Universitat de Girona

PRIMARY SUCCESSION IN MAN-MADE WETLANDS: BIODIVERSITY, STRUCTURE AND DYNAMICS OF MACROFAUNAL ASSEMBLAGES

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ALBERT RUHÍ I VIDAL 2011 - PhD THESIS - PRIMARY SUCCESSION IN MAN-MADE WETLANDS
Biodiversity, structure and dynamics of macrofaunal assemblages

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PhD THESIS

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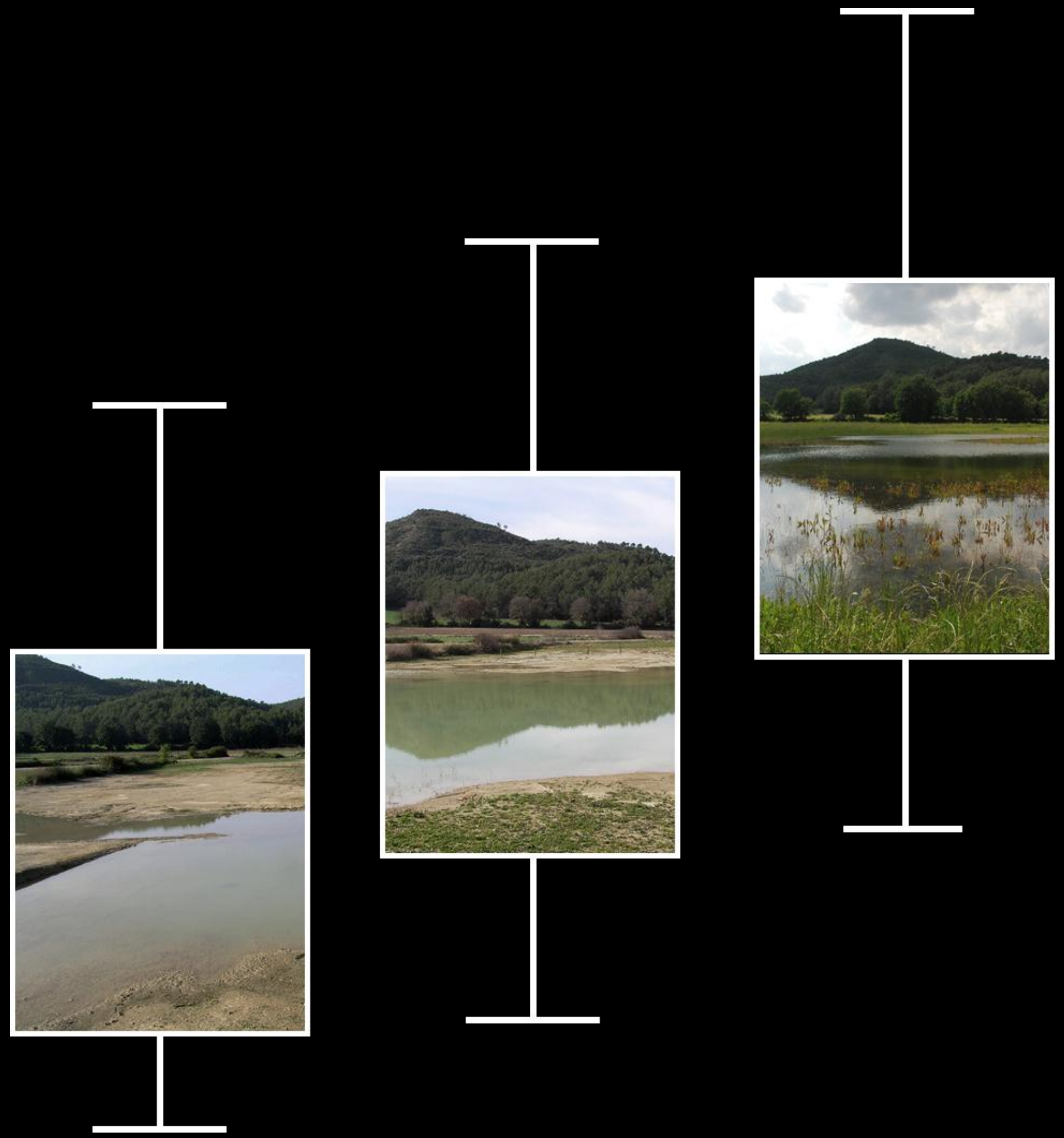

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PhD THESIS

PRIMARY SUCCESSION IN MAN-MADE WETLANDS

Biodiversity, structure and dynamics of macrofaunal assemblages

ALBERT RUHÍ I VIDAL

2011

PROGRAMA DE DOCTORAT EN CIÈNCIES EXPERIMENTALS I SOSTENIBILITAT

Dirigida per:

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Universitat de Girona	Universitat de Girona

Memòria presentada per optar al títol de Doctor per la Universitat de Girona

El Dr. Dani Boix i Masafret, professor agregat del departament de Ciències Ambientals de la Universitat de Girona, i la Dra. Stéphanie Gascón i Garcia, professora titular del departament de Ciències Ambientals de la Universitat de Girona,

CERTIFIQUEN:

Que aquest treball titulat "Primary succession in man-made wetlands: biodiversity, structure and dynamics of macrofaunal assemblages", que presenta Albert Ruhí i Vidal, per a l'obtenció del títol de Doctor, ha estat realitzat sota la seva direcció i que compleix els requeriments per poder optar a Menció Europea.

Dr. Dani Boix i Masafret   Dra. Stéphanie Gascón i Garcia

El doctorand:

Albert Ruhí i Vidal

Girona, octubre 2011

Aquesta tesi doctoral és, innegablement, el fruit de quatre anys de dedicació intensa a la recerca en el camp de l'ecologia aquàtica. Però també ho és de la passió per la Natura que he tingut des de ben petit: de les cuques minúscules més properes als ocells més acolorits i llunyans; dels hàbitats propers i sovint menystinguts fins als tan idealitzats paisatges exòtics. És, en certa manera, la destil·lació científica d'una manera de veure i entendre la vida, marcada per la fam de córrer món, la predisposició a deixar-se sorprendre i la convicció que som tots part d'un gran ecosistema. Pateixo una afecció irreversible, la dels que hem estat seduïts per aquesta meravella que és la Natura. Espero compartir-la amb tots vosaltres.

Per això vull dedicar aquesta tesi a la meva família i la meva parella, per entendre i participar de la meva passió. També vull agrair molt sincerament l'esforç de tots els qui m'heu acompanyat en aquest viatge tan estimulant. Una menció especial la mereixeu els meus directors i els companys del Grup de recerca en limnologia de llacunes i aiguamolls mediterranis (LLAM), que a més a més m'heu fet de mestres i amics. També us dec molt als companys del Grup de recerca en Ecologia aquàtica continental (GRECO), compartint àpats, ciència i limitat espai vital al seminari; i als doctorands de fora la casa (Universitat de Barcelona; Centre d'Estudis Avançats de Blanes, CEAB-CSIC) amb qui hem emprès –i n'estic segur, continuarem fent-ho– il·lusions i projectes comuns.

I also would like to thank those who made my Summer 2009 research stage at the University of Kalmar in Sweden (now Linnaeus University) as pleasant as it was; and last but not least, the colleagues and friends of the University of Georgia who have converted the American ending of my PhD into an unforgettable experience. Thank ya'll!

"We cannot win this battle to save species and environments without forging an emotional bond between ourselves and nature as well - for we will not fight to save what we do not love."

Stephen Jay Gould (1941 – 2002)

"Nature first, then theory. Or, better, Nature and theory closely intertwined while you throw all your intellectual capital at the subject. Love the organisms for themselves first, then strain for general explanations, and, with good fortune, discoveries will follow.
If they don't, the love and the pleasure will have been enough."

Edward Osborne Wilson (1929)

CONTENTS

SUMMARY

Man-made wetlands are often created to compensate for the loss or degradation of natural wetlands, but little is known about the processes taking place in these artificial environments, especially at the community level. Throughout this thesis, we have assessed the phenomena of primary succession over different time (short-, mid- and long-term) and spatial scales (local, regional, interregional levels), applying different approaches (taxonomic and functional) and subject groups (invertebrates and amphibians).

In the **first chapter**, we performed a short-term study (during the first year after creation) of the macrofaunal communities colonizing a group of nine man-made wetlands in three neighboring areas in the NE Iberian Peninsula (Baix Ter, Pla de l'Estany, Plana de la Selva; three wetlands each). We had three aims: first, to explore if any invertebrate assemblage structure change was taking place within a year of the creation of the ecosystem; second, to evaluate the effect of local factors on the invertebrate assemblage at each site; and third, to compare the information obtained from taxonomic and functional approaches. We observed a rapid colonization combined with a lack of temporal changes in assemblage parameters within that year, implying that more time is needed to detect successional changes in invertebrate assemblages. Furthermore, local factors, especially those related to hydrological stability, explained notable differences both in the assemblage parameters and in the taxonomic and functional compositions of the invertebrate fauna. Finally, taxonomic and functional approaches produced very similar results, suggesting that, in recently created eco-

systems, the high dominance of a small number of taxa makes the functional approach a simple biological traits analysis of the few dominant species.

The next logical step in our research was to assess the community development following the phase dominated by the early colonizers. Thus, in the **second chapter** we approached the topic of successional trajectories from a mid-term (3 years) perspective. The same nine wetlands were studied for another two years (thus, 0 to 3 years from creation), as was a set of 91 natural wetlands spread all over Catalonia, which were taken as the reference for natural macroinvertebrate communities. Successional models based on deterministic trajectories are currently being questioned, while, at the same time, new models proposing several possible trajectories have been developed. They generally integrate two key ideas from succession theory: convergence vs. divergence in species composition among successional sites, and progression towards vs. deviation from a desired reference state. These ideas have been created and tested in plant succession frameworks, and, based on these findings, we proposed and tested our own model. In this case, we integrated the differential colonization existing between active and passive disperser macrofauna and the nested patterns that appear as a consequence, into this model based on four possible trajectories. We predicted that (i) highly nested structures would be found in the pioneering assemblages (1st year after creation) decreasing towards lower values in the mid-term (3rd year), due to the shift from pioneering aerial dispersers towards passive dispersal taxa; (ii) these idiosyncratic taxa should cause divergent successional trajectories among areas; and (iii) these divergent trajectories would be reflected in lower local, but higher regional, diversity values in the mid-term rather than in the short-term pioneer assemblages. Our results corroborated the first two hypotheses, but diversity trends did not follow the expected pattern. The divergent successional trajectories did not manage to compensate on a regional level the local biodiversity losses that occurred as a consequence of the decline of pioneering colonizers over time. This observation may have important implications for conservation, since new wetlands are usually designed to substitute or mitigate natural ones in short time periods (the majority, < 5 years). Our conclusion is that different areas in the same region, within that timeframe, would probably present low levels of idiosyncrasy. As a consequence, in order to be successful wetland creation programs need to consider longer time periods.

The **third chapter** moves from a regional to an interregional scale. A research stay at Linnaeus University (Sweden) allowed us to test how colonization/successional processes may be affected by latitudinal-driven effects. We compared macrofaunal communities from a group of three man-made wetlands in Catalonia (Pla de l'Estany) with a group of three man-made wetlands in southern Sweden, from a mid-term time perspective (0 to 3 years from creation). We hypothesized that climate characteristics may condition the community structure and its dynamics, as well as the biological strategies, of the taxa undergoing the successional process. Summers are hot and dry and winters cool and wet in the Iberian Peninsula (Mediterranean climate), whereas milder summers and colder, wetter winters characterize the Scandinavian Peninsula (cold temperate climate). As a consequence, we predicted finding less structured communities in the Mediterranean ponds than in the cold temperate ones as well as higher successional rates in the Mediterranean ponds, with contrary episodes of highest and lowest change throughout the year. We also predicted significantly different biological traits composition between the regions, due to a dominance of traits that favor resilience, or resistance, to major disturbance events in the Mediterranean region compared to those in the cold temperate region. Whereas our hypotheses on community structure and biological traits composition were mostly corroborated, the succession dynamics was explained by climate features in the cold temperate region but not in the Mediterranean ponds. We therefore suggest that the intrinsic hydrological variability of Mediterranean lentic systems may be a major factor behind community changes in wetlands being created in this region. Finally, in order to generalize the observed pattern, we performed a meta-analysis of the temporal trends of taxonomic distinctness parameters from other successional studies across Europe, which supported the differences we had observed between the latitudinal extremes.

As man-made aquatic systems, and therefore ecological research in these ecosystems, have been promoted for longer in Northern Europe, we developed a project to monitor the same Swedish wetland system (Kalmar Dämme) during the summer of 2009, in order to obtain a long-term perspective of the communities inhabiting these wetlands over a 13-year period after construction (1997–2009). This allowed us to assess primary succession, in the **fourth chapter**, by exploring species composition, biological traits, and community structure changes from long-term perspectives. We observed the hypothesized successional changes that had previously been barely evident, revealing a complex community structure in the advanced phase. Three successional phases were observed, each typified by different species. At the advanced phase, dominant biological traits shifted to favor animals with longer life-cycle durations, aerial dispersal strategies, and certain feeding types (i.e., filter-feeders, fine sediment collectors, predators, and parasites). Furthermore, we selected the Coleoptera assemblage to represent the macroinvertebrate community in an evaluation of the extent to which other regional man-made wetlands of different age classes (<3 years and ≥10 years from creation) were similar to natural wetlands in the region (>50 years). No significant differences in Coleoptera assemblages were found between natural wetlands and man-made wetlands ≥10 years. However, man-made wetlands ≥10 years had significantly higher coleopteran species richness than man-made wetlands <3 years due to the convergence of pioneering species remaining from early successional stages with representative specialized taxa from natural wetlands. This chapter makes an interesting contribution, since our results suggest that 10 years may be enough time for the macrofaunal communities of man-made wetlands to resemble, in composition and structure, to those of natural wetlands.

Finally, in the **fifth chapter** we assess the conservation value of man-made Mediterranean temporary ponds (MTPs) for amphibians, a group in decline in the Mediterranean region mainly due to wetland destruction. Although the disappearance of lentic habitats in other regions of the world has been ameliorated by the creation and restoration of wetlands, these tactics remain untested in the Mediterranean region. To evaluate the colonization dynamics of man-made MTPs, we monitored two artificial MTPs (one in a high amphibian diversity area, Plana de la Selva, and the other in a low amphibian diversity area, Baix Ter) over two years from the creation of these wetlands. We selected five reference wetlands in each area, and amphibian communities of man-made MTPs were compared to those of the reference wetlands. We found that, right from the first year, artificial MTPs were a valuable habitat for regional amphibian fauna. We focused on the reproductive success of the natterjack toad, *Bufo calamita,* the main beneficiary of man-made MTPs in those areas. Using drift fences equipped with pit-fall traps, we measured the abundance of both reproductive adults entering the pond and post-metamorphic individuals exiting it. Using mark-recapture methods, we analyzed the time and energy costs associated with reproduction in the artificial MTPs. We observed highly variable colonization dynamics between sites, between hydroperiods, and within hydroperiods, and these dynamics often depended on meteorological factors. Our results suggest that even over a short time scale, native amphibian species such as *B. calamita* can benefit from wetland creation in the Mediterranean region. Moreover, when compared to other amphibian colonization studies of man-made wetlands across Europe and North America, the proportion of regionally present species that colonized and successfully bred was among the highest in both high and low amphibian diversity areas.

Overall, our main findings regarding time scales show a 3-phase successional pattern in Mediterranean man-made wetlands' communities, where at the short term (1 year) colonization processes dominate; at mid term perspectives (2 to 7 years) succession signs begin to be conspicuous, and later on (≥ 10 years) parameters such as species richness reach an asymptote. At that moment, some biological strategies dominate, and biodiversity surrogates indicate that communities are indistinct between man-made and natural wetlands.

Regarding spatial effects, we corroborated that both local and regional factors affect the establishing communities. Particularly, the low hydrological stability of the Mediterranean region has enhanced biological traits favoring resilience and resistance to disturbances when comparing Mediterranean and cold temperate aquatic communities. Even within the Mediterranean region, low levels of hydrological stability have significant effects on the successional dynamics. In these cases, local communities are highly nested within regional natural ones, and so are not able to make net contributions to regional richness. We also showed the influence of the regional pool of recruiters over local communities, both in the case of invertebrates and amphibians. Especially for the latter group, man-made Mediterranean temporary ponds (MTPs) can play an important role in their conservation.

RESUM

Les zones humides de nova creació són sovint concebudes per compensar la pèrdua i degradació de les naturals, però el coneixement dels processos que tenen lloc en aquests ambients artificials encara és superficial, especialment a nivell de comunitat. Al llarg d'aquesta tesi, hem analitzat el fenomen de la successió primària a diferents escales temporals (a curt, mitjà i llarg termini) i a diferents escales espacials (a nivell local, regional i interregional), mitjançant diverses aproximacions (taxonòmiques i funcionals) i subjectes (invertebrats i amfibis).

Al **primer capítol**, vam desenvolupar un estudi a curt termini (durant el primer any després de la seva creació) de les comunitats de macrofauna que van colonitzar un conjunt de 9 zones humides de nova creació distribuïdes en 3 àrees properes del Principat (Baix Ter, Pla de l'Estany, Plana de la Selva; 3 llacunes a cada àrea). Vam plantejar tres objectius: el primer, explorar si es produïen canvis en l'estructura de la comunitat d'invertebrats dins del primer any des de la creació de l'ecosistema; el segon, avaluar l'efecte dels factors locals sobre les comunitats d'invertebrats de cada lloc; i el tercer, comparar la informació obtinguda amb les aproximacions taxonòmica i funcional. Vàrem observar una colonització ràpida combinada amb una absència de canvis en els paràmetres de la comunitat, fet que suggeria que cal més temps per poder detectar canvis successionals en comunitats d'invertebrats. D'altra banda, els factors locals –especialment aquells relacionats amb l'estabilitat hidrològica– semblaven explicar les diferències notables observades tant en els paràmetres de la comunitat com en les composicions taxonòmiques i funcionals d'aquestes comunitats. Finalment, les aproximacions taxonòmiques i funcionals varen proporcionar resultats molt similars,

donant a entendre que en sistemes recentment creats l'alta dominància d'un petit grup de taxons converteix l'aproximació funcional en un mer anàlisi dels trets biològics d'aquestes espècies dominants.

L'objectiu lògic subsegüent era el d'analitzar el desenvolupament de la comunitat després d'aquesta fase dominada pels colonitzadors. Amb aquesta finalitat, al **segon capítol** vam abordar el tema de les trajectòries successionals a mitjà termini (3 anys). Les mateixes 9 llacunes es varen estudiar durant 2 anys més (per tant, dels 0 als 3 anys des de la creació), així com un conjunt de 91 llacunes naturals escampades per Catalunya, que varen ser preses com a referència de les comunitats naturals de macroinvertebrats. Els models successionals basats en trajectòries determinístiques actualment estan essent qüestionats, al mateix temps que s'han anat desenvolupant nous models proposant diverses trajectòries possibles. Generalment, aquests models integren dues idees clau de la teoria de la successió: convergència vs. divergència en composició d'espècies entre àrees, i progressió vs. desviació d'un cert estat de referència. Aquestes idees han estat creades i testades en marcs de successió vegetal, i basant-nos-hi ens vàrem proposar crear i testar el nostre propi model. En particular, vam integrar la colonització diferencial que existeix entre la macrofauna dispersora activa i passiva, i els patrons aniuats que sorgeixen com a conseqüència d'aquest fet, en aquest model basat en 4 possibles trajectòries. Vàrem predir que (i) estructures altament aniuades es trobarien a les comunitats pioneres (1r any des de la creació) amb valors decreixents cap al mitjà termini (3r any); que (ii) la fauna idiosincràtica provocaria trajectòries successionals divergents entre àrees; i que (iii) aquestes trajectòries successionals divergents es reflectirien en baixos nivells de diversitat local i alts nivells de diversitat regional a mitjà més que a curt termini. Els resultats obtinguts validen les dues primeres hipòtesis, mentre que les tendències observades en les diversitats no segueixen el patró predit. Les trajectòries successionals divergents no varen aconseguir compensar regionalment les pèrdues de biodiversitat local que varen succeir com a conseqüència del declini progressiu dels colonitzadors pioners. Aquesta observació pot tenir implicacions importants per a la conservació, ja que les zones humides de nova creació normalment es dissenyen per a substituir o mitigar les naturals en períodes de temps curts (la majoria d'ells, < 5 anys). La nostra conclusió és que dins aquests límits temporals, les àrees diferents d'una mateixa regió probablement presenten nivells baixos d'idiosincràsia. En conseqüència, perquè els projectes de creació de noves llacunes siguin exitosos, han de considerar períodes de temps més llargs.

El **tercer capítol** passa d'una escala geogràfica regional a una d'interregional. Una estada de recerca a la Linnaeus University (Suècia) va permetre testar com els processos de colonització/successió poden estar afectats per efectes derivats de la latitud. Vàrem comparar les comunitats de macrofauna d'un grup de 3 llacunes de nova creació de Catalunya (Pla de l'Estany) amb un grup de 3 llacunes de nova creació del sud de Suècia, a mitjà termini (0 a 3 anys des de la creació). Vam predir que les característiques climàtiques condicionarien l'estructura de la comunitat i la seva dinàmica, així com les estratègies biològiques, dels taxons que duen a terme la successió. Els estius són càlids i secs i els hiverns frescos i humits a la Península Ibèrica (sota clima mediterrani), mentre que estius més suaus i hiverns més freds i humits a la Península Escandinava (sota un clima temperat fred). En conseqüència, vam predir trobar comunitats menys estructurades a les llacunes mediterrànies que no pas a les temperades fredes; taxes de successió més altes –amb episodis contraris de màxim i mínim canvi al llarg de l'any–; i una composició de trets biològics significativament diferent entre regions, degut a la dominància de trets que afavoreixen la resiliència i la resistència enfront de pertorbacions a la regió Mediterrània més que no pas a la temperada freda. Mentre que les hipòtesis sobre l'estructura de comunitats i la composició de trets biològics es varen complir majoritàriament, la dinàmica de la successió s'explicava per característiques climàtiques a la regió temperada freda però no en la Mediterrània. En aquest sentit, suggerim que la variabilitat hidrològica intrínseca dels sistemes lenítics mediterranis pot ser el principal factor conduint el canvi de les comunitats a les zones humides que es creen en aquesta àrea. Finalment, amb la voluntat de generalitzar el patró observat, vàrem dur a terme un meta-anàlisi de les tendències temporals de paràmetres de distinció taxonòmica d'altres estudis al llarg d'Europa, que varen donar suport a les diferències que nosaltres havíem observat entre els extrems latitudinals estudiats.

Degut al fet que al nord d'Europa els sistemes aquàtics de nova creació s'han promogut des de fa temps, així com la recerca ecològica en aquests ambients, vam desenvolupar un projecte per monitoritzar la mateixa zona humida de Suècia (Kalmar Dämme) durant l'estiu del 2009, amb la finalitat d'obtenir una perspectiva a llarg termini de les comunitats que viuen en aquestes llacunes al llarg d'un període de 13 anys des de la seva construcció (1997-2009). Aquest fet va permetre estudiar, al **quart capítol**, la successió primària a través dels canvis en composició, trets biològics i estructura de la comunitat en una perspectiva a llarg termini. Vàrem observar els canvis successionals hipotetitzats, obtenint una estructura de la comunitat complexa en la fase tardana. Vàrem observar tres fases, cadascuna tipificada per diferents espècies. A la fase avançada, els trets biològics dominants afavorien animals amb cicles de vida llargs, dispersió aèria i algunes estratègies tròfiques particulars (filtradors, col·lectors de sediments fins, predadors i paràsits). A més a més, l'associació de coleòpters va servir per avaluar fins a quin punt altres zones humides artificials de diferents edats (< 3 i ≥10 anys) eren similars, en composició, a les zones humides naturals de la regió (>50 anys). No es varen trobar diferències significatives en la comunitat de coleòpters entre les zones humides naturals i les creades feia ≥10 anys. En canvi, la riquesa de coleòpters a les zones humides de ≥10 anys era significativament més alta que a les de <3 anys, a causa de la convergència d'espècies pioneres que persistien d'estadis successionals anteriors amb taxons especialitzats representatius de les comunitats naturals. Aquest capítol ofereix una contribució interessant, ja que els resultats suggereixen que 10 anys pot ser un temps suficient perquè les comunitats de zones humides de nova creació presentin característiques, respecte la composició i estructura de les seves comunitats, similars a les comunitats naturals.

Finalment, al **cinquè capítol** vam avaluar el potencial de conservació de les Basses Temporànies Mediterrànies (BTMs) de nova creació per als amfibis, un grup en declivi a la regió mediterrània degut principalment a la destrucció de zones humides. Tot i que la desaparició d'hàbitats lenítics en altres regions del món s'ha compensat amb la creació i restauració de zones humides, aquestes estratègies romanen desconegudes a l'àrea mediterrània. Per tal d'avaluar la dinàmica de la colonització de BTMs artificials, vam seguir dues àrees (una d'alta diversitat d'amfibis, Plana de la Selva; i una altra de baixa diversitat d'amfibis, Baix Ter) al llarg de dos anys des de la creació d'aquestes zones humides. Vàrem seleccionar 5 llacunes de referència a cada àrea, i les comunitats d'amfibis de les BTMs artificials es varen comparar a les comunitats de referència. Vàrem observar que, ja des del primer any, les BTMs artificials eren un hàbitat valuós per als amfibis presents a nivell regional. Ens vàrem centrar en avaluar l'èxit reproductor del gripau corredor (*Bufo calamita*), el principal beneficiat de les BTMs artificials en aquestes àrees. Fent servir un tancat equipat amb trampes de caiguda, es va mesurar l'abundància tant dels adults reproductors que entraven a les BTMs artificials com dels individus post-metamòrfics que en sortien. Utilitzant tècniques de marcatge i recaptura, vam analitzar els costos de temps i energia associats amb la reproducció en BTMs artificials. Vam detectar una dinàmica de la colonització altament variable entre àrees, dins d'hidroperíodes i entre hidroperíodes, dinàmiques que sovint depenien de factors meteorològics. Els nostres resultats suggereixen que fins i tot dins escales de temps reduïdes, les espècies autòctones d'amfibis com *B. calamita* poden beneficiar-se de la creació de zones humides a la regió mediterrània. A més a més, comparant els resultats obtinguts amb els d'estudis en zones humides al llarg d'Europa i Amèrica del Nord, en el nostre cas la proporció d'espècies presents a nivell regional que va colonitzar i reproduir-se amb èxit va ser d'entre les més altes tant a l'àrea de baixa com d'alta diversitat d'amfibis.

En resum, les nostres aportacions pel que fa a les escales temporals mostren un patró de successió basat en 3 fases, on a curt termini (1 any) dominen els processos de colonització; en perspectives de mitjà termini (2 a 7 anys) els signes de successió comencen a ser conspicus, i més tard (≥ 10 anys) paràmetres com la riquesa d'espècies arriben a una asímptota. En aquesta fase avançada, algunes estratègies biològiques dominen, i els índexs de biodiversitat indiquen que les comunitats poden ser indistintes entre les llacunes naturals i les de nova creació.

Pel que fa als efectes espacials, hem corroborat que tant factors locals com regionals afecten les comunitats que s'hi estableixen. En particular, la baixa estabilitat hidrològica de la regió Mediterrània ha afavorit trets biològics que proveeixen resiliència i resistència enfront de pertorbacions, sobretot quan es comparen amb les comunitats pròpies del clima temperat fred. Fins i tot dins la mateixa regió Mediterrània, nivells baixos d'estabilitat hidrològica poden tenir efectes importants en la dinàmica de la successió. En aquests casos, les comunitats locals estan altament aniuades en les naturals a nivell regional, i per tant difícilment poden fer contribucions netes a la riquesa regional. També hem mostrat la influència del pool regional de colonitzadors sobre les comunitats locals, tant en el cas dels invertebrats com en el dels amfibis. Especialment per aquest darrer grup, les Basses Temporànies Mediterrànies (BTMs) de nova creació poden jugar un paper important per a la seva conservació.

GENERAL INTRODUCTION

Defining wetland

Achieving a precise definition of *wetland* has long been a matter of debate (Batzer and Sharitz 2006). Although consensus exists on its interconnected three-component basis (hydrology, physicochemical environment, and biota), the apparently clear concepts of shallow water or saturated conditions, unique wetland soils and vegetation and fauna adapted to wet conditions, have contributed to the difficulties in separating wetlands from other ecosystems (Mitsch and Gosselink 2007). Since its definition is crucial in terms of policy, the US Fish and Wildlife Service (USFWS) proposed a definition (Cowardin et al. 1979) which considers wetlands as *'lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water'*. However, as ecologists should adopt biologically useful definitions (Batzer and Sharitz 2006), we have selected the one proposed recently by Keddy (2010): '*A wetland is an ecosystem that arises when inundation by water produces soils dominated by anaerobic processes, which, in turn, forces the biota, particularly rooted plants, to adapt to flooding*'. In Europe, shallow and small water bodies (1 m^2 to about 5 ha) that hold water permanently or temporarily are also known as *ponds* (Oertli et al. 2005, Céréghino et al. 2008). Nevertheless, since ponds are considered to be within wetlands by the Ramsar Convention, here we will refer to small wetlands or ponds indistinctively.

Ecological relevance of wetlands

Although wetlands cover less than 9% of the Earth's surface, they contribute up to 40% of the globe's ecosystem services on an annual basis (Zedler and Kercher 2005), offering mainly flood protection, water quality enhancement, and carbon sequestration (Hey and Philippi 1995, Jeng and Hong 2005, Mitsch and Gosselink 2007, Moreno-Mateos et al. 2009). They also contribute disproportionately to biodiversity, hosting many wetland obligate species (Boylan and MacLean 1997, Zedler and Kercher 2005, Daniels and Cumming 2008), and are thus valuable sites for biological conservation (Linton and Goulder 2000). The origin of the rich biota associated with wetlands has been connected to the high biological productivity of these environments (Gopal and Junk 2000, Boix et al. 2001) and to their transitional nature; characterized by the presence of both resident and transient species coming from adjacent terrestrial or aquatic environments (Lefeuvre et al. 2003, Boix et al. 2007). Small wetlands in particular are important because, at the regional level, they support considerably more species and more rare species than other water body types (Williams et al. 2004). This pattern, well documented throughout Europe (Angélibert et al. 2004, Abellán et al. 2006, Davies et al. 2008, Della Bella et al. 2008), may also occur globally (e.g., Guadagnin et al. 2005, Markwell and Fellows 2008). The high species richness has been attributed to their small catchments: they reflect local natural variations better than larger water bodies such as rivers and lakes. Also, they are often protected from land-derived pollutants, something rare in water bodies with larger catchments which cannot remain pristine within humanly degraded landscapes (Biggs et al. 2005). Furthermore, the numerical and areal cover of small water bodies has been proven to be much greater than was previously assumed, hence processes that are most active in small lakes and ponds may assume global significance if further studies focus on the global role and contribution of small water bodies (Downing et al. 2006).

Decline of wetlands in a changing world

In contrast to their important ecological functions, wetlands worldwide have some of the fastest loss rates of any type of ecosystem (Balmford et al. 2002, Coleman et al. 2008). Estimates of historical wetland area are crude because, despite some exceptions (e.g., Jeffries in press), few countries have accurate historical wetland data from a century or two ago. However, it is estimated that about 50% of the global wetland area has been lost as a result of human activity (Gibbs 1995, Daniels and Cumming 2008). Although much of this loss occurred in the northern countries during the first half of the 20th century, conversions of wetlands to other land uses have also accelerated wetland loss in tropical and subtropical areas since the 1950s (Moser et al. 1996, OECD 1996, He and Zhang 2001, Green et al. 2002, Zhang et al. 2010). However, quality estimates of extensive wetland losses and their causes exist only for North America and Europe.

