lonicera caprifolium L. ◪ ◈ ◉
Lonicera etrusca Santi ◈
Lotus angustissimus L. ◉ ▲
Lotus corniculatus L. subsp. *corniculatus* ◪ ◈ ◉
Lotus dorycnium L. subsp. *herbaceus* (Vill.) Kramina & D.D.Sokoloff ◪ ◈ ◉
Lotus hirsutus L. ◪ ◈
Lotus tenuis Waldst. & Kit. ex Willd. ◪ ◈ ◉
Luzula forsteri (Sm.) DC. ◉
Lycopus europaeus L. ◪ ◈ ◉
Lysimachia arvensis (L.) U.Manns & Anderb. ◈ ◉ ■
Lythrum hyssopifolia L. ◉ ▲
Lythrum salicaria L. ◪ ▲
Malus domestica (Suckow) Borkh. ◪ ■

Malus sylvestris (L.) Mill. ◪
Malva setigera K.F.Schimp. & Spenn. ◈
Medicago arabica (L.) Huds. ◈ ◉ ■
Medicago lupulina L. ◪ ◈ ◉ ■
Medicago minima (L.) L. ◪ ◈
Medicago orbicularis (L.) Bartal. ◪ ◈ ■
Medicago polymorpha L. ◈ ◉ ■
Medicago sativa L. ◪ ◈ ◉ ■
Melica uniflora Retz. ◈ ■
Mentha aquatica L. subsp. *aquatica* ◪ ◈ ◉ ▲
Mentha longifolia (L.) L. ◉ ▲ ■
Mentha pulegium L. subsp. *pulegium* ◪ ◉ ▲
Mentha suaveolens Ehrh. subsp. *suaveolens* ◈ ▲
Mercurialis annua L. ◪ ◈ ◉ ■
Microthlaspi perfoliatum (L.) F.K.Mey. ◈
Molinia arundinacea Schrank ◪
Myosotis arvensis (L.) Hill subsp. *arvensis* ◉ ■
Myosotis ramosissima Rochel subsp. *ramosissima* ◉
Myriophyllum spicatum L. ◈ ▲
Nigella damascena L. ◈ ■
Nitella tenuissima (Desvaux) Kutzing ◪ ▲
Nymphaea × marliacea Lat.-Marl. ◈ ▲ ■
Odontites vernus (Bellardi) Dumort. subsp. *serotinus* Corb. ◪ ◈ ◉ ■
Oenanthe pimpinelloides L. ◪ ◈ ◉
Olea europaea L. ◈ ■
Onobrychis caput-galli (L.) Lam. ◪ ◈
Ononis spinosa L. subsp. *spinosa* ◪ ■
Origanum vulgare L. subsp. *vulgare* ◪
Ornithopus compressus L. ◪
Ostrya carpinifolia Scop. ◪ ◈
Osyris alba L. ◈
Papaver rhoeas L. subsp. *rhoeas* ◉ ■
Parthenocissus quinquefolia (L.) Planch. ◉ ■
Paspalum distichum L. ◈ ◉ ▲ ■
Pentanema squarrosum (L.) D.Gut.Larr., Santos-Vicente, Anderb., E.Rico & M.M.Mart.Ort. ◪ ◈ ◉
Persicaria lapathifolia (L.) Delarbre subsp. *lapathifolia* ◉ ▲ ■
Persicaria maculosa Gray ◈ ◉ ▲ ■
Petasites hybridus (L.) G.Gaertn., B.Mey. & Scherb. subsp. *hybridus* ◈ ■
Petrorhagia prolifera (L.) P.W.Ball & Heywood ◈
Phalaris brachystachys Link ◈ ■
Phalaris coerulescens Desf. ◪ ◉
Phillyrea latifolia L. ◪
Phleum nodosum L.
Phleum pratense L. subsp. *pratense* ◪ ◈ ◉
Phleum subulatum (Savi) Asch. & Graebn. subsp. *subulatum* ◉
Phragmites australis (Cav.) Trin. ex Steud. ◪ ◈ ◉ ▲ ■
Picris hieracioides L. subsp. *hieracioides* ◪ ◈ ◉ ■
Pilosella officinarum Vaill. ◪

Pilosella piloselloides (Vill.) Soják subsp. *piloselloides* ◪
Pinus nigra J.F.Arnold subsp. *nigra* ◪ ■
Plantago lanceolata L. ◪ ◈ ◉ ■
Plantago major L. ◪ ◈ ◉ ■
Plantago maritima L. subsp. *serpentina* (All.) Arcang. ◪ ▲
Poa annua L. ◉
Poa bulbosa L. subsp. *bulbosa* ◉
Poa compressa L. ◪ ■
Poa nemoralis L. subsp. *nemoralis* ◪ ■
Poa pratensis L. subsp. *pratensis* ◪ ◈ ◉
Poa sylvicola Guss. ◈ ◉
Poa trivialis L. ◪ ◉ ▲ ■
Polygala flavescens DC. subsp. *flavescens* ◪
Polygonum aviculare L. subsp. *aviculare* ◪ ◈ ◉ ■
Polypogon viridis (Gouan) Breistr. subsp. *viridis* ◪ ◈ ▲
Populus alba L. ◉
Populus nigra L. subsp. *nigra* ◪ ◈ ◉ ▲
Populus tremula L. ◪
Portulaca oleracea L. ◉ ■
Potamogeton coloratus Hornem. ◪ ▲
Potamogeton crispus L. ◈ ◉ ▲
Potamogeton natans L. ◪ ◈ ▲
Potamogeton nodosus Poir. ◪ ◈ ▲
Potamogeton schweinfurthii A.Benn. ◈ ▲
Potentilla pedata Willd. ex Hornem. ◪
Potentilla recta L. subsp. *recta* ◪ ◈ ■
Potentilla reptans L. ◪ ◈ ◉ ■
Poterium sanguisorba L. subsp. *sanguisorba* ◪ ◈
Prunella laciniata (L.) L. ◪ ◈ ◉
Prunella vulgaris L. subsp. *vulgaris* ◪ ◈ ■
Prunus avium (L.) L. ◈ ◉
Prunus cerasifera Ehrh. ◈ ◉ ■
Prunus persica (L.) Batsch ◉ ■
Prunus spinosa L. subsp. *spinosa* ◪ ◈ ◉
Pseudotsuga menziesii (Mirb.) Franco ◪ ■
Pulicaria dysenterica (L.) Bernh. ◪ ◈ ◉ ▲ ■
Pulicaria odora (L.) Rchb. ◈
Pyracantha coccinea M.Roem. ◪ ◈
Pyrus communis L. subsp. *pyraster* (L.) Ehrh. ◪ ◈
Quecus cerris L. ◪ ◈
Quercus ilex L. ◪ ◈ ◉
Quercus petraea (Matt.) Liebl. subsp. *petraea* ◉
Quercus pubescens Willd. subsp. *pubescens* ◪ ◈ ◉
Ranunculus bulbosus L. ◈
Ranunculus lanuginosus L. ■
Ranunculus repens L. ◪ ◈ ▲ ■
Ranunculus sardous Crantz ◪ ◉ ▲ ■
Ranunculus sceleratus L. ◉ ▲
Raphanus raphanistrum L. subsp. *raphanistrum* ◪ ◈ ◉ ■

Rhamnus alaternus L. subsp. *alaternus* ◈
Robinia pseudoacacia L. ◪ ◈ ◉ ■
Rosa arvensis Huds. ◪ ◈
Rosa canina L. ◪ ◈ ◉
Rosa sempervirens L. ◪ ◈ ◉
Rubia peregrina L. ◪ ◈
Rubus caesius L. ◪ ◈ ◉ ■
Rubus ulmifolius Schott ◪ ◈ ◉
Rumex conglomeratus Murray ◪ ◈ ◉ ■
Rumex crispus L. ◪ ◈ ◉ ■
Rumex obtusifolius L. subsp. *obtusifolius* ◈ ■
Rumex pulcher L. subsp. *pulcher* ◉ ■
Salix alba L. ◪ ◈ ▲
Salix caprea L. ◪
Salix cinerea L. ◪ ▲
Salix hastata L. ◪
Salix purpurea L. ◪ ◉ ▲
Salix triandra L. subsp. *triandra* ◪ ▲
Sambucus ebulus L. ◪ ■
Sambucus nigra L. ◉ ■
Samolus valerandi L. ◪ ◈ ▲
Saponaria officinalis L. ◉ ■
Scabiosa columbaria L. subsp. *columbaria* ◪
Schoenoplectus lacustris (L.) Palla ◪ ▲
Schoenoplectus tabernaemontani (C.C.Gmel.) Palla ◪ ▲
Scirpoides holoschoenus (L.) Soják ◪ ◈ ▲
Scolymus hispanicus L. subsp. *hispanicus* ◈ ■
Scorpiurus muricatus L. ◪ ◈ ■
Scorpiurus subvillosus L. ◪ ◈
Scorzonera laciniata L. subsp. *laciniata* ◪ ■
Scorzoneroides autumnalis (L.) Moench ◪
Sedum cepaea L. ◈
Serratula tinctoria L. subsp. *tinctoria* ◪
Setaria italica (L.) P.Beauv. subsp. *italica* ◉ ■
Setaria italica (L.) P.Beauv. subsp. *viridis* (L.) Thell. ◉
Sherardia arvensis L. ◪ ◈ ■
Silene latifolia Poir. ◉ ■
Silene vulgaris (Moench) Garcke subsp. *vulgaris* ◈ ■
Sinapis arvensis L. subsp. *arvensis* ◪ ■
Sixalix atropurpurea (L.) Greuter & Burdet ◈ ■
Solanum nigrum L. ◉ ■
Sonchus arvensis L. subsp. *arvensis* ◪ ■
Sonchus asper (L.) Hill subsp. *asper* ◪ ◈ ◉ ■
Sonchus oleraceus L. ◪ ◈ ◉ ■
Sorbus domestica L. ◪
Sorbus torminalis (L.) Crantz ◉
Sorghum halepense (L.) Pers. ◉ ▲ ■
Spartium junceum L. ◪ ◈
Stachys germanica L. subsp. *germanica* ◈ ■

