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Contribution of artificial waterbodies to biodiversity: A glass half empty or half full?

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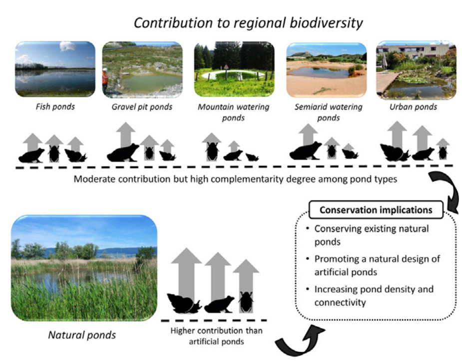
HIGHLIGHTS

- Artificial ponds will replace natural ponds in our future human-dominated landscapes.
- We assess the relative contribution of different types of artificial and natural ponds to regional biodiversity.
- Artificial ponds hosted on average about 50% of the regional species pool, then making a moderate contribution.
- Natural ponds supported higher alpha richness than artificial ones, especially in the case of freshwater snails.
- Conservation strategies should focus on conserving existing natural ponds and creating new "near-natural" ponds.

GRAPHICAL ABSTRACT



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ABSTRACT

Artificial ponds are increasingly created for the services they provide to humans. While they have the potential to offer habitats for freshwater biodiversity, their contribution to regional diversity has hardly been quantified. In this study, we assess the relative contribution of five types of artificial ponds to regional biodiversity of five different regions, studying amphibians, water beetles and freshwater snails. This biodiversity is also compared with that observed in natural ponds from three of the investigated regions. Our results indicate that artificial ponds host, on average, about 50% of the regional pool of lentic species. When compared to natural ponds, the artificial ponds always supported a substantially lower alpha richness (54% of the natural pond richness). The invertebrate communities presented high values of beta diversity and were represented by a restricted set of widely distributed species, and by numerous rare species. There were discrepancies among the taxonomic groups: overall, amphibians benefited most from the presence of artificial ponds, since 65% of the regional lentic species pools for this group was found in artificial ponds, whereas 43% and 42% was observed in the case of beetles and snails, respectively. However, each invertebrate group was promptly the most benefited animal group in a single pond type. Therefore, artificial pond types were complementary among them in terms of contribution to regional diversity of the three animal groups. Based on these results, we forecast that future human-dominated landscapes in which most ponds are artificial will be particularly impoverished in terms of freshwater biodiversity, underlining the need to conserve existing natural ponds and to create new "near-natural" ponds. However, if properly

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designed and managed, artificial ponds could make a substantial contribution to support freshwater biodiversity at a regional scale. Furthermore, the number and diversity of artificial ponds must be high in each considered landscape.

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1. Introduction

Freshwater environments are considered among the most threatened ecosystems in the world, despite the disproportionately high values of biodiversity and multiple ecosystem services that they support (Dudgeon et al., 2006; Millenium Ecosystem Assessment, 2013). Historically, concern about the conservation and management of freshwater ecosystems has focused on running waters, such as rivers and streams, or large lakes. However, smaller waterbodies such as ponds have been reported as representing a significant proportion of the total freshwater surface on Earth, because of their high densities in most landscapes (Downing et al., 2006). During the last two decades, an increasing body of literature has demonstrated the high potential of ponds to increase freshwater biodiversity and to act as critical habitats for wildlife (Oertli et al., 2010; Céréghino et al., 2014; Biggs et al., 2016), especially for amphibians (Gómez-Rodríguez et al., 2009; Arntzen et al., 2017), macroinvertebrates (Florencio et al., 2014; Hill et al., 2016a, 2019; Wissinger et al., 2016) and freshwater macrophytes (Nicolet et al., 2004; Della Bella et al., 2008; Akasaka and Takamura, 2012). Indeed, ponds have been reported to be the most species-rich aquatic habitats at regional scale, supporting a high diversity of rare and unique species (Williams et al., 2004; Davies et al., 2008).

Despite their high ecological and cultural values for society, ponds have been mostly neglected by water and wildlife managers and no legislation frameworks exists to protect them, with the exception of Mediterranean temporary ponds which are listed as a priority in the EU Habitats Directive (Céréghino et al., 2008; European Pond Conservation Network, 2008; Hill et al., 2018). Consequently, the number of ponds has dramatically declined over the last two centuries, and loss rates of over 50% have been reported in several regions of the world, occasionally reaching 90% in human-dominated landscapes (Hull, 1997; Oertli et al., 2005a; European Pond Conservation Network, 2008). Land use changes, particularly toward agriculture uses, often lead to the physical destruction of ponds or to their eutrophication and chemical pollution (Declerck et al., 2006). However, these same land use changes frequently promote the construction of different types of artificial ponds throughout the world (Oertli, 2018).

Artificial ponds are created for economic and socio-cultural reasons, which include a variety of functions such as flow regulation, stormwater drainage, fish production, gravel extraction, providing livestock with drinking water, for their aesthetic value or for leisure activities, among others (European Pond Conservation Network, 2008; Oertli, 2018). Moreover, multifunctional artificial waterbodies have recently been reported as providing suitable habitats for several threatened species, even improving their survival rates (Dafforn et al., 2015; Fait et al., 2020). Artificial waterbodies tend to be managed more frequently than natural ponds, because of the need to maintain the quality of the water good enough to allow the various usages mentioned above. If well designed and managed, artificial ponds also have the potential to support high biodiversity, while offering the functions for which they were created (Oertli and Parris, 2019). However, such view has little scientific support and it has been very scarcely explored, except in some particular countries such as UK (Hassall, 2014) or South Africa (Deacon et al., 2018). Indeed, the contribution of artificial ponds to regional biodiversity conservation remains as a research gap in pond management (Oertli and Parris, 2019). The few existing studies on selected types of artificial ponds suggest that they can, at least partly, contribute to the regional biodiversity. For example, gravel pit ponds were calculated to host 57% of the regional species pool of waterbirds in southern France (Santoul et al., 2009), while irrigation ponds hosted 40% of the regional richness in aquatic insects in south-western France (Ruggiero et al., 2008), and a slightly lower relative contribution was reported for water beetles in irrigation and watering ponds in south-eastern Spain (Picazo et al., 2010). In the case of macrophyte assemblages, artificial ponds were seen to support 65% of regional diversity in Central Europe, although the contribution was significantly lower than for natural ponds (Bubíková and Hrivnák, 2018). If well designed, artificial ponds can provide suitable habitats even for threatened species, as is the case for beetles and dragonflies in small Alpine reservoirs (Fait et al., 2020) and for amphibians in small manmade waterbodies in semiarid regions of Spain (Egea-Serrano et al., 2006). However, all these studies had a limited range, as they focused on a single type of artificial ponds of a single region, and mostly investigated only one taxonomic group.

This stresses the crucial need to conduct studies focused on different types of artificial waterbodies, following a multi-taxa approach (Lemmens et al., 2013; Oertli, 2018). Knowing the contribution of different types of artificial ponds to regional biodiversity is a prerequisite if freshwater biodiversity is to be conserved in our increasingly anthropised landscapes, and is essential for good pond and wildlife management (Picazo et al., 2010; Martínez-Sanz et al., 2012; Lemmens et al., 2013). Furthermore, the ways in which artificial ponds can replace or complement natural ponds is a keystone for future biodiversity conservation (Deacon et al., 2018; Oertli, 2018). However, to date, this question remains surprisingly underexplored and only few studies have compared the diversity of artificial and natural ponds.

For this reason, we assess the relative contribution of five types of artificial ponds to the lentic biodiversity of five different landscapes, through the analysis of three contrasting taxonomic groups: amphibians, water beetles and freshwater snails. These three groups differ widely in their ecology, including their dispersal abilities, life cycles and feeding modes. For example, amphibians are terrestrial active dispersers, water beetles are aerial active dispersers and freshwater snails are passive dispersers. As study cases, we selected five types of artificial ponds constituting a good representation of the artificial ponds widespread in Europe and elsewhere. They included fish ponds, gravel pit ponds, mountain watering ponds, semiarid watering ponds and urban ponds. Answers to the following main questions were sought: (1) What is the relative contribution of artificial ponds to regional biodiversity? (2) Does one animal group benefit more than others from artificial ponds? (3) Can artificial ponds compensate the loss of natural ponds in terms of the biodiversity they support?