In the case of the US, assessments of the wetland loss that occurred during the 200-year time span between 1780 and 1980 in its conterminous states show a 53% reduction from the original total extension: from about 900,000 km^2 to 420,000 km^2 (Dahl 1990). Furthermore, 45% of the wetland surface in the US is concentrated in a single state (Alaska), which has lost only about 1% of its existing wetlands; while 10 states have lost ≥ 70% of their original acreage; (e.g. estimated losses for California are of about 91 %, Dahl 1990). Studies focusing on the causes of extensive coastal wetland losses (3,950 km^2 between 1930 and 1990) in Louisiana and the Mississippi delta (Walker et al. 1987, Templet and Meyer-Arendt 1988, Boesch et al. 1994, Day et al. 2000), in the northern Gulf of Mexico (Turner 1997), in the southeastern states (Johnston 1994) or along the US Atlantic coast (Koneff and Royle 2004), revealed that, in most cases, modification of land uses triggered the hydrological changes that led to wetland impoverishment. In Canada, with the exception of the vast boreal regions (where wetland conversions to other uses have been minimal), the overall picture in the prairie and the southern densely populated temperate regions is similar to that of the US. For instance, in southern Ontario, an area that has been well studied (Glooschenko et al. 1993, Bedford 1999 and references therein), figures exceed 70%.

In Europe, the Global Review of Wetland Resources and Priorities for Wetland Inventory (GRoWI) has shown trends similar to those of North America, despite variations between countries (Nivet and Frazier 2004). Mediterranean states such as Italy (≈ 60% of wetland loss between 1938 and 1984), France (≈ 66%, 1909-1993) or Spain (> 60%, 1965-1990) have been particularly affected. Even though the importance of wetlands has been recognized in Council Directive 92/43/CEE, on the conservation of natural habitats and of wild fauna and flora (EC Habitats Directive), small wetlands remain highly vulnerable to threats of human activity (Hull 1997, Wood et al. 2003, Angélibert et al. 2004, Della Bella et al. 2005).

Wetland creation and biodiversity offsetting

Since wetland mosaics are necessary for species that live in multiple local populations sustained by occasional migration (Gibbs 2000), maintaining minimally sufficient wetland densities is fundamental to sustaining wetland biota. Consequently, amphibians are suffering a serious global decline (Houlahan et al. 2000, Stuart et al. 2004, Beebee and Griffiths 2005), with the main causes of potential mass extinction being habitat reduction, pathogens and introduced predators (Wake and Vredenburg 2008). In the Mediterranean region in particular, wetland destruction is the main cause of amphibian decline, shown by the fact that 89% of the endangered species have suffered habitat loss (Cox et al. 2006). Mediterranean temporary ponds (MTPs), regarded as priority conservation habitats by the European Commission’s Habitats Directive 92/43/CEE, are decreasing due to agricultural and urban development, and their global long-term preservation seems critical (Zacharias et al. 2007). Since MTPs are habitats of vast biological value (Boix et al. 2001, Grillas et al. 2004), especially for amphibians (Jakob et al. 2003, Díaz-Paniagua et al. 2010), the impact of decreasing densities of MTP mosaics could particularly affect this faunal group.

Overall, the ecosystem approach to restoration is critical in any global strategy, since biodiversity loss and ecosystem degradation will continue at high rates under any current developing scenario (Comín 2010). In the US and Canada, the no net loss (NNL) principle is the cornerstone of wetland habitat conservation polices (Harper and Quigley 2005b). In the US, the Army Corps of Engineers applies this principle when it allows wetlands to be affected under Section 404 of the Clean Water Act, which permits ‘unavoidable’ destruction of wetlands only if it is to be compensated by the restoration of the degraded wetlands or the creation of new ones. Hence, it requires the proponent to compensate for environmental damage and habitat losses incurred during the dredging and filling of wetlands, thus ensuring no overall net loss of wetlands by acreage and function (Krucynski 1990). In Canada, Fisheries and Oceans Canada (DFO) also applies the NNL principle when it issues an authorization for development activity affecting fish habitat. However, in 2001 a comprehensive review showed that in the US the NNL of wetlands goal was not being reached, mainly due to poor compliance with the conditions stipulated within the permits, the absence of appropriate monitoring and enforcement, and the failure to adopt landscape-level approaches rather than local solutions (Race and Fonseca 1996, Kelly 2001, National Research Council - Committee on Mitigating Wetland Losses 2001, Sudol and Ambrose 2002). Further research has identified the main challenges in offsetting wetland biodiversity as being the difficulty in replacing the same wetland hydrology and nutrient functioning (Cole and Shafer 2002, Hoeltje and Cole 2009, Hossler et al. 2011), as well as integrating the objectives of wetland creation or restoration into different landscape scales (Moreno-Mateos and Comin 2010). In Canada, studies monitoring compensation projects have been specific to certain development activities, habitat types or compensation techniques, providing more qualitative than quantitative assessments (Harper and Quigley 2005a, b). However, overall, and despite many authors' claims that mitigation tools remain largely untested, important developments in policy and regulation concerning wetland conservation, mitigation and compensation have occurred in North America (Rubec and Hanson 2009). Currently, wetland recovery trends are being intensively monitored in both countries (Dahl 2006, Bartzen et al. 2010).

Outside North America, there is the same need to compensate for wetland loss, but a global homologous 'no net loss' policy is still lacking (but see ten Kate et al. 2004, for exceptional regulations in Switzerland under the Federal Law for the Protection of Nature and Landscape, in the EU under the Habitats and Birds Directive, and in Brazil under the Forest Regulation and National System of Conservation Units). Focusing on Europe, a wide range of human activities have been responsible for the creation of lentic habitats, and the importance of values such as water supply, floodwater retention, recreation and education or wildlife management and research have been recognized (Williams et al. 1999, Oertli et al. 2005, Jeffries in press). As well as nutrient retention, the goal of biodiversity conservation in agricultural areas has gained popularity and some authors support the proposal that wetlands may be able to achieve both aims simultaneously (Comín et al. 2001, Biggs et al. 2005, Hansson et al. 2005). Extensive wetland creation programs have been specially promoted in agricultural landscapes (e.g., > 12.000 ha in Sweden, Swedish Board of Agriculture 2000), and, in some cases, the conservation benefits have been tested and published (e.g., Rannap et al. 2009, Gallardo et al. in press). However, current knowledge on the effectiveness of wetland creation for biodiversity purposes is affected by a two-fold bias. The first, regarding the geographical area where the majority of these projects have been developed, namely central and northern rather than southern Europe (e.g. Rannap et al. 2009, Thiere et al. 2009, Svitok et al. 2011). However, there is a need to adapt the current paradigm in limnology (represented by the cold, temperate climate, stratifying lakes and single-channeled rivers) to the quite distinct characteristics of Mediterranean limnosystems (Álvarez-Cobelas et al. 2005), which are less hydrologically predictable. The second bias is caused by the differential attention that vertebrates have received (i.e., birds and amphibians), in contrast to wetland invertebrates, the diversity of which, globally, has been overlooked (Boix et al. 2001, Williams et al. 2008, Gascón et al. 2009).

Man-made wetlands and temporal scales: colonization and succession

Conservation issues aside, created and restored wetlands are also valuable as study units for pure ecology, thanks to their quasi-experimental conditions. In this sense, although succession has been traditionally described in ecosystems that were recovering from major disturbances, such as fires, droughts or hurricanes (e.g. Force 1981, Smith 1982, Kaufman 1983), created and restored aquatic habitats have proven to be ideal systems for testing the dynamics of this process (Levin et al. 1996, Flory and Milner 2000, Herrmann et al. 2000, Matthews et al. 2009, Matthews and Spyreas 2010).

Succession refers to changes observed in an ecological community following a perturbation that opens up a relatively large space (Connell and Slatyer 1977). These changes involve a sequence of species and important variations in community structure (Odum 1960, Gutierrez and Fey 1980), and usually include two subsequent stages in time: the initial colonization and the changes in assemblage structure (Fisher 1983). Whereas new ponds are usually rapidly colonized by active dispersers (Koskenniemi 1994, Gee et al. 1997, Herrmann et al. 2000, Lods-Crozet and Castella 2009), changes observed in aquatic macroinvertebrate assemblages over short time scales are combinations of seasonal and successional processes (Herrmann et al. 2000, Hillman and Quinn 2002). Given enough time, pioneer active dispersers should progressively decrease in favor of passive dispersers (Batzer and Wissinger 1996), and changes in structure should appear (Velasco et al. 1993b).

Similarly, general increases in biomass and diversity over time were proposed long ago in ecological theory papers (Margalef 1968, Odum 1971, Gutierrez and Fey 1980, Legendre et al. 1985). However, 'humped-shaped' relationships between both parameters have recently been described as appearing when the scales of measurement are large enough to cross various stages of succession (Guo 2003). Thus, studies have shown rapid sustained increases in abundance/density and macroinvertebrate species richness during the first years of succession (e.g. Voshell and Simmons 1984, Bass 1992, Fairchild et al. 2000). However, when studies last longer, asymptotic patterns tend to appear (20 year study of a deglaciated stream, Milner and Robertson 2010).

Despite the associated controversy, new wetlands are often designed to replace natural wetlands over short time periods (Mitsch and Wilson 1996, Pechmann et al. 2001, Lesbarrères et al. 2010). Thus, it seems critical to analyze the changes that take place in the macrofaunal assemblages of newly created habitats during the very early phases of colonization and succession, and to compare these changes with those occurring over the medium and long term (Figure I1).

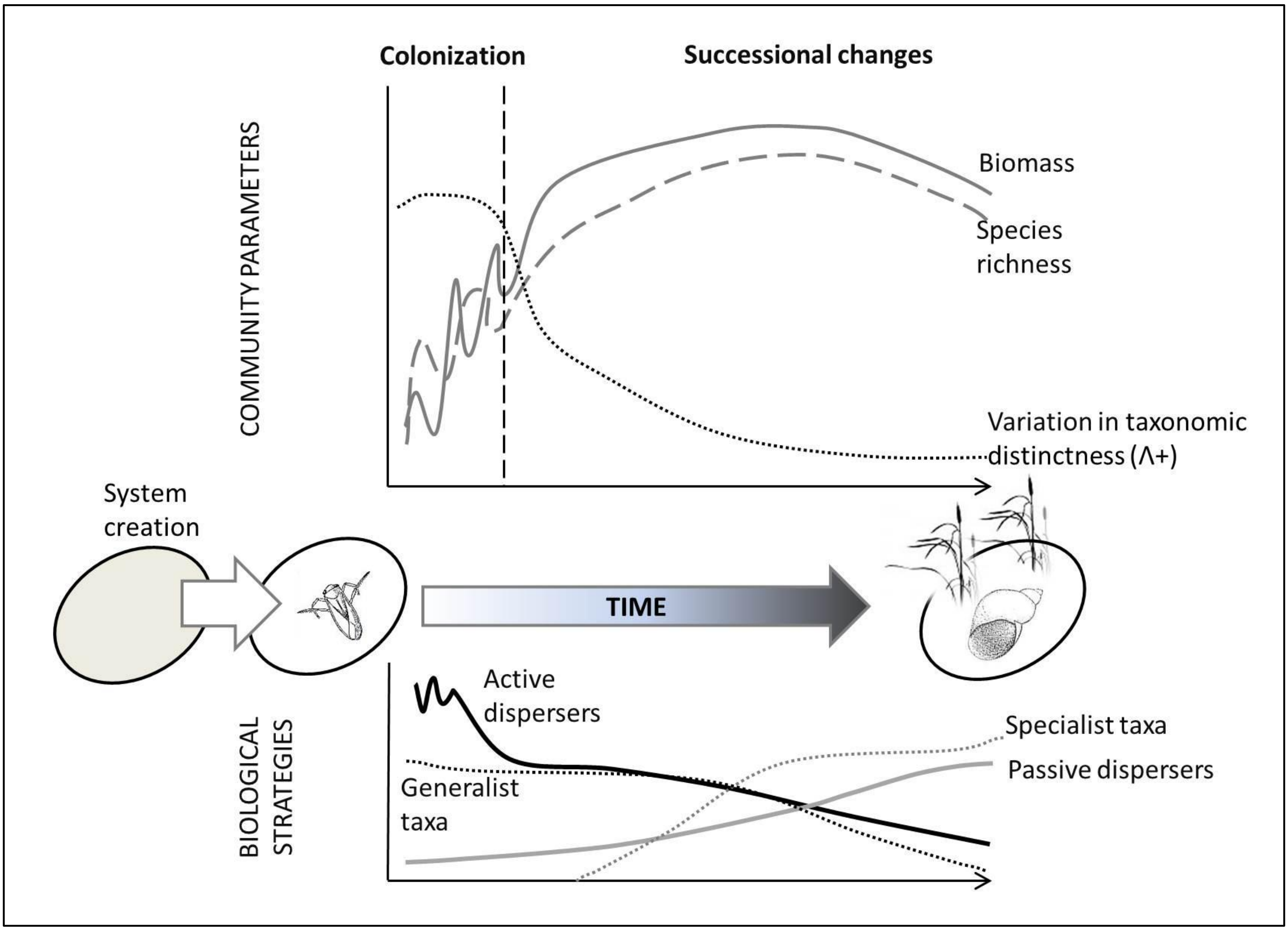

Figure I1. Hypothesized temporal changes on community parameters and organisms characteristics in a man-made wetland through primary succession.

Spatial effects of colonization/succession of man-made wetlands

Research connecting environmental variables and invertebrate community structure tends to be carried out in large geographic areas and indicates a hierarchy of strong ecological factors but rarely takes into account the relative importance of specific factors that can occur against a background of local conditions (Cottenie et al. 2003, Svitok et al. 2011). Ponds that are close together can differ widely in their history; and differences in local factors (e.g., in fish stocking, the impact of pond use, egg banks, water regime or mesohabitat) can have a relevant influence on the community structure (Savage et al. 1998, Della Bella et al. 2005, Jeffries 2008).

However, regional and large-scale factors, such as climate, are important in driving colonization/succession dynamics and their composition, through species and trait "filtering" processes (Poff 1997). Consequently, differences should be expected in the process dynamics between latitudes: on one hand, due to meteorological effects on invertebrate colonization (Boda and Csabai 2009b, Boix et al. in press); and on the other, because higher structure levels of pioneer communities have already been associated with temperate regions rather than low latitudes. This is due to the dominance, in cold areas, of a few pioneering species that establish facilitative interactions from the start in the early stages of primary succession (Kaufmann 2001, Felinks and Wiegand 2008). An extra regional consideration, the effects of which are inherent to Mediterranean ecosystems, is the variability of its climate (Álvarez-Cobelas et al. 2005, Beklioglu et al. 2007). Therefore, creating wetlands in the Mediterranean region may not only imply particular colonization/succession dynamics, but also achieve community compositions dominated by traits that favor resilience and resistance towards hydrological disturbances. This is in contrast to the lack of necessary strategies to overcome these ecological bottlenecks in the temperate regions (Bêche et al. 2006, Bonada et al. 2007). Accordingly, the structural and functional adaptations observed between lotic ecosystems in the Mediterranean and temperate regions (Townsend and Hildrew 1994, Bonada et al. 2007) could serve as a basis for the exploration of whether similar patterns occur when comparing wetland communities latitudinally.

Links between the spatial and temporal components

The spatial and temporal components of primary succession are entangled on several points. On one hand, allogenic phases have been described as occurring at the beginning and end of secondary succession processes in temporary water bodies (Lake et al. 1989, Boix et al. 2004b). Whether this environmental influence plays a similar role in primary succession dynamics remains unanswered. Some studies have shown the influence of existing regional communities on the colonization of created or ephemeral systems (Wissinger et al. 2008, Hart and Davis 2011). Consequently, the differential colonization between active and passive dispersers, within the regional pool of potential colonizers, may cause nested patterns, (i.e., local species-poor sites containing subsets of the regional assemblages found in species-rich sites, Atmar and Patterson 1993, Cook and Quinn 1995, Florencio et al. 2011).

On the other hand, classical deterministic ideas supporting predictable temporal changes throughout succession have been debated recently (e.g., Zedler and Callaway 1999, 2000). Indeed, modern case studies have often failed to support these predictions (del Moral 2007, Matthews and Spyreas 2010) (Figure I2). While the idea of climax has been substituted for reference communities (Matthews et al. 2009), it would be interesting to assess how trajectories from pioneer towards more mature or reference communities are related to changes in nestedness, and how this assembling phenomena is related to local and regional diversity trends (Cook and Quinn 1995, Baselga 2010).

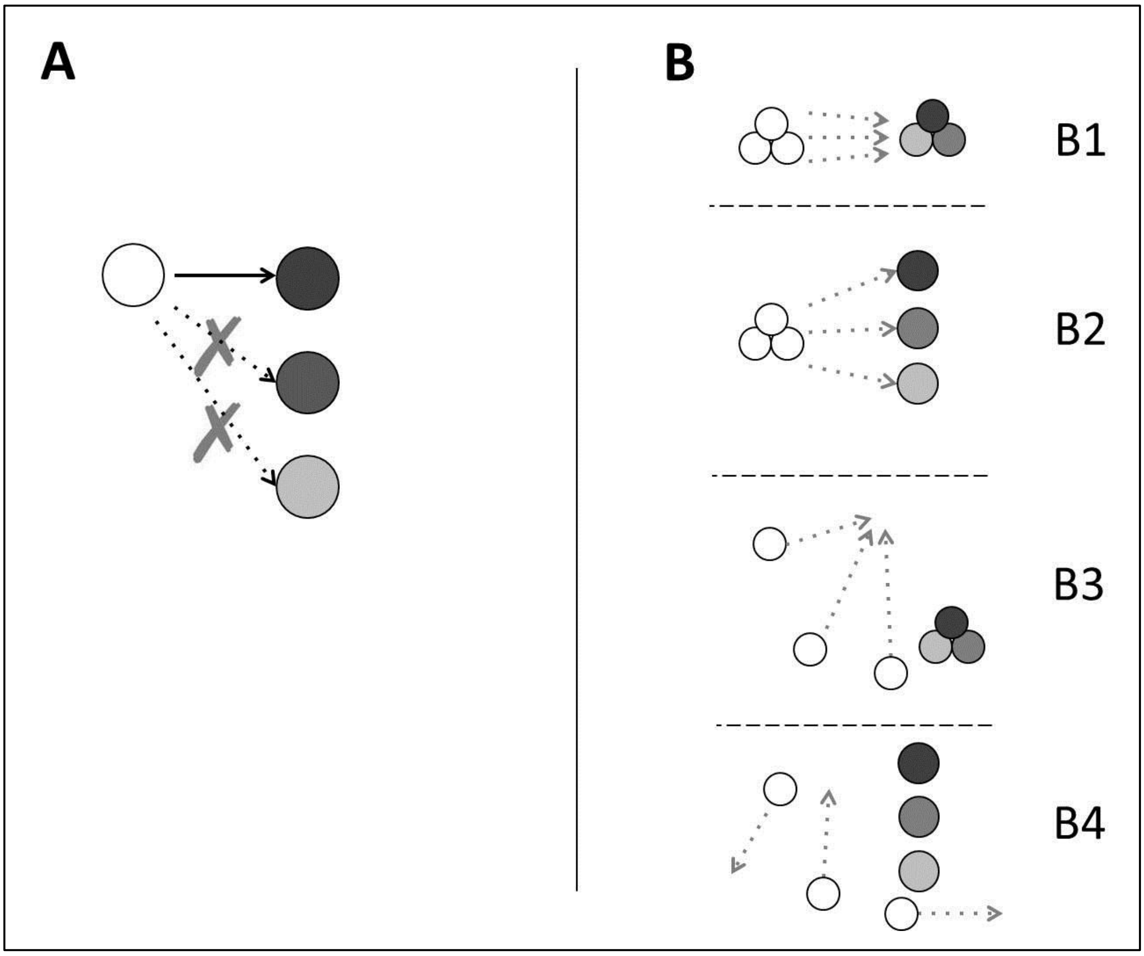

Figure I2. Two antagonistic successional models. Whereas Model A is the traditional deterministic framework, predicting a single particular trajectory towards the climax community (otherwise, as trajectories marked with a cross, restoration would be considered to have failed), modern studies (Model B, described by Matthews and Spyreas 2010) accept several trajectories towards different reference communities and departing from several possible situations. Hence, given a set of restoration sites (empty circles) and reference sites (full circles), four patterns are possible for successional trajectories (arrows): (B1) convergence in species composition among restoration sites and progression towards the reference composition, (B2) divergence among sites and progression towards different references, (B3) convergence among sites but deviation from references, and (B4) divergence among sites and deviation from the reference targets.

New methodological approaches

The phylogenetic relatedness among species found in an area can provide interesting additional information, according to the increasing belief that assemblages consisting of only related species should be regarded as less diverse than others which host more distantly related species (Abellán et al. 2006). Therefore, as well as classical taxonomic assemblage parameters (e.g., abundance, richness, evenness, Shannon-Wiener diversity), taxonomic distinctness has been widely employed in marine systems (Warwick and Clarke 1995, Rogers et al. 1999, Brown et al. 2002, Warwick and Light 2002, Leonard et al. 2006), thanks to its convenient statistical properties (Clarke and Warwick 1998, Clarke and Warwick 2001a). Despite still being little used in freshwater habitats (but see Abellán et al. 2006, Heino et al. 2007, Gascón et al. 2009, Tan et al. 2010), within the framework of primary succession studies, it may allow for the evaluation of whether colonizers arriving in newly created wetlands are mainly from the same (or close) taxonomic groups or if they come instead from less taxonomically-related groups.

In addition, ecosystem level processes are affected by the functional characteristics of the organisms involved rather than by their taxonomic identity (Hooper et al. 2002, Verberk et al. 2008). As a consequence, functional analyses of assemblage compositions can be useful to understand the ecosystem (Higgins and Merritt 1999, Bazzanti and Bella 2004, Boix et al. 2006, Gascón et al. 2008). Several procedures for analyzing the functional status of invertebrate assemblages and ratios of functional groups have been successfully used as surrogates for ecosystem attributes, mostly in rivers (Cummins 1973, Cummins and Klug 1979). The sets of species can be formed following the criteria of species displaying similar effects on major ecosystem processes (e.g., functional feeding groups, Merritt and Cummins 1996); or, less commonly, species that have adopted similar responses to the environment (e.g., life-history strategy groups based on the type of dispersion, the needs of water to reproduce and the capacity to survive desiccation in the pond; Wiggins et al. 1980). Some studies have shown that taxon- and size-based approaches can be complementary when exploring differences in assemblages either between locations or different periods (Rodríguez and Magnan 1993, Boix et al. 2004b, Brucet et al. 2006, Quintana et al. 2006). It would therefore be interesting to explore whether functional approaches, such as traits analyses, also provide complementary information in respect to classic taxonomic insights.

AIMS AND THESIS OUTLINE

The general aim of this thesis was to characterize macrofaunal colonization and primary succession in man-made wetlands, with reference to biodiversity, structure and dynamic aspects. The particular aims of this thesis were:

1) Characterize the changes in assemblage structure, and in taxonomic and functional compositions, which communities undergo throughout primary succession from short-term (*chapter 1*), in mid-term (*chapters 2 & 3*) and long-term perspectives (*chapter 4*);
2) Explore how local factors (*chapter 1*) and regional factors such as climate (*chapter 3*) may affect the successional dynamics and the composition of the establishing community;
3) Disentangle how temporal and spatial components interact in directing successional trajectories through nestedness and diversity patterns (*chapter 2*);
4) Identify the community complexity features that characterize the advanced phase of a successional process (*chapter 4*);
5) Determine the minimum time that a created aquatic ecosystem needs to overcome the pioneering colonizer assemblage (*chapters 1 & 5*), as well as achieve a similar community, in terms of structure and composition, to that of natural wetlands (*chapter 4*);
6) Assess the effectiveness of creating wetlands as biodiversity conservation tools, regarding both macroinvertebrate (*chapters 2 & 4*) and amphibian communities (*chapter 5*);
7) Explore how taxonomic versus functional approaches may be complementary or redundant in applied aquatic ecology studies (*chapter 1*).

CHAPTERS AND PUBLICATIONS

Chapter 1. Spatial and temporal patterns of pioneer macrofauna in recently created ponds: taxonomic and functional approaches

A. Ruhí, D. Boix, J. Sala, S. Gascón & X.D. Quintana

Status: published in *Hydrobiologia (2009) 634:137-151*

Chapter 2. Nestedness and successional trajectories of macroinvertebrate assemblages in created wetlands

A. Ruhí, D. Boix, J. Sala, S. Gascón & X.D. Quintana

Status: submitted to Oecologia

Chapter 3. How do early successional patterns differ between man-made wetlands in the cold temperate and Mediterranean regions?

A. Ruhí, J. Herrmann, S. Gascón, J. Sala & D. Boix

Status: in review in *Limnologica*

Chapter 4. Change in biological traits and community structure of macroinvertebrates through primary succession in a man-made Swedish wetland

A. Ruhí, J. Herrmann, S. Gascón, J. Sala, J. Geijer & D. Boix

Status: In press in *Freshwater Science (formerly Journal of the North American Benthological Society)*

Chapter 5. Man-made Mediterranean Temporary Ponds as a tool for amphibian conservation

A. Ruhí, O. San Sebastian, C. Feo, M. Franch, S. Gascón, À. Richter-Boix, D. Boix & G. Llorente

Status: in review in *Annales de Limnologie – International Journal of Limnology*

CHAPTER 1. Spatial and temporal patterns of pioneer macrofauna in recently created ponds: taxonomic and functional approaches

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Abstract

Man-made ponds are often created to compensate for the loss and degradation of wetlands, but little is known about the processes taking place in these artificial environments, especially at a community level. The macrofaunal assemblage and wàter chemistry of newly created ponds in three nearby areas in the NE Iberian Peninsula were studied during the first year of life of these ponds in order to (i) detect if any invertebrate assemblage structure change was taking place, (ii) evaluate the effect of local factors on the invertebrate assemblage in each site, and (iii) compare the information obtained by taxonomic and functional approaches. Although invertebrate colonization was rapid, no relevant changes in assemblage parameters were related to time, implying that more time may be needed to detect successional changes in invertebrate assemblages. Local factors—especially those related to hydrological stability—produced notable differences both in the assemblage parameters and in the taxonomic and functional compositions of the invertebrate fauna. Finally, information provided by the functional approach was redundant with respect to that obtained by the classical taxonomic approach: in these newly created systems, the high dominance of a small number of taxa makes the functional approach a simple biological traits analysis of the few dominant species.

Introduction

Artificial ponds are very valuable to society, since they are often created for purposes such as water supply, floodwater retention, recreation and education, or wildlife management and research (Oertli et al. 2005). They are also often the result of mitigative measures to compensate for habitat destruction and the subsequent loss of species (National Research Council - Committee on Mitigating Wetland Losses 2001), but there is still little knowledge of the ecological function of these habitats, especially at the invertebrate community level (e.g., Gee et al. 1997, Herrmann et al. 2000). In this sense, a deeper knowledge of the biodiversity hosted in these environments is needed to evaluate if newly created ponds are appropriate management tools for biological conservation. Although biodiversity analyses have often been based only on species richness, it is important to take into account, among others, aspects concerning taxonomic relatedness (Warwick and Clarke 1995). Thus, assemblages comprising only taxonomically related species should be regarded as less diverse than others that host more distantly related species (Abellán et al. 2006).

In general, newly created ponds are rapidly colonized by plants and invertebrates, particularly, when they are close to, or connected to, other wetlands (Gee et al. 1997, Fairchild et al. 2000). Any successional process includes not only this initial rapid colonization but also subsequent changes in structure and organization of the assemblage (Fisher 1983). Hence, although it has been reported that the main increase in species richness takes place over the first year, assemblage structuring patterns—e.g., decreasing of the dominance values, shift from predators toward grazers and detritivores—can take longer (Barnes 1983, Friday 1987). Therefore, a lack of structure changes in assemblages of newly created ponds during their first year of life is hypothesized in this study.

Local factors, such as fish stocking, pond use, egg banks, water regime, hydroperiod length, or habitat heterogeneity, can relevantly influence the community structure (e.g., Schneider and Frost 1996, Della Bella et al. 2005, Gascón et al. 2005). Even in highly interconnected ponds, local environmental constraints can be strong enough to prevail over regional homogenizing forces and structure local communities (Cottenie et al. 2003). In this study, we hypothesize that local factors will greatly influence the resulting assemblage.

Since ecosystem-level processes are affected by the functional characteristics of the organisms involved rather than by their taxonomic identity (Hooper et al. 2002, Verberk et al. 2008), functional analyses, taking into account both functional parameters and biological traits, have proved to be useful methods (Higgins and Merritt 1999, Gascón et al. 2008). Moreover, functional approaches can provide information that is complementary to taxonomical data (Rodríguez and Magnan 1993, Boix et al. 2004b, Brucet et al. 2005). Therefore, in this study, taxonomic and functional approaches are expected to provide complementary, not redundant, information.

The aims of this study were: (i) to analyze changes that take place in macrofaunal assemblages of newly created habitats during the very early phase of colonization and succession, along the first year of creation of these ponds; (ii) to study the importance of local factors and to establish whether they can explain differences in the pond assemblage structure among nearby ponds; and (iii) to compare results obtained by taxonomic and functional approaches, and check if these procedures are complementary or redundant.

Materials and methods

Study site

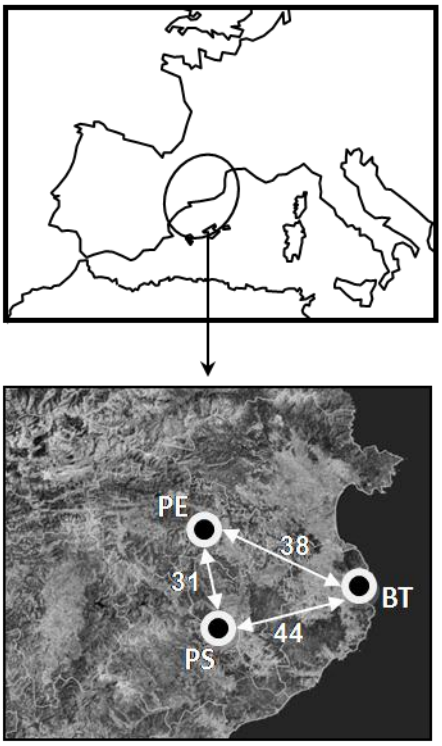

Fig. 1 Map of the study area with the location of the three studied sites, and distances (in km) between them.

The study was carried out in the NE Iberian Peninsula, in three different but nearby plain areas (Fig. 1): Pla de l'Estany (hereafter, PE), Plana del Baix Ter (hereafter, BT), and Plana de la Selva (hereafter, PS). In each site, several man-made ponds for habitat and species recovery and mitigative measures were constructed, and three ponds in each site were selected for this study (Table 1). All ponds at all sites were shallow (depth < 2 m), were flooded for the first time in the summer of 2006 and were monitored during their first year of life, from September 2006 until September 2007. The main water supplies were different in the three sites (Table 1): ponds in PE were fed by a karstic stream, ponds in BT by a coastal aquifer, and ponds in PS by rainfall. Ponds located in this last site did not complete their first hydroperiod, drying up in summer due to a strong drought (Fig. 2). The study sites presented different abundances of the Eastern mosquitofish (*Gambusia holbrooki*) and the red swamp crawfish (*Procambarus clarkii*), as well as the percentage of the surface covered by aquatic vegetation, estimated by visual analysis in the field (Table 1). Some natural ponds were selected for having similar characteristics and being situated near the constructed ones, acting as controls to compare their invertebrate assemblages: two natural ponds were selected near PE (adding up 6 samples), one natural pond was selected near BT (13 samples), and another one near PS (5 samples). This data was obtained in the framework of a project focused on water quality assessment (Boix et al. 2005).

Sampling and sample processing

Newly created ponds were sampled quarterly, during the same week in all three areas. Physical and chemical water parameters and water level were measured in situ using a Crison 524 conductivity meter (for conductivity), an EcoScan ph6 (for pH), a Hach HQ10 Portable LDO meter (for temperature and dissolved oxygen), and a graduated gauge (for water level). Water samples were collected on every sampling day, filtered through GF/C Whatman filters, and frozen upon arrival at the laboratory. Analyses of dissolved inorganic nutrients (ammonium, NH_4^+; nitrite, NO_2^-; nitrate, NO_3^-; and soluble reactive phosphorus, PO_4^{3+}) from filtered samples were carried out according to Grasshoff et al. (1983). According to Talling and Driver (1963), chlorophyll-a content was later extracted from filters using 80% methanol and measured. Aquatic macrofauna was sampled using a 250 µm mesh size dip-net of 20 cm in diameter, and the sampling procedure was based on 20 dip-net sweeps in rapid sequence, covering all different microhabitats. This methodology was performed identically in the newly created and in the natural ponds. Samples were preserved in situ in 4% formalin. Subsequently, the invertebrate fauna was sorted, identified to the lowest taxonomic level possible, and 25 individuals of each taxa were randomly chosen and measured. Biomass was estimated

Table 1 General characteristics of the ponds created at each site and mean values (standard deviation, in italics) of the water and environmental variables measured in each pond. Variables significantly related to the invertebrate assemblage, according to the CCA and the forward selection, are shown in bold (*P* < 0.05).