Stachys recta L. subsp. *recta* ◈
Sulla coronaria (L.) B.H.Choi & H.Ohashi ◪ ■
Symphyotrichum squamatum (Spreng.) G.L.Nesom ◪ ◈ ◉ ■
Tanacetum vulgare L. subsp. *vulgare* ◉ ■
Teucrium chamaedrys L. subsp. *chamaedrys* ◈
Teucrium scordium L. subsp. *scordioides* (Schreb.) Arcang. ◪ ◈
*Thalictrum lucidu*m L. ◪
Thinopyrum acutum (DC.) Banfi ◪ ◈ ◉
Thymus longicaulis C.Presl subsp. *longicaulis* ◪
Typha angustifolia L. ◪ ◈ ◉ ▲ ■
Typha latifolia L. ◪ ◉ ▲ ■
Tolpis virgata (Desf.) Bertol. subsp. *virgata* ◉
Tordylium maximum L. ◉ ■
Torilis arvensis (Huds.) Link subsp. *arvensis* ◪ ◈ ◉ ■
Torilis nodosa (L.) Gaertn. subsp. *nodosa* ◈ ■
Tragopogon porrifolius L. ◉
Trifolium angustifolium L. subsp. *angustifolium* ◪ ◈ ◉ ■
*Trifolium campestr*e Schreb. ◪ ◈ ◉ ■
Trifolium echinatum M.Bieb. ◪ ◈ ■
Trifolium glomeratum L. ◉ ■
Trifolium hybridum L. ◪
Trifolium lappaceum L. ◪ ◉
Trifolium pratense Schreb. ◪ ◈ ◉
Trifolium repens L. ◪ ◈ ◉ ■
Trifolium resupinatum L. ◪ ◈ ◉ ■
Trifolium scabrum L. ◪ ◈
Trifolium squarrosum L. ◪ ◈
Trifolium stellatum L. ◪
Trifolium tomentosum L. ◈ ■
Trigonella alba (Medik.) Coulot & Rabaute ◈ ◉ ■
Trigonella officinalis (L.) Coulot & Rabaute ◪ ◈ ■
Trigonella sulcata (Desf.) Coulot & Rabaute ◈ ■
Triticum turgidum L. subsp. *durum* (Desf.) Husn. ◉ ■
Triticum vagans (Jord. & Fourr.) Greuter ◪ ◈
Tussilago farfara L. ◪ ◈ ◉ ■
Ulmus minor Mill. subsp. *minor* ◪ ◈ ◉
Urospermum dalechampii (L.) Scop. ex F.W.Schmidt ◈ ■
Urtica dioica L. ◈ ◉
Verbascum thapsus L. subsp. *thapsus* ◉ ■
Verbena bonariensis L. ◪ ◈ ◉ ■
Verbena officinalis L. ◪ ◈ ◉ ■
Veronica anagallis-aquatica L. subsp. *anagallis-aquatica* ◈ ◉ ▲
Veronica arvensis L. ◈ ◉ ■
Veronica barrelieri H.Schott ex Roem. & Schult. subsp. *barrelieri* ◪
Veronica persica Poir. ◉ ■
Viburnum lantana L. ◉
Viburnum tinus L. subsp. *tinus* ◈
Vicia angustifolia L. ◪ ■

Vicia cracca L. ◪ ◈ ◉
Vicia dasycarpa Ten. ◪ ◈ ◉
Vicia disperma DC. ◪ ◈ ◉
Vicia lutea L. ◪ ■
Vicia psudocracca Bertol. ◉
Vicia sativa L. ◪ ◉ ■
Vicia villosa Roth ◉ ■
Viola alba Besser subsp. *dehnhardtii* (Ten.) W.Becker ◪ ◈ ■
Viola hirta L. ◪ ◈
Viola odorata L. ◈ ■
Viola reichenbachiana Jord. ex Boreau ◪ ◈ ◉ ■
Xanthium orientale L. ◪ ◈ ◉ ■
Xanthium spinosum L. ◉ ■
Xeranthemum cylindraceum Sm. ◪ ◈
Zannichellia palustris L. ◈ ◉ ▲

Table S4: Eco-morphological variables of ponds with their mean values (Mean) and standard deviation (SD) for each pondscape ALE (agricultural land-use extent).

	Pondscape					
Variable name	**High ALE**		**Intermediate ALE**		**Low ALE**	
	Mean	SD	Mean	SD	Mean	SD
Pond area (m^2)	2343.1	3153.9	3833.5	4951.6	1150.2	1668.1
Pond margin slope (%)	50.8	30.5	35.8	19.9	28.8	23.5

Table S5: Differences in species richness of all the species and groups of species, between plot position, according to pondscape ALE (agricultural land-use extent). ALL = all species, WIS = Wetlands Indicator Species, SYN = Synanthropic species. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

		ALL	**WIS**	**SYN**
	Pairs of ALE	t-test	t-test	t-test
All plots	Low ALE-Intermediate ALE	0.32413	negative	negative
	Intermediate ALE-High ALE	2.8271**	2.229*	2.229*
	High ALE-Low ALE	3.135***	2.2861*	2.2861*
In-water plots	Low ALE-Intermediate ALE	0.19485	0.29721	0.29721
	Intermediate ALE-High ALE	3.6545***	3.5537**	3.5537**
	High ALE-Low ALE	3.6285**	3.4754**	3.754**
Out-water plots	Low ALE-Intermediate ALE	0.41518	0.21095	0.21095
	Intermediate ALE-High ALE	1.5797	1.1835	1.1835
	High ALE-Low ALE	1.8844*	0.94992	0.94992

Table S6: Differences in species composition of all the species and groups of species, between plot position, according to pondscape ALE (agricultural land-use extent). ALL = all species, WIS = Wetlands Indicator Species, SYN = Synanthropic species. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

		ALL	**WIS**	**SYN**
	Pairs of ALE	t-test	t-test	t-test
All plots	Low ALE-Intermediate ALE	1.1565	1.2053	1.0049
	Intermediate ALE-High ALE	1.7098**	1.8673***	1.3442**
	High ALE-Low ALE	2.0282***	2.114***	1.3498*
In-water plots	Low ALE-Intermediate ALE	0.89965	0.9727	1.045
	Intermediate ALE-High ALE	2.0176**	2.0524***	1.5235*
	High ALE-Low ALE	2.33***	2.456***	1.7357*
Out-water plots	Low ALE-Intermediate ALE	1.4223**	1.5623**	1.1407
	Intermediate ALE-High ALE	1.5031***	1.3611*	1.6039***
	High ALE-Low ALE	1.7823***	1.6545***	1.7652***

Table S7: Results of the indicator species analysis for the total plant communities between plots position according to the three pondscale ALE (agricultural land-use extent). Species names follow the Portal to the Flora of Italy (2024). * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