In order to shed light on these questions, several biodiversity metrics (including alpha, beta and gamma diversity, and species rarity) were assessed in 239 artificial ponds: 83 fish ponds in France, 41 gravel pit ponds, 22 mountain watering ponds and 55 urban ponds in Switzerland, and 38 semiarid watering ponds in Spain. In addition, biodiversity data of 130 natural ponds, located in the three Swiss regions hosting the artificial ones, were used to compare between ponds of both origins. We hypothesised that artificial ponds can contribute significantly to regional biodiversity, and therefore are useful for freshwater biodiversity conservation. More specifically, active disperser animal groups are expected to benefit more than passive dispersers from artificial ponds, linked to their higher ability for colonization of these new created habitats. Therefore, it is also expected that artificial ponds would not be able to compensate the loss of natural ponds in terms of supported biodiversity, for all types of animal groups.

2. Materials and methods

2.1. Study regions and pond types

We measured the biodiversity metrics of 239 artificial ponds from three European countries: France, Spain and Switzerland (Fig. 1). Five different types of artificial ponds were investigated: fish ponds (hereafter, FP), gravel pit ponds (GP), mountain watering ponds (MWP), semiarid watering ponds (SWP) and urban ponds (UP). Their main characteristics are summarized in Table 1, and a representative picture for each pond type is presented in Fig. 2.

The FP studied ($n = 83$) are located on the plateau of the Dombes region (Department of Ain), in eastern France. This is a pondscape covering >1000 km^2 with about 1100 ponds for fish production, but also for crops and livestock. Many of them were created in the thirteenth century, but are actively managed: they are totally emptied every autumn or winter to harvest the fish, and most are dried for one year every four years, to return them to their original condition (Arthaud et al., 2011). Pond size varies widely from 22,400 to 790,000 m^2. These ponds, with an average water depth that rarely exceeds 0.9 m, are characterized by highly nutrient-rich water, which is the basis for fish production. Most FP are partly covered by dense aquatic vegetation and bordered by reed or sedge belts. The waterfowl communities are particularly dense and species-rich: see Wezel et al. (2014) for more detailed information. GP ($n = 41$) are spread over the eastern and western plateaus of Switzerland (between 374 and 721 m.a.s.l.). Dug for gravel extraction activities, the mean depth of these ponds rarely exceeds 50 cm and their area is usually smaller than 500 m^2. GP are characterized by a stone bed. The submerged and emergent vegetation is generally well represented, but varies widely in abundance and diversity. The MWP ($n = 22$) are located in Jura Vaudois Natural Park, south-western Switzerland, between 1116 and 1528 m.a.s.l. These artificial ponds were mainly created to store water for cattle to drink and generally have a plastic bed. Therefore, most MWP (90%) are lacking aquatic

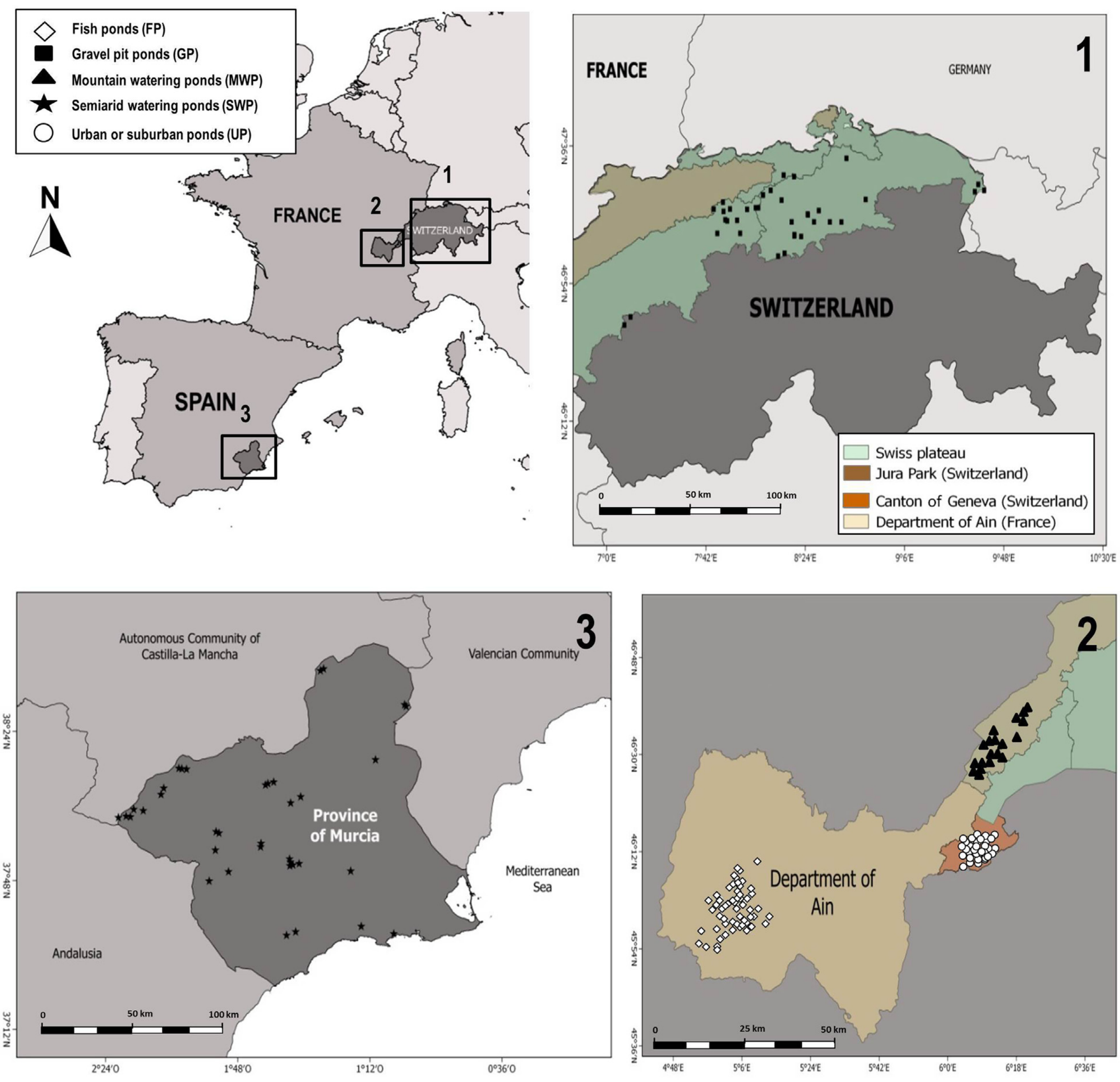

Fig. 1. Distribution of the artificial ponds along the investigated regions in France, Spain and Switzerland. Each region hosts also natural ponds and other types of artificial waterbodies (not investigated here), which are not represented in the figure. Coordinates are provided in decimal degrees (datum WGS84). The symbols used to represent each pond type are indicated in the upper left-hand corner. Additional information about the geographical regions where the studied ponds were located can be found in Appendix A: Table A1.

Table 1
Main environmental variables characterizing the five studied pond types. Median, minimum and maximum (in brackets) are indicated for each variable. Rainfall and air temperature are calculated as annual averages. All variables were recorded for each sampled pond, except pond density which was provided at regional scale by Oertli and Frossard (2013).