Site	Situation	Water supply	Hydroperiod	Vegetation cover	*P. clarkii* and *G. holbrooki*	Pond	T (ºC)	Ox. (mg/L)	**Conductivity (µS.cm^{-1})**	pH	**Chl a (µg/l)**	DIN (mg/l)	SRP (mg/l)	**Water level (cm)**	**Distance to the nearest natural pond (m)**
Pla de l'Estany	Inland plain	Karstic stream	> 12 months	High (> 60%)	Present	PE1	18.7	9.60	**1145.0**	8.67	**2.304**	0.034	0.002	**102**	**2614**
							6.8	*4.83*	***150.2***	*1.10*	***3.503***	*0.014*	*0.001*	***42***	-
						PE2	16.9	6.83	**1236.0**	8.22	**32.087**	0.048	0.008	**61**	**2603**
							7.9	*2.38*	***661.3***	*0.32*	***66.392***	*0.034*	*0.006*	***36***	-
						PE3	19.5	8.58	**1153.8**	8.37	**3.396**	0.103	0.004	**96**	**2464**
							7.1	*1.49*	***337.6***	*0.42*	***2.896***	*0.103*	*0.004*	***47***	-
Plana del Baix Ter	Coastal plain	Coastal aquifer	> 12 months	Medium (30 – 60%)	Present	BT1	17.0	7.60	**1393.6**	8.30	**3.918**	0.040	0.002	**119**	**3042**
							6.8	*0.50*	***226.3***	*0.68*	***1.753***	*0.024*	*0.002*	***9***	-
						BT2	17.2	8.42	**2834.0**	8.57	**12.194**	0.042	0.009	**112**	**3114**
							6.7	*2.17*	***940.1***	*1.41*	***12.663***	*0.033*	*0.015*	***37***	-
						BT3	16.3	6.52	**718.6**	8.14	**7.464**	0.093	0.012	**86**	**3097**
							6.8	*1.21*	***327.4***	*0.59*	***4.942***	*0.089*	*0.015*	***12***	-
Plana de la Selva	Inland plain	Rainfall	6 - 9 months	Low (< 30%)	Absent	PS1	17.6	6.86	**309.0**	7.64	**3.243**	0.341	0.001	**25**	**3256**
							4.6	*0.53*	***455.8***	*0.54*	***4.587***	*0.367*	*0.001*	***7***	-
						PS2	16.4	5.89	**63.0**	7.51	**2.583**	0.375	0.014	**20**	**3236**
							4.5	*1.69*	***36.5***	*0.24*	***0.960***	*0.271*	*0.023*	***7***	-
						PS3	16.0	7.19	**63.8**	7.46	**3.200**	0.344	0.001	**24**	**3260**
							5.2	*1.31*	***28.5***	*0.30*	***3.127***	*0.185*	*0.000*	***3***	-

as dry mass, which was calculated from individual lengths using existing equations for macroinvertebrates (Smock 1980, Meyer 1989, Lindegaard 1992, Traina and Ende 1992, Montes et al. 1993, Smit et al. 1993, Quintana 1995, Benke et al. 1999, Cabral and Marques 1999, Koutrakis and Tsikliras 2003, Boix et al. 2004b)

Assemblage parameters: taxonomic and functional approaches

The analyzed taxonomic parameters of the assemblage were species richness (S), Shannon–Wiener diversity (H'), and complementary measures of taxonomic distinctness. Three taxonomic distinctness indices were chosen for this study: taxonomic distinctness (Δ^*), average taxonomic distinctness (Δ^+), and variation in taxonomic distinctness (Λ^+). The first metric is based on quantitative data, whereas the last two are based on presence/absence data. Both the first (Δ^*) and the second (Δ^+) represent the average path length in the phylogenetic tree connecting two random species of those collected, but are not always highly correlated, suggesting that they capture different aspects of relatedness (Clarke and Gorley 2006). Λ^+ measures the variance in pairwise lengths between each pair of species and reflects the unevenness of the taxonomic tree (Clarke and Warwick 2001a). Neither total taxonomic distinctness ($S\Delta^+$) nor taxonomic diversity (Δ) was used - $S\Delta^+$ as it is redundant with the species richness, and Δ as it closely tracks traditional diversity measures, depending highly on the dominance of species (Clarke and Warwick 2001a). The taxonomic levels taken into account for this analysis were species, genus, family, order, class, subphylum, and phylum, and the same branch length was weighted for each taxonomic level. Three assemblage functional parameters were also chosen: total numerical abundance (N), total biomass (B), and size diversity (μ). For size diversity (μ), the method recently described by Quintana et al. (2008) was followed.

Assemblage composition: taxonomic and functional approaches

The assemblage composition was studied both from a taxonomic point of view (at species and order levels) and using a functional approach. Two functional groups were created, one according to functional feeding groups and the other to life-history strategy groups. Following Merritt & Cummins (1996), six feeding-type groups were created: predators (PR), filterers (FI), scrapers (SC), piercing-herbivores (PH), collectors (CO), and shredders (SH). Moreover, each taxon was assigned to a life-history strategy group based on Wiggins et al. (1980). Groups 1, 2, and 3 include species that are dormant during the unfavorable season, but differ in the dispersion capacity and the timing of oviposition. Group 1 includes species with passive dispersal, group 2 includes species with active dispersal that need water for oviposition, and group 3 includes species with active dispersal that do not need water for oviposition. Group 4 includes species that cannot remain in the basin during the unfavorable season. A fifth group, added to the original classification, included taxa which need water to disperse and reproduce and cannot survive desiccation, as described by other authors (Hillman and Quinn 2002, Gascón et al. 2008) Assignations of found species to the corresponding functional feeding and life-history group are shown in the Appendix—Supplementary Material.

Data analysis

The extent to which study sites differ in their hydrological stability was studied using the method described by Brownlow et al. (1994), which implies cluster analysis of the water level frequencies for each pond (group average as a conglomeration method and Manhattan distance as a similarity measure). In order to analyze the importance of local environmental variables among sites and over time, a principal component analysis

(PCA) was conducted. The variables included in the environmental matrix were: conductivity, pH, temperature, dissolved oxygen, water level, concentration of dissolved inorganic nitrogen (DIN) as the sum of concentrations of NH_4^+, NO_2^- and NO_3^-, soluble reactive phosphorus (SRP), and concentration of chlorophyll-a (Chla). All environmental variables, except pH, were log-transformed using $\log_{10}$ (Var + 1). ANOVA tests were performed to check the significance of the positions of samples (using sample scores as dependent variable) classified by site or time (used as factors). Bonferroni post-hoc tests were also used to compare similarity among sites in ANOVA results. The environmental variables listed above, plus the distance to the nearest natural pond, were related to species variability by means of a canonical correspondence analysis (CCA) of the species matrix. A forward selection of the environmental variables was performed using Monte Carlo permutation tests (999 random permutations), retaining the variables with $P < 0.05$. This was computed from the ‘forward.sel’ function available in the R ‘packfor’ library (Dray 2004). In order to quantify the ‘‘locality effect’’, a variation partitioning was performed using the function ‘varpart’ in the vegan library, written in R language (Oksanen et al. 2005). Thus, ‘‘locality effect’’ was assessed not only considering the variance explained by the locality itself but also the shared variability between locality and environmental variables. In order to perform this analysis, three matrices were used: the species matrix, the locality matrix, and the significant environmental variables matrix. The species matrix contained the abundance of taxa by samples, the locality matrix included three dummy variables identifying samples from the same site (PE, BT, and PS), and the environmental variables matrix was the result of the selection of the significant environmental variables performed by the forward selection procedure previously described.

Changes in the assemblage parameters among sites and over time were tested by a mixed linear model, with site and time as fixed effects and time as a random effect, nested within the site. The inclusion of time in the random part of the model allows for the control of pseudoreplication problems due to sampling the same pond over time. The tested taxonomic parameters of the assemblage were species richness (S), Shannon–Wiener diversity (H’), average taxonomic distinctness (Δ^+), variation in taxonomic distinctness (Λ^+), and taxonomic distinctness (Δ^*). The tested functional parameters of the assemblage were total numerical abundance (N), total biomass (B), and size diversity (μ). Numerical abundance, biomass, and species richness were log-transformed to ensure a better fit of errors to a normal distribution.

Changes in the assemblage composition among sites and over time were tested with an analysis of similarities (ANOSIM) test. This type of test operates on a resemblance matrix and is similar to a standard univariate ANOVA, but does not need either normality or homoscedasticity of data. The chosen option was the two-way nested layout, where the two factors were hierarchic (time factor nested within site factor), and the results showed a global R that oscillated from 0 and 1 and a *P*-value expressed in percentage. When R was 0 or close to 0, similarities within groups (i.e., in samples within the same site) and between groups (i.e., in samples between different sites) were equivalent. In contrast, when higher values of R were obtained, more samples within the group resembled each other than they did between groups, differentiating groups that would correspond to samples from different sites (Clarke and Warwick 2001a). The distance matrix was built with Bray–Curtis similarity, based on a rectangular, original standardized, and square-root transformed matrix, and the ANOSIM test operated 999 permutations in all cases. This test was applied to eight compositional matrices, which were the result of two approaches (taxonomic and functional), two levels for each approach (species and orders for the taxonomic approach; functional feeding groups and life-history strategy groups for the functional approach) and two matrices for each level (numerical abundance and biomass). A similarity percentages (SIMPER) test was used to analyze and detect the characteristic species of a site. Specifically, the test performed was a two-way SIMPER analysis with the numerical abundance species composition matrix, with site and time as factors and a cut off for low contributions at 90%. Finally, a non-parametric multidimensional scaling (MDS) was performed to compare the assemblage structure of samples from the newly created ponds to those of natural ponds situated nearby. Abundances were square-root transformed and Bray–Curtis was selected as a similarity distance. Subsequently, a two-way nested ANOSIM (natural/artificial factor nested within the site factor) was used to test differences when comparing assemblages among sites and pond types.

The cluster analysis, the ANOSIM and SIMPER tests, the MDS and the calculations of the assemblage parameters were performed with PRIMER v. 6.0 for Windows. The PCA was performed with CANOCO 4.5, and R v. 2.8.1 was used for the CCA, the forward selection of the environmental variables and the variation partitioning test. ANOVA tests, Bonferroni post-hoc tests, and mixed linear models were performed with the software package SPSS 15.0.

Results

Pond characterization

In accordance with the temporary behavior of PS ponds, the analysis of the hydrological stability resulted in a cluster that separated PS ponds from the rest (Fig. 3). When studying the site factor, the position of the samples in the PCA (Fig. 4) showed significant differences among sites for axis 1 (ANOVA, $F_{2,37} = 21.701$; $P < 0.001$). Again, PS was different from the other sites with the post-hoc test ($P < 0.001$), while BT and PE were not distinguishable ($P = 1.000$). Low levels of conductivity and water column depth were characteristic of PS, as well as high levels of dissolved nitrogen in comparison with ponds in PE and BT, more related to higher conductivities and water levels (Table 1). Ponds in PE and BT also had more variability within axis 2, associated with the concentration of chlorophyll values. Nevertheless, no significant differences in sample positions were detected for the second axis (ANOVA, $F_{2,37} = 2.14$; $P < 0.100$). On the other hand, water and environmental characteristics did not differ over time since the position of the samples in the PCA did not show significant differences either for axis 1 (ANOVA, $F_{4,35} = 2.088$; $P < 0.100$), or for axis 2 (ANOVA, $F_{4,35} = 1.871$; $P < 0.100$). According to the forward selection, the environmental variables which appeared to significantly affect the assemblage were distance to the nearest natural pond ($F = 5.705$; $P = 0.001$), conductivity ($F = 2.465$; $P = 0.010$), concentration of chlorophyll ($F = 2.300$; $P = 0.024$), and water level ($F = 2.291$; $P = 0.014$). These four variables alone explained 10% of the variance, whereas the shared variability between these variables and the site explained 14% and the site by itself explained only 1%. The high percentage of shared variability implies that each locality had characteristic environmental conditions.

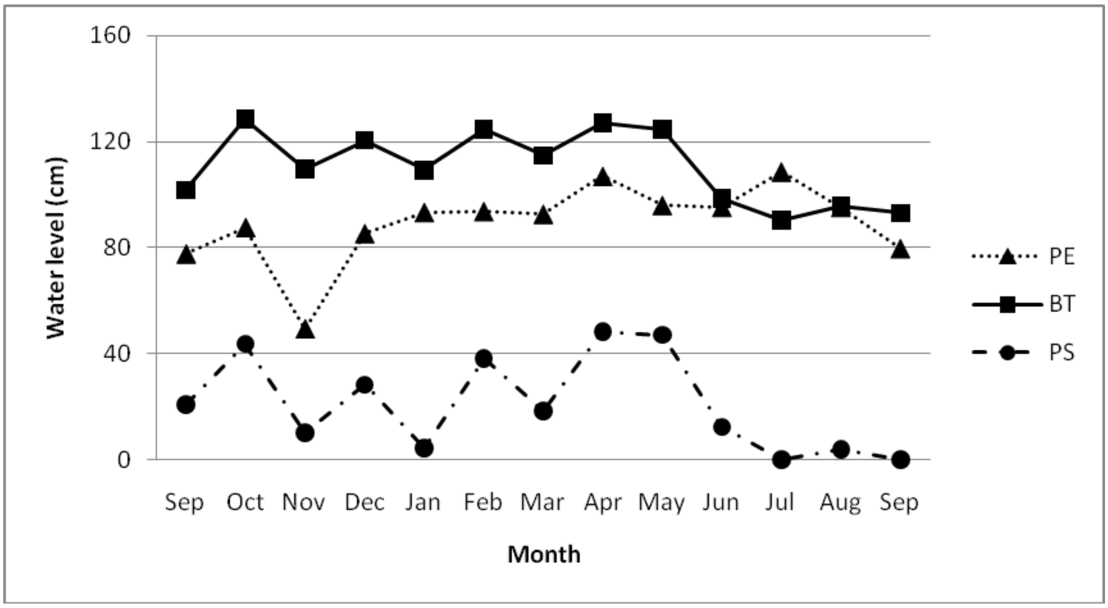

Fig. 2 Water level (cm) of the ponds studied in (PE) Pla de l'Estany, (BT) Plana del Baix Ter, and (PS) Plana de la Selva, during the first complete year after flooding of these ponds (September 2006–September 2007).

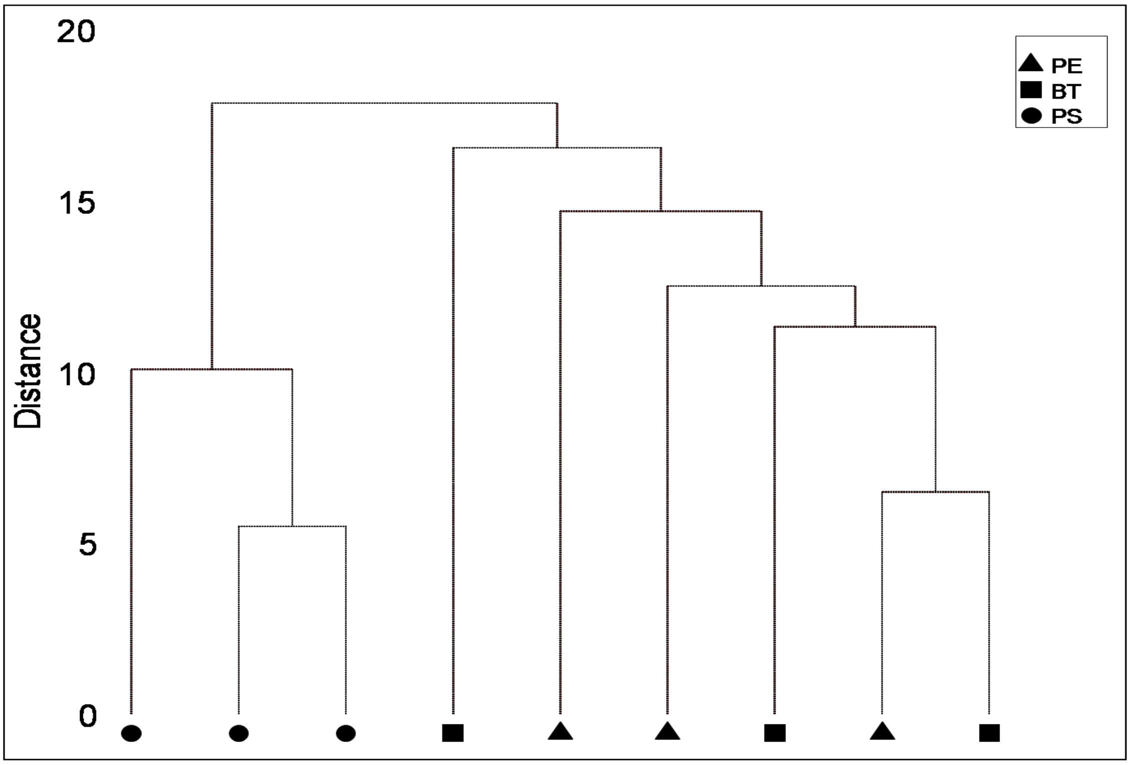

Fig. 3 Clustering of the distances of the newly created ponds according to their hydrological stability. PE Pla de l'Estany, BT Plana del Baix Ter, and PS Plana de la Selva.

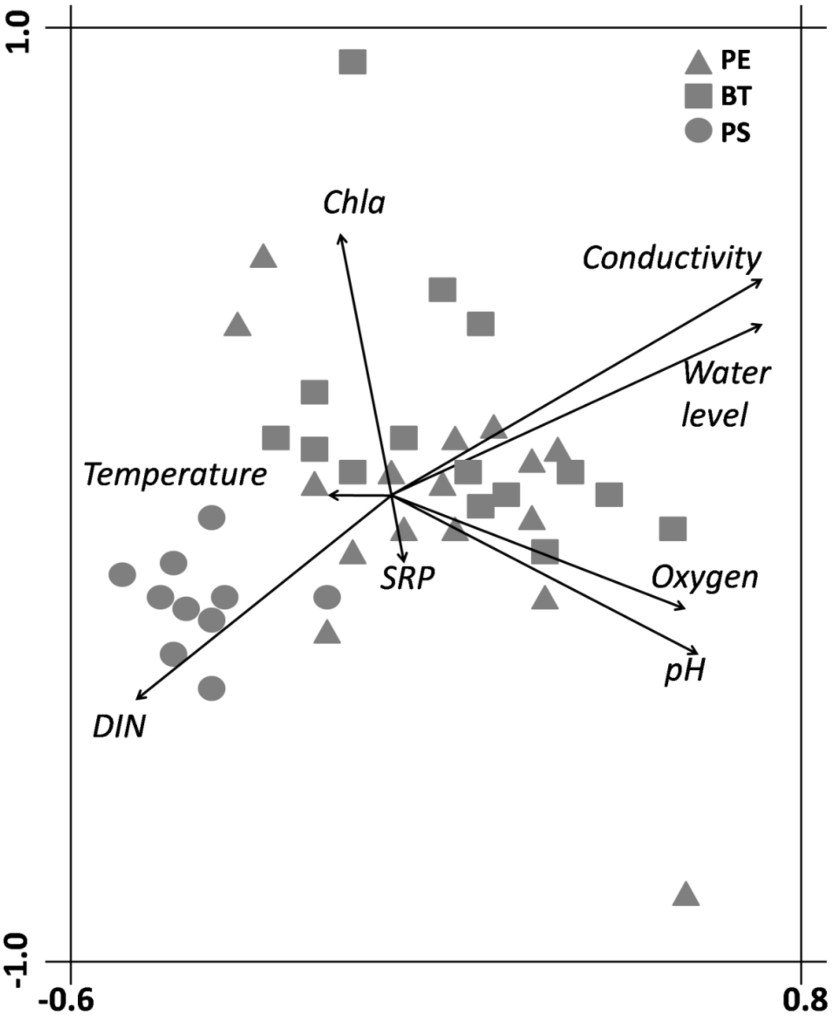

Fig. 4 Sample position in relation to water and environmental variables in the space created by the first two axes of the PCA. Axis 1 explains 54.3% of the variability; axis 2 explains 24.2%. DIN concentration of dissolved inorganic nitrogen, SRP soluble reactive phosphorus, Chl a concentration of Chlorophyll-a, PE Pla de l’Estany, BT Plana del Baix Ter, and PS Plana de la Selva.

Pioneer assemblages: composition and abundance

A total of 87 species were detected, of which 57.5% were exclusively found at one site and 19.5% of them were found at all sites. Species richness was, however, concentrated in a few taxonomic groups, as only three families were responsible for more than a third of the total richness. Chironomidae (18 taxa), Dytiscidae (7 taxa), and Corixidae (5 taxa), and the corresponding orders (Diptera, 27 taxa; Coleoptera, 18 taxa; and Heteroptera, 12 taxa) were the richest groups within Insecta. Moreover, insects alone, with 66 species, represented more than 75% of the macrofaunal richness. Although the three main dominating orders in number of individuals were the same at all sites (Ephemeroptera, Heteroptera, and Diptera), the dominant one was different for each site: Ephemeroptera for PE, Heteroptera for BT, and Diptera for PS. In contrast, none of these groups dominated in biomass in the corresponding site. In PE and BT, a small number of individuals of Malacostraca (more than 99% of them were red swamp crawfish) represented 73% (PE) and 48% (BT) of the total macrofaunal biomass. In contrast, in PS insects represented practically the whole biomass. It is remarkable that two out of the three areas (PE and BT) were colonized early (during the first year of life) by the red swamp crawfish and the Eastern mosquitofish, whereas in PS these invasive species were not detected (Figs. 5A, B).

When analyzing functional feeding strategies, collectors represented the main feeding group in PE, both in biomass and in numerical abundance, collectors and predators were the dominant feeding groups in BT, and predators dominated in PS (Fig. 5C). Analyzing life-history strategies, results for abundance and biomass were only similar in PS, where the fourth strategy was dominant, followed by the second strategy. The fourth strategy comprises species active in dispersal, which need water to reproduce and can leave the pond during a dry phase; and taxa comprised in the second strategy show the same behavior but remain during an eventual desiccation of the pond, often as an egg or immature stage. In PE and BT, the dominant strategy for biomass was the fifth, which contained the crawfish. In contrast, when analyzing numerical abundance, the main strategy was the second in PE and the fourth in BT (Fig. 5D).

Analyzing the effect of time on species richness, it was observed that during the first sampling period (September 2006), 51% of the cumulative species richness (44 out of 87) had already arrived at least in one site. A close look showed that this percentage differed among sites, ranging from around 40% in PE and PS to 50% in BT.

Nevertheless, the increase in species richness obtained during the first period (June to September 2006) was the highest at all sites.

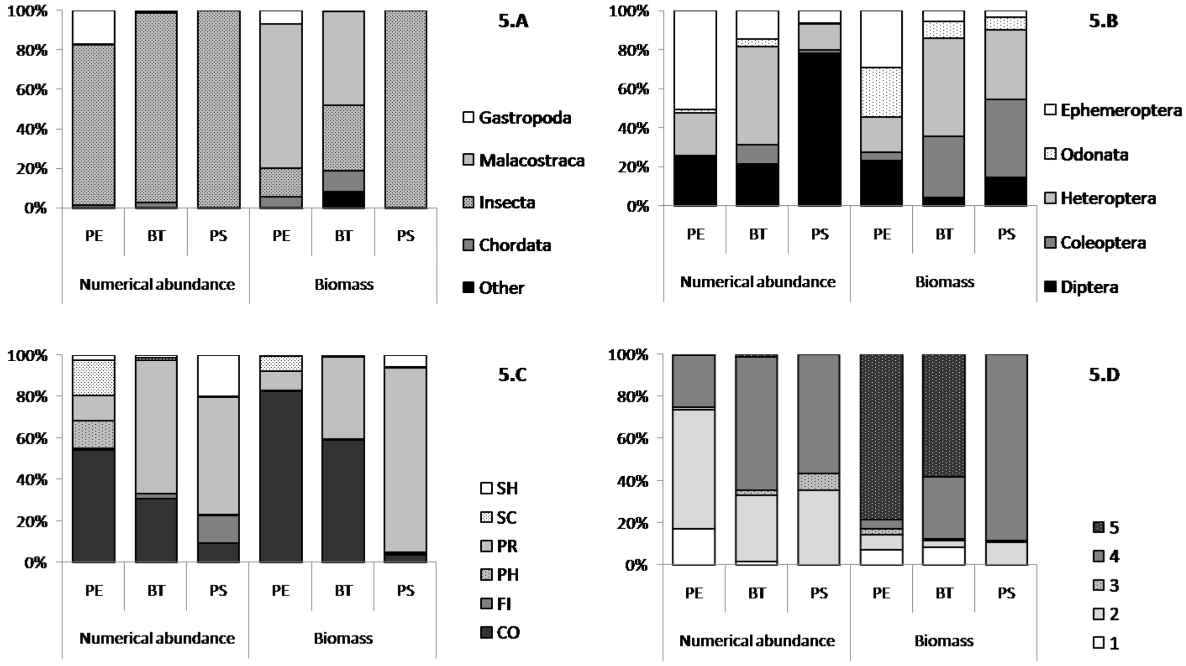

Fig. 5 Relative importance of the main taxonomic groups and of the main functional groups by means of numerical abundance and biomass. In A, orders with a total abundance of less than 50 individuals and a total biomass lower than 1 g have been included in the ‘‘other’’ category (including the orders of the following classes: Leptolida, Oligochaeta, and Arachnida), except for Chordata. In B, only Insecta orders are shown. For C, CO collectors, FI filterers, PH piercingherbivores, PR predators, SC scrapers, and SH shredders. For D, numbers in the legend represent the particular life-history strategy group (see text for the biological characteristics of the five life-history strategy groups). PE Pla de l’Estany, BT Plana del Baix Ter, and PS Plana de la Selva.

Assemblage structure among sites and over time

Assemblage parameters: taxonomic and functional approaches

Log-transformed species richness ($F_{2,11}$ = 6.163, P = 0.006) and variation in taxonomic distinctness ($F_{2,11}$ = 6.696, P = 0.005) were the only taxonomic parameters of the assemblage significantly related to site factor (Table 2). These variables showed their highest values in PE and their lowest in PS, indicating that sites with higher richness also had a higher unevenness in their taxonomic tree. In contrast, none of the five assemblage taxonomic parameters showed significant differences when related to the time factor, and only one was marginally significant: species richness ($F_{2,11}$ = 2.155, P = 0.053). Analyzing the functional parameters of the assemblage, both total numerical abundance ($F_{2,11}$ = 7.313, P = 0.003) and total biomass ($F_{2,11}$ = 5.722, P = 0.009), presented significant differences for the site factor. The highest values of total numerical abundance were obtained in PE, while lower values of total biomass were measured in PS than at the other two sites. Total biomass was the only parameter related to the time factor ($F_{2,11}$ = 4.718, P = 0.001), showing its highest values at the end (Fig. 6); and total numerical abundance gave a marginally significant result ($F_{2,11}$ = 2.140, P = 0.054). At BT and PS, adult Coleoptera and Heteroptera contributed highly to biomass at the beginning, with a relevant decrease during autumn and winter, and an increase in spring. In contrast, in PE Coleoptera and Heteroptera were only relevant in biomass at the beginning, and other groups dominated during winter and spring, mainly crawfish from June onwards.

Table 2 Assemblage parameters compared among sites and over time. The results of the linear mixed models (site = fixed factor, time = random factor nested inside site) are shown. Significant results are shown in bold ($P < 0.05$).

	Assemblage parameter	**Site**		**Time**	
		$F_{2.11}$	***p***	**$F_{2.11}$**	***p***
Taxonomic	Species richness (S)	**6.163**	**0.006**	2.155	0.053
	Shannon-Wiener diversity (H’)	1.300	0.290	0.557	0.845
	Average taxonomic distinctness (Δ^+)	0.138	0.872	1.289	0.285
	Variation in taxonomic distinctness (Λ^+)	**6.696**	**0.005**	0.981	0.487
	Taxonomic distinctness (Δ^*)	0.790	0.464	1.470	0.202
Functional	Total numerical abundance	**7.313**	**0.003**	2.140	0.054
	Total biomass	**5.722**	**0.009**	**4.718**	**0.001**
	Size diversity (μ)	3.017	0.066	1.562	0.169

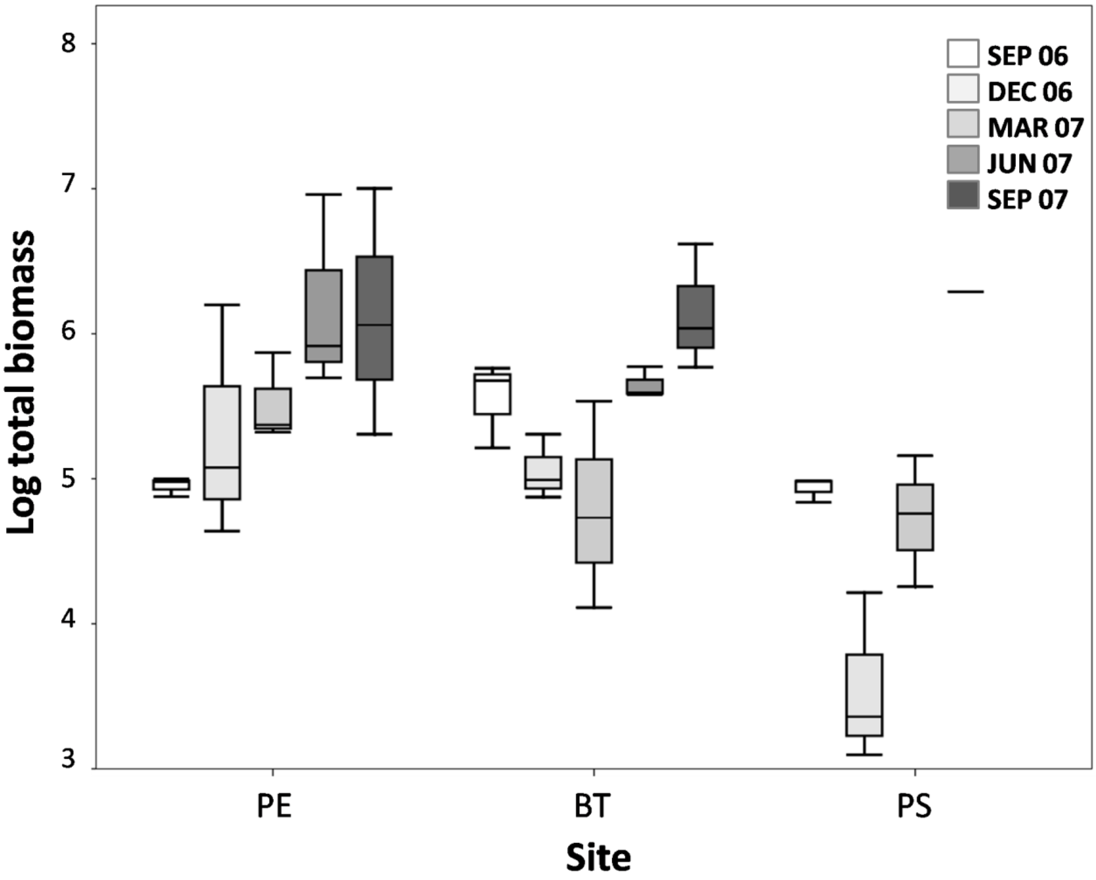

Fig. 6 Box-plots showing the total biomass over time. PE Pla de l'Estany, BT Plana del Baix Ter, and PS Plana de la Selva.