	Low ALE		Intermediate ALE		High ALE	
	Species	**IndVal**	**Species**	**IndVal**	**Species**	**IndVal**
All plots	*Carex flacca* subsp. *flacca*	0.458**	*Rubia peregrina*	0.434**	*Torilis arvensis* subsp. *arvensis*	0.450**
	Lotus dorycnium	0.414**	*Mentha aquatica* subsp. *aquatica*	0.373*	*Avena sterilis* subsp. *sterilis*	0.437**
	Prunus spinosa subsp. *spinosa*	0.411*	*Carex pendula*	0.358**	*Acer campestre*	0.391**
	Xeranthemum cylindraceum	0.393**	*Medicago lupulina*	0.339**	*Lactuca sativa* subsp. *serriola*	0.375**
	Quercus cerris	0.374**	*Laurus nobilis*	0.298**	*Convolvulus arvensis*	0.373**
	Ulmus minor subsp. *minor*	0.298*	*Medicago minima*	0.297**	*Symphyotrichum squamatum*	0.349**
	Lotus hirsutus	0.297**	*Clematis vitalba*	0.284*	*Galium aparine*	0.315**
	Juncus subnodulosus	0.296**	*Eupatorium cannabinum* subsp. *cannabinum*	0.279**	*Lysimachia arvensis*	0.296**
	Linum trigynum	0.293**	*Spartium junceum*	0.261**	*Equisetum ramosissimum*	0.293*
	Agrimonia eupatoria subsp. *eupatoria*	0.290*	*Fallopia convolvulus*	0.236**	*Epilobium tetragonum*	0.292**

Typa latifolia	0.285**	*Viola alba*	0.232*	*Cirsium arvense*	0.291*
Knautia integrifolia	0.277**	*Geranium colombinum*	0.229*	*Anisantha sterlis*	0.280*
Fraxinus angustifolia	0.262*	*Asparagus acutifolius*	0.211*	*Erigeron sumatrensis*	0.276**
Oenanthe pimpinelloides	0.260*	*Malva setigera*	0.211*	*Sonchus asper*	0.274**
Lathyrus hirsutus	0.258**	*Teucrium chamaedrys* subsp. *chamaedrys*	0.211*	*Convolvulus sepium*	0.258**
Centaurea jacea subsp. *gaudinii*	0.236*	*Viburnum tinus* subsp. tinus	0.211*	*Cyperus longus*	0.251*
Hippocrepis comosa subsp. *comosa*	0.236*	*Ostrya carpinifolia*	0.211*	*Chenopodium album* subsp. *album*	0.236**
Leucanthemum vulgare subsp. *vulgare*	0.236*			*Elymus repens* subsp. *repens*	0.236**
Lathyrus aphaca subsp. *aphaca*	0.233*			*Lythrum hyssopifolia*	0.236**
Knutia arvensis	0.224*			*Erigeron canadensis*	0.231*
Phalaris coerulescens	0.221*			*Lolium multiflorum*	0.230*
Euphorbia cyparissias	0.211*			*Juncus bufonius*	0.214*
Genista pilosa	0.211*			*Atriplex prostata*	0.211*
Schoenoplectus lacustris	0.211*			*Echinochloa crus-galli* subsp. *crus-*	0.211*

					galli	
	Bromopsis erecta	0.195*			*Lotus angustissimus*	0.211*
In-water plots	*Typha latifolia*	0.404**	*Veronica anagallis-aquatica* subsp. *anagallis-aquatica*	0.293*	*Zannichellia palustris*	0.250*
	Juncus subnodulosus	0.368**	*Potamogeton nodosus*	0.288*	*Chara globularis*	0.246*
	Typha angustifolia	0.309 *	*Chara gymnophylla*	0.258*		
	Lemna minor	0.276*	*Myriophyllum spicatum*	0.258*		
	Schoenoplectus lacustris	0.258 *	*Nymphaea × marliacea*	0.258*		
	Schoenoplectus tabernaemontani	0.258*				
Out-water plots	*Carex flacca* subsp. *flacca*	0.648**	*Rubia peregrina*	0.613**	*Torilis arvensis* subsp. *arvensis*	0.636**
	Lotus dorycnium subsp. *herbaceus*	0.586**	*Medicago lupulina*	0.479**	*Avena sterilis* subsp. *sterilis*	0.619**
	Prunus spinosa subsp. *spinosa*	0.581**	*Laurus nobilis*	0.422**	*Acer campestre*	0.553**
	Xeranthemum cylindraceum	0.556**	*Medicago minima*	0.420**	*Lactuca sativa* subsp. *serriola*	0.530**
	Quercus cerris	0.529**	*Clematis vitalba*	0.401**	*Convolvulus arvensis*	0.527**

Lotus hirsutus	0.419**	*Eupatorium cannabinum* subsp. *cannabinum*	0.394**	*Symphyotrichum squamatum*	0.494**
Juniperus communis	0.419**	*Bromus hordeaceus* subsp. *hordeaceus*	0.380**	*Galium aparine*	0.445**
Linum trigynum	0.415**	*Carex pendula*	0.373**	*Bidens frondosa*	0.424**
Agrimonia eupatoria	0.410**	*Spartium junceum*	0.369**	*Lysimachia arvensis*	0.418**
Knautia integrifolia	0.391**	*Crepis capillaris*	0.366*	*Equisetum ramosissimum*	0.414**
Phleum pratense subsp. *pratense*	0.387**	*Ranunculus lanuginosus*	0.347**	*Epilobium tetragonum*	0.413**
Tussilago farfara	0.383**	*Fallopia convolvulus*	0.333**	*Cirsium arvense*	0.411**
Fraxinus angustifolia	0.371**	*Viola alba*	0.328**	*Rumex conglomeratus*	0.399**
Oenanthe pimpinelloides	0.368**	*Scorpiurus muricatus*	0.327**	*Anisantha sterlis*	0.397**
Lathyrus hirsutus	0.365**	*Pyracantha coccinea*	0.326**	*Erigeron sumatrensis*	0.390**
Juncus articulatus subsp. *articulatus*	0.345*	*Geranium colombinum*	0.324**	*Sonchus asper* subsp. *asper*	0.387**
Centaurea jacea subsp. *gaudinii*	0.333**	*Asparagus acutifolius*	0.298**	*Convolvulus sepium*	0.365**
Hippocrepis comosa subsp. *comosa*	0.333**	*Malva setigera*	0.298**	*Cyperus longus*	0.354**

Leucanthemum vulgare subsp. *vulgare*	0.333**	*Teucrium chamaedrys* subsp. *chamaedrys*	0.298**	*Chenopodium album* subsp. *album*	0.333**
Lathyrus aphaca subsp. *aphaca*	0.330**	*Viburnum tinus* subsp. tinus	0.298**	*Elymus repens* subsp. *repens*	0.333**
Astragalus monspessulanus subsp. *monspessulanus*	0.320**	*Ostrya carpinifolia*	0.298*	*Lythrum hyssopifolia*	0.333**
Knutia arvensis	0.317**	*Catapodium rigidum* subsp. *rigidum*	0.282**	*Erigeron canadensis*	0.327**
Phalaris coerulescens	0.313**	*Lolium arundinaceum* subsp. *arundinaceum*	0.271*	*Lolium multiflorum*	0.325**
Potentilla recta subsp. *recta*	0.307*	*Petasites hybridus* subsp. *hybridus*	0.258*	*Lolium perenne*	0.318**
Linum usitatissimum subsp. *usitatissimum*	0.300**	*Pulicaria odora*	0.258*	*Juncus bufonius*	0.303**
Euphorbia cyparissias	0.298**	*Trigonella sulcata*	0.258*	*Atriplex prostata*	0.298**
Genista pilosa	0.298**	*Trifolium echinatum*	0.258*	*Echinochloa crus-galli* subsp. *crus-galli*	0.298**
Genista tinctoria	0.298*	*Vicia disperma*	0.256*	*Lotus angustissimus*	0.298*
Trifolium squarrosum	0.298*	*Clinopodium nepeta* subsp. *nepeta*	0.254	*Poa trivialis*	0.296*

Rubus caesius	0.296*	*Persicaria maculosa*	0.294*
Bromopsis erecta	0.276*	*Vicia sativa*	0.274*
Lonicera caprifolium	0.274*	*Artemisia vulgaris*	0.268*
Achillea ageratum	0.258*	*Anthemis cotula*	0.258*
Betonica officinalis	0.258*	*Epilobium hirsutum*	0.258*
Galatella linosyris subsp. *linosyris.*	0.258*	*Festuca myuros* subsp. *myuros*	0.258*
Linum tenuifolium	0.258*	*Persicaria lapathifolia* subsp. *lapathifolia*	0.258*
Molinia arundinacea	0.258*	*Popupus alba*	0.258*
Ononis spinosa subsp. *spinosa*	0.258*	*Quercus petraea* subsp. *petraea*	0.258*
Schoenoplectus lacustris	0.258*	*Solanum nigrum*	0.258*
Achillea millefolium subsp. *millefolium*	0.250*	*Sorbus torminalis*	0.258*
Cytisus scoparius	0.249**	*Tolpis virgata* subsp. *virgata*	0.258*
		Tordylium maximum	0.258*
		Triticum turgidum subsp. *durum*	0.258*