	Fish ponds	Gravel pit ponds	Mountain watering ponds	Semiarid watering ponds	Urban ponds
Abbreviation	FP	GP	MWP	SWP	UP
n ponds	83	41	22	38	55
ALTITUDE (m.a.s.l.)	279 (246–312)	449 (374–449)	1 348 (1 116–1 528)	882 (270–1 584)	417 (375–449)
RAINFALL (mm/year)	834 (805–861)	1 104 (980–1 584)	1 461 (1 038–1 461)	405 (306–601)	987 (956–1 044)
AIR TEMP. (° C)	10.9 (10.9–11.1)	8.8 (3.6-9.1)	5.6 (5.6–9.1)	14.6 (10.8–17.5)	9.8 (9.0–9.9)
CONDUCTIVITY (μS/cm)	NA	377 (137–1 002)	20 (6–273)	529 (86–2 590)	356 (119–760)
POND SIZE (m^2)	98 406 (22 426–790 190)	40 (2-4 450)	141 (17–442)	18 (1–432)	120 (2–3 754)
MEAN DEPTH (cm)	72 (28–110)	38 (3–150)	215 (143–300)	30 (5–200)	44 (6–200)
AQUATIC VEGETATION (mean species richness)	11.5 (+/- 7.7)	13 (+/- 6)	0.2 (+/- 0.5)	Unavailable data	7.5 (+/- 6.5)
POND DENSITY IN THE LANDSCAPE (*n* ponds/km2)	1.1	0.4	0.3	0.1	1.5

vegetation. They are fenced to avoid their direct use by cattle, since they are equipped with a gravity system that feeds metal drinking troughs located at lower altitude. Water depth ranges from 1.50 to 3 m and the average pond size rarely exceeds 250 m^2. SWP ($n = 38$) are found throughout the Province of Murcia, a semiarid Mediterranean region in south-eastern Spain. Most SWP were created for cattle drinking purposes in recent centuries, but a few of them were built or transformed for hunting or aesthetic purposes. Pond size and water depth rarely exceed 350 m^2 and 1 m, respectively. Macrophyte beds are moderately developed in these ponds whereas no surrounding vegetation is generally

Fig. 2. Picture of a representative pond for each of the five types of artificial ponds and a typical natural pond investigated in this study. a) fish ponds (FP); b) gravel pit ponds (GP); c) mountain watering ponds (MWP); d) semiarid watering ponds (SWP); e) urban ponds (UP); and f) natural pond in lowlands (NPL).

found in pond shoreline. SWP are located in a rural landscape dominated by Mediterranean forest and rain-fed agriculture. Lastly, the UP studied ($n = 55$) are located in urban areas (>16% impervious surface in 500-m buffer area) of the Canton of Geneva, in south-western Switzerland. Most of them are characterized by scarce littoral vegetation and artificial substrates. Moreover, 43% of the UP host non-native fish populations. Water depth and UP size rarely exceed 0.5 m and 800 m^2, respectively. Apart from these artificial ponds, the respective regions host other types of natural and near natural waterbodies which also support lentic aquatic communities.

2.2. Data collection

Three contrasting freshwater animal groups were studied for differing in their ecological requirements, dispersal ability and feeding modes: amphibians, water beetles (larvae and adults) (Coleoptera) and freshwater snails (Gastropoda). Field surveys for these groups were carried out between 2007 and 2018 (FP, 2007–2009; GP, 2013; MWP, 2017; SWP, 2018; UP, 2012–2013). The study groups were sampled following the PLOCH/IBEM protocol (Oertli et al., 2005b; Indermuehle et al., 2010), which was developed for surveying and assessing pond biodiversity. For aquatic macroinvertebrates (beetles and snails), ponds were visited once in late spring or early summer. Such unique sampling session allows gathering a species list that is representative of the sampled pond, even if the sampling is not exhaustive (especially for insects). Moreover, the sampling of larvae (beetles) partly compensated the absence of the adults that are more active later in the summer. The PLOCH sampling strategy is acknowledged to sample >70% of the beetles and 90% of the snails (Oertli et al., 2005b). The invertebrates were sampled by means of sweeps using a standardised dipnet with a rectangular frame (14 × 10 cm side, mesh size 0.5 mm) that allows efficient sampling within areas of dense aquatic vegetation. For each sample, the dipnet was swept through the water intensively for 30 s, the number of sampling events per study pond being proportional to the pond size. Therefore, the sampling effort was proportional to pond size. Overall, five samples were collected for ponds with a pond size smaller than 170 m^2 and six samples for larger ponds. Nevertheless, for the larger ponds, the sample number was increased proportionally to the size and attained 21 samples for the largest FP. In the case of SWP, three samples were collected from ponds larger than 100 m^2 and one sample from the remaining ponds due to their small size (<50 m^2). Each sampling was stratified according to the mesohabitats present, which were characterized by different substrates and vegetation structures present in a given pond. The collected material was preserved in 70% ethanol and was identified at species level whenever possible (93% of the recorded taxa). Macroinvertebrate samples were collected for 82 FP, 36 GP, 21 MWP, 35 SP and 55 UP.

Amphibian surveys were conducted with the aim of gathering an exhaustive species list for each pond. This was achieved through 1-h field visits on windless and rainless nights. Amphibians (adults, sub-adults and larvae) were surveyed by flashlight, the identification of calls and dip netting. Two visits were conducted for all ponds, with additional visits in the case of some pond types: one more visit for MWP and SWP, and two more for GP. Sampling visits for MWP and SWP were conducted during the day due to the small pond size and low habitat heterogeneity, which allowed breeding amphibian species to be confidently detected. Amphibians were sampled in all the study ponds, except FP, of which only 33 out of 83 ponds were surveyed. More detailed information about the sampling methods focused on these animal groups and pond types is presented in Ilg and Oertli (2017), Indermuehle et al. (2010), Oertli et al. (2005b) and Wezel et al. (2014).

2.3. Pond species pools

Only species associated with standing waters ("lentic" habitats), and therefore potentially living in ponds, were included in our analyses based on the above-mentioned field surveys. Taxa living exclusively in running waters ("lotic" habitats) may occur in ponds, especially if there is a tributary present, but were discarded. The information on habitat preference (lotic or lentic) for water beetles and freshwater snails was obtained at genus level from Tachet et al. (2010), provided by the ecological trait "*current velocity*". Only species described as lentic or generalist species were kept. Moreover, taxa mainly composed of terrestrial species were also excluded. Therefore, the species pool of true aquatic and lentic taxa included eight beetle families (Dytiscidae, Gyrinidae, Haliplidae, Hydraenidae, Hydrochidae, Hydrophilidae, Hygrobiidae and Noteridae) and eight snail families (Acroloxidae, Bithyniidae, Hydrobiidae, Lymnaeidae, Physidae, Planorbidae, Valvatidae and Viviparidae). Furthermore, two amphibian species which do not use lentic habitats for breeding were also excluded: *Salamandra atra* and *S. salamandra*. However, *S. salamandra* shows different habitat preferences in the Province of Murcia (Spain), where the SWP are located, which are exclusively selected by this species for breeding (Egea-Serrano et al., 2006), so it was included for this region.

2.4. Regional species pools

The regional richness for the three animal groups in each region was obtained from data sources that included public databanks and the published literature. Only species that potentially live in ponds were included (= "lentic" taxa). Therefore, this "lentic regional richness" included taxa inhabiting all types of lentic waterbodies present in a given region: both natural and artificial ponds, and also ditches, wetlands and lakes.

Lentic regional species pools for the period 1996–2019 were provided by the Swiss fauna databank (CSCF-KARCH, Neuchâtel, Switzerland) for regions located in Switzerland: Swiss plateau (for GP), Jura Vaudois Natural Park (for MWP) and Canton of Geneva (for UP). Additional information about the obtained data can be found in Appendix A: Table A1.

Recently published and group-specific literature provided species occurrence data for the regions where SWP (Province of Murcia, Spain) and FP (Department of Ain, France) were located. Regional species pools (= lentic regional diversity) for FP region are available for the Department of Ain, through GHRA (2015) for amphibians, in Prudhomme (2018) for beetles and in Audibert and Bertrand (2010) for snails. Regional species pools for SWP region are available for the Province of Murcia in Torralva-Forero et al. (2005) and Fernández-Cardenete et al. (2013) for amphibians, in Sánchez-Fernández et al. (2003) and Millán et al. (2014) for beetles, and in García-Messeguer et al. (2017) for snails.