Assemblage composition: taxonomic and functional approaches

When analyzing the site factor, the two-way nested ANOSIM tests showed significant differences for all levels of both approaches (taxonomic and functional), testing either the numerical abundance matrix or the biomass matrix (Table 3). However, only at species level were all pairwise comparison tests significant. In this case, all R values were high (>0.8), indicating that the species composition was different in each area, either analyzing the numerical abundance or analyzing the biomass matrix.

Table 3 Taxonomic and functional assemblage parameters compared among sites and over time. The results of the two-way nested ANOSIM test (time nested within site factor) are shown. For pairwise comparisons, PE Pla de l'Estany, BT Plana del Baix Ter, and PS Plana de la Selva. *N. ab.* = numerical abundance matrix, *Biom.* = biomass matrix. Significant results (global tests and pairwise comparisons) are shown in bold ($P < 0.01$).

			Site		***Time***	
			N. ab.	Biom.	N. ab.	Biom.
Taxonomic approach	**Species**	global R	**0.871**	**0.811**		
		global p	**0.001**	**0.001**	ns ($p > 0.01$)	
		$R_{\text{PE-BT}}$	**0.874**	**0.805**	–	
		$R_{\text{PE-PS}}$	**0.963**	**0.825**		
		$R_{\text{BT-PS}}$	**0.881**	**0.881**		
	Orders	global R	**0.756**	**0.656**		
		global p	**0.001**	**0.001**	ns ($p > 0.01$)	
		$R_{\text{PE-BT}}$	**0.840**	**0.790**	–	
		$R_{\text{PE-PS}}$	**0.831**	0.594		
		$R_{\text{BT-PS}}$	0.681	**0.669**		
Functional approach	**Feeding groups**	global R	**0.799**	**0.663**		
		global p	**0.001**	**0.001**	ns ($p > 0.01$)	
		$R_{\text{PE-BT}}$	**0.976**	**0.772**	–	
		$R_{\text{PE-PS}}$	**0.963**	0.719		
		$R_{\text{BT-PS}}$	**0.550**	0.600		
	Life-history strategy groups	global R	**0.743**	**0.631**		
		global p	**0.001**	**0.001**	ns ($p > 0.01$)	
		$R_{\text{PE-BT}}$	**0.896**	**0.752**	–	
		$R_{\text{PE-PS}}$	**0.813**	0.525		
		$R_{\text{BT-PS}}$	0.594	0.744		

For the rest of the levels (orders, functional feeding groups, and life-history strategy groups), although global tests were significant ($P<0.01$), pairwise comparisons were not always significant. Differences were higher with numerical abundance matrices (higher values of R and a higher number of significant pairwise comparison tests) than with biomass matrices; and only comparisons between two sites (PE vs. BT) were significant for all levels and matrices. The time factor was not significantly related to changes in the taxonomic or functional assemblage composition. On the other hand, the results of the two-way SIMPER analysis with numerical abundance of species composition allowed us to identify the characteristic species of each site (Table 4). Thus, although, some species were characteristic in samples of all sites—*Cloeon inscriptum* and *Sigara lateralis* contributed highly to similarity among samples for all three sites—others were particularly common only in one site, such as *Physella acuta* and *Procladius choreus* in PE, *Anisops sardeus* and *Psectrocladius* gr. *sordidellus* in BT, or *Chaoborus flavicans* and *Anopheles* gr. *maculipennis* in PS.

Table 4 Characteristic species (two-way SIMPER analysis, factors = site and time). The first four species in % of similarity have been selected.

PE **(32.7 % average similarity)**		**BT** **(25.0% average similarity)**		**PS** **(59.9 % average similarity)**	
Species	**%**	**Species**	**%**	**Species**	**%**
Cloeon inscriptum	24.7	*Anisops sardeus*	31.5	*Chaoborus flavicans*	47.8
Sigara lateralis	16.4	*Sigara lateralis*	24.5	*Cloeon inscriptum*	17.4
Physella acuta	9.3	*Cloeon inscriptum*	10.7	*Anopheles* gr. *maculipennis*	15.7
Procladius choreus	8.6	*Psectrocladius* gr. *sordidellus*	4.9	*Sigara lateralis*	12.0

Comparison of newly created and natural ponds' assemblages

The MDS showed that samples from newly created ponds appeared separated from the assemblages of the corresponding natural ponds in each site (Fig. 7). The ANOSIM analysis detected significant differences between newly created and natural ponds (R = 0.347; *P* = 0.001), but not among sites (R = 0.222; *P* = 0.867). This implies that, when comparing natural to newly created ponds, the large differences between the typology of the pond (natural–artificial) reduces the existent site differences until make them non-significant.

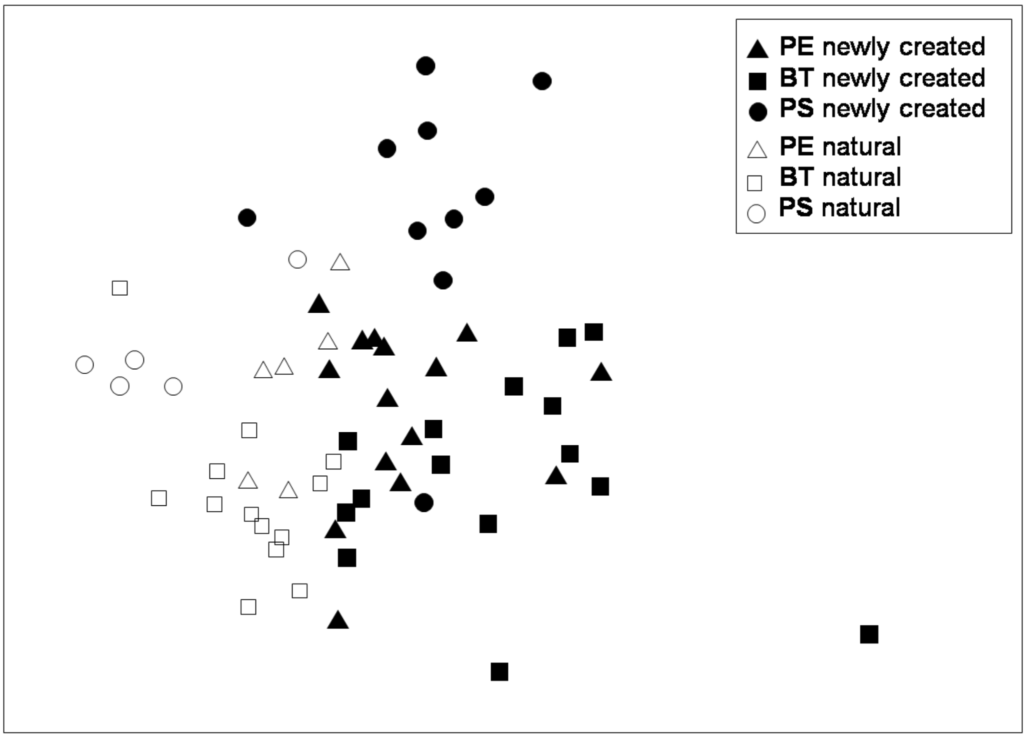

Fig. 7 MDS plot of the invertebrate assemblages of newly created ponds and those of nearby natural ponds (stress = 0.19). PE Pla de l'Estany, BT Plana del Baix Ter, and PS Plana de la Selva.

Discussion

Assemblage structure changes

Succession and colonization have traditionally been considered as equivalent and inseparable processes, but succession includes colonization and the subsequent changes in structure and organization of the assemblage (Velasco et al. 1993b). The rapid colonization of the studied ponds was fairly predictable, as it is described as being common in newly created ponds (Gee et al. 1997, Fairchild et al. 2000), and it is also known in other aquatic environments, such as newly created streams or channels (Malmqvist et al. 1991), experimentally flooded lakes and wetlands (Herrmann et al. 2000), or impounded reservoirs (Bass 1992). In our case, about 50% of the species found in this study were already captured at the first sampling after flooding (1–2 month period). Studies going deeper into colonization mechanisms show that newly created, small and isolated ponds can be compared to oceanic islands, with a colonization rate that results from species immigration and extinction, and tends to be quicker, when dispersal distances are short and active dispersal mechanisms are efficient (Barnes 1983, Havel and Shurin 2004, Csabai and Boda 2005).

Although the colonization of newly created ponds was quick, only one assemblage parameter (total biomass) proved to be related to time during their first year of life. Since there was no significant increase in the total numerical abundance of individuals, the increasing biomass can probably be explained by secondary production inside the pond (individual growth), and the arrival of larger-bodied species. Despite a biomass shift at two sites (BT and PS) during colder months (December 2006 and March 2007), when biomass was a bit lower, no more relevant changes in assemblage parameters were related to time. Other findings are consistent with these results and have demonstrated that pioneer communities usually last longer (Barnes 1983, Friday 1987). Fairchild et al. (2000) found that young ponds were colonized early by large predatory beetles and acquired beetle assemblages comparable in species richness to those of older ponds, but taxa dependent on particular plant species occurred later. This led to the conclusion that several years are necessary after site construction to host these rarer specialist taxa. The lack of these specialist taxa in the newly created ponds, together with the great dominance of a small number of pioneer colonizers, may explain the distance between assemblages of these ponds and those in natural ones.

Importance of local factors

Conductivity and water level are two covarying local factors: low conductivity values and low water column levels at PS are due to the fact that ponds in this site depended exclusively on rainfall, and the year during which this study took place was very dry. Higher conductivity values in BT and PE are attributed to the coastal influence and the karstic stream, respectively, whereas more regular and higher water column depths are related to their small dependence on rainfall.

Although salinity has been widely described as a community constraint (Williams and Williams 1998, Boix et al. 2007), in this case, values did not reach 5 mS/cm, described as a threshold for invertebrate communities (Frey 1993, Boix et al. 2005). Instead, differences found in assemblage parameters (species richness (S), variation in taxonomic distinctness (Λ^+), total numerical abundance, and total biomass) could be related to the hydrological stability of each site. Being true that, in some cases, temporary ponds certainly contain a smaller number of taxa than permanent ponds (Della Bella et al. 2005), Williams (2006) has called for a review of assumptions that temporary environments support lower biodiversity. In some studies, comparing species richness of temporary and permanent environments, water permanence has not appeared to have a relevant effect on species richness (Boix et al. 2008), and some other authors have pointed out that a large number of species are well-adapted and associated with intermittent drying (e.g., Williams 1996). On the other hand, hydroperiod lengths have been described as one of the main environmental factors influencing macrofaunal assemblages (Schneider and Frost 1996), but the predictability of these hydroperiods has proven to be even more relevant than the length of hydroperiods themselves, with regard to the ability of animal communities to predict water fluctuations (Williams 2006). Hydrological stability, including drying out and water level fluctuations, summarizes the physical factors that ultimately determine benthic fauna (Gascón et al. 2005). This stability seems to be related to differences between the two permanent sites and the least hydrologically stable site. Thus, hydrological stability has also probably altered the attraction and probability of colonization for macroinvertebrates, as described by other authors (Williams 2006).

It is interesting to observe that higher levels of hydrological stability in PE and BT were not reflected in more phylogenetic evenness in the arriving taxa. A high variation in taxonomic distinctness (Λ^+) indicates that although more species arrived, they were not only equally distributed among taxonomic groups but also concentrated in a few taxonomic levels, each of which tended to be relatively more species-rich (Clarke and Warwick 2001b). This may be due to the fact that short term (one year) macroinvertebrate colonization processes in newly created ponds are mainly driven by a few taxonomic groups, which is in agreement with the observed high dominance in numerical abundance of a few taxa. Whereas in PE collectors dominated, PS and BT were dominated by predators, *Chaoborus flavicans* and *Anisops sardeus*, respectively. Both predators have been described as having an important effect on community structure (Luecke and Litt 1987, Lindholm and Hessen 2007). The dominance of predators has been related to the first months of the hydroperiod in natural temporary ponds and also in newly created ones (Friday 1987, Layton and Voshell 1991, Fairchild et al. 2000), supporting the idea that assemblages in these two sites were more pioneering than those in PE. The life-history strategy group analysis is coherent with this statement: although dominant strategies presented active dispersion at all sites (which is expected for young ponds, e.g., Velasco et al. 1993a, Fairchild et al. 2000), in PE, the first strategy (species with passive dispersal) had a significant presence, probably as the superficial stream made it possible for passive dispersers to reach this site.

Trophic state (using concentration of chlorophyll as a surrogate) and connectivity are factors which have also appeared to affect pioneering assemblages. The relationship between trophic state and macrofaunal assemblages' structure in the Mediterranean area has not always been strong (García-Criado et al. 2005, Boix et al. 2008). On the other hand, connectivity to natural ponds is known to be important, since colonization and extinction of aquatic insects in a water body is mainly explained by pond and landscape characteristics (Jeffries 2005). Nevertheless, both connectivity and trophic state covaried with other previously commented factors, making the importance by themselves difficult to establish. For example, the temporary and least hydrologically stable site was also the most isolated, with less chlorophyll content and lower conductivity values. Therefore, it is interesting to remark that covariation is expressed by the high shared variability found in the variation partitioning analysis between the environmental variables and the locality factor, which would imply that each site presented several characteristic conditions that affected colonization processes differently.

Finally, the vegetation cover and the abundance of invasive species are other local factors that may determine the assemblage structure. In our case, on one hand, the high aquatic vegetation cover, important for providing refuge, and structural heterogeneity (Savage et al. 1998, Della Bella et al. 2005), must have had a strong connection with the great dominance of *Cloeon inscriptum* in the well-vegetated site, since it is an herbivore–detritivore larva (Merritt and Cummins 1996). On the other hand, the low hydrological stability of PS may have been a constraint for the colonization of the red swamp crawfish and the Eastern mosquitofish. This has probably had consequences, since the red swamp crawfish, the main invasive species in terms of biomass, causes negative impacts on the trophic web and on assemblage biodiversity (Geiger et al. 2005, Gherardi and Acquistapace 2007); and the introduced Eastern mosquitofish also profoundly alters the functioning of the ecosystem through trophic cascades (Blanco et al. 2004).

Taxonomic and functional approaches

Despite the literature defending the idea that taxonomic and functional approaches are complementary (Rodríguez and Magnan 1993, Brucet et al. 2005), in this study, only a single functional parameter (total biomass) presented a significantly different response when relating it to a factor (time), while the results for the rest of the assemblage parameters coincided with the taxonomic approach. A similar result was obtained in the case of taxonomic/functional composition approaches. Although the use of functional groups has also become popular to study ecosystem processes (e.g., Gladden and Smock 1990, Gascón et al. 2008), results provided by both approaches were redundant in our case. The functional assignations have become biased by the great dominance of a small number of species, and the functional analysis has lost a large part of its meaning by really only showing the roles of the most dominant taxa. This explanation can be added to other drawbacks associated with assigning species to groups, and with the arbitrary scale on which differences between species qualify as functionally significant (Hooper et al. 2002, Wright et al. 2006).

Conclusions

In conclusion, although a quick colonization has been observed, subsequent successional changes in the assemblage structure have not yet manifested. In addition, local factors—especially those related to hydrological stability—have highly affected both the assemblage parameters and the composition. Finally, although analyses from a functional point of view have proved to be interesting tools for studying aquatic communities, they are not appropriate in short term studies of newly created environments since the dominance of a few taxa causes them to provide practically redundant information with respect to the traditional taxonomic approach.

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Appendix

Assignations of found taxa to the corresponding functional feeding and life-history strategy groups. Families are listed alphabetically within each order. For developmental stage category, A = adults; L = larvae; N = nymphs; P = pupae. For functional feeding groups (FFG), PR = predators; FI = filterers; SC = scrapers; PH = Piercing-herbivores; CO = Collectors and SH = Shredders. For life-history strategy groups (LHSG), the number represents the particular life-history strategy group (see text for the biological characteristics of the 5 life-history strategy groups). For each taxon, the maximum number of individuals per sample (Max.) and the occurrence (Oc., percentage of samples in which the taxon is present) is also shown for each site. PE = Pla de l'Estany; BT = Plana del Baix Ter; PS = Plana de la Selva.

					PE		**BT**		**PS**	
Taxa	**Dev. stage**	**FFG**	**LHSG**	**Biomass equation**	**Max.**	**Oc.(%)**	**Max.**	**Oc.(%)**	**Max.**	**Oc.(%)**
Ph. CNIDARIA										
Cl. LEPTOLIDA, O. CAPITATA										
F. HYDRIDAE										
***Hydra* sp.**	A	PR	1	-	32	13	0	0	0	0
Ph. MOLLUSCA										
Cl. GASTROPODA, O. PULMONATA										
F. PHYSIDAE										
***Physella acuta* (Draparnaud 1805)**	A	SC	1	Boix et al., 2004	1474	67	18	13	0	0
F. FERRISSIIDAE										
***Ferrissia* sp.**	A	SC	1	Boix et al., 2004	32	7	0	0	0	0
Ph. ANNELIDA										
Cl. OLIGOCHAETA, O. LUMBRICULIDA										
F. LUMBRICULIDAE	A	CO	1	Smit et al., 1993	2	7	0	0	0	0
Cl. OLIGOCHAETA, O. TUBIFICIDA										
F. ENCHYTRAEIDAE	A	CO	1	Lindegaard, 1992	0	0	0	0	4	7
F. NAIDIDAE	A	CO	1	Smit et al., 1993	0	0	8	20	0	0
F. TUBIFICIDAE	A	CO	1	Smit et al., 1993	0	0	4	20	4	7

Ph. ARTHROPODA										
Cl. ARACHNIDA, O. PROSTIGMATA										
F. ARRENURIDAE										
***Arrenurus* (*Megaluracarus*) sp.**	A	PR	2	Smit et al., 1993	1	7	0	0	4	7
F. HYDRACHNIDAE										
***Hydrachna globosa* (De Geer 1778)**	A / L	PR	2	Smit et al., 1993	1	7	0	0	4	7
***Hydrachna* (*Hydrachna*) sp.**	A / L	PR	2	Smit et al., 1993	4	20	0	0	0	0
F. HYDRODROMIDAE										
***Hydrodroma despiciens* (O. F. Müller 1776)**	A / L	PR	2	Smit et al., 1993	51	27	13	7	4	7
F. HYDRYPHANTIDAE										
***Hydryphantes ruber* De Geer 1778**	A	PR	2	Smit et al., 1993	8	7	0	0	0	0
F. PIONIDAE										
***Piona* sp.**	A	PR	2	Smit et al., 1993	160	13	0	0	0	0
Cl. MALACOSTRACA, O. DECAPODA										
F. ATYIDAE										
***Atyaephyra desmaresti* (Millet 1831)**	A	CO	5	Benke et al., 1999	10	20	0	0	0	0
F. CAMBARIDAE										
***Procambarus clarkii* (Girard 1852)**	A	CO	5	Montes et al., 1993	1	13	6	47	0	0
Cl. INSECTA, O. EPHEMEROPTERA										
F. BAETIDAE										
***Cloeon inscriptum* Bengtsson 1914**	N	CO	2	Benke et al., 1999	7190	93	458	47	100	53
F. CAENIDAE										
***Caenis luctuosa* (Burmeister 1839)**	N	CO	2	Benke et al., 1999	32	40	0	0	10	7
Cl. INSECTA, O. ODONATA										
F. AESHNIDAE										
***Anax imperator* Leach 1815**	N	PR	4	Benke et al., 1999	7	33	21	7	2	7
F. COENAGRIONIDAE										
***Coenagrion mercuriale* (Charpentier 1840)**	N	PR	3	Benke et al., 1999	0	0	0	0	2	7
***Ischnura elegans* (Vander Linden 1820)**	N	PR	3	Benke et al., 1999	58	53	17	40	0	0
F. LESTIDAE										
***Lestes* cf. *viridis* (Vander Linden 1825)**	N	PR	3	Smock, 1980	6	7	0	0	0	0
F. LIBELLULIDAE										
***Orthetrum cancellatum* (Linnaeus 1758)**	N	PR	4	Benke et al., 1999	1	7	0	0	0	0
***Sympetrum fonscolombii* (Selys 1840)**	N	PR	4	Benke et al., 1999	75	47	48	13	6	7

Cl. INSECTA, O. HETEROPTERA										
F. CORIXIDAE										
Cymatia rogenhoferi (Fieber 1864)	A / N	PR	4	Benke et al., 1999	220	40	0	0	0	0
Micronecta scholtzi (Fieber 1860)	A / N	PH	4	Benke et al., 1999	2445	47	0	0	0	0
Paracorixa concinna (Fieber 1848)	A	PH	4	Benke et al., 1999	1	7	0	0	0	0
Sigara lateralis (Leach 1817)	A / N	CO	4	Benke et al., 1999	177	73	372	73	33	47
Sigara cf *nigrolineata* (Fieber 1848)	A	CO	4	Benke et al., 1999	0	0	1	13	0	0
F. GERRIDAE										
Aquarius paludum (Fabricius 1794)	A / N	PR	4	Benke et al., 1999	2	13	1	7	7	20
Gerris argentatus Schummel 1832	A / N	PR	4	Benke et al., 1999	8	13	4	20	0	0
Gerris lacustris (Linnaeus 1758)	A / N	PR	4	Benke et al., 1999	6	20	82	7	59	7
F. NOTONECTIDAE										
Anisops sardeus Herrich-Schaeffer 1849	A / N	PR	4	Smock, 1980	217	67	435	73	307	13
Notonecta maculata Fabricius 1794	A	PR	4	Smock, 1980	0	0	1	7	5	7
F. PLEIDAE										
Plea minutissima Leach 1817	A	PH	4	Smock, 1980	1	7	0	0	0	0
F. VELIIDAE										
Microvelia pygmaea (Dufour 1833)	A	PR	4	Benke et al., 1999	0	0	130	27	0	0
Cl. INSECTA, O. COLEOPTERA										
F. DRYOPIDAE										
Dryops algiricus (Lucas 1846)	A	SC	2	Meyer, 1989	0	0	0	0	1	7
F. DYTISCIDAE										
Agabus sp.	L	PR	2	Boix et al., 2004	2	13	0	0	1	13
Agabus nebulosus (Forster 1771)	A	PR	2	Smock, 1980	2	13	0	0	2	13
Eretes sp.	L	PR	4	Boix et al., 2004	1	7	0	0	1	13
Eretes griseus (Fabricius, 1781)	A	PR	4	Smock, 1980	16	27	13	20	18	33
Hydroglyphus geminus (Fabricius 1792)	A	PR	4	Smock, 1980	0	0	338	40	5	7
Hygrotus confluens (Fabricius, 1787)	A	PR	4	Smock, 1980	0	0	0	0	2	13
Laccophilus hyalinus (De Geer 1774)	A	PR	4	Smock, 1980	3	7	0	0	0	0
Rhantus suturalis (MacLeay 1825)	A	PR	4	Smock, 1980	0	0	1	27	0	0
Yola bicarinata (Latreille 1804)	A	PR	4	Smock, 1980	0	0	0	0	1	7

F. HELOPHORIDAE										
***Helophorus* sp.**	L	SH	2	Meyer, 1989	1	7	0	0	0	0
***Helophorus alternans* Gené 1836**	A	SH	2	Smock, 1980	0	0	2	7	0	0
***Helophorus asturiensis* Kuwert 1885**	A	SH	2	Smock, 1980	4	7	1	7	0	0
***Helophorus minutus* complex**	A	SH	2	Smock, 1980	0	0	1	7	0	0
***Helophorus* cf. *lapponicus* Thomson 1853**	A	SH	2	Smock, 1980	1	7	0	0	0	0
F. HYDRAENIDAE										
***Aulacochthebius exaratus* (Mulsant 1844)**	A	SC	4	Smock, 1980	0	0	0	0	5	13
***Ochthebius* (*Asiobates*) sp.**	A	SC	4	Smock, 1980	2	7	0	0	0	0
***Ochthebius dilatatus* Stephens 1829**	A	SC	4	Smock, 1980	0	0	12	20	0	0
F. HYDROPHILIDAE										
***Enochrus* sp.**	L	PH	4	Meyer, 1989	1	7	0	0	0	0
***Helochares lividus* (Forster 1771)**	A	PH	2	Smock, 1980	2	7	0	0	1	13
F. NOTERIDAE										
***Noterus clavicornis* (De Geer 1774)**	A	PR	4	Smock, 1980	1	7	0	0	0	0
Cl. INSECTA, O. TRICHOPTERA										
F. ECNOMIDAE										
***Ecnomus* sp.**	L	SH	3	Meyer, 1989	1	7	0	0	0	0
Cl. INSECTA, O. DIPTERA										
F.CERATOPOGONIDAE										
***Bezzia* sp.**	L	PR	2	Meyer, 1989	0	0	8	7	0	0
***Culicoides* sp.**	L	PR	2	Meyer, 1989	65	40	4	7	4	20
	P	PR	2	Smock, 1980						
F.CHAOBORIDAE										
Chaoborus flavicans (Meigen 1830)	L	PR	4	Traina & Ende, 1992	18	20	0	0	168	67
	P	PR	4	Quintana, 1995						

F. CHIRONOMIDAE										
***Ablabesmyia* sp.**	L / P	PR	4	Smock, 1980	251	47	8	13	0	0
***Cladotanytarsus* sp.**	L / P	CO	2	Smock, 1980	36	20	33	7	0	0
***Cladopelma* sp.**	L	CO	2	Smock, 1980	241	7	0	0	0	0
***Corynoneura* sp.**	L	CO	4	Smock, 1980	556	20	0	0	0	0
***Cricotopus* sp.**	L	CO	2	Smock, 1980	235	33	29	53	5	7
***Endochironomus* sp.**	L	SH	2	Smock, 1980	35	13	0	0	0	0
***Kiefferulus tendipediformis* (Goetghebuer 1921)**	L / P	CO	2	Smock, 1980	334	67	79	53	91	7
***Labrundinia neopilosella* Beck & Beck, 1966**	L	PR	4	Smock, 1980	1	7	0	0	0	0
***Meropelopia* sp.**	L	PR	4	Smock, 1980	38	33	0	0	0	0
***Microchironomus* sp.**	L	CO	2	Smock, 1980	167	7	0	0	0	0
cf. *Paramerina* sp.	P	FI	4	Smock, 1980	1	7	0	0	0	0
***Paratanytarsus* sp.**	L	FI	2	Smock, 1980	35	33	46	27	182	7
***Parachironomus* sp.**	L	PR	2	Smock, 1980	8	7	0	0	0	0
***Polypedilum nubifer* (Skuse 1889)**	L / P	SH	2	Smock, 1980	189	67	25	27	652	13
***Polypedilum scalaenum* (Schrank 1803)**	L	SH	2	Smock, 1980	0	0	8	7	0	0
***Procladius choreus* (Meigen 1804)**	L / P	PR	4	Smock, 1980	128	80	25	40	858	27
***Psectrocladius* gr. sordidellus (Zetterstedt 1838)**	L	CO	2	Smock, 1980	546	67	115	40	8	7
***Tanytarsus* cf. *mendax* Kieffer 1925**	L / P	CO	2	Smock, 1980	70	20	99	27	0	0
F.CULICIDAE										
***Aedes vexans* (Meigen 1830)**	L	CO	3	Quintana, 1995	0	0	4	7	0	0
***Anopheles* gr. *maculipennis* Meigen 1818**	L	FI	3	Quintana, 1995	36	20	25	20	100	20
	P	FI	3	Smock, 1980						
***Culex pipiens* Linnaeus 1758**	L	FI	4	Quintana, 1995	1	7	0	0	0	0
***Culex theileri* Theobald 1903**	L	FI	4	Quintana, 1995	1	7	3	20	0	0
F. EPHYDRIDAE										
***Scatella* sp.**	P	CO	4	Meyer, 1989	2	7	9	7	0	0
F. SYRPHIDAE	L	CO	4	Meyer, 1989	1	7	0	0	0	0

Ph. CHORDATA										
Cl. OSTEICHTHYES, O. CYPRINIFORMES										
F. CYPRINIDAE										
***Barbus meridionalis* Risso 1827**	A	PR	5	Koutrakis & Tsikliras, 2003	1	7	0	0	0	0
***Squalius laietanus* Doadrio, Kottelat & de Sostoa, 2007**	A	CO	5	Koutrakis & Tsikliras, 2003	2	7	0	0	0	0
Cl. OSTEICHTHYES, O. CYPRINODONTIFORMES										
F. POECILIIDAE										
***Gambusia holbrooki* Girard 1859**	A	PR	5	Cabral & Marques, 1999	11	20	25	13	0	0
Cl. AMPHIBIA, O. ANURA										
F. DISCOGLOSSIDAE										
***Discoglossus pictus* Otth 1837**	L	FI	4	Boix et al., 2004	4	13	0	0	0	0
F. PELODYTIDAE										
***Pelodytes punctatus* (Daudin 1802)**	L	CO	4	Boix et al., 2004	11	7	0	0	0	0
F. RANIDAE										
***Pelophylax perezi* (Seoane, 1885)**	L	CO	4	Boix et al., 2004	0	0	44	7	0	0

CHAPTER 2. Nestedness and successional trajectories of macroinvertebrate assemblages in created wetlands

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Abstract

Current successional models, mainly based on vegetal succession, propose several possible trajectories by integrating two key ideas from succession theory: convergence vs. divergence in species composition among areas, and progression towards vs. deviation from a desired reference state. We believed this framework could be applied as well to faunal succession if differential colonization between active and passive dispersers, and the nested patterns that are generated as a consequence, were taken into account. We studied 9 newly created wetlands located in 3 different areas, 0 to 3 years from wetland creation, and a set of 91 wetlands spread all over the region, taken as reference for natural macroinvertebrate communities. We predicted to find (i) highly nested structures in the pioneering assemblages decreasing towards lower values at the mid-term, due to the shift from pioneering aerial dispersers towards passive dispersal taxa; (ii) passive idiosyncratic taxa provoking divergent successional trajectories among areas; and (iii) these divergent trajectories causing lower local but higher regional diversity values in the mid-term rather than in pioneer assemblages. Results mostly agreed with hypotheses (i) and (ii), diverging from the anticipated patterns only in the case of the temporary wetlands' area. However, overall diversity trends (iii) did not follow the expected pattern: the divergent successional trajectories did not manage to compensate regionally the local biodiversity losses that occurred as a consequence of the decline of pioneering colonizers through time. Hence, we call to reconsider the idea that wetland creation for mitigation purposes may offset, within mid-term perspectives ($\leq$ 3 years), regional losses of biodiversity, since within such temporal scenarios they may not achieve the idiosyncratic taxa from the natural wetlands.

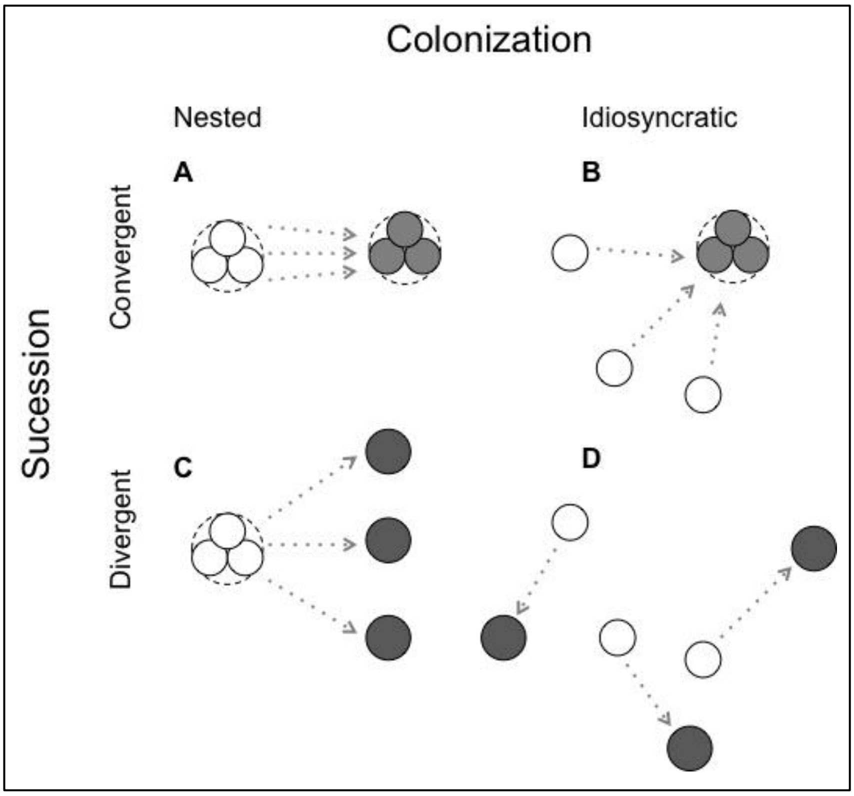
Introduction

Succession refers to changes observed in an ecological community following a perturbation that opens up a relatively large space (Connell and Slatyer 1977). These changes involve a sequence of species and important variations in community structure (Odum 1960, Gutierrez and Fey 1980). Environmental policies that use ecological restoration to compensate for the loss of natural ecosystems usually assume that these trajectories are deterministic, a view inspired by the classical model of vegetation succession and climax communities (Clements 1936). Since modern successional case studies failed to support these predictions (e.g., del Moral 2007), Matthews and Spyreas (2010) developed a new framework to assess ecosystem succession, replacing the idea of *climax* for *reference* communities. This model integrates two key ideas from succession theory: convergence vs. divergence in species composition among areas, and "progression towards" vs. "deviation from" a desired reference state. In this sense, trajectories can be synthesized as 4 possible combinations: (a) convergence in species composition among restorations and progression towards the reference target, (b) divergence among restorations and progression towards different targets, (c) convergence among restorations but deviation from the reference targets, and (d) divergence among restorations and deviation from the reference targets.