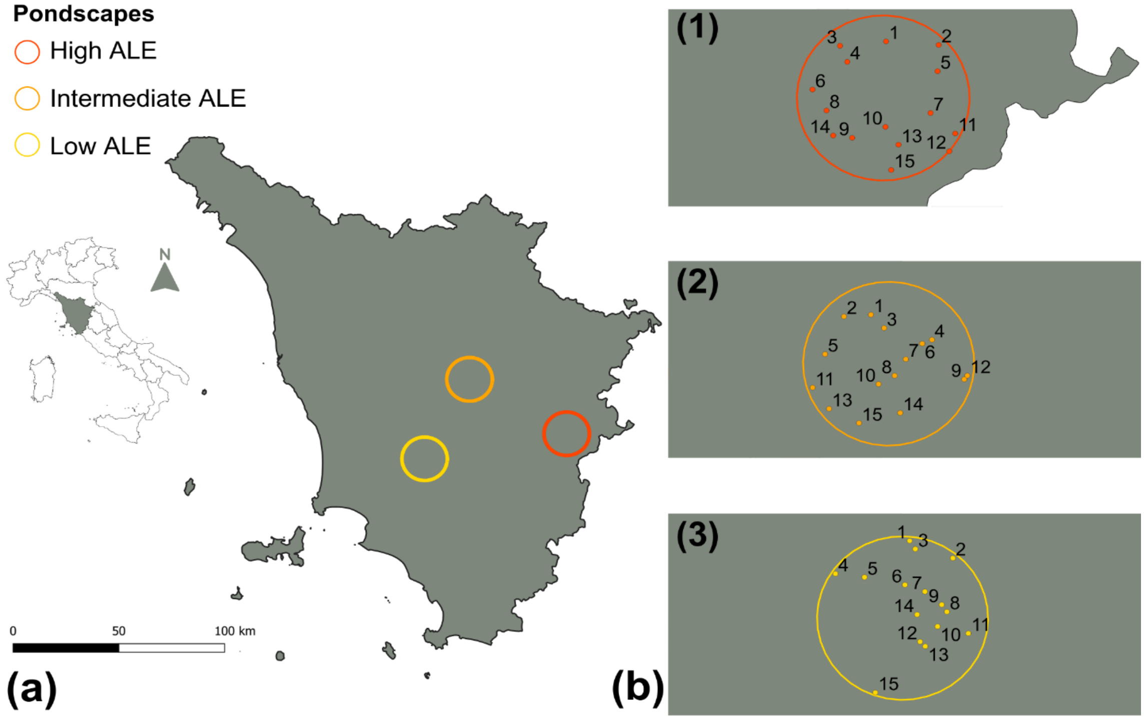

Figure S1: (a) Location of the three study areas (pondscapes) in Tuscany and position of the region with respect to Italy; (b) Distribution of the surveyed ponds within each pondscape; (1) High ALE pondscape; (2) Intermediate ALE pondscape; (3) Low ALE pondscape. ALE = Agricultural land-use extent.

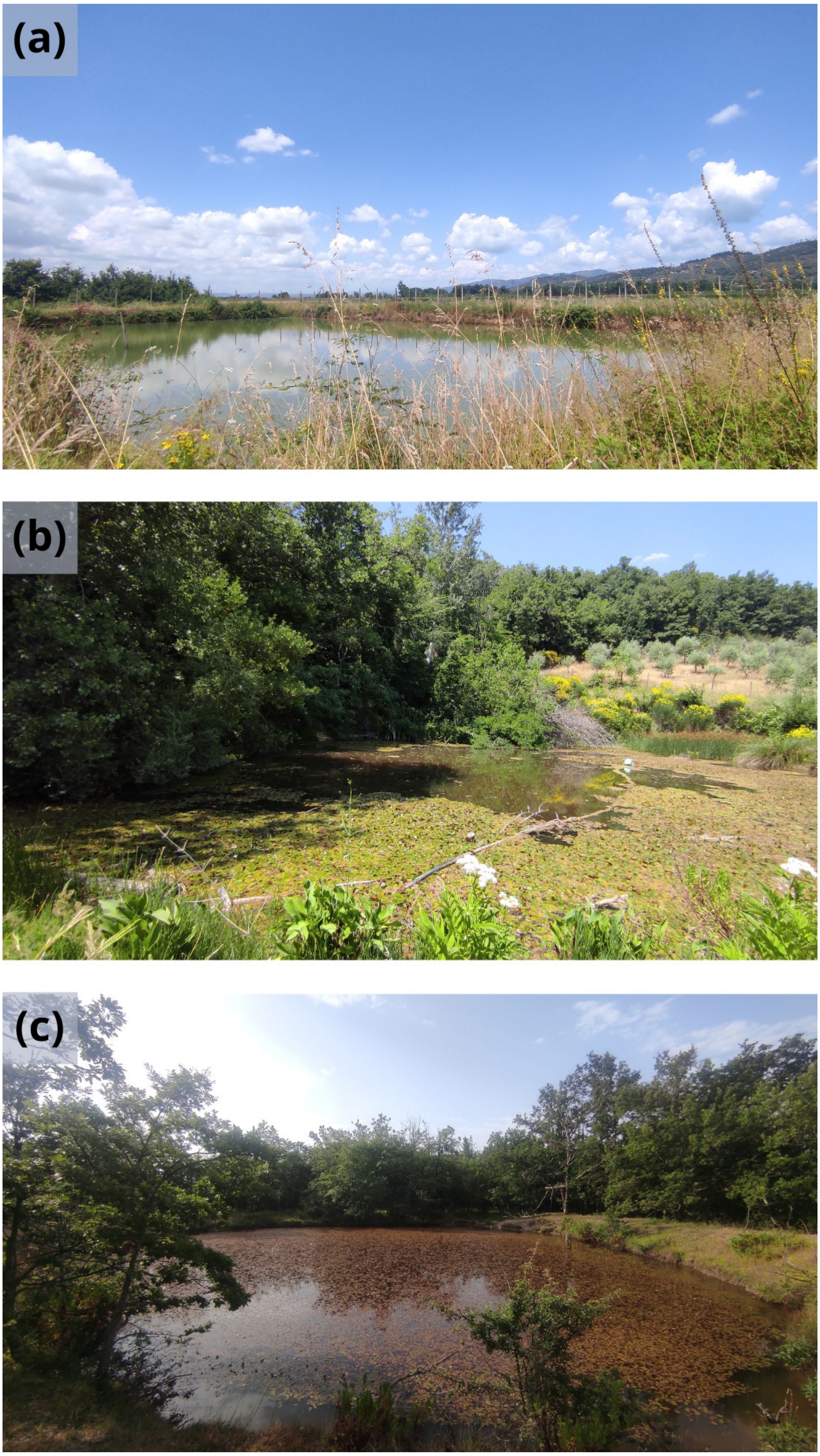

Figure S2: Examples of ponds of the three agricultural land-use extent (ALE): (a) High ALE; (b) Intermediate ALE, and (c) Low ALE.

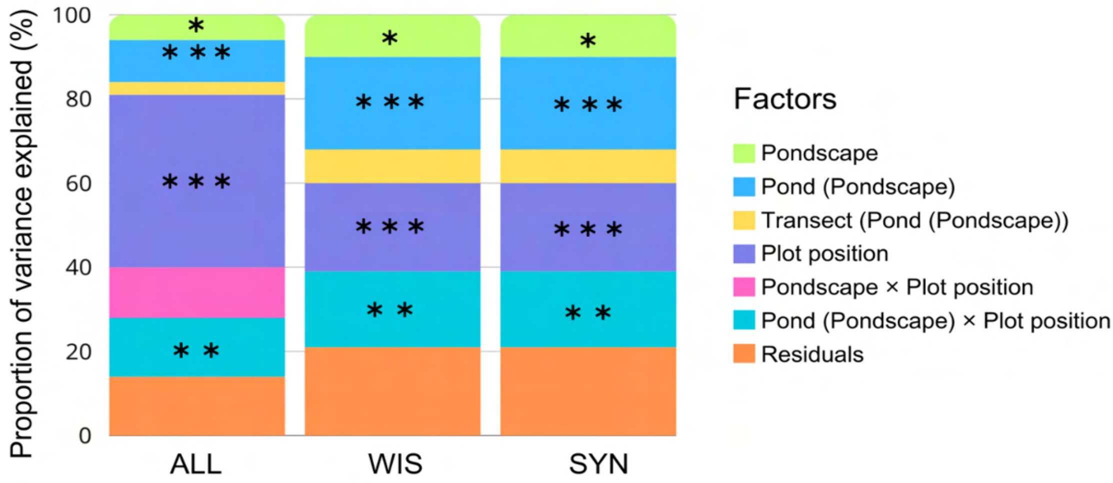

Figure S3: Estimates of components of variance (expressed as %) of species richness calculated for each factor of the PERMANOVA analysis for all species (ALL), Wetlands Indicator Species (WIS), and Synanthropic species (SYN). Nested factors are reported within brackets; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