2.5. Comparisons with natural ponds

For three artificial pond types (GP, MWP and UP, all located in Switzerland), data on natural ponds were available for the same regions in which they are found or for the neighbouring region with similar characteristics, which offered the opportunity to make comparisons between natural and artificial ponds. Data on natural ponds were nevertheless not available for Province of Murcia and Department of Ain (regions hosting SWP and FP, respectively). Most of the data on natural ponds were collected between 1996 and 2004 (Oertli et al., 2002; Ilg and Oertli, 2017). The ponds classified as "natural ponds" were either of natural origin or manmade but with near natural aspect (natural shore or surrounding habitat and no artificial structures or management practices), so that they closely reflected natural ponds. They are denoted in this study with an abbreviation indicating the region where they are located: natural ponds in lowlands (NPL), natural ponds in mountain areas (NPM) and natural ponds near urban areas (NPU). All three types of natural ponds were located in Switzerland and their characteristics are detailed in Table A2. NPL ($n = 52$) were spread over rural areas in Swiss lowlands, between 212 and 1100 m.a.s.l., while NPM ($n = 24$)

were located in mountain areas between 1112 and 1780 m.a.s.l., and NPU ($n = 54$) in periurban or rural areas of Canton of Geneva (<15% impervious surface in a 500 m buffer area). NPM were placed in a neighbouring mountain region from MWP (>70 km away), and regional diversity for the former pond type was not available, so it was possible to compare the richness values between both pond types but not their relative contributions to regional diversity. Therefore, three artificial pond types and their respective three natural pond types (placed in the same regions) were compared as follows: GP vs NPL, MWP vs NPM, and UP vs NPU.

2.6. Data analysis

Species presence/absence matrices were used for all the analyses made. Abundance was never considered in this study because of the lack of necessary data, especially for amphibians. Such approach based on presence/absence data can have some limitations (see Jiménez-Valverde et al. (2009) and Nielsen et al. (2005)). Nevertheless, the incidence-based approach is fully relevant for the objective of this study.

Alpha diversity (pond richness) was measured as the number of taxa recorded in each studied pond. Gamma diversity was measured as the cumulative richness (collective diversity) of a given type of pond, and it represents the regional richness linked to the considered pond type (hereafter called “pond-type regional richness”). For quality check of our data, we used a “true richness” estimator which is widely used when sampling is not exhaustive (Magurran, 2003), as it was the case here. “True richness” refers to the real richness present in a certain pond type (as a sampling is never exhaustive), and it includes the observed species (in the sampling) plus the undetected species (species undiscovered by the sampling). The true richness estimator Chao2 was calculated (Chao, 1984; Colwell and Coddington, 1995), since this is considered one of the most accurate nonparametric estimators to estimate true diversity (detected and undetected) in ponds (Foggo et al., 2003). Chao2 is an incidence-based estimator that uses the frequencies of species occurring in a single site (singletons) and species occurring in exactly two sites (doubletons) within a sample (in our case “pond type”) to estimate the number of undetected species. Species accumulation curves were also calculated (100 permutations) to determine and visualise the sampling efficiency (sampling completeness) linked to the investigated ponds. The contribution of each pond type to the regional diversity of lentic taxa was calculated as the proportion between the pond-type regional diversity and the lentic regional diversity of the region where that pond type occurs.

Taxonomic richness can nevertheless mask some dramatic patterns; for example, the regional species pool for a pond type can include frequent species (hosted in most ponds) beside rare species (infrequent species, hosted in only one or two ponds). Indeed, the most species-rich sites almost always fail to represent rare species (Albuquerque and Beier, 2015). Therefore, differences in the occurrence of rare species among pond types (among different types of artificial ponds and between artificial and natural ponds) were also explored following two techniques: rank frequency curves and the Index of Relative Rarity. The rank frequency curves were drawn according to the proportional occurrence (n occupied ponds/n ponds per pond type) of the recorded species (Magurran, 2003). A species was considered rare (rarity cut-off point) when it occurred in <5% of all the sampled ponds for a given pond type (Leroy et al., 2012). Rank frequency curves are considered a suitable tool for visualizing the proportion of rare species supported by different habitat types. However, this technique does not provide a single rarity value for each studied site, thus making it difficult to perform statistical comparisons among pond types. For this reason, we also used the Index of Relative Rarity (IRR) proposed by Leroy et al. (2012, 2013), which assigns values to sites based on rarity cut-off points and the proportion of rare species. As the IRR was developed to explore rarity in species-rich communities, such as invertebrate assemblages, we only applied it to the data obtained for water beetles and freshwater snails, following the same procedure as Astudillo-Scalia and de Albuquerque (2019), who used the *rWeights* function and Gaston's method (rare species are the 25% of the species with the lowest occurrence) to set the rarity cut-off point.

In addition, beta diversity was calculated for ascertaining whether artificial ponds in a given region have similar or dissimilar communities, and hence for assessing whether the artificial ponds complement each other to make a collective contribution to the regional species pool. Moreover, we compared beta diversity values between artificial and natural ponds to see if artificial ponds complement each other better than natural ones. Variation in the species composition within each pond type was explored following the beta diversity approach described by Baselga (2010), using multiple site dissimilarity measures calculated from site-by-species matrices. Overall beta diversity (β_{SOR}, Sørensen's dissimilarity) was measured as the sum of two components: the spatial turn-over in species composition (β_{SIM}, Simpson's dissimilarity) and the dissimilarity due to species loss that produces nested assemblages (β_{sne}, nestedness-driven dissimilarity). Thus, if β_{SOR} for a given pond type is higher than for any other type, the former has ponds with more diverse communities among them than the second pond type. Furthermore, if β_{SIM} is also higher in the first pond type than in the second type, more unique (=singleton) species per pond occur in the first one. On the other hand, to explore whether communities from artificial ponds are represented by subsets of those communities from natural ponds (nested pattern), we used the NODF metric (nestedness measure based on overlap and decreasing fills, Almeida-Neto et al., 2008). This metric quantifies independently whether poorer communities constitute subsets of progressively richer ones as well as whether uncommon species occur in sites where the most common species are found (Ulrich et al., 2009). Following Cerini et al. (2020), NODF was compared with 500 null matrices to calculate Z-scores and RN scores (relative nestedness) using the “Proportional column and row totals” algorithm (Strona et al., 2014). The online tool NeD (https://ecosoft.alwaysdata.net/; Strona et al., 2014) was used for nestedness analysis and for packing matrices according to maximum nestedness.

Rank-based Mann-Whitney U tests were conducted to explore differences in alpha richness and species rarity between artificial and natural pond types located in the same region. Differences in absolute terms among pond types located in different regions were unexplored because of the dissimilar climate and biogeographical features strongly affect the species distribution, thus precluding any comparison. All analyses were performed in R software v.3.4.4. (R Core Team, 2016), using the libraries *betapart* (Baselga and Orme, 2012), *rarity* (Leroy et al., 2013) and *vegan* (Oksanen et al., 2017).

3. Results

3.1. Sampled biodiversity

A total of 121 lentic taxa were recorded: 21 amphibian species, 26 freshwater snail taxa and 74 water beetle taxa (see list in Table A3). We observed 55 taxa in FP, 55 in GP, 12 in MWP, 35 in SWP and 45 in UP (Table 2). For all three animal groups and for most of the pond types, the sampling efficiency was generally higher than 70% (Table 2), indicating adequate survey efficiency (Sánchez-Fernández et al., 2008). The high values of the sampling efficiency were also indicated graphically by the estimated pond-type regional richness (Chao2), which was only slightly higher than the accumulated species richness (Fig. 3). Sampling efficiency was best for amphibians in all pond types, while it was generally lower for freshwater snails and water beetles. The lower sampling efficiency for macroinvertebrates is congruent with previous studies because of the great survey effort needed to reach high completeness in species-rich communities (Oertli et al., 2005b; Sánchez-Fernández et al., 2008). Indeed, some

Table 2
Taxonomic richness metrics characterizing the lentic biodiversity of the five types of artificial ponds investigated in this study. Lentic regional species richness refers to the pool of species inhabiting the region where a pond type occurs, and it includes the richness from the considered pond type (pond-type regional richness) plus the richness from all lentic waterbodies. FP: fish ponds; GP: gravel pit ponds; MWP: mountain watering ponds; SWP: semiarid watering ponds; and UP: urban ponds.