Unlike plants, macrofaunal pioneering colonization is quick and mainly carried out by active dispersers (Koskenniemi 1994, Herrmann et al. 2000, Lods-Crozet and Castella 2009, Ruhí et al. 2009). Because newly created wetlands are colonization sinks from the surrounding ecosystems (i.e., source), and colonization occurs more rapidly when nearby water bodies exist (Gee et al. 1997, Fairchild et al. 2000), in high connectivity scenarios pioneering assemblages of man-made wetlands would merely be local subsets of the communities inhabiting the regional natural wetlands. However, the importance of active colonizers in a community undergoing succession may progressively decrease at mid-term perspectives, in favor of passive dispersers (Batzer and Wissinger 1996, Ruhí et al. in press). As a consequence of this differential colonization potential between active and passive dispersers, the phenomenon known as nestedness may appear in created wetlands with respects to natural wetlands at regional scale, similarly to what has been described between temporary (i.e., sinks) and permanent (i.e., sources) lentic communities (Wissinger et al. 2008, Florencio et al. 2011). Nested distributions occur when species-poor sites contain subsets of the assemblages found in species-rich sites, and the degree of nestedness thus quantifies the overlap in species composition between high and low diversity areas (McAbendroth et al. 2005). Besides, idiosyncratic taxa are those departing from the general nested pattern, occurring more frequently than expected in species-poor sites, or less frequently in species-rich ones. They often have limited dispersal capacities or require specialized conditions (Atmar and Patterson 1993), and present a potential interest for conservation (Heino et al. 2005, McAbendroth et al. 2005). Furthermore, nestedness may decrease through time in a given man-made ecosystem, and divergent successional trajectories caused by this decrease could result in loosing local diversity levels at each individual site, but increasing regional diversity values overall (Cook 1995, Crist et al. 2003, Baselga 2010).

Our view is that the extent to which local communities are nested within the regional ones, and the temporal variations of this nestedness, should be related with the successional trajectories of macroinvertebrate assemblages in created wetlands. Hence, the previous model for successional trajectories (Matthews and Spyreas 2010) could be as well applied to macrofauna if the differential colonization between active and passive dispersers, and the nested patterns generated as a consequence, were taken into account (Figure 1). This would, in turn, show the connection between nestedness and diversity measures in a set of created systems, and help explaining the role of colonization in generating nested patterns (Florencio et al. 2011).

Fig 1. Schematic models of the possible successional trajectories of aquatic macrofaunal communities through primary succession. Light circles represent pioneering communities, dark circles represent mid-term communities. Big dotted circles represent highly nested communities, whereas the absence of dotted circles accounts for idiosyncratic ones (modified from Matthews and Spyreas 2010).



We studied a set of newly created wetlands located in different areas, from 0 to 3 years from wetland creation, and a broad set of natural wetlands spread over the region, which were taken as reference for natural macroinvertebrate communities. We raised three hypotheses: First, we predicted to find highly nested structures in the pioneering assemblages (1st year after creation) decreasing towards lower values at the mid-term (3rd year), due to the effects of differential colonization. Second, we hypothesized the random-driven arrival of passive dispersers to provoke divergence of trajectories among areas, despite departing from similar compositions (Figure 1, trajectory C). Third, we anticipated these divergent successional trajectories to be reflected into lower local but higher regional diversity values in the mid-term rather than in pioneering assemblages, in parallel with decreasing nestedness and increasing idiosyncrasy through time.

Materials and methods

This research uses two different macroinvertebrate data sets generated by two studies: a study of natural wetlands' communities and a study of man-made wetlands communities. The natural wetlands study was focused on insects and crustaceans of 91 regional wetlands, which were visited 1-2 times during a single year. The man-made wetlands study was carried out with the whole macrofaunal community of 9 newly created wetlands in 3 different areas (3 wetlands each), sampled each season throughout a period of 3 years from their creation. Whereas the first section of the paper merges the data from both data sets, the second section is exclusively built upon the man-made wetlands study.

Study area

The natural wetlands study was carried out in 91 wetlands located throughout Catalonia, NE Iberian Peninsula. The selected water bodies are part of the official Wetland Inventory of Catalonia. This inventory is an attempt to list and characterize all regional water bodies with some natural heritage value. All sampled wetlands were below 800 m a.s.l. to ensure that they were influenced by Mediterranean climatic conditions, and presented a maximum depth of 6 m. Two sampling surveys were conducted during 2003 in order to encompass temporal variability, the first one in February and the second one in June. All water bodies were sampled twice except 17 temporary freshwater bodies that dried out before the second sampling survey. Additional information on faunal composition, water and environmental characteristics of these wetlands is provided in Boix et al. (2008).

The man-made wetlands study was carried out in three different but nearby (< 50km) plain areas in Catalonia, NE Iberian Peninsula: Plana del Baix Ter (hereafter, BT), Pla de l'Estany (hereafter, PE) and Plana de la Selva (hereafter, PS). In each area, 3 man-made wetlands (sites) for habitat and species recovery and mitigative measures were constructed. All ponds at all sites were shallow (depth <2 m), were flooded for the first time in the summer of 2006 and were monitored during their first 3 years of life, from September 2006 until September 2009. Wetlands were sampled quarterly (12 visits), during the same week in all three areas.

Sampling and sample processing

For the natural wetlands study, aquatic macrofauna was sampled using a 250 µm mesh size dip-net of 20 cm in diameter, and the sampling procedure was based on 20 dip-net sweeps in rapid sequence, covering all different mesohabitats. Samples were preserved in situ in 4% formalin. Subsequently, the invertebrate fauna was sorted and identified in the laboratory. Macrocrustaceans (Anostraca, Notostraca, Mysida, Amphipoda, Isopoda, Decapoda) and several orders of insects (Ephemeroptera, Odonata, Heteroptera, Coleoptera, Lepidoptera and Trichoptera) were taken into account, and these groups were identified to species level.

For the man-made wetlands study, the sampling methodology was performed identically. However, all the macrofaunal community was considered. Except for Oligochaeta (which were left to family level), all groups were identified to species level. Moreover, physical and chemical water parameters and water level were measured on every sampling day in situ, using a Crison 524 conductivity meter (for conductivity), an EcoScan ph6 (for pH), a Hach HQ10 Portable LDO meter (for temperature and dissolved oxygen), and a graduated gauge (for water level). Water samples were collected, filtered through GF/C Whatman filters, and frozen upon arrival at the laboratory. Analyses of dissolved inorganic nutrients (ammonium, NH_4^+, nitrite, NO_2^-, nitrate, NO_3^-, and soluble reactive phosphorus, PO_4^{3+}) from filtered samples were carried out according to Grasshoff et al. (1983). Following the method described by Talling & Driver (1963), chlorophyll-a content was extracted from filters using 80% methanol and measured.

Data analyses

Data analyses were divided in two sections. The first one is focused in analyzing nested patterns in man-made wetlands when comparing them to regional natural communities (hereafter, "Nestedness of man-made communities within regional natural communities"). The second section analyses the successional trajectories and diversity trends only in man-made wetlands, in order to explore if succession provokes divergent or convergent trajectories among areas, and if these trajectories lead to particular diversity trends (hereafter, “Successional trajectories and diversity trends in man-made wetlands”).

Nestedness of man-made communities within regional natural communities

For this first section of the paper, we created a macrocrustaceans + insects binary matrix (presence-absence) encompassing samples from natural and man-made wetlands. With this data, we explored similarities between man-made and natural wetlands’ communities, we assessed the extent to which man-made communities were nested within the regional natural communities, and we compared these values among years.

In order to test for significant composition differences among wetland origins, we performed one analysis of similarities (ANOSIM) test over both man-made and natural wetlands’ samples. To this end, we built a binary matrix comprising all samples from man-made and natural wetlands (118 species * 256 samples; hereafter, *total matrix*). The ANOSIM test operates on a resemblance matrix and is similar to a standard univariate analysis of variance (ANOVA), but requires neither normality nor homoscedasticity of data. We compared composition between *wetland origins* (natural vs. man-made). Natural wetlands were visited at most twice (2 visits) and man-made wetlands up to 12 times (12 visits). However, since visits 1 - 2 of natural wetlands were not directly comparable to visits 1 - 2 of man-made wetlands, we considered *visit* as a factor, nested within *wetland origin*. The analysis returns a global R and a p-value expressed as a percentage. When R is negative or close to 0, similarities within groups (i.e., samples within the same wetland origin) and among groups (i.e., samples of different wetland origins) are equivalent. In contrast, when *R* values approach 1, samples are more similar within than among groups, and groups of samples from different wetland origins are therefore differentiated. In turn, the different number of visits was controlled by considering *visit* as a nested factor (Clarke and Warwick 2001a). We performed 999 permutations over a Bray-Curtis distances matrix. Next, we used a 2-dimensional nonparametric multidimensional scaling (MDS) to visualize community patterns (99 restarts, 0.01 minimum stress, Kruskal fit scheme 1). In order to assess if man-made wetlands' communities progressively resembled to those of natural wetlands, we performed a similarity percentages test (SIMPER, Bray-Curtis distances matrix) comparing the man-made wetland community of each year and area with that of the natural wetlands. Similarity percentages of man-made towards natural wetlands, and similarity among man-made sites within each area, were obtained.

Besides, in order to explore if community differences between wetland origins were due to active or passive dispersers, we splitted the *total matrix* into 2 new matrices, one comprising only insect species (*active dispersers matrix*; 106 species * 256 samples) and the other comprising only crustacean species (*passive dispersers matrix*; 12 species * 256 samples). We performed six analyses of similarities (ANOSIM) tests, one over active dispersers (insects) and another over passive dispersers (crustaceans), with samples of natural wetlands and man-made wetlands of the 1st, 2nd and 3rd year.

Secondly, we aimed to assess nestedness on the *total*, the *active dispersers,* and the *passive dispersers matrix*. To this end, we used the software ANINHADO to order matrices according to the number of presences per row (wetlands) and to draw a diagonal between species presences and absences (Guimarães and Guimarães 2006). From this basis, the software uses the classical Nestedness Temperature Calculator method to obtain parameter *T*, based on unexpected absences (Atmar and Patterson 1993). *T* usually reaches high values in disordered systems and low values in ordered ones. However, following Bascompte et al. (2003) here we use *N*, a parameter which indicates the degree of nestedness (i.e., order) with values between 0 (minimum nestedness) and 1 (maximum nestedness), calculated as $N = (100-T)/100$. ANINHADO allows the degree of nestedness present within a system to be compared to 4 separate null models (Guimarães and Guimarães 2006). Whenever significant nestedness was obtained with the fixed-fixed model, it was also obtained using the other three. Thus, following similar studies (Florencio et al. 2011) we selected the fixed-fixed model for being more restrictive and incurring fewer Type I errors (Almeida-Neto et al. 2008). We identified idiosyncratic species as those whose N values were lower than the value of the original matrix, and nested species as those with higher than that value (Atmar and Patterson 1993). We aimed to explore the effect of the uneven sample number on nestedness, a common problem in this type of studies. To this end, we used a sample-based rarefaction procedure, taking the minimum number of samples per wetland and month (Gotelli and Colwell 2001). Since in all cases we obtained similar nested patterns to those produced with the whole data set, here we only present the latter.

Generalized additive models (GAMs) were fitted to appraise the temporal variation of nestedness (from visit 1 to visit 12), since they better detect nonlinear structures (de Eyto and Irvine 2007). We used the function ‘gam’, part of the ‘mgcv’ library, written in R statistical software (Wood 2001). Nestedness values were used as response variable, and *visit* (as surrogate of time) and *area* (BT, PE, PS) as explanatory variables.

Visit was included as a smoothing term, while *area* was included as a nominal variable (factor). The interaction between *visit* and *area* was also included in the model, so we obtained 3 regressions lines, one for each area. This interaction is necessary in order to analyze if there are significant changes in the nestedness values trends through time among the different areas. To this end, we first performed the more complex model, which allows to obtain a regression line for each area; GAM1), and then we performed a simpler model (GAM2) merging the areas (i.e. factor categories) that showed similar trends through time, obtaining one regression line for the merged areas that would be compared to the non-merged one. We kept the model (GAM1 or GAM2) with the lower AIC value. This procedure of merging factor categories to obtain a more parsimonious model is described in Crawley (2007).

Successional trajectories and diversity trends in man-made wetlands

For this second section of the paper, we used the samples of the man-made wetlands study (years 0 to 3) considering abundances of the whole community. With this data, we explored successional trajectories and established links between nestedness and local/regional diversity trends in man-made wetlands.

First, in order to assess if changes in the environmental variables through time differed among areas, a MANCOVA was performed (*area* factor as fixed effect, *visit* as covariable). The variables included in the environmental matrix were water temperature (TEMP), concentration of oxygen (OX), conductivity (COND), water pH (PH), concentration of clorophyll-a (CHLA), concentration of dissolved inorganic nitrogen

(DIN), concentration of soluble reactive phosphorus (SRP) and water level (WL). All variables, except pH, were log-transformed using $\log_{10}$ (Var+1).

In order to assess successional trajectories, over the man-made wetlands samples (72 taxa * 91 samples), we performed a 2-dimensional nonparametric multidimensional scaling (MDS) to visualize community patterns (99 restarts, 0.01 minimum stress, Kruskal fit scheme 1). Next, 3 analyses of similarities (ANOSIM) allowed testing for significant composition differences among areas at each year (1^{st}, 2^{nd} and 3^{rd}), setting the simple layout of the test with *area* as factor and a cut off for low contributions at 90%. Finally, a similarity percentages test (SIMPER) allowed us to identify which species explained more dissimilarity among mid-term communities (3^{rd} year) of each area). Taxa which contributed more to dissimilarity, with values of Av. dissimilarity / SD > 1, were considered useful to discriminate areas. For all these analyses the abundance matrix had been previously standardized (by samples), fourth-root transformed and converted into a resemblance matrix using Bray-Curtis distances.

Our last aim was to explore how successional trajectories were related to local and regional diversity components. To this end, we calculated species richness and α, β and γ diversities for each visit (1-12). Abundance was variable among samples, so we calculated richness using a rarefaction procedure with the function rarefy deriving from the vegan library (Oksanen et al. 2010). This function, inspired by Heck et al. (1975), calculates the estimated species richness for a number of individuals by simulating random draws of a fixed number of individuals based on the least abundant sample. Rarified Species Richness (Srar) is not an estimate of the total community richness, but it permits an unbiased comparison between samples of unequal abundance. Regarding diversity parameters, according to recent theoretical frameworks we named the three diversity components as local diversity (α), regional-to-local diversity ratio (β) and regional diversity (γ) (Tuomisto 2010a, b). We compared the diversity components of the same visit. Hence, in our case we obtained local diversity (α) by calculating the Shannon-Wiener diversity index (using $\log_2$) after pooling species abundance per each area in a given visit, averaging abundances between samples within areas in order to keep the same unit effort (Legendre et al. 2005). In order to calculate regional diversity (γ) we used the same index after pooling the species abundance of all areas in a given visit. Regional-to-local diversity ratio (β), which indicates the variation in species composition among areas, was obtained as the ratio between γ and α diversity. Finally, GAMs (same layout as previously) were fitted to appraise the temporal variation of rarified species richness (Srar), local diversity (α), regional-to-local diversity (β) and regional diversity (γ). In order to compare temporal trends between areas, the comparison of the AIC values of models merging the similar areas (GAM 2) and the areas apart (GAM 1) was carried out as previously described in the nestedness analyses subsection.

MDS, ANOSIM and SIMPER routines were performed with PRIMER-E 18 v.6.1.11 & PERMANOVA+ v.1.0.1; Nestedness was calculated with ANINHADO 3.0; MANCOVA tests were performed with the software package PASW v.18, and GAMs analyses and rarefied species richness were calculated with R software v. 2.12.1.

Results

Nestedness of local man-made wetlands' communities within regional natural wetlands' communities

Nestedness of local man-made wetlands' communities within regional natural ones

The global ANOSIM test showed significant compositional differences between man-made and natural wetlands (*wetland origin*: R = 0.048, p = 0.011), whereas no differences were related to time (*visit*: R = 0.178, p = 0.251). The MDS showed a different position for samples from natural wetlands and those from man-made wetlands (years 1 to 3) (Figure 2). When analyzing compositional differences year by year, ANOSIM tests showed differentiated communities between natural and man-made wetlands at the 1st, 2nd and 3rd year, being these differences not explained by the active but by the passive dispersers' subset (Table 1). Overall, the SIMPER analysis showed man-made communities of BT and PE resembling more to natural communities than those from PS, an area that had a higher among-sites similarity than BT and PE (Figure 3).

Year	***Community***	***R***	***p***
1	Whole	0.148	0.1 %
1	Passive disp.	0.149	0.1 %
1	Active disp.	0.008	9.8 %
2	Whole	0.099	2.1 %
2	Passive disp.	0.075	0.9 %
2	Active disp.	0.007	15 %
3	Whole	0.121	4.8 %
3	Passive disp.	0.123	1.0 %
3	Active disp.	0.019	20 %

Table 1. ANOSIM tests comparing the whole community, the passive dispersers community and the active dispersers community between wetland origins (natural / man-made), at the 1st, 2nd and 3rd year from creation of man-made wetlands.

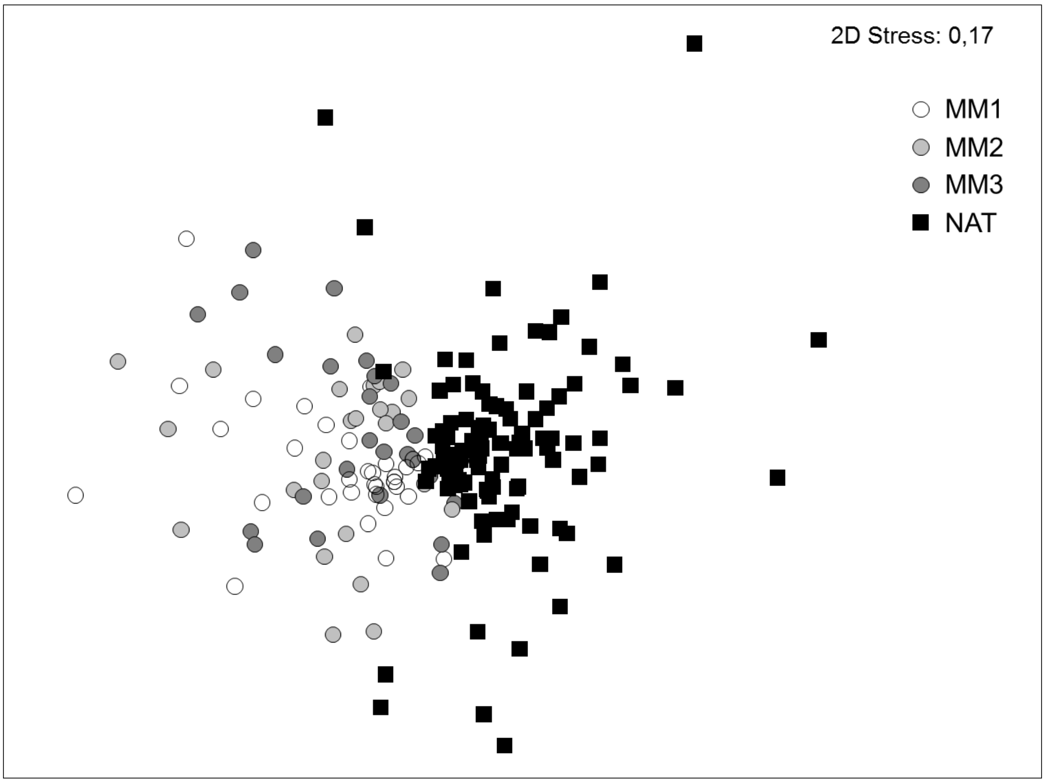


Fig 2. Non-parametric multidimensional scaling (MDS) representing the samples from pioneering man-made wetlands of the 1st year (MM1), 2nd year (MM2) and 3rd year (MM3) after creation, and samples from the natural wetlands (NAT).

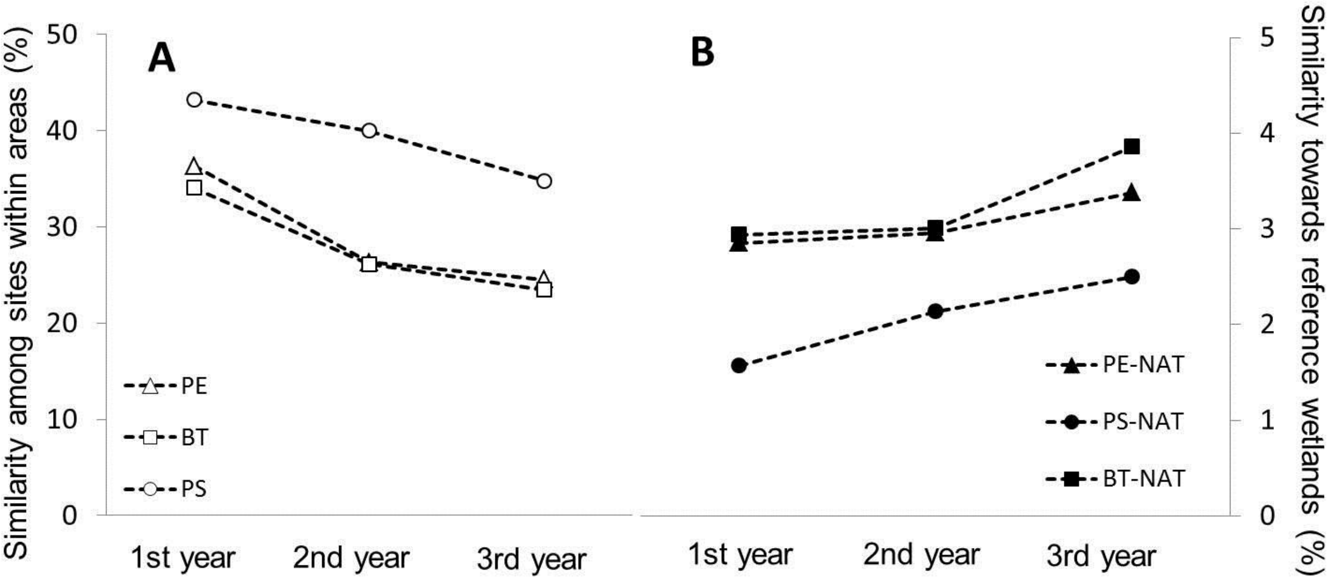


Figure 3. Representation of the values of composition similarity among-sites within each area (A); and the values of composition similarity between man-made and natural wetlands' communities (B).

Regarding nestedness analyses of pioneering colonizers within natural communities, the *total matrix* presented very similar nestedness values to the *active dispersers matrix* (total matrix: N = 0.964; active dispersers matrix: N = 0.963). Contrarily, the *passive dispersers matrix* was much less nested (N = 0.738). The analysis of nested and idiosyncratic taxa showed that active dispersers highly contributed to the nested structure, since 64% of them showed a nested pattern (Table 2). The richest orders were also those with a high number of nested species (Coleoptera, 28 species; Heteroptera, 17 species; Odonata, 14 species), but this fact was however variable among families within each group (Table 2). On the other hand, passive dispersers were highly idiosyncratic, with only 2 species (9%) contributing to the nested pattern.

Nestedness tended to decrease through succession globally in man-made wetlands, from higher (1st year) to lower values (3rd year) than those presented by the natural wetlands: $N_{1st\ year} = 0.9666 \pm 0.0033$; $N_{2nd\ year} = 0.9573 \pm 0.0083$; $N_{3rd\ year} = 0.9503 \pm 0.0096$; $N_{Natural} = 0.9613 \pm 0.0035$. The GAM analysis corroborated a significant global decreasing trend through time (Table 3, Figure 4). Comparing nestedness trends by area, in PS this parameter tended to increase, whereas in BT and PE the contrary was true. Temporal trends between BT and PE were considered similar since the GAM model merging both areas presented a lower AIC value ($AIC_{GAM\ 2} = 393.9$) than that considering the three areas separately ($AIC_{GAM\ 1} = 403.1$) (Figure 4).

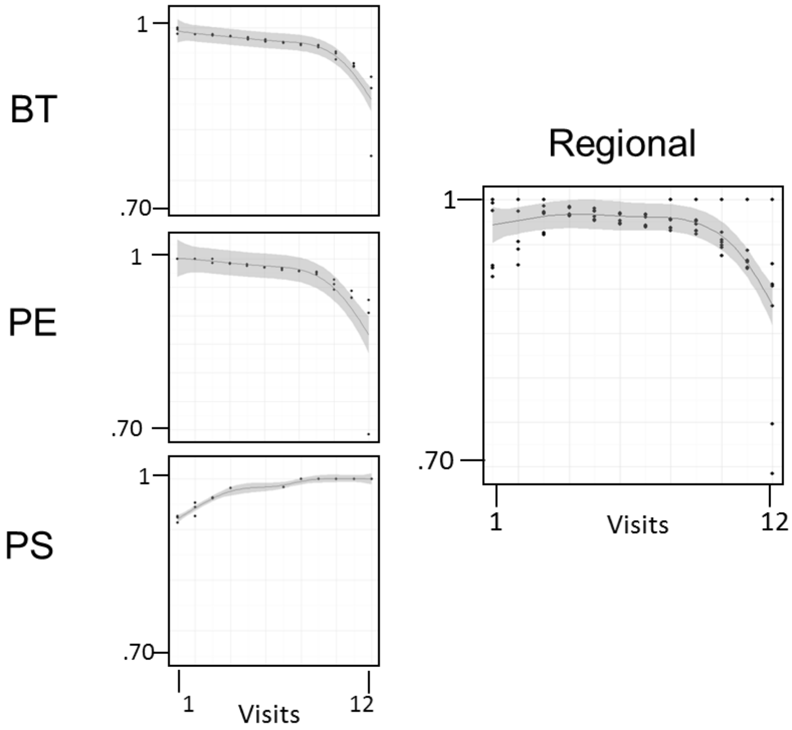


Fig. 4. Generalized additive models (GAMs) representing Nestedness through time, regionally and at each area (BT, PE, PS).

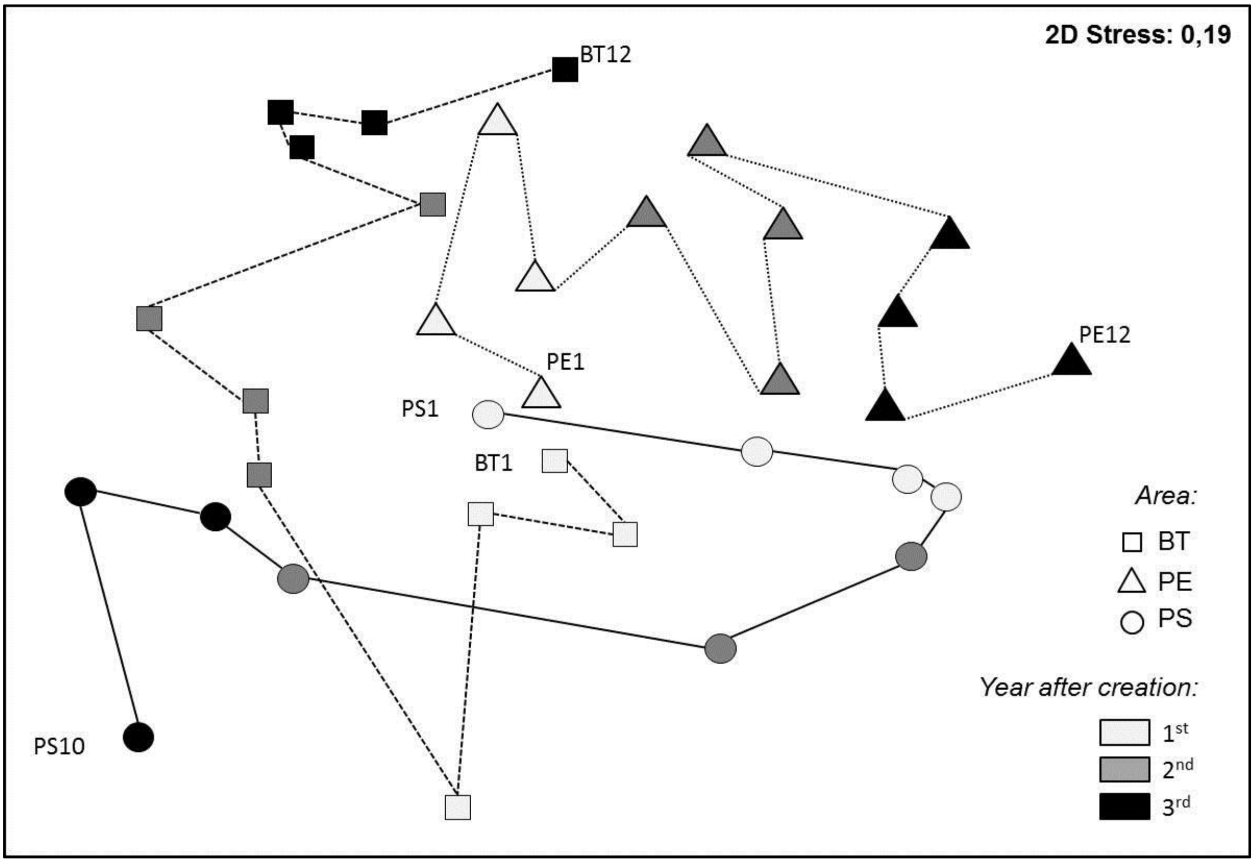


Fig. 5. Non-parametric multidimensional scaling (MDS) showing the successional trajectories of the man-made wetlands' communities through time (in the 12 visits performed in the three first years after wetland creation). Samples were area-averaged (site-centroids) for each visit..

Table 2. Number of species per Order and Family that show an idiosyncratic (IDIO) or a nested (NEST) pattern. * = Orders represented by only one family.

TAXONOMIC GROUP	*IDIO*	*NEST*
INSECTS (active dispersers)	*35*	*63*
EPHEMEROPTERA		2
Baetidae		1
Caenidae		1
ODONATA	3	14
Aeshnidae		2
Coenagrionidae		3
Gomphidae		1
Lestidae	1	3
Libellulidae	2	5
HETEROPTERA	9	17
Corixidae	4	7
Gerridae	2	2
Hydrometridae		1
Mesoveliidae	1	
Nepidae	2	
Notonectidae		5
Pleidae		1
Veliidae		1
COLEOPTERA	20	28
Dryopidae		1
Dytiscidae	7	9
Elmidae	1	1
Haliplidae	1	
COLEOPTERA (cont.)	20	28
Helophoridae	2	3
Hydraenidae	2	6
Hydrophilidae	7	4
Hygrobiidae		1
Noteridae		3
*LEPIDOPTERA	1	
TRICHOPTERA	2	2
Ecnomidae		1
Limnephilidae	2	1
MACROCRUSTACEANS (passive dispersers)	*10*	*2*
*ANOSTRACA	1	
*NOTOSTRACA	1	
*MYSIDA	1	
*AMPHIPODA	1	
ISOPODA	3	1
Asellidae		1
Idoteidae	1	
Sphaeromatidae	1	
Trachelipodidae	1	
DECAPODA	3	1
Atyidae		1
Cambaridae	1	
Palaemonidae	2	

Table 3. Values of nestedness (N), rarefied species richness (Srar) and diversity parameters (local diversity, α; local-to-regional diversity, β) compared by areas. For the whole region, nestedness, rarefied species richness and regional diversity (γ) were also calculated. Mean, standard deviation (SD), and statistical values of the GAM models examining each parameter through time are also shown (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ┼ $p < 0.10$; n.s. = non-significant).