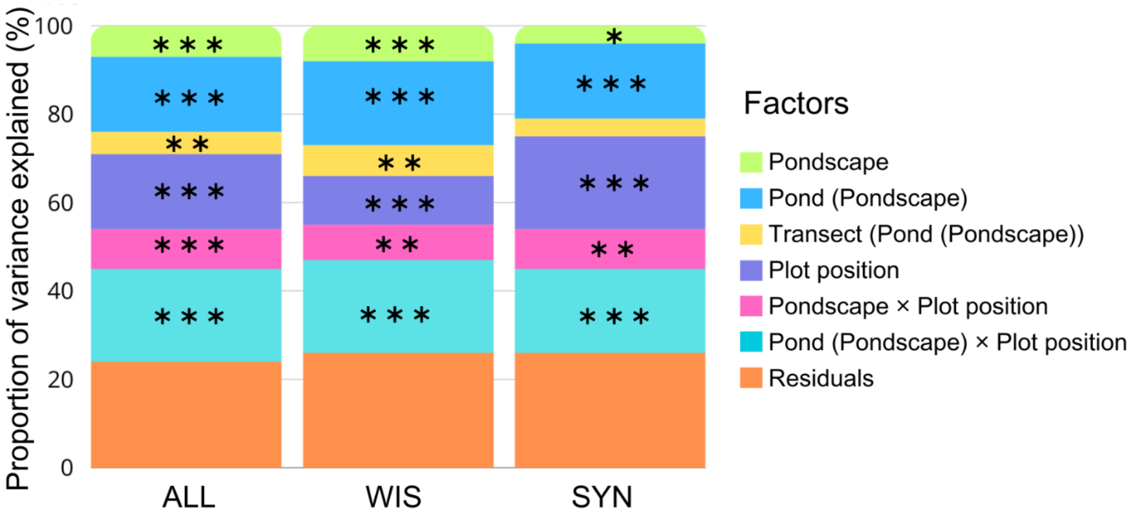

Figure S4: Estimates of components of variance (expressed as %) of species composition calculated for each factor of the PERMANOVA analysis for all species (ALL), Wetlands Indicator Species (WIS), and Synanthropic species (SYN). Nested factors are reported within brackets; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

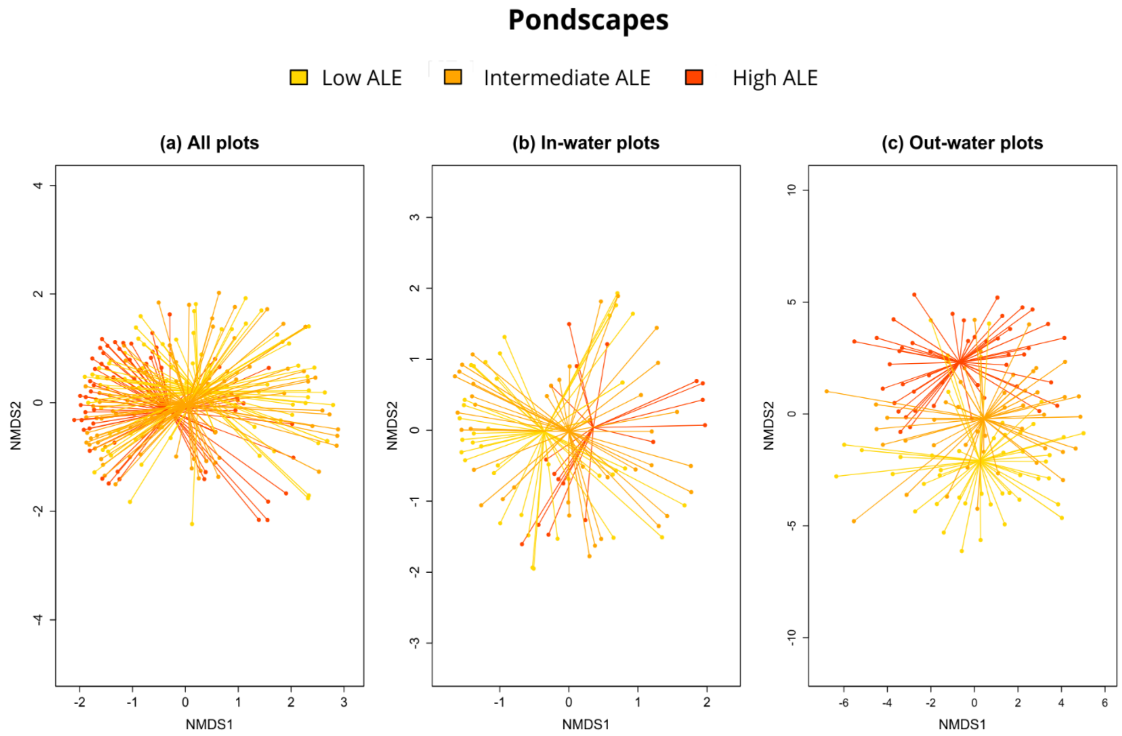

Figure S5: Non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity and ordispider function, in relation to the pondscapes agricultural land-use extent (ALE) for (a) all plots (stress = 0.2), (b) in-water plots (stress = 0.2) and (c) out-water plots (stress = 0.2).

References

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Supplementary material to chapter 3

We selected ponds within each pondscape by extracting water bodies classified under the "Water Bodies" category (5.1.2) of the Corine Land Cover map (ISPRA, 2018) using QGIS. Around each pondscape, we applied a 10 km buffer divided into a 500 m × 500 m grid, which was overlaid on the extracted water bodies. From this grid, ponds were randomly chosen with the constraint of including only one pond per grid, using the QGIS tool *Random selection within subsets*. To address potential access limitations, the procedure was repeated three times, ensuring a minimum straight-line distance of 1 km between selected ponds.

Table S1: Average monthly minimum and maximum temperatures (°C) and annual precipitation (mm) for the studied bioclimatic areas. MED. = mediterranean (https://www.sardegnaambiente.it/arpas/attivita/); TEMP-Sub-MED. = temperate sub-mediterranean (https://www.lamma.toscana.it/clima-e-energia/climatologia/clima-siena) and TEMP.-CON. = temperate continental (https://www.arpae.it/it/temi-ambientali/clima/dati-e-indicatori/tabelle-climatiche).

Factors	MED.	TEMP-Sub-MED.	TEMP.-CON.
Average maximum temperatures (°C)	31.1	30.7	32.3
Average minimum temperatures (°C)	7.9	3.0	-0.2
Annual precipitation (mm)	453	823	778

Table S2: Eigenvalues of the first six axes from the Principal Coordinates Analysis (PCoA) based on the truncated Euclidean distance matrix of pond coordinates. The values indicate the amount of spatial variance explained by each axis.

PCoA axis	Explained variance (%)
1	71.05
2	7.57
3	5.62
4	4.05
5	1.0
6	0.54

Table S3: Summary of the statistics of physico-chemical and climatic predictors used for the analysis. DO = dissolved oxygen; NO_3 = nitrate ion; NH_4 = ammonium ion; bio_12 = annual precipitation amount; epot = potential evapotranspiration.

Factor type	Predictors	Mean	Min-Max	SD
Physico-chemical	DO	83.34	7-207	41.92
	NO_3	0.96	0-10.21	2.00
	NH_4	1.96	0-90.5	9.57
Climatic	bio_12	790.64	502.5-126.5	137.13
	epot	146.68	135.44-219	10.04

Table S4: Species Contributions to Beta Diversity (SCBD) and species frequencies (number of plot occurrences). The species are ordered according to decreasing SCBD values. NEHY = non-emergent hydrophytes; WERP = wetland emergent rooted plants.