	FP	GP	MWP	SWP	UP
Amphibia					
Mean richness per pond (alpha richness)	2.3	4.9	1.8	2.1	2.0
Pond-type regional richness					
– Observed	9	13	3	8	9
– Estimated (Chao2 true richness)	9.5	13.0	3.0	8.0	9.0
Sampling efficiency (Observed/Estimated)	95%	100%	100%	100%	100%
Regional richness of lentic species	15	15	11	10	13
Contribution of pond type to lentic regional diversity (pond type/lentic regional)	63%	87%	27%	80%	69%
Coleoptera					
Mean richness per pond (alpha richness)	1.6	4.3	0.8	1.8	0.7
Pond-type regional richness					
– Observed	28	33	9	24	19
– Estimated (Chao2 true richness)	38.0	43.1	30.0	32.3	27.1
Sampling efficiency (Observed/Estimated)	74%	77%	30%	74%	70%
Regional richness of lentic species	67	117	52	116	72
Contribution of pond type to lentic regional diversity (pond type/lentic regional)	57%	37%	58%	28%	38%
Gastropoda					
Mean richness per pond (alpha richness)	2.5	0.9	0.0	0.2	1.0
Pond-type regional richness					
– Observed	18	9	0	3	17
– Estimated (Chao2 true richness)	20.0	12.0	0.0	4.0	29.3
Sampling efficiency (Observed/Estimated)	90%	75%	–	75%	58%
Regional richness of lentic species	33	42	18	16	32
Contribution of pond type to lentic regional diversity (pond type/lentic regional)	61%	29%	0%	25%	92%
Amphibia + Coleoptera + Gastropoda					
Total number of recorded taxa	55	55	12	35	45
Average contribution to lentic regional diversity	60%	51%	28%	44%	67%

macroinvertebrate species can easily be missed due to the sampling time (see Hill et al., 2016b).

Compared with natural ponds, artificial pond types (GP, MWP, UP) supported a significantly lower alpha richness in most of the paired comparisons (Fig. 4; Table A4), reaching on average only 54% of the natural pond richness. The alpha richness of freshwater snails was always significantly higher in natural pond types, and this was also the case for the pooled richness of the three animal groups.

3.2. Contribution of artificial pond types to regional diversity

3.2.1. Taxonomic richness

On average, considering the three groups together, the artificial ponds hosted 50% of the regional species pool (Fig. A1d): 65% for amphibians, 43% for water beetles and 42% for freshwater snails. Despite similar average values for both invertebrate groups, artificial ponds seemed to make a more balanced contribution to the regional species pool of water beetles, since all pond types contributed >25% in the case of this animal group (Fig. A1b). In addition to these discrepancies observed among the taxonomic groups, there were also marked differences among the five artificial pond types. For example, in the case of snails, the contribution to the regional species pool was 0% in MWP and 92% in UP. For beetles, the contribution was 28% in SWP and 58% in MWP. For amphibians, the contribution was 27% in MWP and 87% in GP. Considering all three groups together (Fig. A1d), UP was the artificial pond type with the highest average contribution (67%). This artificial pond type contribute largely to the regional species pool of snails (Fig. A1c), with 92% of the regional snail species occurring in UP. The among-group most similar average contribution was observed in FP (60%), which hosted 63% of the amphibians, 57% of the beetles and 61% of the snails. On the other hand, GP and SWP made lower average contributions (51% and 44%, respectively), both with a similar pattern: high contributions for the amphibians (≥80% in both types) and relatively low contributions for beetles (37% in GP and 28% in SWP) and freshwater snails (29% in GP and 25% in SWP). The lowest overall contribution (28%) was shown by MWP, which, on the other hand, made a higher contribution to the beetles (58%).

3.2.2. Species frequency in the pond-types communities

Contrasting results were found for the proportion of rare species (species occurring in <5% of the ponds) in the pond-types communities, depending on the animal group considered (Fig. 5a-c). All the studied amphibian species were widely distributed in the five types of artificial ponds, since no rare species were generally observed (Fig. 5a). However, in the case of the invertebrates (Fig. 5b-c), a great number of rare species was observed in all five pond types. The invertebrate communities present in the five types of artificial ponds were often represented by a set of few widely distributed species and of numerous rare species. For example, most of the recorded species of beetles (on average, 55%) were rare, particularly in MWP and UP (78% and 74%, respectively). For freshwater snails, an average of 45% of the recorded taxa corresponded to rare species, with a particularly large proportion in UP (53%).

The comparison between artificial ponds (GP, MWP, UP) and natural ponds (Fig. A2) pointed to the same patterns, and no great differences in the proportion of rare species between artificial and natural ponds (Table A6; Fig. A2) were evident from either of the analytical methods used. In general terms, the rank frequency curves showed a similar pattern for all three animal groups in artificial pond types and their respective natural ponds. According to the rank frequency curves, there were no significant differences in the IRR values between artificial and natural ponds for water beetles or freshwater snails (Table A6).

In a further analysis, we assessed the complementarity of artificial ponds and the singularity of their communities at regional scale by measuring β-diversity. Overall β-diversity was high (0.90) for the three animal groups in all artificial pond types (Fig. 6), pointing to the great variation in species composition among ponds of the same type. β-diversity was clearly dominated by the spatial turn-over component for the three animal groups in all the artificial pond types, since this component represented >70% of the total dissimilarity in most cases. An exception was observed for amphibians in MWP, where the nestedness component was slightly higher than the turn-over. Artificial ponds generally had similar values of β-diversity to natural ponds, both in terms of overall β-diversity and the two components (Fig. A3). The only exception was in one of the comparisons made for amphibians (MWP vs. NPL), when a higher contribution of the nestedness component was observed for the artificial pond type. The patterns obtained from nestedness analyses (e.g. packed matrices presented in Fig. A4) indicated that artificial pond communities were partially nested into natural pond communities. For half of the mixed matrices (artificial plus natural ponds), the artificial pond communities were clustered in the right end, whereas these ponds were interspersed with natural ponds for the remaining half of the mixed matrices. Importantly, natural ponds hosted several species which were not found in the artificial ponds situated in the same regions (Table A7), especially for water beetles: 39 beetle species were exclusively found in NPL, 20 in NPM and 36 in NPU. However, some artificial pond types also hosted exclusive species within their respective regions, though comparatively much less than natural pond types: 13 beetle species were exclusively found in GP, 4 in MWP and 3 in UP. In most cases, natural ponds also made a greater contribution to regional diversity than artificial ponds (Fig. A5).