	Parameter	**Mean**	**SD**	***F***	**df**	***p***
BT	N	0.960	0.045	15.85	3.776	***
	Srar	6.78	4.17	5.871	0.8562	*
	α	1.583	0.860	8.231	1.465	***
	β	2.646	0.644	12.544	7.090	***
PE	N	0.969	0.053	15.84	4.370	***
	Srar	13.86	4.55	2.350	1.587	┼
	α	2.188	0.707	1.519	4.247	n.s.
	β	3.118	0.257	1.967	5.263	┼
PS	N	0.970	0.030	10.12	1.346	***
	Srar	8.15	5.23	2.177	5.708	*
	α	1.741	0.603	0.457	0.3129	n.s.
	β	2.289	0.549	12.281	7.834	***
Regional	N	0.966	0.045	11.39	4.544	***
	Srar	9.85	5.58	2.343	5.101	*
	γ	3.619	0.394	5.498	3.358	**

Successional trajectories and diversity trends in man-made wetlands

Only water level showed a significant different response through time among areas ($F_{2,89} = 6.677$; $p = 0.002$). The rest of environmental variables showed similar responses at each area, since no significant interactions were obtained. Although 3 out of the 7 analyzed environmental variables differed among man-made areas (water level, $F_{2,89} = 26.560$, $p < 0.001$; conductivity, $F_{2,89} = 6.983$, $p = 0.002$; DIN, $F_{2,89} = 9.381$, $p < 0.001$), none of them changed significantly through time.

The MDS exploring successional trajectories of macroinvertebrate communities at each area (inter-sites centroids) through time (visits) showed that communities tended to diverge among areas (Figure 5). The ANOSIM confirmed this observation: *area* was not significant when testing differences among samples of the 1st year after creation (R = 0.403, $p = 0.100$), indicating a common starting point. However, it showed significant differences among samples of the 2nd year after creation (R = 0.553; $p = 0.025$), with the post-hoc pairwise test differentiating PE - BT (R = 0.719; $p = 0.029$), but neither PE - PS (R = 0.536; $p = 0.133$) nor BT - PS (R = 0.286; $p = 0.200$). Similarly, the ANOSIM for the 3rd year after creation showed significant differences among areas (global R = 0.634, $p = 0.004$), and all of them differed significantly from the rest (all pairwise tests R $\geq$ 719; $p \leq 0.029$), indicating an increasing divergence. SIMPER analyses allowed us to identify the taxa that contributed more to the dissimilarity observed among areas in the 3rd year after creation. The 3 taxa typifying BT against PS/PE were passive dispersers (Tubificidae, *Physella acuta, Procambarus clarkii*), as the main taxa typifying PE against PS/PE (Enchytraeidae). Contrarily, all taxa typifying PS against BT/PE were active dispersers (Figure 6). Globally, active dispersers were much more abundant throughout the study than passive ones (see appendix for taxonomic lists).

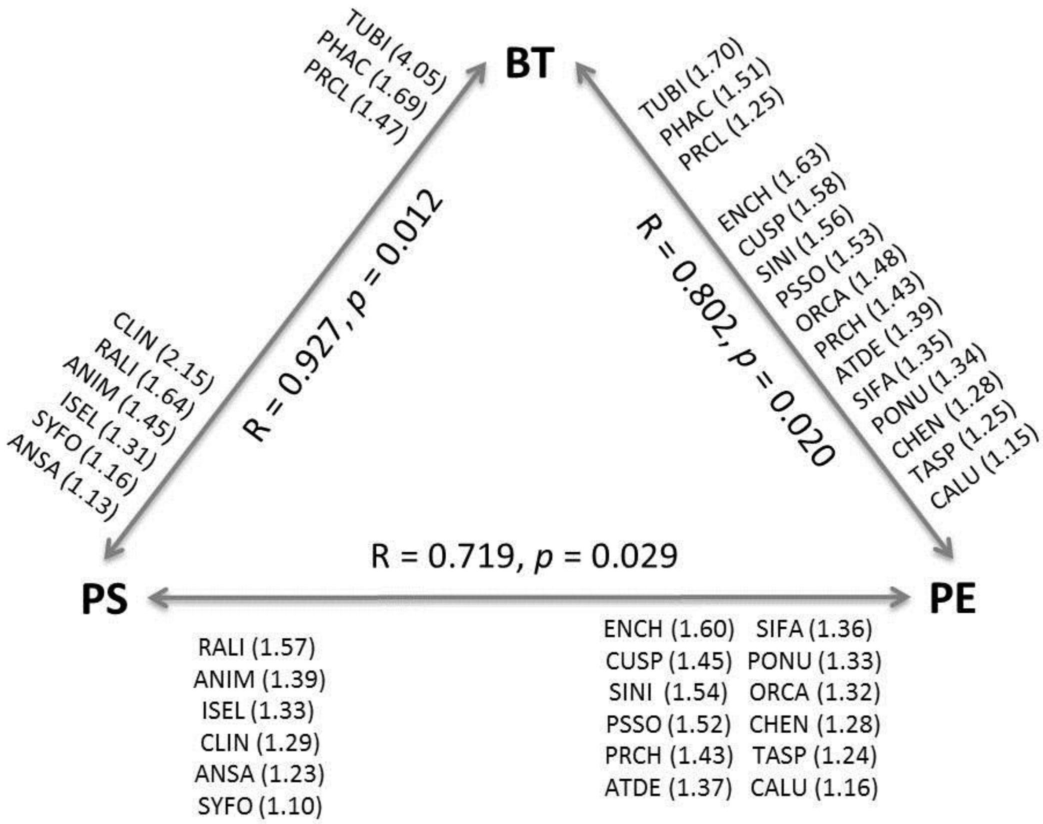


Fig. 6. Similarity percentages (SIMPER) analysis, showing the species which contributed most to dissimilarity between areas at the 3rd year after wetland creation (in brackets, the contribution in % to this dissimilarity). ANOSIM pairwise tests between areas are also shown. Legend: ANIM = *Anax imperator*, ANSA = *Anisops sardeus*, ATDE = *Atyaephyra desmarestii*, CALU = *Caenis luctuosa*, CHEN = *Chironomus*/*Einfeldia* sp., CLIN = *Cloeon inscriptum*, CUSP = *Culicoides* sp., ENCH = Enchytraeidae, ISEL = *Ischnura elegans*, ORCA = *Orthetrum cancellatum*, PHAC = *Physella acuta*, PONU = *Polypedilum nubifer*, PRCH = *Procladius choreus*, PRCL = *Procambarus clarkii*, PSSO = *Psectrocladius sordidellus*, RALI = *Ranatra linearis*, SIFA = *Sigara falleni*, SINI = *Sigara nigrolineata*, SYFO = *Sympetrum fonscolombii*, TASP = *Tanytarsus* sp., TUBI = Tubificidae.

Looking at the temporal variation of diversity parameters (Table 3, Figure 7), for Srar BT and PE presented a similar temporal pattern, since the model with these two areas merged showed slightly lower AIC value than the model considering them apart ($AIC_{GAM\ 2}$=566.2; $AIC_{GAM\ 1}$=567.5). BT and PE showed a decreasing trend through time, whereas PS showed stochastic but significant oscillations. Regionally, this parameter showed a unimodal curve with the highest values at the end of the 1st towards the 2nd year after creation, similarly to the pattern observed for regional diversity (γ). On the other hand, local (α) and local-to-regional diversity (β) trends were less clear. Whereas α had a significant decrease only in BT, β showed patterns that differed among areas (merging BT-PE vs. PS, $AIC_{GAM\ 2}$=125.2; $AIC_{GAM\ 1}$=79.9) (Figure 7).

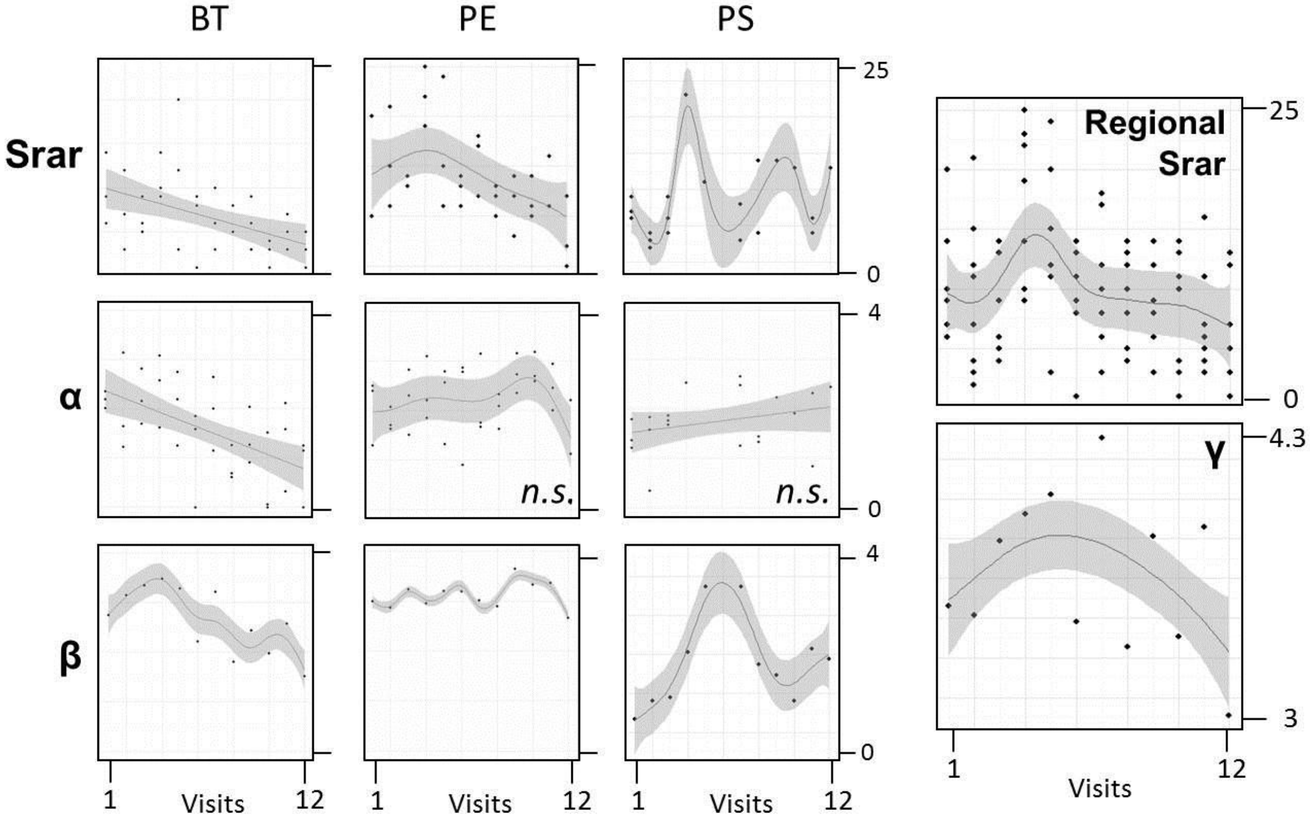


Fig. 7. Generalized additive models (GAMs) representing the analyzed diversity parameters through time: Rarefied species richness (Srar), local diversity (α), local-to-regional diversity (β) and regional diversity (γ). Statistical values of the models examining each parameter through time are shown in Table 3; *n.s.* = non-significant GAM model.

Discussion

Decreasing nestedness and divergent successional trajectories

Nestedness analysis provides a framework for analyzing species occurrences to determine non-random patterns in community composition and to potentially identify the role of colonization-extinction in shaping faunal assemblages (Wissinger et al. 2008, El-Bana 2009, Frick et al. 2009). Our global wetland network showed a high degree of nestedness, with values similar to those found by other studies (e.g., Florencio et al. 2011). Significant levels of nestedness have been described in biotas of aquatic ecosystems, even when they are dominated by taxa with high rates of inter-locality dispersion (Rundle et al. 2002). In our case, active dispersers contributed more to nestedness than to idiosyncrasy, while the opposite was true for passive dispersers. Nested taxa usually show a strong spatial structure, while spatially random distributions have been attributed to idiosyncratic taxa (McAbendroth et al. 2005). In fact, factors structuring nested subsets in wetland networks might be viewed as probabilistic filters, which act at the species level to limit the spatial distribution of species with narrow ecological tolerance (Atmar and Patterson 1993, Mitsuo et al. 2011) or with low dispersal tendency (Wright et al. 1998). In our case, some families within the active dispersers subset contributed particularly high to the nested pattern, either by bearing only nested species (in the case of Coenagrionidae, Notonectidae, Noteridae), or a number of nested species that greatly outnumbered the idiosyncratic ones (Lestidae, Libellulidae, Corixidae, Dytiscidae, Hydraenidae). Pioneering communities are known to be dominated by active dispersers (Herrmann et al. 2000, Lods-Crozet and Castella 2009) and particularly by some groups (i.e., Coleoptera and Heteroptera; Ruhí et al. 2009, Bloechl et al. 2010). Hence, the nested structure of local pioneering subsets within the regional natural community, as observed in this study, was already expected.

This fact is particularly important under the light of successional trajectories, since the initially shared composition (1st year after creation) caused different areas to depart from the same successional point.

Besides, composition similarities among- and within- areas decreased through succession, achieving differentiated communities among areas that rise to significant different communities at the 3rd year. Surprisingly, at the same time these communities slowly approached towards natural wetlands' composition. On one hand, the arrival of active but less pioneer taxa probably explained the approach of man-made towards natural wetlands' communities, since even for some active groups succession can take much longer than the studied period (around 10 years for Coleoptera, Ruhí et al. in press). On the other hand, the progressive arrival of passive dispersers had already been hypothesized (Batzer and Wissinger 1996, Ruhí et al. in press). In our case, despite being numerically unimportant, passive dispersers caused the main compositional differences among areas at the 3rd year after creation.

On balance, the observed trajectory was a combination of a nested colonization and a divergent succession (Figure 1, trajectory C). It has been suggested that divergent trajectories departing from similar initial compositions are common both in vegetation (Pineda et al. 1981, Christensen and Peet 1984, Seabloom and Van Der Valk 2003, del Moral 2007) and faunal successional studies (Chase 2007, Jeffries 2011). However, to our best knowledge, no such research to date has described the relationship between nestedness and this trajectory. Matthews and Spyreas (2010) pointed out that this trajectory can be explained in vegetal succession when the same set of species are planted in all restoration sites regardless of whether those species are well-suited to a site’s specific environmental conditions, causing the initial composition to be similar among sites but to diverge as plant communities respond to underlying environmental gradients among sites. Our study suggests that, at least in macrofaunal succession, this trajectory may be mainly explained by differential colonization: while the initial pioneering colonizer subset is mainly composed by highly nested active colonizers, the progressive stochastic arrival of lower-performance or passive dispersers causes increasing divergence among areas through time. Nevertheless, other factors such as invasive exotic species presence (McIver and Starr 2001) and hydrological disruptions (Jeffries 1994, Chase 2007), both covarying in our case, should also be considered. High nestedness values through time have been described when systems are assembling and deterministic processes become more important, mainly during initial colonization and recurrent perturbations (Patterson 1990, Loo et al. 2002, Bloch et al. 2007). Thus, the low hydrological stability of temporary wetlands of PS probably explains the particularly high and increasing nestedness trend at this area.

Overall, our findings support the view that criticizes predictable temporal trajectories in created or restored wetlands, even when regional factors and initial compositions are similar and well known (e.g., Zedler and Callaway 1999, 2000).

Diversity trends and implications for conservation

Although it would seem logical that the observed divergent successional trajectories could imply progressively more singular communities at each area, and consequently higher regional diversity values, this was not the case in our study. At a local level, Srar showed oscillations at the temporary area and steady decreases at the other two; while regionally, the hump-back trend of Srar was similar to the curve drawn by regional diversity (γ). The similarity between regional Srar and γ is logical since Srar also measures diversity, increasing, for a given number of taxa, with the evenness of species abundance (Lods-Crozet and Castella 2009). Comparing local species richness (Srar) and regional biodiversity trends (Regional Srar, γ), the most plausible interpretation is that local losses of pioneering species were not compensated by the differential arrival (at each area) of taxa with low dispersal abilities and/or specialized requirements. As a consequence, the decline on species gain was combined with constant species losses, leading local and regional diversity values to decrease. This non-linear pattern has already been acknowledged in recent conceptual frameworks (Anderson 2007) and empirical studies (Santos et al. 2011) on ecological succession.

In streams, local-to-regional diversity (β) has been described to indicate the taxa turnover among areas caused by the existence of heterogeneous habitat patchiness and of local filters to the regional pool (Hieber et al. 2005, Stendera and Johnson 2005, Zilli and Marchese 2011). In this sense, our wetland areas did not make important differentiate contributions to the overall biodiversity (Moreno and Halffter 2001, Primack and Carotenuto 2003), contrarily to what has been observed across networks of natural ponds (Bilton et al. 2009, Bagella et al. 2011). Many studies have claimed that pond clusters may be better than single, larger wetlands, for promoting local species (e.g., Jeffries 1991, Oertli et al. 2002, Scheffer et al. 2006). This idea, supported by the fact that even species-poor sites contain specialist taxa not found elsewhere within the region, has been proved mainly in natural systems (Bilton et al. 2009, Florencio et al. 2011). Although studies in created ponds monitored over longer periods have shown similar patterns (e.g., Williams et al. 2008), we suggest that faunal communities of short- and mid-term successional stages may be still too nested within regional natural communities to locally offset, by means of low dispersers and idiosyncratic taxa, the regional loss of the pioneering ones. Consequently, unless habitat differs enough among areas to break the nested pattern (promoting specialist beyond generalist species, Bascompte et al. 2003, Almeida-Neto et al. 2008), early faunal communities may merely be a "filtered" subset of the best regional dispersers.

Long-term studies (spanning > 10 years) in freshwater ecology are still relatively rare (Jackson and Füreder 2006), and this fact has proven to be critical when creating/restoring ecosystems for biodiversity offsetting (Mitsch and Wilson 1996, Pechmann et al. 2001, Lesbarrères et al. 2010). Our findings suggest that not only the evaluation of wetlands created for mitigation purposes should expand beyond mid–term scenarios (> 3 years), but also that unless these systems are conceived to operate in longer time perspectives, they will be a sink of generalist faunas without achieving the idiosyncratic taxa of the natural wetlands.

Acknowledgements

This work was supported by a PhD grant and a Scientific Research grant (CGL2008 05778/BOS) from the Ministerio de Ciencia y Tecnología of the Spanish Government. We thank Mònica Martinoy and Jaume Gifre for field and laboratory assistance.

Appendix. SIMPER analysis (1st year after creation) showing the species contributing more to each *area* composition similarity. Av.Ab. = Average abundance of the species in the area; S/SD = ratio between average similarity values and standard deviation of similarity values within the area; Cont. % = contribution of the species to the within-area similarity (%). A cut-off for species contributing cumulatively up to 99% of similarity has been established.

Group BT (1st year)

Species	**Av.Ab.**	**S/SD**	**Cont.%**
Sigara lateralis	0.75	0.93	32.94
Anisops sardeus	0.75	0.97	31.24
Cloeon inscriptum	0.50	0.51	12.49
Procambarus clarkii	0.42	0.40	7.95
Hydroglyphus geminus	0.33	0.30	4.34
Ischnura elegans	0.33	0.31	3.57
Rhantus suturalis	0.25	0.21	1.88
Ochthebius dilatatus	0.25	0.21	1.77
Microvelia pygmaea	0.25	0.21	1.60
Gerris argentatus	0.17	0.12	0.83
Eretes griseus	0.17	0.12	0.70

Group PE (1st year)

Species	**Av.Ab.**	**S/SD**	**Cont.%**
Cloeon inscriptum	0.92	1.76	29.21
Sigara lateralis	0.83	1.27	27.06
Anisops sardeus	0.67	0.78	13.33
Cymatia rogenhoferi	0.50	0.51	6.49
Sympetrum fonscolombii	0.50	0.52	5.95
Ischnura elegans	0.50	0.52	5.78
Eretes griseus	0.33	0.29	3.05
Micronecta scholtzi	0.33	0.30	2.78
Anax imperator	0.33	0.31	2.05
Caenis luctuosa	0.25	0.21	1.05
Gerris lateralis	0.25	0.22	0.88
Agabus bipustulatus	0.17	0.12	0.88
Helophorus* cf. *lapponicus	0.17	0.12	0.88

Group PS (1st year)

Species	**Av.Ab.**	**S/SD**	**Cont.%**
Cloeon inscriptum	0.73	0.83	41.03
Sigara lateralis	0.73	0.80	39.06
Eretes griseus	0.45	0.43	10.87
Helochares lividus	0.27	0.23	2.90
Aquarius paludum	0.27	0.22	2.46
Agabus bipustulatus	0.18	0.13	1.53
Anisops sardeus	0.18	0.13	0.59
Aulacochtebius exaratus	0.18	0.13	0.56

Appendix (cont., SIMPER analysis 2nd year after creation)

Group BT (2nd year)

Species	**Av.Ab.**	**S/SD**	**Cont.%**
Sigara lateralis	0.67	0.68	32.21
Anisops sardeus	0.50	0.52	15.71
Ischnura elegans	0.50	0.52	15.71
Gerris argentatus	0.42	0.40	8.86
Hydroglyphus geminus	0.42	0.41	8.55
Procambarus clarkii	0.33	0.29	5.74
Cloeon inscriptum	0.33	0.31	4.97
Aquarius paludum	0.25	0.21	2.54
Rhantus suturalis	0.25	0.21	2.18
Microvelia pygmaea	0.17	0.12	0.95
Helophorus* cf. *lapponicus	0.17	0.12	0.88
Ochthebius dilatatus	0.17	0.12	0.88

Group PE (2nd year)

Species	**Av.Ab.**	**S/SD**	**Cont.%**
Cloeon inscriptum	0.92	2.04	36.50
Ischnura elegans	0.67	0.82	18.49
Micronecta scholtzi	0.67	0.83	16.56
Caenis luctuosa	0.58	0.66	13.17
Sigara lateralis	0.42	0.41	5.44
Anisops sardeus	0.33	0.31	3.37
Atyaephyra desmarestii	0.25	0.22	2.27
Sympetrum fonscolombii	0.25	0.21	1.45
Helochares lividus	0.17	0.12	0.76
Laccophilus hyalinus	0.17	0.12	0.58
Procambarus clarkii	0.17	0.12	0.51

Group PS (2nd year)

Species	**Av.Ab.**	**S/SD**	**Cont.%**
Sigara limitata	0.67	0.58	18.25
Aeshna cyanea	0.67	0.58	10.22
Anax imperator	0.67	0.58	10.22
Cloeon inscriptum	0.67	0.58	10.22
Gerris lateralis	0.67	0.58	10.22
Helochares lividus	0.67	0.58	10.22
Laccophilus hyalinus	0.67	0.58	10.22
Sigara lateralis	0.67	0.58	10.22

Appendix (cont., SIMPER analysis 3rd year after creation)

Group BT (3rd year)

Species	Av.Ab.	S/SD	Cont.%
Sigara lateralis	0.53	0.51	21.29
Cloeon inscriptum	0.50	0.52	19.88
Anisops sardeus	0.50	0.53	17.80
Procambarus clarkii	0.44	0.42	17.34
Ischnura elegans	0.36	0.36	8.59
Hydroglyphus geminus	0.28	0.27	4.32
Gerris argentatus	0.22	0.21	2.89
Ochthebius dilatatus	0.19	0.17	2.59
Rhantus suturalis	0.19	0.18	1.86
Microvelia pygmaea	0.17	0.15	1.33
Eretes griseus	0.14	0.13	0.90
Aquarius paludum	0.11	0.09	0.67

Group PE (3rd year)

Species	Av.Ab.	S/SD	Cont.%
Cloeon inscriptum	0.89	1.70	35.89
Sigara lateralis	0.56	0.62	13.47
Ischnura elegans	0.53	0.59	11.20
Anisops sardeus	0.44	0.46	7.91
Caenis luctuosa	0.42	0.43	6.91
Micronecta scholtzi	0.42	0.44	6.84
Sympetrum fonscolombii	0.39	0.40	5.34
Procambarus clarkii	0.28	0.26	3.19
Cymatia rogenhoferi	0.22	0.21	1.61
Atyaephyra desmarestii	0.19	0.18	1.43
Orthetrum cancellatum	0.17	0.15	1.07
Sigara falleni	0.17	0.15	0.93
Helochares lividus	0.14	0.12	0.79
Aquarius paludum	0.14	0.13	0.50
Agabus bipustulatus	0.11	0.10	0.49
Corixa affinis	0.11	0.09	0.45
Anax imperator	0.14	0.13	0.44
Eretes griseus	0.11	0.09	0.40
Sigara nigrolineata	0.11	0.10	0.36

Group PS (3rd year)

Species	Av.Ab.	S/SD	Cont.%
Cloeon inscriptum	0.70	0.72	37.37
Sigara lateralis	0.55	0.50	23.46
Eretes griseus	0.35	0.31	7.21
Helochares lividus	0.30	0.28	4.04
Ischnura elegans	0.30	0.28	3.58
Sympetrum fonscolombii	0.30	0.28	3.20
Aquarius paludum	0.25	0.22	2.78
Anax imperator	0.30	0.29	2.71
Anisops sardeus	0.25	0.23	2.17
Laccophilus hyalinus	0.25	0.23	2.15
Gerris lateralis	0.25	0.23	1.94
Agabus bipustulatus	0.15	0.13	1.70
Hydroglyphus geminus	0.20	0.17	1.67
Notonecta maculata	0.20	0.18	1.26
Ranatra linearis	0.20	0.18	1.10
Sigara limitata	0.15	0.12	0.97
Rhantus suturalis	0.15	0.13	0.58
Aeshna cyanea	0.15	0.13	0.56
Helophorus alternans	0.10	0.07	0.35
Helophorus obscurus	0.10	0.07	0.35

CHAPTER 3. How do early successional patterns differ between man-made wetlands in the cold temperate and Mediterranean regions?

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Abstract

The region where a newly created wetland is located should have an important effect over its early successional process, since climate may have filtered the dominant biological strategies of the taxa leading this process, and climate characteristics may condition their dynamics. We studied the early successional patterns of macroinvertebrates within two sets of three man made ponds each, located in the cold temperate (Scandinavian Peninsula) and Mediterranean regions (Iberian Peninsula), during the first three years from the creation of these ecosystems. We predicted (1) non random samples of the regional assemblage pool (deterministic assembling) guiding the successional process in the cold temperate wetlands, and random ones (stochastic assembling) in the Mediterranean; (2) higher successional rates in the Mediterranean ponds than in the cold temperate ones, with contrary episodes of highest and lowest change throughout the year; and (3) a significantly different biological traits' composition between regions, due to the dominance of traits that favor resilience from or resistance against hydrological variability in the Mediterranean region rather than in the cold temperate region. Hypotheses on community structure (1) and dominant biological traits composition (3) were mostly supported, observing deterministic assembling mechanisms in the cold temperate ponds and stochastic ones in the Mediterranean; and a dominance of different biological traits between regions, explained by the need (Mediterranean) or the lack of need (cold temperate ponds) to overcome hydrological disturbances. Besides, succession dynamics (2) was explained by climate features in the cold temperate region but not in the Mediterranean ponds. We suggest that the intrinsic hydrological variability of Mediterranean lentic systems may be a major factor driving community changes in wetlands being created in this region. In order to generalize the observed patterns, we performed a meta-analysis of the temporal trends of taxonomic distinctness parameters of other successional studies across a

latitudinal gradient in Europe, which supported the differences we had observed between latitudinal extremes.

Introduction

Beyond the classical uses of created lentic habitats (Oertli et al. 2005), man-made aquatic systems might also offer useful opportunities to disentangle ecological processes, thanks to the quasi-experimental conditions that allow for the testing of hypotheses. Hence, although succession had been traditionally described in ecosystems that were recovering from major disturbances (e.g. Force 1981, Smith 1982, Kaufman 1983), the dynamics of this process also started to be tested in man-made aquatic habitats at the time that marshy wetlands (Levin et al. 1996, Herrmann et al. 2000), pond clusters (Seabloom and Van Der Valk 2003, Bloechl et al. 2010) or reservoirs were being studied (Voshell and Simmons 1984, Bass 1992, Koskenniemi 1994). In turn, the study of primary succession has generated theories on mechanisms by which communities are assembled, including the relative role of deterministic and stochastic pathways (Milner et al. 2008).

Hot dry summers and cool wet winters characterize the Mediterranean climate, whereas milder summers and colder and wetter winters are present in cold temperate regions (Verdonschot et al. 2010). Since colonization of newly created wetlands is mainly carried out by active dispersers, both in the temperate (Koskenniemi 1994, Herrmann et al. 2000, Lods-Crozet and Castella 2009) and Mediterranean regions (Ruhí et al. 2009), differences in the amount of time available for active dispersal between both regions may be reflected into different successional patterns. Moreover, climate may affect the relative role of deterministic and stochastic assembling mechanisms (Milner et al. 2008). Stochastic views have dominated among stream ecologists (Fisher 1983, Townsend 1989, Reice 1994). Although structuring patterns may respond to local constraints (Cottenie et al. 2003, Jeffries 2008), overriding large scale effects (such as climate, sensu Poff 1997) may also facilitate or avoid certain fauna under unfavorable conditions (Flory and Milner 2000, Milner et al. 2008, Milner and Robertson 2010), and thus “filter” the subset of the regional pool able to colonize the new habitat. Lepori and Malmqvist (2009) already proposed that stochastic and deterministic processes interact hierarchically in streams, being the relative strength of each modified by disturbance. Besides, Milner et al. (2008) found cold temperatures to favor this override of deterministic beyond stochastic assembling mechanisms in Alaskan stream communities. Other studies in the temperate region have shown that assemblages are dominated by a few pioneering species that establish species-species facilitative interactions already in early stages of primary succession (Kaufmann 2001, Felinks and Wiegand 2008), whereas in low latitudes many species can play an active role during colonization at the same time (e.g. Benzie 1984). However, much of this work has been carried out in streams (but see Matthews and Spyreas 2010, Jeffries 2011), and there is still little evidence of deterministic vs. stochastic assembling mechanisms in wetlands through primary succession.

On the other hand, the dependence of active dispersers on favorable meteorology may imply an effect of climate (i.e. the achievement of certain temperature thresholds) over colonization rates (Bilton et al. 2001, Boda and Csabai 2009a) and so it may affect the subsequent succession pattern. Moreover, climate may also shape the community through critical episodes such as unexpected dry periods (Jeffries 2003, 2008) or very low temperatures (Verdonschot et al. 2010). Aquatic communities in Mediterranean wetlands depend primarily on hydrological factors (Gascón et al. 2005, 2008) and show high values of inter- and intraannual variability (Álvarez-Cobelas et al. 2005, Beklioglu et al. 2007). In the Mediterranean, the predominance of traits favoring resilience from and resistance against hydrological disturbances has been related to the high occurrence of these events, contrasting to the lack of needed strategies to overcome such ecological bottlenecks in the temperate region (Bêche et al. 2006, Bonada et al. 2007). In this sense, although structural and functional adaptations between aquatic ecosystems in the Mediterranean and temperate regions have been claimed to be largely unknown (Gasith and Resh 1999), evidence described in streams and rivers can serve as basis to predict patterns in wetlands (Townsend and Hildrew 1994, Bonada et al. 2007).