Species	SCBD	Frequency	Life forms
Typha angustifolia	0.06	23	WERP
Chara vulgaris	0.06	19	NEHY
Mentha aquatica subsp. *aquatica*	0.04	17	WERP
Potamogeton natans	0.04	16	NEHY
Phragmites australis	0.03	9	WERP
Juncus inflexus	0.02	9	WERP
Lemna minuta	0.02	7	NEHY
Agrostis stolonifera	0.02	10	WERP
Spirodela polyrhiza	0.02	9	NEHY
Veronica anagallis-aquatica subsp. *anagallis-aquatica*	0.02	9	WERP
Lemna aequinoctialis	0.02	2	NEHY
Lemna minor	0.02	11	NEHY
Ranunculus peltatus	0.02	6	NEHY
Eleocharis palustris subsp. *palustris*	0.02	11	WERP
Lemna gibba	0.02	6	NEHY
Juncus articulatus	0.02	9	WERP
Potamogeton pusillus	0.02	5	NEHY
Ceratophyllum demersum	0.02	6	NEHY
Potamogeton nodosus	0.02	6	NEHY
Myriophyllum spicatum	0.02	4	NEHY
Schoenoplectus tabernaemontani	0.01	4	WERP
Lycopus europaeus	0.01	9	WERP
Alisma plantago-aquatica	0.01	8	WERP
Helosciadium nodiflorum	0.01	2	WERP
Salix purpurea subsp. *purpurea*	0.01	2	WERP
Salvinia natans	0.01	5	NEHY
Juncus subnodulosus	0.01	7	WERP
Wolffia arrhiza	0.01	4	NEHY
Bolboschoenus maritimus	0.01	4	WERP
Potamogeton crispus	0.01	4	NEHY
Juncus effusus	0.01	4	WERP
Zannichellia palustris	0.01	5	NEHY
Chara globularis	0.01	4	NEHY
Scirpoides holoschoenus	0.01	5	WERP
Teucrium scordium	0.01	2	WERP
Carex pendula	0.01	3	WERP

Nuphar lutea	0.01	2	NEHY
Typha latifolia	0.01	4	WERP
Ranunculus lanuginosus	0.01	2	WERP
Cynodon dactylon	0.01	3	WERP
Pulicaria dysenterica	0.01	3	WERP
Lemna trisulca	0.01	3	NEHY
Potamogeton gramineus	0.01	2	NEHY
Juncus fontanesii subsp. *fontanesii*	0.01	1	WERP
Chara crassicaulis	0.01	1	NEHY
Potamogeton trichoides	<0.01	2	NEHY
Glyceria notata	<0.01	3	WERP
Epilobium tetragonum	<0.01	4	WERP
Lythrum junceum	<0.01	2	WERP
Schoenoplectus lacustris	<0.01	2	WERP
Samolus valerandi	<0.01	2	WERP
Chara gymnophylla	<0.01	1	NEHY
Mentha pulegium subsp. *pulegium*	<0.01	2	WERP
Stuckenia pectinata	<0.01	2	NEHY
Bidens frondosa	<0.01	2	WERP
Populus nigra	<0.01	3	WERP
Sorghum halepense	<0.01	2	WERP
Rumex conglomeratus	<0.01	2	WERP
Alisma lanceolatum	<0.01	2	WERP
Carex hirta	<0.01	1	WERP
Juncus compressus	<0.01	1	WERP
Persicaria maculosa	<0.01	1	WERP
Rubus caesius	<0.01	1	WERP
Ranunculus repens	<0.01	2	WERP
Nitella tenuissima	<0.01	1	NEHY
Rumex crispus	<0.01	2	WERP
Potentilla reptans	<0.01	2	WERP
Echinochloa crus-galli	<0.01	2	WERP
Carex microcarpa	<0.01	1	WERP
Persicaria lapathifolia subsp. *lapathifolia*	<0.01	1	WERP
Rorippa amphibia	<0.01	1	WERP
Salix alba	<0.01	2	WERP
Ranunculus trichophyllus	<0.01	2	NEHY
Convolvulus arvensis	<0.01	1	WERP
Convolvulus sepium	<0.01	1	WERP
Equisetum ramosissimum	<0.01	1	WERP
Glyceria fluitans	<0.01	1	WERP

Limniris pseudacorus	<0.01	1	WERP
Lythrum salicaria	<0.01	1	WERP
Ranunculus baudotii	<0.01	1	NEHY
Lotus tenuis	<0.01	2	WERP
Nasturtium officinale	<0.01	1	WERP
Nymphaea ×marliacea	<0.01	1	NEHY
Potamogeton schweinfurthii	<0.01	1	NEHY
Ranunculus saniculifolius	<0.01	1	NEHY
Callitriche stagnalis	<0.01	1	NEHY
Damasonium bourgaei	<0.01	1	WERP
Ludwigia hexapetala	<0.01	1	WERP
Potamogeton coloratus	<0.01	1	NEHY
Salix cinerea	<0.01	1	WERP
Cerinthe major subsp. *major*	<0.01	1	WERP
Ranunculus sardous	<0.01	1	WERP
Trifolium squarrosum	<0.01	1	WERP
Veronica beccabunga subsp. *beccabunga*	<0.01	1	WERP
Bellium bellidioides	<0.01	1	WERP
Carex divulsa	<0.01	1	WERP
Juncus bufonius	<0.01	1	WERP
Ranunculus ophioglossifolius	<0.01	1	NEHY
Cyperus fuscus	<0.01	1	WERP
Cyperus glomeratus	<0.01	1	WERP
Lindernia dubia	<0.01	1	WERP
Cyperus badius	<0.01	1	WERP
Poa sylvicola	<0.01	1	WERP
Ranunculus sceleratus	<0.01	1	WERP
Hypochaeris radicata	<0.01	1	WERP
Prunella vulgaris	<0.01	1	WERP
Baldellia ranunculoides	<0.01	1	WERP
Trifolium resupinatum	<0.01	1	WERP

Table S5: Species life form and dispersal distance classes, from class 6 (400 m to 1500 m) to class 1 (0.1 m to 1m). The species are ordered according to decreasing dispersal distance classes values. NEHY = non-emergent hydrophytes; WERP = wetland emergent rooted plants.

Species	Life form	Dispersal distance
Callitriche stagnalis	NEHY	6
Ceratophyllum demersum	NEHY	6
Lemna gibba	NEHY	6
Lemna minor	NEHY	6
Lemna minuta	NEHY	6
Lemna trisulca	NEHY	6
Myriophyllum spicatum	NEHY	6
Ranunculus trichophyllus	NEHY	6
Salvinia natans	NEHY	6
Wolffia arrhiza	NEHY	6
Echinochloa crus-galli	WERP	6
Eleocharis palustris	WERP	6
Glyceria fluitans	WERP	6
Glyceria notata	WERP	6
Ranunculus sceleratus	WERP	6
Rorippa amphibia	WERP	6
Rubus caesius	WERP	6
Epilobium tetragonum	WERP	5
Equisetum ramosissimum	WERP	5
Lycopus europaeus	WERP	5
Phragmites australis	WERP	5
Populus nigra	WERP	5
Pulicaria dysenterica	WERP	5
Salix alba	WERP	5
Salix cinerea	WERP	5
Salix purpurea	WERP	5
Typha angustifolia	WERP	5
Typha latifolia	WERP	5
Carex hirta	WERP	3
Hypochaeris radicata	WERP	3
Potentilla reptans	WERP	3
Ranunculus lanuginosus	WERP	3
Schoenoplectus lacustris	WERP	2
Sorghum halepense	WERP	2
Agrostis stolonifera	WERP	2

Alisma lanceolatum	WERP	2
Alisma plantago-aquatica	WERP	2
Bidens frondosa	WERP	2
Bolboschoenus maritimus	WERP	2
Carex divisa	WERP	2
Carex microcarpa	WERP	2
Carex pendula	WERP	2
Cerinthe major	WERP	2
Convolvulus arvensis	WERP	2
Convolvulus sepium	WERP	2
Cyperus glomeratus	WERP	2
Helosciadium nodiflorum	WERP	2
Juncus articulatus	WERP	2
Juncus effusus	WERP	2
Juncus inflexus	WERP	2
Juncus subnodulosus	WERP	2
Limniris pseudacorus	WERP	2
Lotus tenuis	WERP	2
Lythrum junceum	WERP	2
Lythrum salicaria	WERP	2
Mentha aquatica	WERP	2
Nasturtium officinale	WERP	2
Persicaria lapathifolia	WERP	2
Persicaria maculosa	WERP	2
Rumex conglomeratus	WERP	2
Rumex crispus	WERP	2
Scirpoides holoschoenus	WERP	2
Teucrium scordium	WERP	2
Veronica anagallis-aquatica	WERP	2
Veronica beccabunga	WERP	2
Ranunculus peltatus	NEHY	2
Bellium bellidioides	WERP	1
Cynodon dactylon	WERP	1
Cyperus fuscus	WERP	1
Juncus bufonius	WERP	1
Juncus compressus	WERP	1
Juncus fontanesii	WERP	1
Prunella vulgaris	WERP	1
Ranunculus repens	WERP	1
Ranunculus sardous	WERP	1
Samolus valerandi	WERP	1