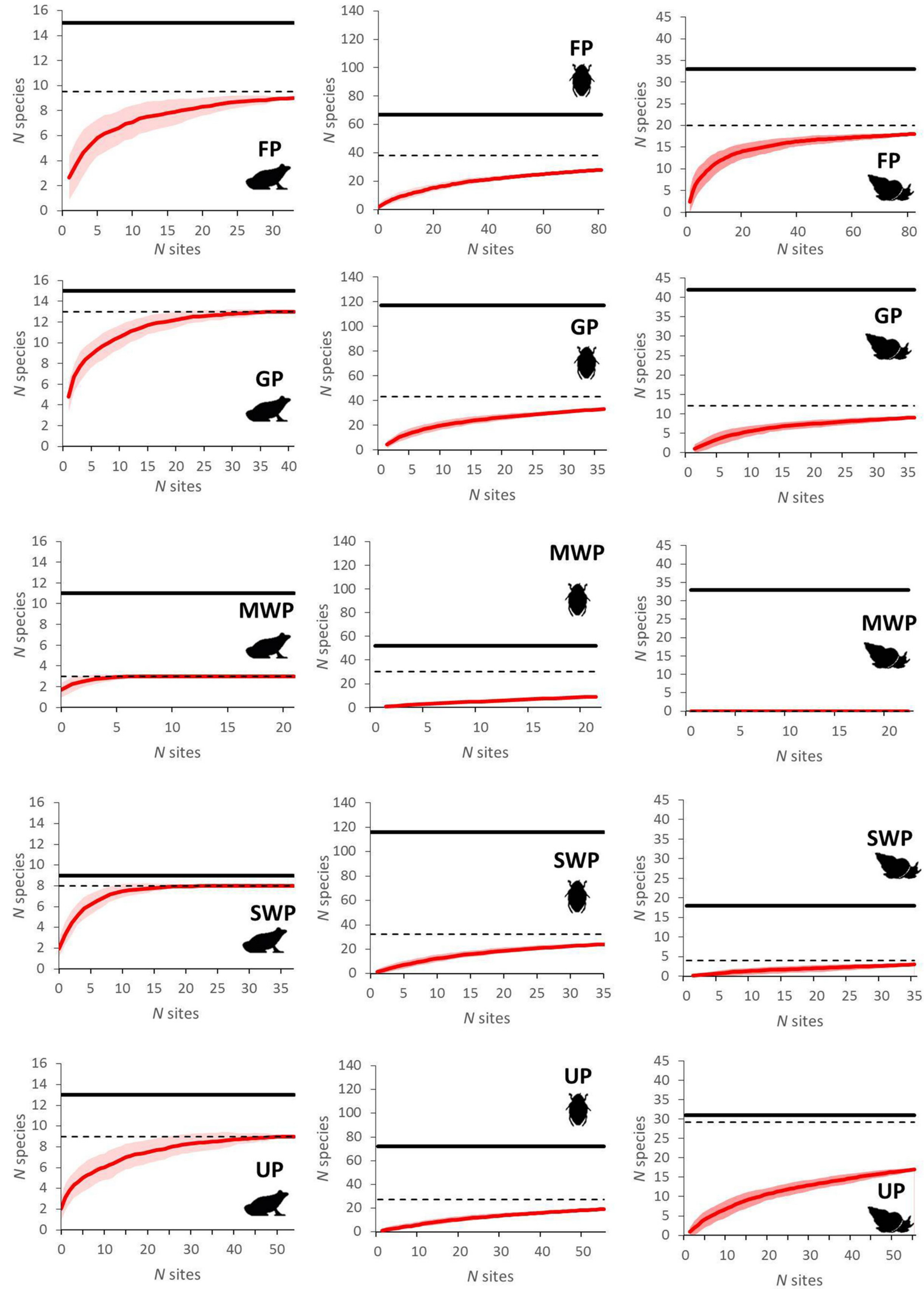

Fig. 3. Species accumulation curves (SACs) for the three animal groups in the five artificial pond types investigated in this study. Mean accumulated richness is indicated as a dark red line, with light red shadow showing the standard deviation. The lentic regional richness (pool of species occurring in all lentic waterbodies of the region) is indicated by a continuous black line. The pond-type regional richness (Chao2 true richness) is added (dashed line), as a quality control indicating sampling efficiency. FP: fish ponds; GP: gravel pit ponds; MWP: mountain watering ponds; SWP: semiarid watering ponds; and UP: urban ponds. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

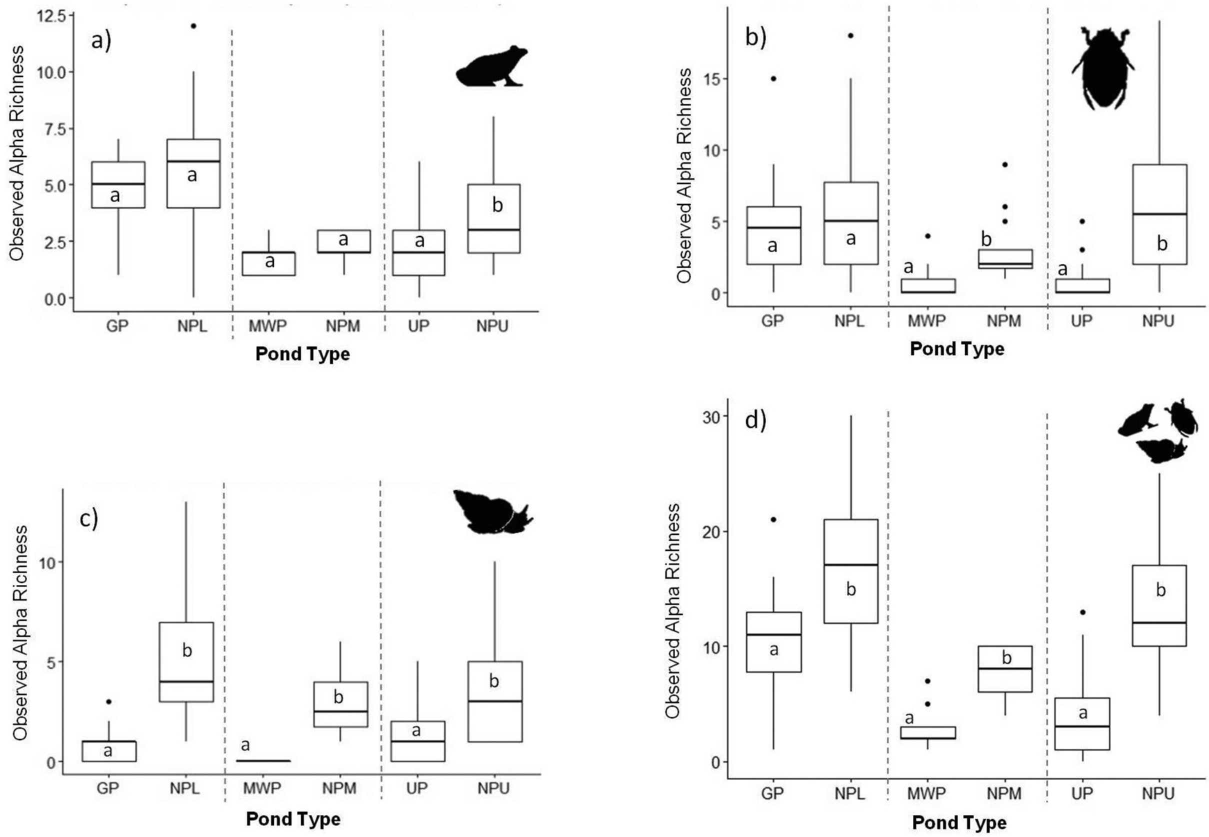

Fig. 4. Boxplots comparing alpha richness of amphibians (a), water beetles (b), freshwater snails (c) and all groups together (d) for artificial and natural pond types located in the same region. Mann-Whitney test results are shown with different letters within boxes (a or b) for each paired comparison between three types of artificial ponds (GP, MWP, UP) and natural pond types located on the same region. Same letters indicate groupings based on lack of statistical difference among pond types. Dashed lines separate paired comparisons. *P*-values can be found in Table A5. GP: gravel pit ponds; NPL: natural ponds in lowlands; MWP: mountain watering ponds; NPM: natural ponds in mountain areas; UP: urban ponds; and NPU: natural ponds near urban areas.

4. Discussion

4.1. Artificial ponds contribute partially to regional diversity

The artificial ponds investigated in this study hosted half of the regional species pool, highlighting their effective contribution to regional biodiversity conservation that nevertheless remains relatively moderate. This was partly due to the lower potential of individual artificial ponds to maintain biodiversity at local scale. Indeed, compared to natural ponds, artificial pond types (e.g. GP, MWP, UP) supported a significantly lower alpha richness, reaching only 54% of the natural pond richness on average. However, the beta richness of artificial ponds was high, underlining their potential for enriching regional biodiversity if they are constructed in large numbers or in areas with a low number of natural ponds. Notwithstanding, the same pattern in beta diversity was also observed for natural ponds, that collectively made a higher contribution to regional diversity than the artificial ponds. Importantly, artificial ponds, even if they had a markedly lower species richness than natural ponds, were similar to them in terms of beta diversity and the proportion of rare species they supported, suggesting that the artificial origin of these ponds does not affect their ability to provide habitat for some rare species and to contribute to regional diversity. However, a high number of beetle and snail species were exclusively found in natural ponds, pointing to the limitation of artificial ponds to replace natural ones in the future human-dominated landscapes. Nevertheless, it should be noted that data on natural ponds in our study were only available for the three investigated regions in Switzerland, so further studies are needed to shed light on this question also in other regions.

About half of the invertebrate species represented in each artificial pond type were rare at the regional scale, as were found in <5% of the investigated artificial ponds. Such pattern was also observed for the natural ponds. This stresses the complementarity of ponds at the regional scales and underlines the importance of the pond density in a pondscape, that has to be large. As recalled by Hill et al. (2018), it is collectively that ponds support high taxonomic richness and conservation value. On a larger scale, these pond networks are also part of a larger network of freshwater habitats ("freshwater landscape"), including also running waters and lakes, where plants and animals move around (Sayer, 2014).

There were nevertheless discrepancies among the taxonomic groups according to artificial pond type. On the one hand, the contribution of artificial ponds to the regional species pool was low for invertebrates. For example, in the case of snails, some artificial pond types (especially MWP and SWP) contributed particularly poorly to the regional species pool (lentic regional diversity), while the contribution of artificial ponds to the regional species pool was better in the case of amphibians. Some pond types (GP and SWP) even supported a large proportion of the amphibian species occurring at regional scale.