In this study we followed the macroinvertebrate communities of two sets of three man-made ponds each, located in the Scandinavian and Iberian Peninsulas, during the first three years from creation of these systems. We predicted that climate differences between regions should have favored different strategies in communities colonizing these created habitats, whereas climate-dependent environmental variables should influence the succession patterns that take place at each region. In particular, we tested three hypotheses: (1) Random compositions from the regional pool (i.e., stochastic assembling mechanisms) should be expected in the Mediterranean region, due to higher colonization chances by the regional fauna, whereas non-random samples (i.e., deterministic assembling mechanisms) should be expected in Scandinavian ponds due to the dominance of a few pioneering colonist species; (2) Succession should be quicker in Mediterranean than in cold temperate ponds, due to the better average conditions for active dispersers throughout the year, and favorable/critical phases (those undergoing more/less community change, respectively) should differ between regions according to the best/harshest season for active dispersers within each year; and (3) The composition of biological traits should differ between both climatic regions, due to the expected higher abundance of traits that favor resistance against or resilience from hydrological disturbances in the Mediterranean region than in the cold temperate region (Table 1).

Table 1 (next page). Biological traits and categories for invertebrates considered in the present study; hypotheses for the dominance of each category in either KD or BA (White cells = lower values; grey cells = higher values) and corresponding rationale. The rationale for the hypotheses based on biological traits was derived from predictions made by Townsend and Hildrew (1994) and Bonada et al. (2007).

Trait	Category		Hypothesis		Rationale
			KD	BA	
1. Potential number of cycles per year	1.1	< 1	▨		In KD, the low occurrence of major disturbances (i.e. floods or droughts) should require less resilience capacity and permit less-frequent reproduction. In BA, a better resilience capacity should be achieved through shorter cycles after disturbances.
	1.2	1	▨		
	1.3	> 1		▨	
2. Reproduction	2.1	ovoviviparity		▨	In KD, isolated eggs and aquatic clutches should be expected according to the low occurrence of major disturbances. In BA, a better resilience capacity should be expected, through ovoviviparity or asexual reproduction (no need for sexual partner) after disturbances, and an increased resistance against droughts through terrestrial clutches.
	2.2	isolated eggs, free	▨		
	2.3	isolated eggs, cemented	▨		
	2.4	clutches, cemented or fixed	▨		
	2.5	clutches, free	▨		
	2.6	clutches, in vegetation	▨		
	2.7	clutches, terrestrial		▨	
	2.8	asexual reproduction		▨	
3. Dispersal	3.1	aquatic	▨		Dryness in BA should favour flying to other less-dry sites, whereas aerial passive and aquatic strategies should dominate in KD, without major disturbances.
	3.2	aerial passive	▨		
	3.3	aerial active		▨	
4. Resistance forms	4.1	eggs, statoblasts		▨	In BA biological traits related to the increased resistance against droughts should be expected. In contrast, in KD the low occurrence of major disturbances should require no resistance forms.
	4.2	cocoons		▨	
	4.3	housings against desiccation		▨	
	4.4	diapause or dormancy		▨	
	4.5	none	▨		
5. Respiration	5.1	tegument	▨		Since higher temperatures make the oxygen uptake more difficult, specialized techniques to overcome this inconvenience (plastron and aerial respiration) should be expected in BA.
	5.2	gill	▨		
	5.3	plastron		▨	
	5.4	spiracle (aerial)		▨	
6. Temperature	6.1	psychrophilic	▨		Psychrophilic taxa, capable of growth and reproduction in cold temperatures, should dominate in KD, whereas adaptations towards high temperatures and broad minim-maximum ranges should be predominantly found in BA.
	6.2	thermophilic		▨	
	6.3	eurythermic		▨	

Materials and methods

Study regions

The study was carried out in six ponds in two man-made wetland systems (three ponds each), located respectively in the Scandinavian (Kalmar Dämme, hereafter KD) and Iberian Peninsulas (Banyoles, hereafter BA) (Figure 1). KD is a constructed freshwater wetland system located on the south-eastern coast of Sweden, excavated and flooded for the first time in late 1996. This wetland system consists of several elongate ponds less than 2 m deep and vegetated mainly with belts of common reed (*Phragmites australis*). It was designed to reduce the urea levels discharged at the nearby airport and to promote regional aquatic biodiversity (Herrmann et al. 2000).

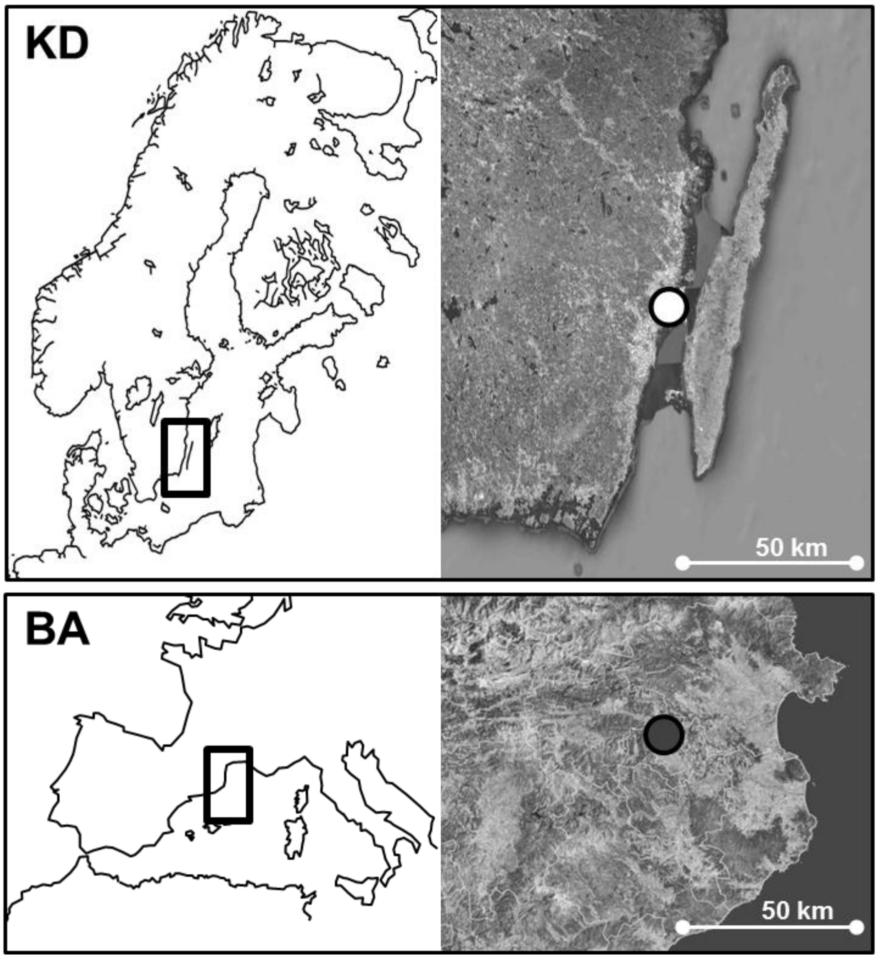

Fig. 1. Study regions (KD, BA). The location of the ponds is: KD1 = 56°40'8.84"N, 16°17'18.92"E; KD2 = 56°40'1.70"N, 16°17'41.76"E; KD3 = 56°39'49.20"N, 16°17'26.34"E; BA1 = 42°7'50.38"N, 2°44'52.65"E; BA2 = 42°7'55.33"N, 2°44'46.45"E; BA3 = 42°8'4.46"N, 2°44'49.61"E).

On the other hand, BA is a constructed wetland system consisting of three shallow ponds (depth < 2 m), vegetated mainly by *P. australis* and bulrush (*Typha latifolia*). The goal of the construction of these ponds was to enhance amphibian populations, within the framework of the LIFE-Nature project LIFE03 NAT/E/000067. . Wetlands in both regions were close (< 5 km) to other ponds (17 and 25 ponds bigger than 50 m2 in BA and KD, respectively) and located near major lentic habitats (Banyoles lake in BA; the Baltic Sea marshes in KD). The macroinvertebrate assemblages of KD ponds had already been described in Herrmann et al. (2000), whereas the detailed macrofaunal composition of BA ponds has been published in Ruhí et al. (2009). Meteorological variables, obtained from the Swedish Meteorological and Hydrological Institute (SMHI) for KD region and from the Catalan Meteorological Service (SMC-Meteocat) for BA region, show the main characteristics of the respective climates (Figure 2).

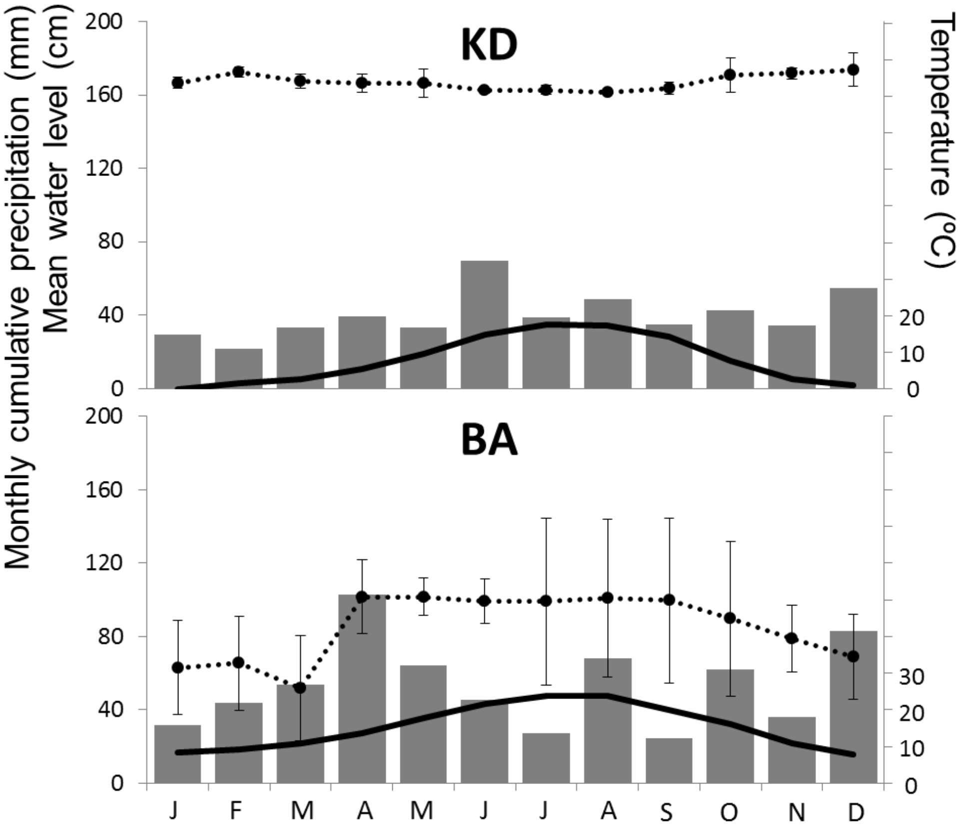

Figure 2. Main meteorological variables in KD and BA regions during the study. Bars represent the monthly cumulative precipitation (mm), continuous lines represent the monthly mean temperatures (°C) and discontinuous lines the mean water levels (cm) among ponds.

In addition, a literature-based meta-analysis was performed including data from man-made wetlands in 7 extra sites in order to determine if the patterns observed in KD and BA were generalized: Norway (Hov and Walseng 2003), Sweden (Herrmann 2011), Scotland (Lancaster et al. 2004) and England (Barnes 1983) in the cold temperate region; and Italy (Solimini et al. 2003) and two different sites in Catalonia (Ruhí et al. 2009) in the Mediterranean region.

Sampling and sample processing

Each pond was monitored during its three first years from creation (from winter 1996 until autumn 1999 in KD; and from winter 2006 to autumn 2009 in BA), and received 10 visits (four the 1st year, four the 2nd year and two the 3rd year) evenly spaced throughout each year. At each pond the water level (deepest point) was measured, and 3 replicates of water samples were collected, filtered and frozen upon arrival at the laboratory. Analyses of dissolved inorganic nutrients (ammonium, NH_4^+; nitrite, NO_2^-; nitrate, NO_3^- and soluble reactive phosphorus, PO_4^{3+}) from filtered samples were carried out according to Grasshoff et al. (1983).

In KD ponds, aquatic macroinvertebrates were sampled using a long-handled D-shaped dip-net (25 cm of inner width, 500-µm mesh). The dip-net was swept over a linear transect of 10 m approx., covering all microhabitats. In BA ponds, aquatic macroinvertebrates were sampled using a long-handled circled dip-net (20 cm diameter, 250-µm mesh), with a sampling procedure based on 20 dip-net sweeps (0.5 m approx. each) in a rapid sequence, also covering all different microhabitats. Although the sampling instruments between both wetland systems were slightly different, the applied effort was very comparable since the procedures operated very similarly, and both the opening of the devices (approx. 0.3 m^2) and the approximate integrated sampled length (10 m of bottom wetland) were the same. Moreover, as a solution to overcome the flaw of having used different mesh sizes between regions (500-µm in KD, 250-µm in BA), only specimens > 0.5 mm were considered in this study. In KD, samples were preserved in situ in 70 % ethanol, and in BA, in 4 % formalin. In both regions the invertebrate fauna was sorted, measured and identified in the laboratory, and the identification was carried out mostly at species level, except for Oligochaeta and Chironomidae, which were left at this resolution. Due to its lower taxonomical resolution, these groups were taken into account only when their inclusion did not imply a bias in the analyses. Platyhelminthes (Turbellaria), Annelida (Oligochaeta, Hirudinea), Mollusca (Bivalvia, Gastropoda) and Arthropoda (Malacostraca, Arachnida, Insecta) were the phylums and classes considered in this study.

Data analysis

In order to test for differences in water and environmental variables between regions, ANCOVAs were performed (*region* factor as fixed effect, *visit* as covariable). The variables included in the environmental matrix were: atmospheric temperature (monthly average), rain (monthly cumulative values), water level, concentration of dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP) and pH. All variables, except pH, were log-transformed using $\log_{10}$ (Var+1). Coefficients of variation were calculated for each variable. Additionally, hydrological stability was studied using the method described by Brownlow et al. (1994), based on cluster analysis of the water level frequencies for each pond, using group average as a conglomeration method and Manhattan distance as a similarity measure.

With the purpose of comparing between regions the extent to which the communities were random or non-random samples of the regional pool at the first year of existence (early samplings) and at the end of the study (late samplings), we selected a similarity profile routine (SIMPROF), a permutation procedure which tests for significant structure in a given matrix. If community structure was low, no significant differences should be found between our profile and the profile obtained by random combinations of the regional fauna. In contrast, a structured community should significantly differ from the random profile generated by the null model, indicating a dominance of pioneering taxa leading the colonization. Regional faunas were collated by pooling, for each region, the taxonomic lists of all samples and sites produced in this study. Then, the respective regional faunas were pooled into two separate lists (KD/BA regions) and four matrices were built, with the early (1-4) and late samplings (7-10) for each region. We then executed the test, which ordered Bray-Curtis similarities in composition for each group of samples. These similarities were plotted against their rank (Clarke et al. 2008), and the resulting profile was then compared with that expected under a simple null hypothesis of no meaningful structure within the matrix.

In turn, succession patterns were approached three different ways. Firstly, we aimed to analyze the structural and compositional changes that the community underwent during the study at each region. To this end, a non-parametric multidimensional scaling (MDS) allowed us to visualize if those changes presented a temporal pattern. Dissimilarity among ponds for a given visit was represented with a bubble gradient over the MDS diagram, and mean dissimilarities between successive samplings were calculated for each region. In order to test for differences between successive samplings, an ANOSIM (analysis of similarities) test was performed. This type of test operates on a resemblance matrix and is similar to a standard univariate ANOVA, but needs neither normality nor homoscedasticity of data. In order to compare the community (species abundance composition matrix) between regions, we aimed to take into account the time component, by choosing the 2-factor layout with *region* as the main factor (KD / BA) and *visit* (1 to 10) as a nested factor within *region*. The results showed a global R that ranged from 0 to 1 and a *p*-value expressed in percentage. When R was 0 or close to 0, similarities within groups and between groups were equivalent. In contrast, when higher values of R were obtained, more samples within the group resembled each other than they did between groups, differentiating groups that would correspond to samples from different levels of the factor. The distance matrix was built with Bray-Curtis similarity, based on a rectangular, originally standardized, and fourth-root transformed matrix.

Secondly, succession was also assessed by means of temporal changes in 4 biodiversity measures. These biodiversity parameters were: Armstrong index (A), Rarefied species richness (S), Average taxonomic distinctness (Δ+) and Variation in taxonomic distinctness (Λ+). The species turnover for each taxonomic group was calculated as the percentage of species that appeared and disappeared during the time between two consecutive visits. In order to compare the change rate between samples, succession rate was calculated following Armstrong index (Armstrong 1969) following the equation:

$$A_{ab} = \left[\sum_{i=1}^{n} \left(\frac{f_{ib} - f_{ia}}{b - a} \right)^{2} \right]^{1/2} \qquad f_{ia} = \frac{\frac{x_{ia}}{X_a} \log \frac{x_{ia}}{X_a}}{H_a}$$

where A_{ab} is the daily rate of assemblage change, taking into account the species contribution to the diversity change, b-a is the time interval in days, f_{ia} and f_{ib} are the contributions of the species i to the diversity of the days a and b, respectively, x_{ia} is the abundance of the species i at day a, X_a is the abundance of the whole assemblage at day a, and H_a is the diversity of the assemblage at day a. Rarefied species richness (S) was calculated using the rarefaction function ‘rarefy’ from ‘vegan’ library, written in R language (Oksanen et al. 2010). This procedure, inspired by Heck et al. (1975), calculates the estimated species richness for a number of individuals, simulating random draws of a fixed number of individuals, based upon the least abundant sample. Although rarefied species richness (S) is not an estimate of the total community richness, it permits an unbiased comparison between samples of unequal abundances. Therefore, it can also be regarded as a diversity measure, since for a given number of taxa it will increase with the evenness of the distribution of abundances among them (Lods-Crozet and Castella 2009). Two taxonomic distinctness indices (Average taxonomic distinctness, Δ+; and Variation in taxonomic distinctness, Λ+) were also chosen. Although biodiversity analyses have often been based only on species richness, assemblages comprising only taxonomically related species should be regarded as less diverse than others which host more distantly related species (Warwick and Clarke 1995, Abellán et al. 2006). Moreover, these indices show statistical properties robust to variations in experimental designs (Krishnakumar 2008) and are particularly recommendable when dealing with differing or uncontrolled degrees of sampling effort (Clarke and Warwick 2001b). Average taxonomic distinctness (Δ^+) represents the average path length in the phylogenetic tree connecting two random species of those collected, while Variation in taxonomic distinctness (Λ^+) measures the variance in pairwise lengths between each pair of species and reflects the unevenness of the taxonomic tree (Clarke and Warwick 2001b, Clarke and Gorley 2006). The taxonomic levels taken into account in this analysis were species, genus, family, order, class, subphylum, and phylum, and the same branch length was weighted for each taxonomic level. All four biodiversity parameters (A, S, Δ+ and Λ+) were tested for differences between regions by means of ANCOVAs (*region* factor as fixed effect, *visit* as covariable).

Thirdly, in order to explore the generality of the previously observed succession patterns, we performed a literature-based meta-analysis with our data and that obtained from seven other European sites (i.e. Barnes 1983, Hov and Walseng 2003, Solimini et al. 2003, Lancaster et al. 2004, Ruhí et al. 2009, Herrmann 2011). These studies were selected for meeting the criteria of (i) being focused on the macroinvertebrate community of man-made wetlands; (ii) dealing with the whole macroinvertebrate community, mostly at species level; and (iii) presenting ≥ 6 samples within the period 0 to 3 years of wetland age. Due to the different methodologies used in the chosen literature, taxonomic distinctness indices based on presence-absence data –Average taxonomic distinctness (Δ+) and Variation in taxonomic distinctness (Λ+)– were selected as surrogates for biodiversity, because of their statistical robustness towards different sampling efforts. These measures were calculated for each sample and their values were modeled by wetland age for each site, using linear and quadratic regressions.

Finally, in order to identify regional differences in biological traits composition, each trait category was assigned to each genus (ranging from 0 = no affinity; to 5 = high affinity), according to their affinity for each category. This technique, known as fuzzy coding (Chevenet et al. 1994) uses scores that in this case were extracted from Tachet et al. (2002) and were assigned to each taxa for each of the six biological traits considered and hypothesized in this study (Table 1). This procedure allowed us to build the species traits matrix, which was analysed by means of ANOSIM (same layout as previously stated). For each trait, a SIMPER (similarity percentages) allowed us to identify which categories explained more dissimilarity between regions. The test was performed under the simple layout, with *region* as factor and a cut off for low contributions at 90%. Categories which contributed more to dissimilarity, with values of Av. dissimilarity / SD > 1, were considered significant to discriminate regions.

SIMPROF, MDS, ANOSIM, SIMPER and clustering routines were performed with PRIMER-E v.6.1.11; ANCOVA tests and regressions were performed with the software package PASW v.18; and biodiversity parameters were calculated with PRIMER-E v.6.1.11 (taxonomic distinctness indices) and with R software v. 2.12.1 (Rarefied species richness).

Results

Regional differences on water and environmental variables

No significant interactions between *region* and *visit* factors were detected by the ANCOVA, indicating similar temporal trends of water and environmental variables between regions. Neither of the analysed water variables significantly varied between regions (DIN, $F_{1,65}=1.455$, $p = 0.232$; SRP, $F_{1,65}=0.033$, $p = 0.857$; pH, $F_{1,65}=3.783$, $p = 0.560$), nor did cumulative precipitation ($F_{1,65}=0.080$, $p = 0.778$). However, atmospheric temperature ($F_{1,65}=17.437$, $p < 0.001$) was higher in BA than in KD region, and water level ($F_{1,65}=76.825$, $p < 0.001$) also differed significantly between regions, with higher values in KD than in BA ponds (Figure 2). Except for nutrient concentrations, the rest of variables showed higher coefficients of variation in the Mediterranean (DIN: 58.8%; SRP: 37.8%; pH: 33.7%; precipitation: 77.9%; temperature: 91.3%; water levels: 43.1%) than in the cold temperate region (DIN: 73.9%; SRP: 40.6%; pH; 25.5%; precipitation: 49.7%; temperature: 38.3%; water levels: 3.5%). This fact was combined with a higher hydrological stability in KD ponds (< 5 % dissimilarity among visits) than in BA ponds (32 % dissimilarity), and a clear differentiation of samples between regions by this factor (Figure 3).

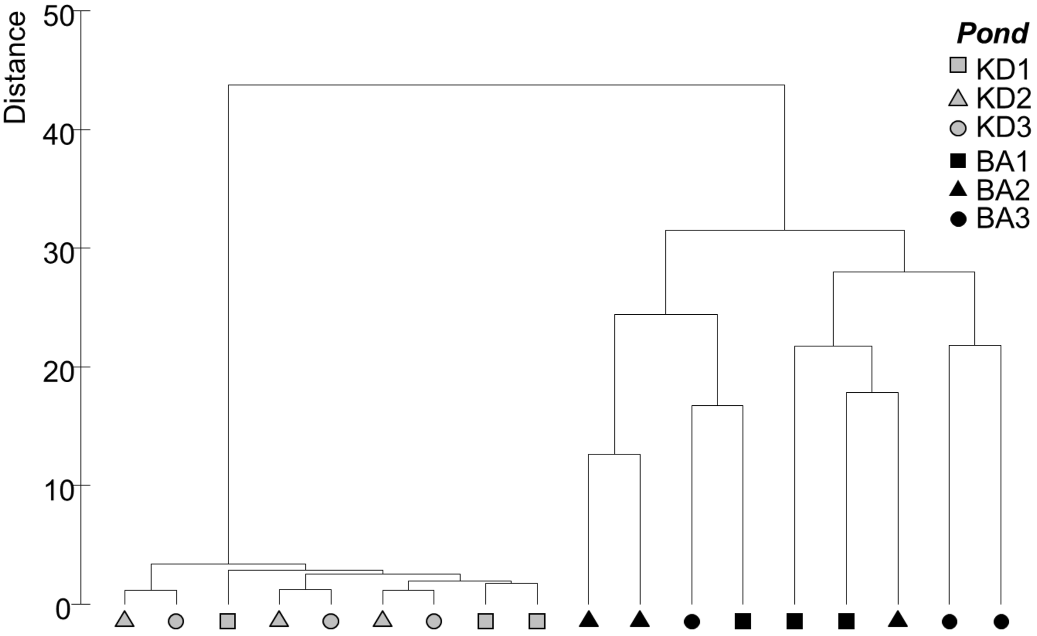

Figure 3. Hydrological stability diagram, following the method described by Brownlow et al. (1994). A clustering of the distances of the water level frequencies for each pond (throughout the study) was made, selecting group average as a conglomeration method and Manhattan distance as a similarity measure. Different symbols correspond to each pond (in grey, KD ponds; in black, BA ponds).

Deterministic vs. stochastic assembling mechanisms

Similarity profiles (SIMPROF) showed ordered similarities between species plotted against their ranks for real and permuted data (Figure 4). In KD region, non-random compositions were detected both in early (R = 5.905, $p = 0.001$) and late samplings (R = 4.529, $p = 0.001$): smaller and larger similarities between species pairs were observed than those expected by chance (higher and lower ranks, respectively). In early samplings, communities in BA were not significantly differently structured from what it would be expected by chance (R = 3.479, $p = 0.077$), whereas in late samplings the structure was higher (R = 2.939, $p = 0.040$).

Therefore, in the Mediterranean the community was assembled stochastically from the regional pool at least in early samplings, whereas in the temperate region deterministic subsets characterized both early and late samplings (Figure 4).

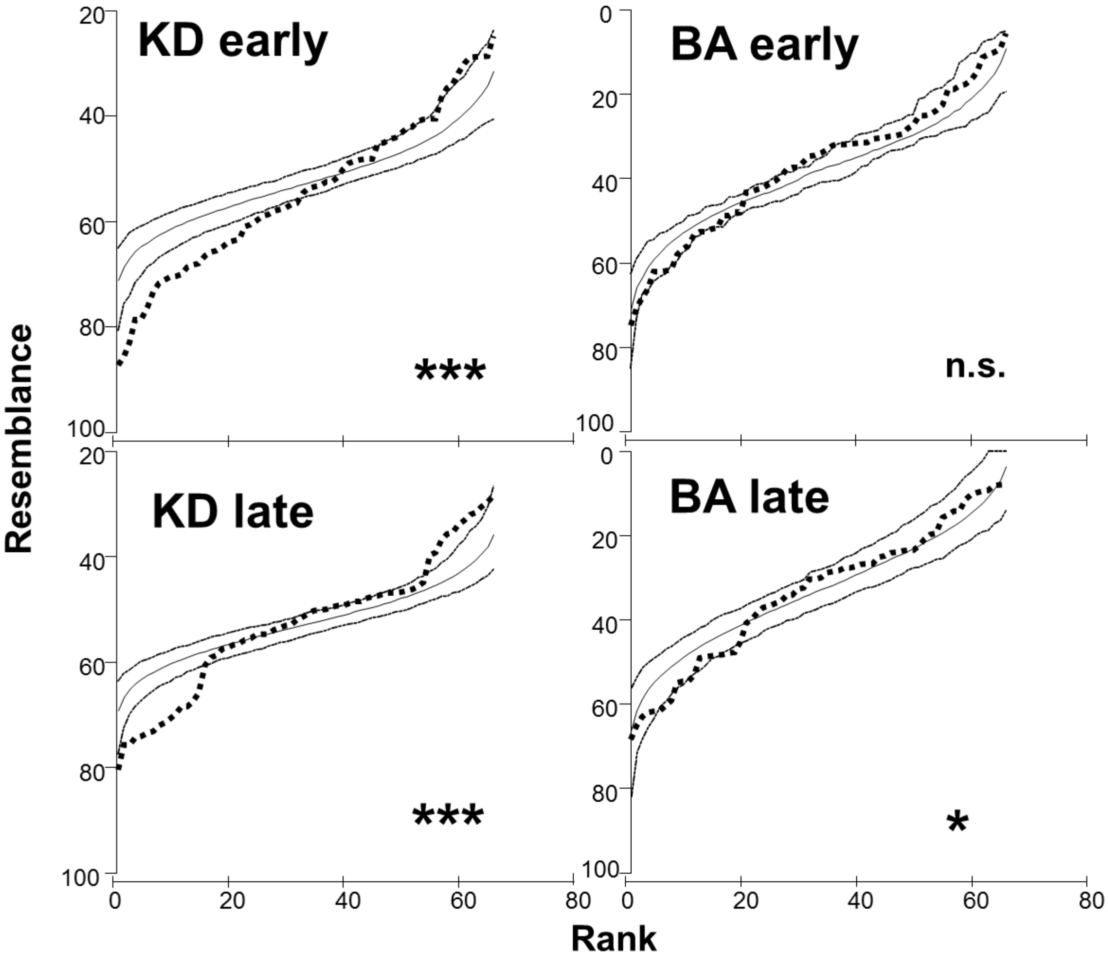

Figure 4. Similarity profiles (SIMPROF) showing ordered similarities between species in KD (early samplings / late samplings) and BA (early samplings / late samplings), plotted against their ranks for real (dashed lines) and permuted data (continuous lines). The mean of 999 permuted matrices and 95% confidence intervals depict the expected similarity profile. Resemblance indicates Bray-Curtis similarities. n.s., $p > 0.05$; *, $p < 0.05$; ***, $p < 0.001$.

Comparison of the succession patterns at regional scale

ANOSIM provided evidence of different compositions among visits within each region (R = 0.773, *p* = 0.001 in KD; R = 0.226, *p* = 0.003 in BA). In KD, the families which contributed > 1% to total abundance were Asellidae, 42.1%; Chironomidae, 33.8%; Corixidae, 9.7%; Baetidae, 4.2% and Planorbidae, 2.3%. In BA, these families were Baetidae, 35.4%; Corixidae, 15.6%; Notonectidae, 14.2% and Coenagrionidae, 1.4%. Furthermore, the overall compositional change (dissimilarity values between initial and final visits) was slightly higher in BA than in KD region (77.8 and 71.9%, respectively). The MDS plotted samples from KD region followed a repetitive circular trajectory through time, with the biggest gaps (corresponding to the highest dissimilarity values) between successive samplings being between samplings 3-4 (59 % dissimilarity) and 7-8 (53% dissimilarity), coinciding with summer periods. On the other hand, no such patterns were observed in samples from BA region (Figure 5).

The comparison of the succession patterns using the biodiversity parameters showed that Variation in taxonomic distinctness (Λ+) differed significantly between regions, whereas Armstrong index (A) was marginally significant (Table 2). More thorough examination into the temporal pattern of these parameters (Figure 6) showed that taxonomic distinctness indices tended to move towards the same direction (higher levels) in both regions (in agreement with the non-significant result of the interaction term between region and visit for these two metrics; Table 2), whereas Rarefied species richness (S) and Armstrong index (A) were divergent between regions (also according to the significant result obtained by the interaction term; Table 2): Rarefied species richness (S) tended to increase more in KD than in BA region, whereas the opposite was true for Armstrong index (A), with higher change rates in BA than in KD region. This latter pattern was divergent also in another important aspect: in KD region Armstrong index presented highest values in summer and lowest in winter, whereas the opposite occurred in BA region (Figure 6).