Trifolium resupinatum	WERP	1
Trifolium squarrosum	WERP	1

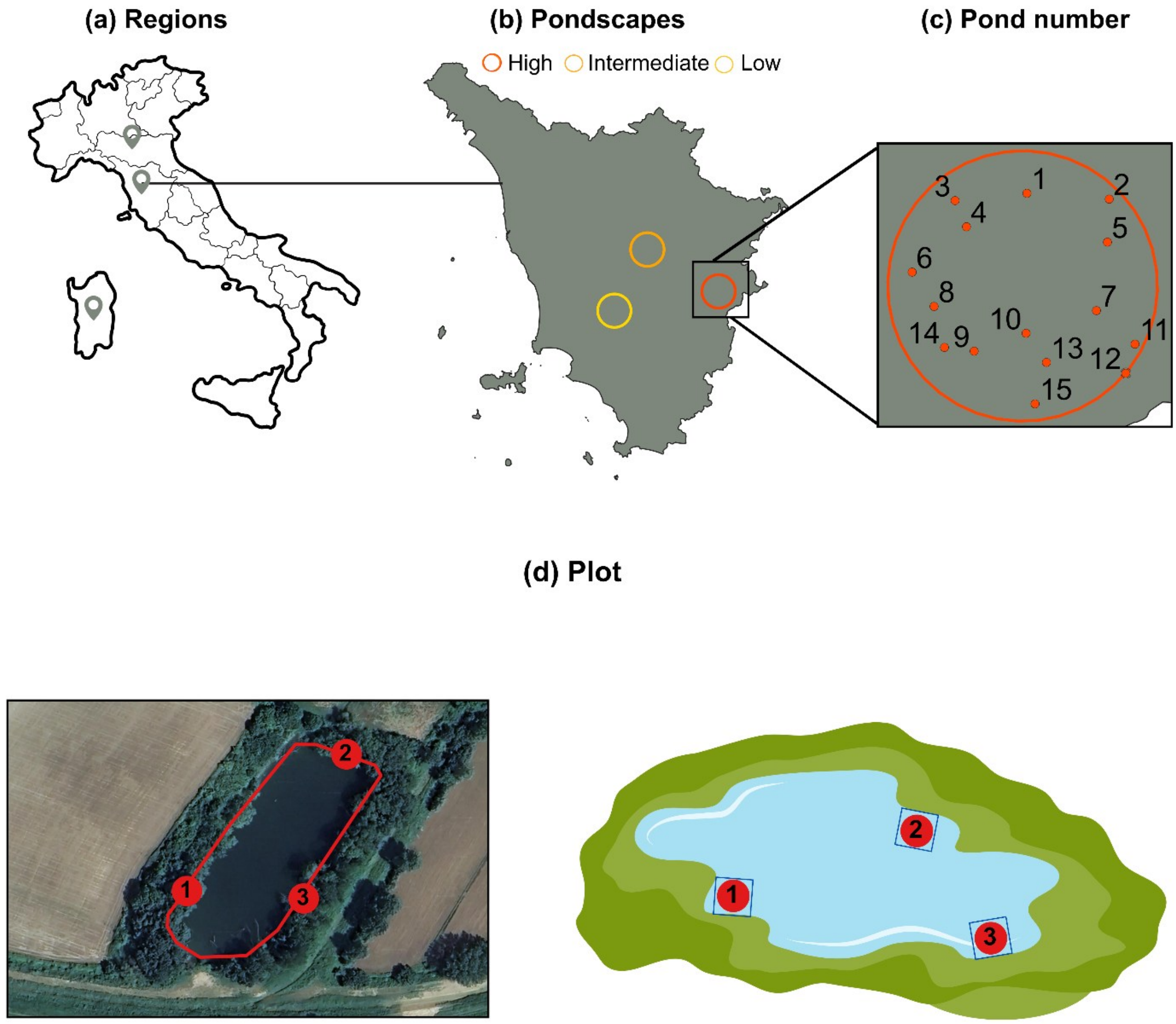

Figure S1: Sampling design spatialization spanning from the (a) regions, (b) selection of the a pondscapes, (c) the selection of the pond and (d) localisation of the plots (2 m × 2 m) within the pond.

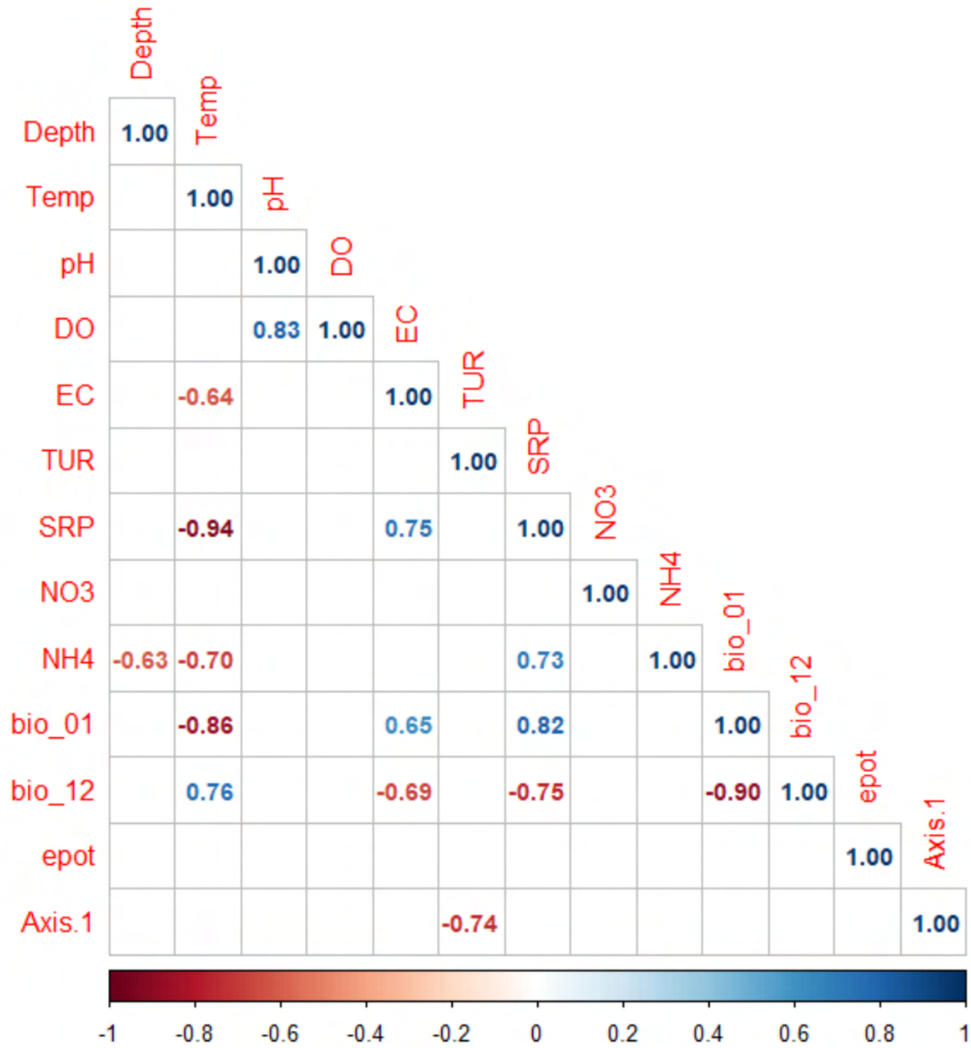

Figure S2: Correlation matrix based on Spearman's correlation coefficient. Significant correlations and correlation coefficients below -0.6 and above 0.6 are reported. Temp = temperature; DO = dissolved oxygen; EC = electrical conductivity; TUR = turbidity; SRP = phosphate ion; NO_3 = nitrate ion, NH_4 = ammonium ion; bio_01 = mean annual air temperature; bio_12 = annual precipitation amount; epot = potential evapotranspiration; Axis.1 = spatial variable.