4.2. Amphibians benefit more from artificial ponds than invertebrates

The average contribution of artificial ponds to the regional species pool was higher for amphibians (65%) than for water beetles (43%) and freshwater snails (42%). Interestingly, SWP held eight of the ten amphibian species inhabiting the investigated region (Province of Murcia). In this region, the natural scarcity of water resources

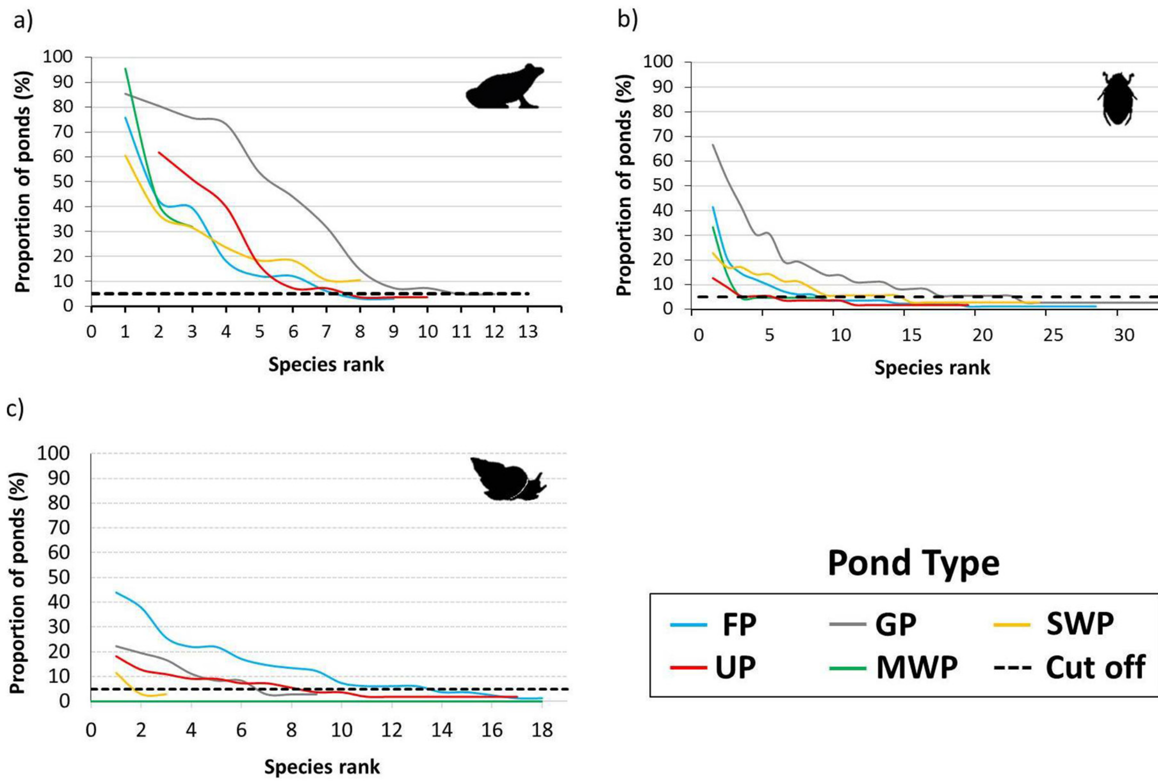

Fig. 5. Rank frequency curves for the three animal groups in the artificial pond types explored in this study. Species are ranked from highest to lowest frequency of occurrence for each pond type. Occurrence frequency is calculated as the proportion between the number of ponds where a species occurs in a given pond type and the total number of ponds belonging to that pond type. The rarity cut-off point was set at 5% and is indicated by a black dashed line. Graphs compare frequency curves among artificial pond types for amphibians (a), water beetles (b) and freshwater snails (c). FP: fish ponds; GP: gravel pit ponds; MWP: mountain watering ponds; SWP: semiarid watering ponds; UP: urban ponds.

and the sharp decline of natural ponds make artificial ponds critical habitats for supporting the amphibian community. Indeed, the groundwater overexploitation derived from the increasing irrigated agriculture (Rupérez-Moreno et al., 2017) is expected to make artificial ponds even more important for biodiversity in the near future. This finding is consistent with previous studies conducted in European arid and semiarid regions, where the availability of natural ponds is very low and artificial ponds often constitute the only alternative breeding sites for amphibians (Valera et al., 2011). Amphibians were also well represented in GP, a type of habitat recognised as particularly important for this pioneer group (Sievers, 2017). Indeed, such ponds are regularly managed (or created), and so continuously offer pioneer conditions.

The discrepancy between the relative contributions of artificial pond types to the regional diversity of the three animal groups may be explained by their different responses to environmental factors and dispersal modes. Freshwater snails, characterized by low dispersal ability, presented lower alpha richness in artificial ponds than in natural ponds in all the paired comparisons. Indeed, artificial ponds often offer pioneer conditions as a result of their recent creation (e.g. GP) or their intense management (e.g. FP), and they are therefore likely to be colonized more efficiently by pioneer groups (such as amphibians or beetles) than by passive dispersers (e.g. snails). However, it should be noted that other environmental factors not considered in this study (e.g. environmental heterogeneity or among-pond connectivity) can affect the spatial distribution of the these animal groups in ponds (Hill

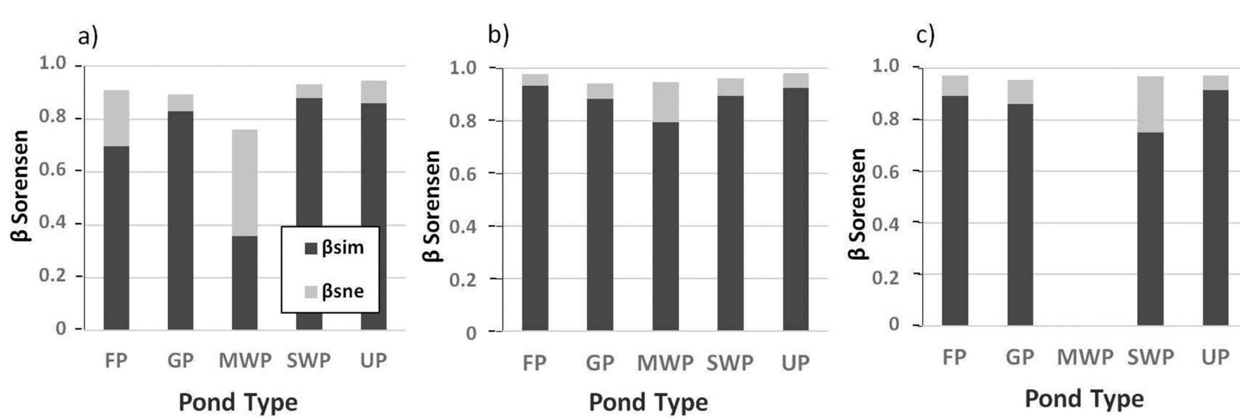

Fig. 6. Contribution of turn-over (βsim) and nestedness (βsne) components to the overall β-diversity (β Sørensen) for amphibians (a), water beetles (b) and freshwater snails (c) in the five types of artificial ponds investigated in this study. The contributions of turn-over and nestedness are indicated with dark and light grey colouring, respectively. The overall β-diversity corresponds to the sum of both components. FP: fish ponds; GP: gravel pit ponds; MWP: mountain watering ponds; SWP: semiarid watering ponds; UP: urban ponds.

et al., 2019; Rosset et al., 2014), so further studies are needed to shed light on this question.

Even though landscape variables have been reported to be important factors in shaping the community composition of the three animal groups, water beetles are particularly influenced by the water's characteristics (Boix et al., 2016), whereas amphibians and freshwater snails are mostly influenced by landscape and pond features (Jumeau et al., 2020; Rosset et al., 2014). In addition, amphibians are terrestrial active dispersers, and this great dispersal ability enables them to rapidly colonize new artificial ponds, where they may even reach similar richness values as they do in natural ponds located in the same region (Arntzen et al., 2017).