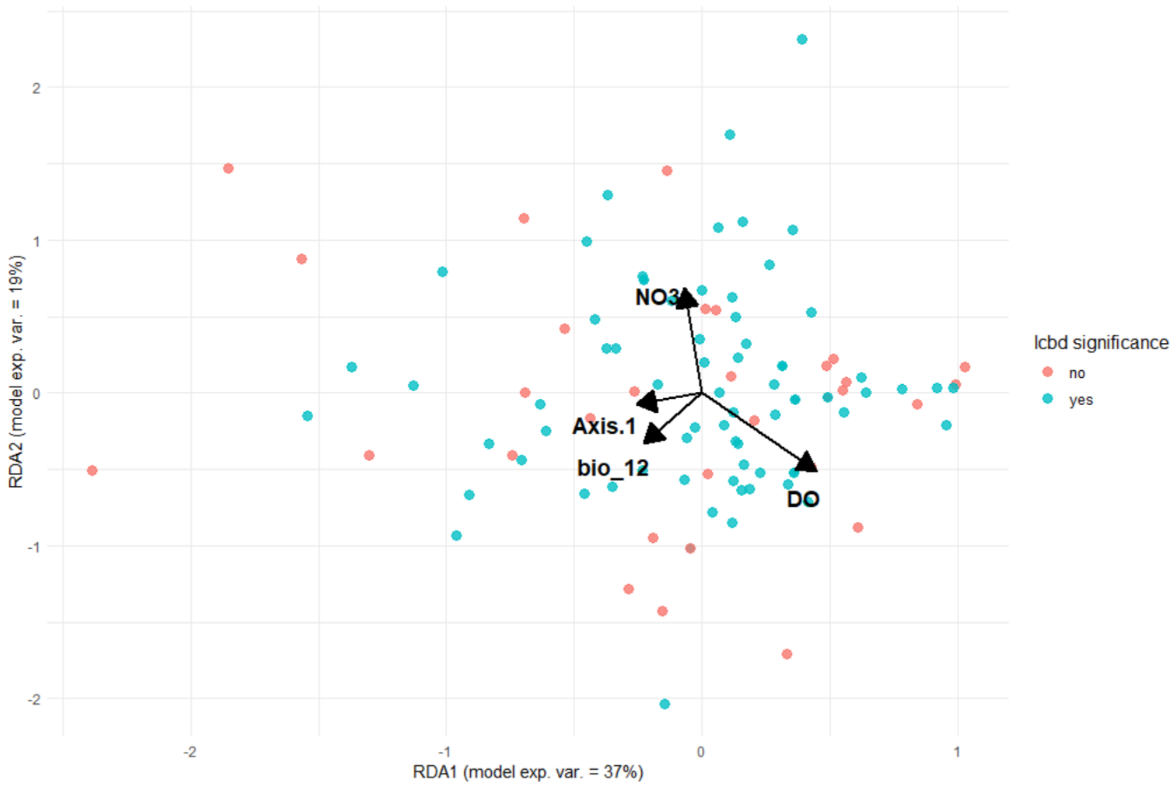

Figure S3: RDA plot of the effects of environmental and spatial variables on sites (ponds). Different colours indicate significant LCBD values attributed to the site. DO = dissolved oxygen; NO_3 = nitrate ion; bio_12 = annual precipitation amount; epot = potential evapotranspiration; Axis.1 = spatial variable.

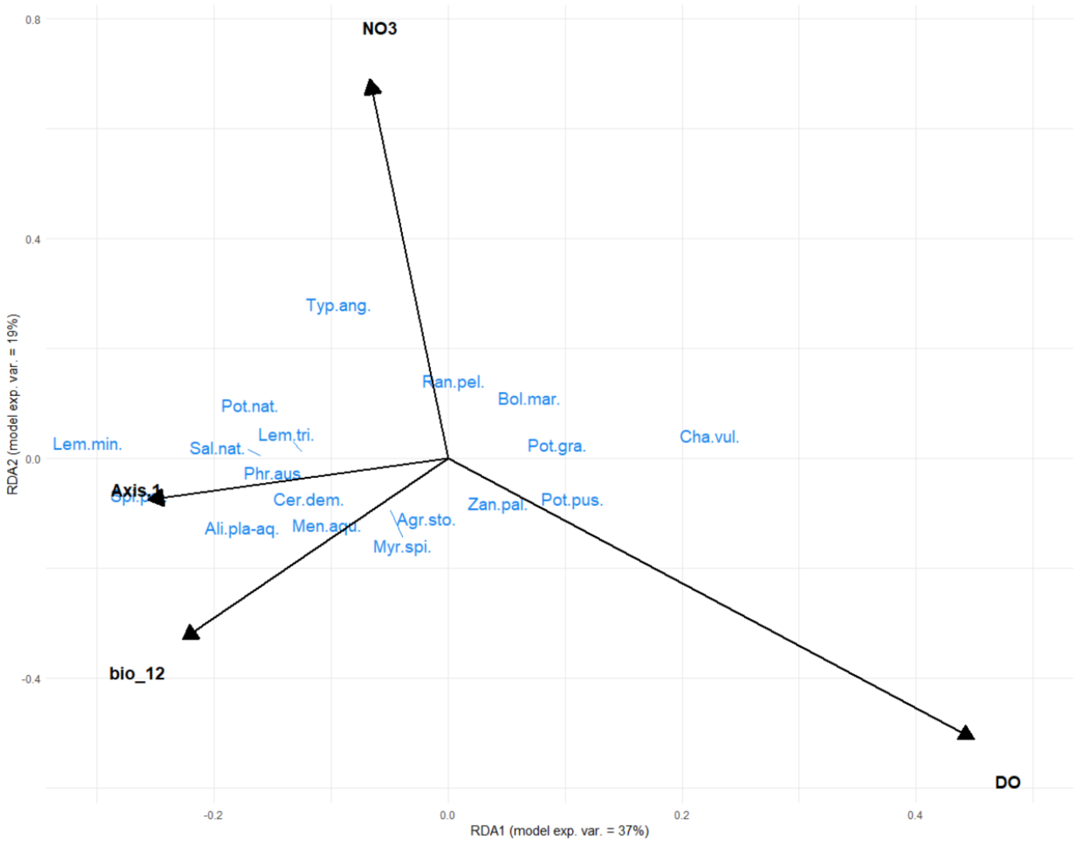

Figure S4: RDA plot of the effects of environmental and spatial variables on species composition. DO = dissolved oxygen, NO_3 = nitrate ion, bio_12 = annual precipitation amount, Axis.1 = spatial variable. Agr.sto. = *Agrostis stolonifera*; Ali.pla-aq = *Alisma plantago-aquatica*; Bol.mar. = *Bolboschoenus maritimus*; Cer.dem. = *Ceratophyllum demersum*; Cha.vul. = *Chara vulgaris*; Lem.min. = *Lemna minor*; Lem.tri. = *Lemna trisulca*; Men.aqu. = *Mentha aquatica* ssp. *aquatica*, Myr.spi. = *Myriophyllum spicatum*, Phra.aus. = *Phragmites australis*; Pot.gra. = *Potamogeton gramineus*; Pot.nat. = *Potamogeton natans*; Pot.pus. = *Potamogeton pusillus*; Ran.pel. = *Ranunculus peltatus*; Sal.nat. = *Salvinia natans*; Spi.pol. = *Spirodela polyrhiza*; Typ.ang. = *Typha angustifolia*; Zan.pal. = *Zannichellia palustris*.

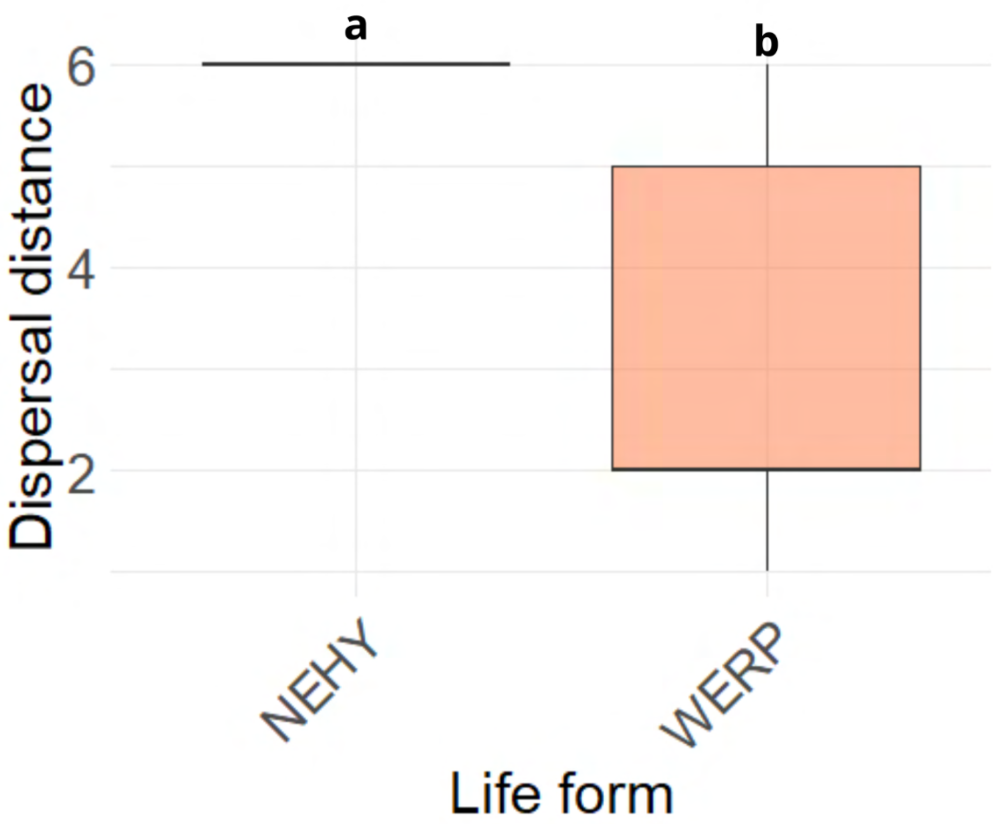

Figure S5: Differences in dispersal distance classes between two major life forms groups. Different letters indicate significant differences between the groups (Welch's t-test, $p < 0.05$). NEHY = non-emergent hydrophytes, WERP = wetland emergent rooted plants

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