As the main function of most artificial ponds is not to provide habitats for wildlife, their design and management is often inappropriate for maximizing their potential to host species-rich communities (Oertli, 2018). Thus, artificial ponds often show monotonous shorelines which provide few suitable habitats for aquatic vegetation (Declerck et al., 2006; Law et al., 2019), thus decreasing their potential to support macroinvertebrate communities (Thornhill et al., 2017). The richness of macroinvertebrate passive dispersers, in our case snails, increases with pond size and width of pond sediment layer (Oertli et al., 2002; Zealand and Jeffries, 2009; Shieh and Chi, 2010). Hence, the larger the pond size, the more species-rich macrophyte communities they will support and the greater the probability of snail colonization (Laseen, 1975; Oertli et al., 2002), since larger ponds provide more suitable habitats and resources for snails (Brönmark, 1985). The patterns mentioned by the above are consistent with our results, since MWP (where no snail species were detected) are relatively small and characterized by the impervious material (e.g. plastic) covering the pond bottoms, hindering or preventing the enrooting of vascular plants. Moreover, the small pond size of MWP might hamper the occurrence of waterfowls, which act as natural vectors for passive snail dispersal. Conversely, FP had the highest snail richness values among the studied pond types, which may be attributed to their greater pond size and abundant bird populations (vectors for passive transport), but also to their earlier creation date. Indeed, these aspects were probably responsible for the greater snail diversity found overall for all types of natural ponds when local richness was being analysed, because of all artificial pond types were much smaller than their respective natural ones. The species richness of freshwater snails was also very low in SWP, possibly as a combined response to small pond size and degree of isolation, as both aspects have been reported to decrease the colonization rates of freshwater snails (Brönmark, 1985).

On the other hand, in the case of water beetles and freshwater snails, it should be noted that the average contribution of artificial ponds to regional diversity, while low, demonstrates that some ponds types can support most of the species occurring in the studied regions. In this regard, the average contribution (taking into account all artificial pond types together) to regional diversity of water beetles in our study (43%) was very similar to the reported contribution for dragonflies in farm ponds (40%) of France (Ruggiero et al., 2008) and for water beetles (42%) in natural ponds in south-eastern Spain (Picazo et al., 2010). Furthermore, the contribution of SWP to the regional species pool of water beetles (28%) is similar to the contribution reported in previous studies (25%) (Picazo et al., 2010) for other types of artificial ponds in the same region.

4.3. Dealing with artificial ponds in human dominated landscapes

Our results suggest that a landscape with only artificial ponds would host only about half of the regional species pool present today. Indeed, this proportion of species inhabiting artificial ponds could be even lower because of natural ponds frequently act as source habitats for most freshwater species. Although natural (or "near-natural") ponds are key ecosystems for promoting and conserving freshwater biodiversity in all landscapes, they are gradually vanishing, mostly through human intervention (e.g. by filling in) but occasionally naturally (by terrestrialization). A priority in biodiversity conservation is therefore to protect existing natural ponds, and to manage them appropriately. Creating new "near-natural" ponds is also a priority in pond-impoverished landscapes.

Current landscapes tend more and more to be human dominated (Kareiva et al., 2007; Yang et al., 2019), with freshwater biodiversity expected to experience a sharp decline in the future (Sala et al., 2000; Pereira et al., 2010). Indeed, the density of artificial ponds is increasing at the expense of the density of natural ponds (Oertli, 2018), and must be taken into account for future biodiversity conservation, although they also have to be managed carefully for this purpose (Briggs et al., 2019).

Firstly, promoting the diversity of different types of artificial pond appears to be key to ensure effective freshwater biodiversity conservation at regional scale, as it has already been suggested (Oertli, 2018). All the artificial pond types described herein were seen to make a considerable contribution to the regional diversity of any animal group; for example, GP and SWP in the case of amphibians, FP and UP for freshwater snails, and FP and MWP for beetles. Although the five types of artificial ponds were investigated in different regions, several types of artificial pond in the same region could act in a complementary way, but this remains to be confirmed in further studies. There is therefore a need to focus conservation efforts at regional scale by maximizing the potential of artificial ponds to support biodiversity. The different types of artificial ponds should be considered as complementary, since the richness of different biotic groups is not always congruent (Rooney and Bayley, 2012; Ilg and Oertli, 2017). However, further studies assessing the species turn-over among artificial pond types located in the same region should be conducted for unravelling the way in which these ecosystems complement each other. In our case, half of the artificial pond communities were partially nested (subsets) within the natural pond communities. This finding indicates that some artificial pond types can provide additional habitat for species already present in natural ponds from the same region, whereas other artificial pond types are needed to host new species not found in natural ones.

Pond density in a given landscape also appears to be as a key issue because, if the ponds are complementary, they must be considered collectively. This is underlined in our results by the numerous rare species hosted by both artificial and natural ponds, which is reflected in the high beta-diversity values and the gradual increase in species accumulation. Pond density, then, needs to be sufficiently high to promote regional biodiversity. In this respect, the studied regions had an artificial pond density of between 0.1 and 1.5 ponds/km^2 (Table 1), which must be regarded as being close to the lower limit and cannot be reduced, since many ponds have already been filled in. Fortunately, many regions of Western Europe have densities higher than two ponds/km^2 (from Downing et al., 2006), the highest pond densities exceeding 20 ponds/km^2 (Oertli and Frossard, 2013).

Design and management protocols should be considered to improve the artificial ponds, as mentioned in a recent review by Oertli and Parris (2019). At regional scale, the low level of suitability of artificial ponds for supporting taxa with limited dispersal ability could be improved by increasing pond connectivity. The diversity of freshwater snails increases with pond density and pond size, partly because of the increased occurrence of birds that act as natural snail vectors (Laseen, 1975; Brönmark, 1985). In this regard, newly created large ponds may constitute an interesting tool for promoting natural dispersal from natural to artificial ponds by passive colonisers. Thus, the co-occurrence of several ponds differing in size and other characteristics (e.g. trophic state, presence of vegetation) in the landscape ("*pondscapes*") and near natural ponds, will increase the colonization rates of passive colonisers in artificial ponds. Such measures would also benefit active dispersers, which will be able to reinforce their metapopulations. At the local scale (ponds), habitat diversification should be promoted, particularly by ensuring the presence of diversified plant communities (e.g. sedge or reed belts and submerged macrophyte beds). Features such as steep slopes and the plastic materials used to make ponds waterproof, should, as much as possible, be avoided during the design of new artificial ponds.

While the replacement of natural ponds in our landscapes by artificial ponds has been poorly researched, the artificialisation of other types of freshwater habitat is not a novel issue, and has already been widely documented in the case of lake shores, streams and rivers (Sondergaard and Jeppesen, 2007; Lu et al., 2019). Nature-based solutions have also been proposed for these other ecosystems, including many types of restoration measures (Brachet, 2015; Geist and Hawkins, 2016). This trend must be applied to pondscapes, were plans for the restoration of natural (or "near natural") habitats should be put into action with some urgency.

In conclusion, the artificialisation of natural habitats in our landscapes, through the replacement of natural ponds by artificial ponds, is a great threat to biodiversity. Concurrently, the creation of artificial ponds is a growing practice throughout the world, due to the increasing need of freshwater resources by today's societies, then offering a great opportunity to create new habitats for freshwater biodiversity. Based on our results we forecast that future human-dominated landscapes, where most ponds will be artificial, will be particularly impoverished in freshwater biodiversity. This underlines the need to conserve and manage existing natural ponds, as well as to create new "near-natural" ponds. Artificial ponds can nevertheless make an important contribution for supporting freshwater biodiversity at regional scale, but for this to happen their design must be improved. Pond density also plays an important role in the landscape, especially for conserving regional invertebrate species pools.

CRediT authorship contribution statement

Jose Manuel Zamora-Marín: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Writing – original draft, Writing – review & editing. **Christiane Ilg:** Methodology, Investigation, Writing – review & editing. **Eliane Demierre:** Methodology, Investigation, Writing – review & editing. **Nelly Bonnet:** Methodology, Investigation, Writing – review & editing. **Alexander Wezel:** Methodology, Investigation, Writing – review & editing. **Joël Robin:** Methodology, Investigation, Writing – review & editing. **Dominique Vallod:** Methodology, Investigation, Writing – review & editing. **José Francisco Calvo:** Resources, Supervision, Visualization, Writing – review & editing, Project administration, Funding acquisition. **Francisco José Oliva-Paterna:** Resources, Supervision, Visualization, Writing – review & editing, Project administration, Funding acquisition. **Beat Oertli:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data Curation, Supervision, Visualization, Writing – original draft, Writing – review & editing, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.141987.

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