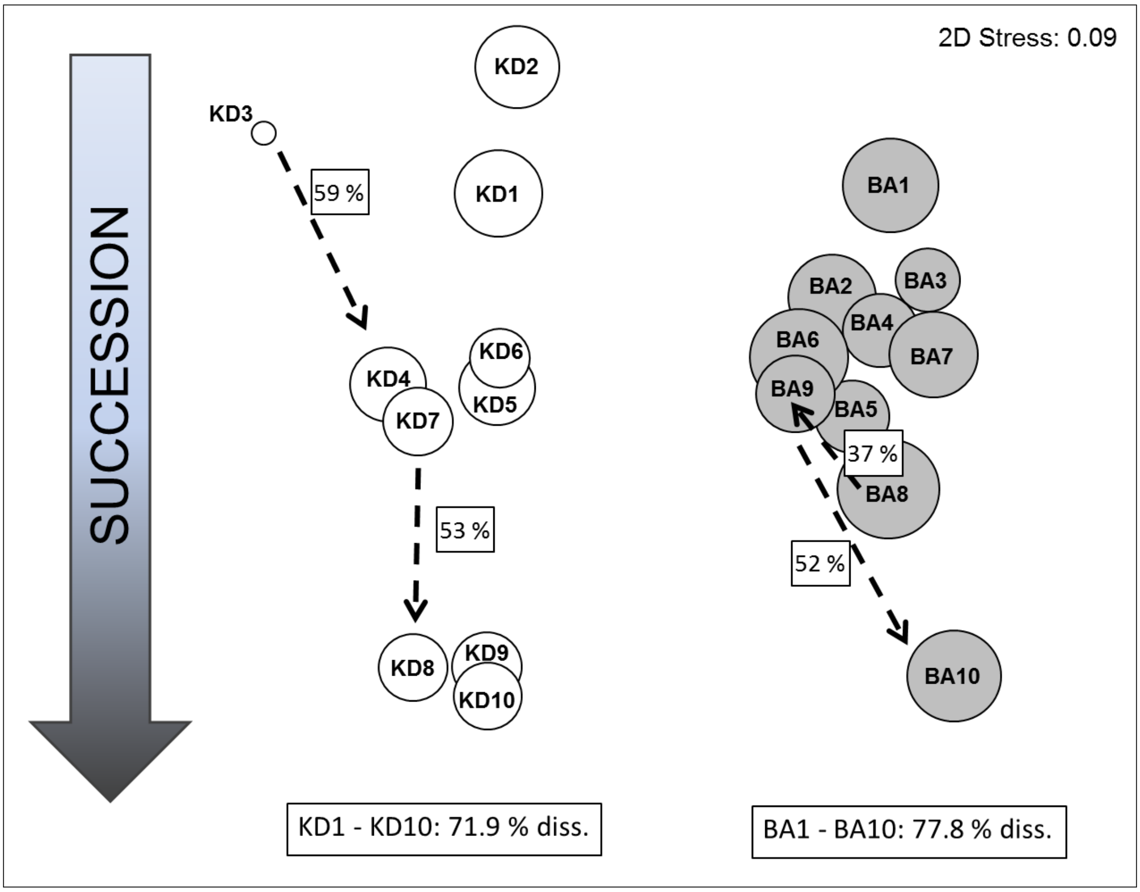

Figure 5. MDS diagram of the invertebrate compositions of KD and BA through the 10 visits. Abundances were fourth-root transformed and Bray-Curtis was selected as a similarity distance. Dissimilarity among ponds for a given region and visit is represented by means of a bubble gradient: the position of the bubble is the among-sites centroid, whereas the size of the bubble represents the among-sites dissimilarity (the bigger the bubble it is, the higher are the compositional differences among wetlands within that area and visit).

Table 2. Biodiversity parameters analysed with ANCOVA, with *region* factor as fixed effect and *visit* factor as covariable (A, Armstrong index; S, Rarefied species richness; Δ+, Average taxonomic distinctness; Λ+, Variation in taxonomic distinctness).

		A			**S**			**Δ+**			**Λ+**	
	df	F	*p*	df	F	*p*	df	F	*p*	df	F	*p*
Region	1	3.845	0.056	1	0.244	0.623	1	0.968	0.330	1	4.598	0.037
Visit	1	0.192	0.663	1	5.149	0.028	1	14.916	0.000	1	15.862	0.000
Region * Visit	1	8.799	0.005	1	11.156	0.002	1	0.047	0.829	1	0.482	0.491

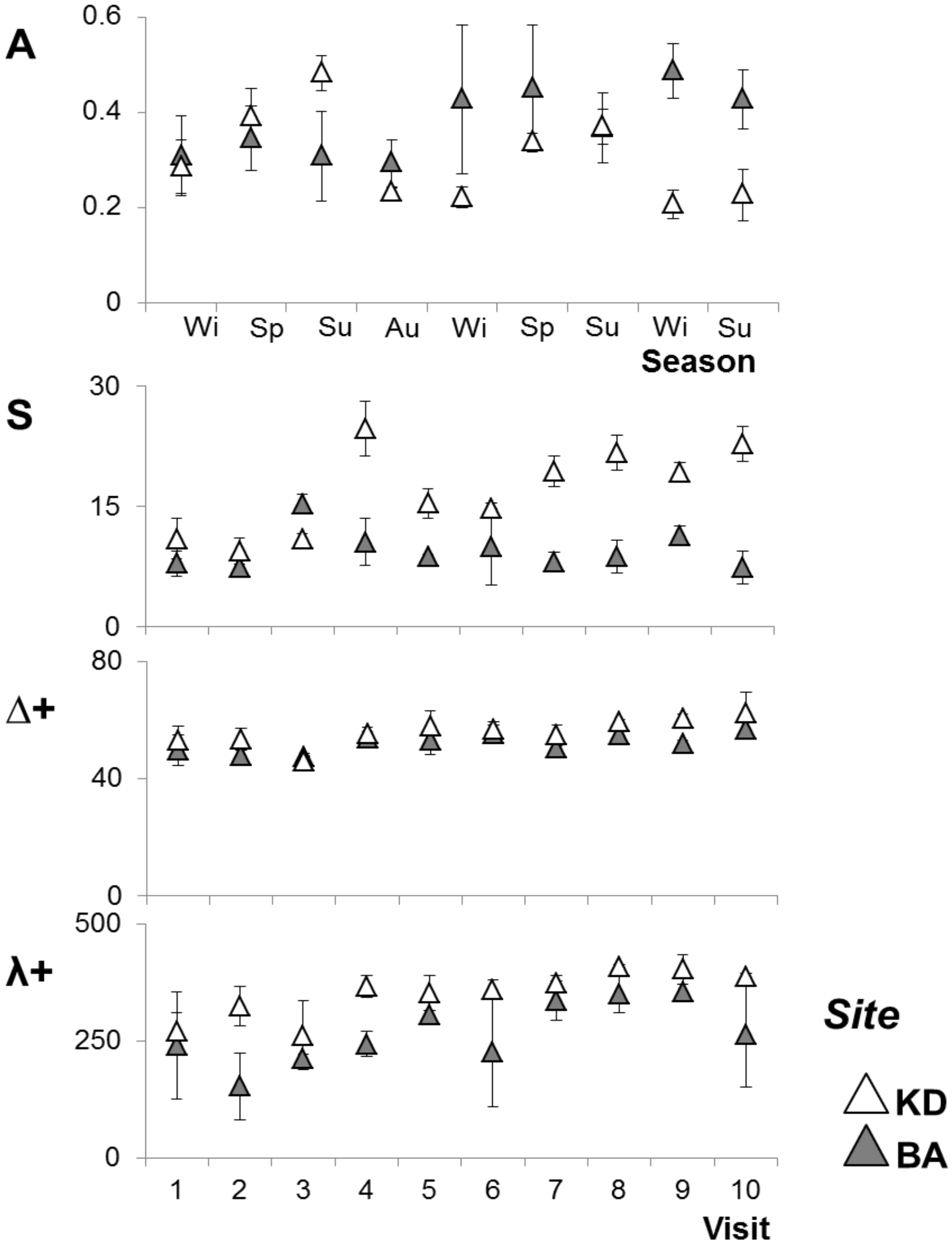

Figure 6. Trends of the succession community parameters through visits (1 to 10) and seasons (Wi = Winter, Sp = Spring; Su = Summer; Au = Autumn): Armstrong index (A), Rarefied species richness (S), Average taxonomic distinctness (Δ+) and Variation in taxonomic distinctness (Λ+).

Meta-analysis of successional patterns between cold temperate and Mediterranean systems

The generality of the observed patterns was tested by means of two taxonomic distinctness indices (selected as biodiversity surrogates) performed over our data as well as sites located at North (NOR, SWE, SCO, ENG) and South latitudes (CBT, CPS, ITA). Whereas mean values of Average taxonomic distinctness (Δ+) and Variation in taxonomic distinctness (Λ+) during the analysed period varied among sites without a clear pattern (Table 3), the temporal changes of these measures through time were more revealing (Figure 7): from the four sites in the South (Mediterranean region), only BA presented a significant linear relationship with time (for Δ+). In contrast, all 5 sites in the North (cold temperate region) presented significant relationships for both Δ+ and Λ+ by wetland age.

Biological traits patterns at regional scale

The analyses detected a significant regional effect for 5 out of the 6 selected traits. Moreover, 9 out the 10 significant categories (explaining higher levels of dissimilarity between regions, Av. diss. / SD > 1) were in agreement with the raised hypotheses. Multivoltine taxa dominated in BA ponds whereas semivoltine taxa were significantly present in KD. Regarding reproduction strategies, ovoviviparity (the only significant divergent catagory) and free clutching were favored in KD region, whereas terrestrial clutches dominated in BA. Organisms with eggs/statoblasts as resistance forms were significantly associated to BA, whereas taxa without any resistance strategy identified KD ponds. Aerial respiration (by means of spiracle) was significantly found in BA; and psychrophilic and thermophylic taxa were significantly found in KD and BA regions respectively (Table 4). Overall, with the exception of ovoviviparity, BA contrasted to KD dominant traits composition because categories associated to that region were mostly that conferring resilience from or resistance against hydrological disturbances.

Table 3. Meta-analysis of several published studies on invertebrate colonization in man-made wetlands across Europe (ordered latitudinally). Mean ± standard deviation values of Average taxonomic distinctness (Δ+) and Variation in taxonomic distinctness (Λ+) for all samples are shown. [* = In some cases studies could present further samples corresponding to > 3 years of wetland age, but only those within the range 0 to 3 years were selected for the sake of comparison.]

Id.	**Site (Country)**	**Study**	**Wetland ages (range)***	**Samples (analysed N)***	**Δ+ (mean±SD)**	**Λ+ (mean±SD)**
NOR	Trogstad (Norway)	Hov and Walseng (2003)	1 to 3 years*	12*	57.9 ± 11.9	389.8 ± 208.1
KD	Kalmar Dämme (Sweden)	This study	0 to 3 years	30	64.0 ± 5.7	380.4 ± 60.9
SWE	Skalby Dämme (Sweden)	Herrmann (2011)	0 to 3 years	32	59.9 ± 5.1	337.1 ± 78.7
SCO	Dunfermline (Scotland, UK)	Lancaster et al. (2004)	1 to 3 years*	12*	62.2 ± 13.2	390.9 ± 156.4
ENG	Dorset (England, UK)	Barnes et al. (1983)	1 to 3 years*	6*	54.0 ± 0.9	221.6 ± 39.4
BA	Pla de l'Estany (Catalonia, Spain)	This study	0 to 3 years	30	61.7 ± 6.9	307.2 ± 137.3
CBT	Baix Ter (Catalonia, Spain)	Ruhí et al. (2009, plus additional data)	0 to 3 year	36	63.5 ± 16.9	198.4 ± 174.4
CPS	Plana de la Selva (Catalonia, Spain)	Ruhí et al. (2009, plus additional data)	0 to 3 year	20	49.5 ± 8.6	76.5 ± 95.8
ITA	Rome (Italy)	Solimini et al. (2003)	1 to 3 years	8	67.4 ± 6.5	394.4 ± 82.5

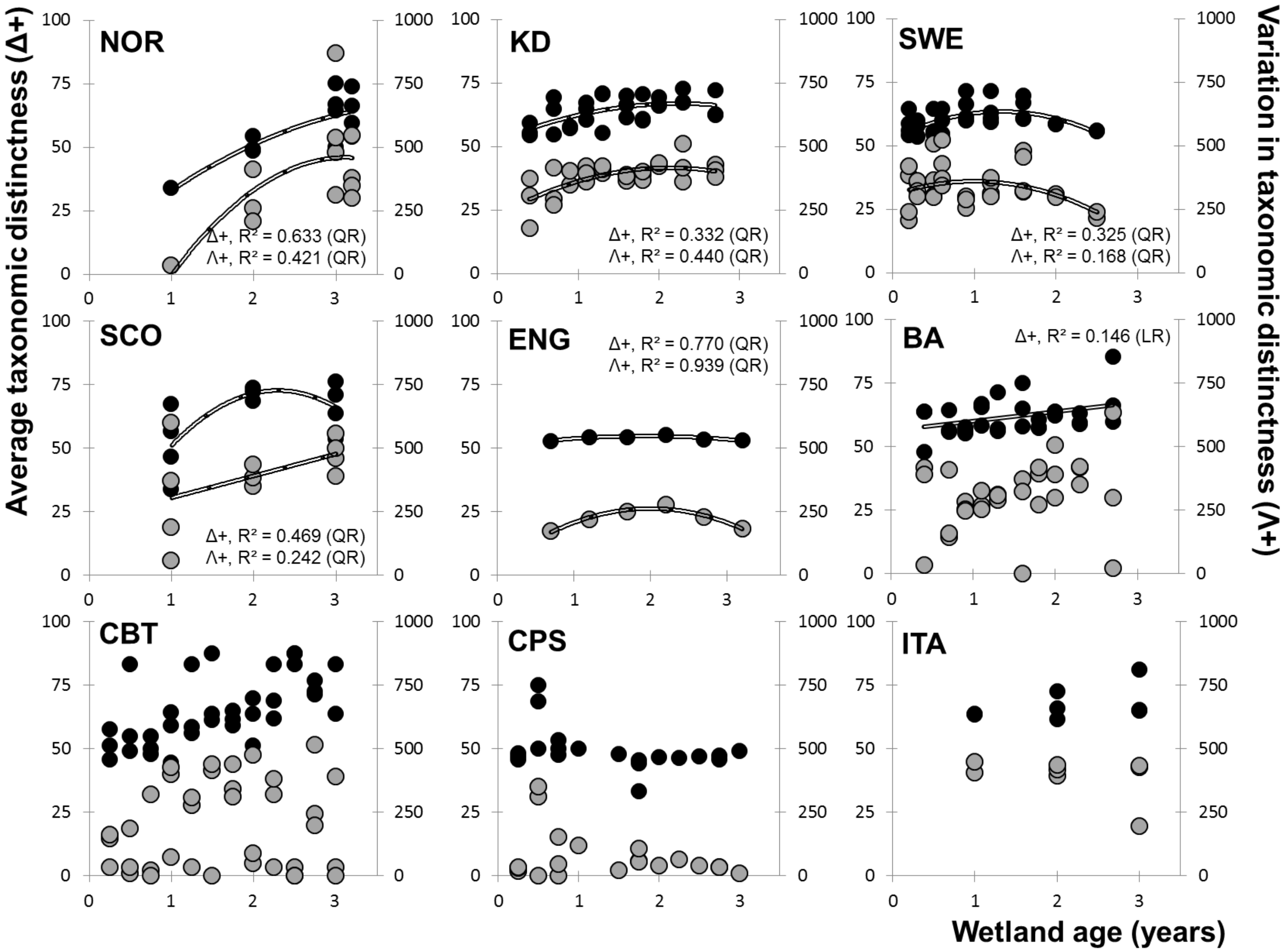

Figure 7. Meta-analysis of the temporal trends among nine European sites of Average taxonomic distinctness (Δ+), in black, and Variation in taxonomic distinctness (Λ+), in grey. Relationships between each biodiversity parameter and wetland age were tested by means of linear and quadratic regressions (the best regression and fit is shown: LR = linear regression, QR = quadratic regression); R^2 of the best relation is shown.

Discussion

Assembling mechanisms and successional patterns

The study of community structure during the colonization of available niches has been an important issue under discussion both in animal (Ranta and As 1982, Kukert and Smith 1992) and plant communities (Kadmon 1995, Butaye et al. 2001). Current conceptual models of spatiotemporal dynamics of primary succession generally assume an initial random composition from the regional pool of recruiters during the very first stages of colonization, followed by a subsequent development of the community that may follow different models depending on the system stability and the strength of positive (facilitation) and negative (competition) interactions between the colonizers (Cutler et al. 2008). In our case, stochastic subsets of the regional fauna were obtained during the early samplings in Mediterranean but not in temperate ponds: in the latter we observed deterministic assembling mechanisms already in early samplings. This fact could be explained by a differential prevalence of high/low colonizers between regions (i.e., if more species were able to colonize in the Mediterranean rather than in the cold temperate region, local random subsets of the regional pool would be more easily obtained). However, we believe this was not the case in our study, since neither global richness values (Table 2), nor the percentage of active/passive dispersers (88% in BA, 86% in KD) differed between areas. Supporting these findings, active dispersers dominating early successional communities have been described from man-made wetlands in both the Mediterranean and cold temperate regions (e.g., Koskenniemi 1994, Herrmann et al. 2000, Ruhí et al. 2009). Alternatively, we believe the precocity of temperate ponds in presenting structure may be a consequence of the lower performance of active dispersers under unfavorable conditions (Bilton et al. 2001). Hence, similarly to what occurs during colonization of extreme ecosystems without previous biological legacy (e.g. glacier forelands, Kaufmann 2001), the dominance of a very small number of pioneer taxa may either facilitate or act as a barrier towards secondary colonizers already in the first stages of succession (Felinks and Wiegand 2008). In contrast, in warmer climates more favorable time to disperse may imply more colonizing opportunities for more taxa simultaneously, and therefore, lower structures reflected into higher resemblances between the local pioneer subset and the regional pool (Benzie 1984, Farnon Ellwood et al. 2009). Macroinvertebrate communities assembling deterministically due to the effect of low temperatures have already been observed in close latitudes (e.g., Milner and Robertson 2010, identified 7ºC as being the threshold between determinstic and stochastic assembling mechanisms in streams in Glacier

Bay, SE Alaska). Overall, our findings support the idea that climate-dependent environmental variables may condition the assembling mechanisms of a community through succession (Milner et al. 2008, Lepori and Malmqvist 2009, Milner and Robertson 2010).

Although a large portion of wetland fauna are noted for their colonizing abilities (Batzer and Wissinger 1996, Batzer et al. 2006), few studies have quantified colonization rates (Bohonak and Jenkins 2003). Decelerating increases in species richness and turnover rates have been identified as regularities characterizing post-colonization phases in ecological succession (Connell and Slatyer 1977, Anderson 2007, Santos et al. 2011). In our study, the measured change of community structure was assessed by means of four parameters. On one hand, the contrasting patterns of Rarefied species richness (S) and Armstrong index (A) observed at a regional scale may reflect two different aspects: (1) contrary to that expected, ponds in the cold temperate region seemed to reach within the same time a more advanced successional phase than those in the Mediterranean region; and (2) in the temperate region, intervals with highest/lowest change between successive samplings were related to favorable/unfavorable conditions for active dispersers, whereas in the Mediterranean this pattern was not detected. The strong correspondence of high successional values (colonization peaks) in KD with summer season can be explained by the achievement of temperature thresholds for certain species, since this variable plays a role in triggering the dispersal of aquatic heteropterans and coleopterans (Velasco et al. 1998). Lundkvist et al. (2002) and Boda and Csabai (2009a) also identified air temperature as an important variable explaining active dispersion in these groups, and a particular studied coleopteran species (*Helophorus brevipalpis*) was proven to disperse a month earlier in Spain (Miguélez and Valladares 2008) than in Sweden (Landin and Stark 1973, Landin 1980). However, while temperature might well explain the expected dynamics in KD ponds (Bilton et al. 2001, Cáceres and Soluk 2002), in BA other factors probably prevailed.

On the other hand, Average (Δ+) and Variation in taxonomic distinctness (Λ+) tended to increase by time in both regions, implying a more taxonomically diverse but uneven tree towards the end of the study: more species arrived, yet these species were not equally distributed but concentrated in a few taxonomic groups, each of which tended to be relatively more species-rich (Clarke and Warwick 2001b). However, the latitudinal meta-analysis showed that this relation was not as clear in the Mediterranean as it was in the cold temperate region. Whereas sites in the Mediterranean region did not present a significant relationship between the selected biodiversity surrogates and wetland age, in the cold temperate sites the relationship was clear and communities presented an inflection point for both parameters between 2-4 years. Although these results could be suffering a time-limited approach (Barnes 1983, Friday 1987, Fairchild et al. 2000, Bloechl et al. 2010), they are consistent with those obtained in a long-term study (13 years) carried out in KD, where high levels of Δ+ were combined with a decreasing Λ+ towards late successional stages, resulting in a taxonomically diverse and even tree (Ruhí et al. in press). Overall, the lack of relation between Δ+ or Λ+ with wetland age in the Mediterranean sites might be a latitudinal confirmation of the previous regional results, namely, higher structure levels and clearer successional patterns in the cold temperate rather than in the Mediterranean region. Although conditions whose effects cannot be separated may operate together in preventing Mediterranean communities from clearer seasonal and successional patterns, we believe the most plausible factor is the high hydrological variability characteristic of these wetlands (Álvarez-Cobelas et al. 2005, Beklioglu et al. 2007). In fact, this has been identified to be the main factor determining the composition and community structure in newly created Mediterranean wetlands (Ruhí et al. 2009) as well as in natural ones (Gascón et al. 2005, 2008).

Biological traits patterns

Selecting forces work at several hierarchical geographical levels, so that large-scale filters may successively constrain the expression of local selective forces or biotic potential, and ultimately a regional pool of species in a locality represents the range of adaptations that have passed through this ecological sieve (Poff 1997). Hence, an analysis of the functional attributes (biological traits) of a particular community should reflect the successive “filterings” this community has undergone (Townsend and Hildrew 1994, Gasith and Resh 1999, Bonada et al. 2007), thus at the same time the functional variability compared between large regional scales should synthesize large-scale filters such as climate characteristics (Poff and Ward 1990).

As we hypothesized, the traits favoring resistance against and resilience from hydrological disturbance (>1 potential number of cycles per year, terrestrial egg clutches, existence of resistance forms to avoid desiccation and thermophylic organisms) had been enhanced in the Mediterranean region, contrasting to those dominating in the cold temperate region (<1 potential number of cycles per year, free clutches, no resistance forms against desiccation and psychrophylic organisms). Similar results were found in stream macroinvertebrate traits by Bonada et al. (2007), such as multivoltinism, terrestrial clutches and aerial respiration typifying Mediterranean vs. cold temperate streams. However, some traits were dependent of the habitat under study. For example, the hypothesis of higher abundances of traits having specialized techniques of respiration in Mediterranean rivers, compared to temperate regions

(Bonada et al. 2007) could not be applied directly to wetlands, taking into account that in these systems, the lack of flow prevents a constant concentration of oxygen in the water, being “lentic” respiratory adaptations similar to that of insects specialized in inhabiting pools in streams (Huryn et al. 2008). On the other hand, the non-significant results for dispersal traits probably showed similar dispersal strategies for lentic organisms regardless of the region, an observation coherent with the high dominance of active dispersers observed in colonization studies in the temperate region (Koskenniemi 1994, Herrmann et al. 2000, Lods-Crozet and Castella 2009) but contrasting with the findings of Bonada et al (2007) for lotic habitats. This interpretation could be also applied to the relationship of ovoviviparity strategies in the cold temperate region, which disagreed with the *a priori* hypothesis, and may probably be explained by the high abundance in the temperate region of a particular family (Asellidae) which holds this strategy (Wilson 1991). Compared with changes in taxonomic composition, biological traits within a region may also be susceptible to change. Bêche and Resh (2007) identified meteorological variability within a site to have a relevant effect over the trait community, noting that biological traits which conferred strategies against the drying out (i.e.. resistance strategies, aerial respiration) were more common during drought than in wet years.

Table 4 (opposite page). Results of the ANOSIM and SIMPER tests over the traits matrix, performed with each of the six biological traits for invertebrates considered in the present study. ‘Hypothesis’ column shows if the obtained result is in consonance with the corresponding raised hypothesis for the particular category. White cells = lower values; grey cells = higher values (Av. abundance per region). n.s. = SIMPER not performed, due to a non-significant ANOSIM test. Categories shown in bold are those explaining more dissimilarity, for which the SIMPER analysis provided values of Av. Diss / SD > 1.

TRAIT	ANOSIM	CATEGORY		SIMPER		Hypothesis
				KD	BA	
1. Potential number of cycles per year	R = 0.068 *p* = 0.009	**1.1**	**< 1**	■		**agreement**
		1.2	1	■		agreement
		1.3	**> 1**		■	**agreement**
2. Reproduction	R = 0.138 *p* = 0.001	**2.1**	**ovoviviparity**	■		**disagreement**
		2.2	isolated eggs, free		■	disagreement
		2.3	isolated eggs, cemented		■	disagreement
		2.4	clutches, cemented or fixed		■	disagreement
		2.5	**clutches, free**	■		**agreement**
		2.6	clutches, in vegetation		■	disagreement
		2.7	**clutches, terrestrial**		■	**agreement**
		2.8	asexual reproduction		■	agreement
3. Dispersal	R = 0.022 *p* = 0.128	3.1	aquatic	n. s.		–
		3.2	aerial passive			
		3.3	aerial active			
4. Resistance forms	R = 0.177 *p* = 0.001	**4.1**	**eggs, statoblasts**		■	**agreement**
		4.2	cocoons		■	agreement
		4.3	housings against desiccation	■		disagreement
		4.4	diapause or dormancy	■		disagreement
		4.5	**none**	■		**agreement**
5. Respiration	R = 0.071 *p* = 0.011	5.1	tegument		■	disagreement
		5.2	gill	■		agreement
		5.3	plastron		■	agreement
		5.4	**spiracle (aerial)**		■	**agreement**
6. Temperature	R = 0.052 *p* = 0.036	**6.1**	**psychrophilic**	■		**agreement**
		6.2	**thermophilic**		■	**agreement**
		6.3	eurythermic	■		disagreement

Moreover, some authors have pointed out that functional responses among organisms may be undergoing a slow but steady shift as a consequence of climate change (Parmesan and Yohe 2003, Parmesan 2006). Because of this reason, it has been suggested that creation and restoration of wetlands should be made with future climate predictions in mind (Erwin 2009). In this sense, we also believe that a better understanding of expected changes in colonization and primary succession patterns is needed to predict the mechanics of ecosystem development, especially in environments subject to high variability and/or disturbance.

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CHAPTER 4. Change in biological traits and community parameters of macroinvertebrates through primary succession in a man-made Swedish wetland

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Abstract

We investigated the successional development of a benthic macrofaunal community in Kalmar Dämme, a man-made wetland in southeastern Sweden, over a 13-y period after construction (1997–2009). We assessed primary succession by monitoring changes in species composition, biological traits, and community structure. Predictable successional changes occurred, and the structure of the community was complex at the advanced phase. Three successional phases were observed, each with typifying species. At the advanced phase, dominant biological traits shifted to favor animals with longer life-cycle durations, aerial dispersal strategies, and certain feeding types (i.e., filter-feeders, fine sediment collectors, predators, and parasites). We selected the Coleoptera assemblage to represent the macroinvertebrate community in an evaluation of the extent to which man-made wetlands in different age classes (<3 y and ≥10 y) were similar to natural wetlands (>50 y). No significant differences in Coleoptera assemblages were found between natural wetlands and man-made wetlands ≥10 y. However, man made wetlands ≥10 y had significantly higher coleopteran species richness than natural and man-made wetlands <3 y because of the convergence of pioneering species persisting from early successional stages with representative specialized taxa from natural wetlands. Our results suggest that 10 y may be sufficient time for the macrofaunal communities of man-made wetlands to resemble those of natural wetlands.

Introduction

Succession can involve large numbers of species and important changes in community structure (Smith 1928, Odum 1960, Gutierrez and Fey 1980). These changes usually are associated with different successional phases, each with its own stable point, moving in a particular direction (Allen et al. 1977, Niell 1981, Legendre et al. 1985). Succession has been studied during the process of recovery after major disturbances, such as fires, hurricanes, or droughts (Force 1981, Smith 1982, Kaufman 1983). However, newly created aquatic habitats also are optimal systems in which to study and test successional dynamics. Research on man-made aquatic systems has expanded over the last decade (Oertli et al. 2005) because they tend to be easy to monitor and regulate. Nevertheless, most studies done in newly created wetlands are short-term (<3 y), which is a critical limitation when assessing ecological functioning (Zedler and Callaway 1999). For example, studies focused on the mitigation of wetland loss to conserve amphibians have shown that detailed, qualitative, and long-term observations are essential for a correct evaluation of their conservation value (Pechmann et al. 2001, Petranka et al. 2003, Petranka et al. 2007). Furthermore, short-term approaches are restrictive when studying invertebrate communities in these systems because the initial years are dominated by pioneer assemblages (Bloechl et al. 2010). Hence, these studies may assess initial colonization successfully, but usually do not detect later changes in assemblage structure and organization (Barnes 1983, Friday 1987). A small number of pioneer colonizers may explain the main differences between assemblages in created vs natural water bodies (Ruhí et al. 2009). Moreover, for some particularly species-rich taxa with specialized feeding structures (e.g., Coleoptera; Lundkvist et al. 2001, Thiere et al. 2009), succession may continue for >10 y (Fairchild et al. 2000).

Increases in biomass and diversity during succession were hypothesized in earlier general ecology papers (Margalef 1968, Odum 1971, Gutierrez and Fey 1980, Legendre et al. 1985), but unimodal (hump-shaped) changes in biomass and diversity over time have been described when the scale of measurement was long enough to include several stages of succession (Guo 2003). In freshwater systems, abundance/density and taxonomic richness of macroinvertebrates tend to increase during the first years of succession (e.g., in new reservoirs; Voshell and Simmons 1984, Bass 1992), but asymptotic patterns tend to appear when studies are longer (e.g., 20-y study of a deglaciated stream; Milner and Robertson 2010). Despite the paucity of published research in newly created wetlands, available studies suggest that new taxonomic groups tend to arrive in a directional successional process (Barnes 1983, Herrmann et al. 2000, Solimini et al. 2003, Ruhí et al. 2009). Thus, changes in community structure should be reflected by measures of taxonomic distinctness (Clarke and Warwick 2001a). Successional changes usually have been described taxonomically, but they also should be apparent in analyses of functional characteristics of the organisms (Hooper et al. 2005, Verberk et al. 2008). Batzer and Wissinger (1996) pointed out that changes in species composition of establishing communities could be a consequence of the favored life-history strategies (i.e., dispersal capacity, desiccation resistance, trophic specialization). The hypotheses and rationale proposed by Townsend and Hildrew (1994) and Bonada et al. (2007) relating the presence of traits favoring resistance/resilience to ecological disturbance in streams also could be relevant to understanding succession in new wetlands.

Our study goal was to describe the main changes of a macrofaunal community in a man-made wetland and to analyze whether the community eventually resembled that of a natural one. The biological traits and community structure of the macroinvertebrate community of a newly created wetland were monitored for 13 y. We predicted that: 1) taxa with short life cycles and active dispersing mechanisms would dominate immediately after flooding and during the initial phases of succession, whereas taxa with long life cycles and passive dispersal mechanisms would increase in importance during the later phases; 2) the dominant feeding type would shift during succession from taxa that consume suspended matter and primary production to those feeding on prey, hosts and abundant fine particulate organic matter; 3) species richness and evenness would increase during early successional stages; 4) species richness and evenness would decrease and cumulative richness and numerical abundance would reach asymptotes during later successional stages; and 5) average taxonomic distinctness would be higher and variation in taxonomic distinctness would be lower in late than early stages during succession (Table 1).

We also compared the macroinvertebrate community in the study wetland with those in other man-made (<3 y and ≥10 y old) and natural wetlands. We used aquatic Coleoptera as a surrogate for the entire insect community because coleopterans have been identified as a potential biodiversity indicator in continental European aquatic ecosystems (Foster et al. 1989, Sánchez-Fernández et al. 2006). We expected the composition of the Coleoptera in old man-made wetlands to converge on composition in natural wetlands subsequent to the arrival of late-colonist specialist taxa to old man-made wetlands. In contrast, we expected the community in young man-made wetlands to be dominated by pioneering generalist taxa and, therefore, different from the community in old man-made wetlands. Thus, we predicted higher species richness in natural and old man-made wetlands than in young ones.

Table 1. Hypotheses and rationale for community structure and biological traits considered in the macroinvertebrate study. + and – indicate expected high and low values, respectively.

Trait	Trait state	Succession early	Succession →adv.	Rationale	References
No. reproductive cycles/y	>1	+	–	Stable environments should favor species with longer life-cycle, long life spans, and late maturity	Townsend and Hildrew 1994, Bonada et al. 2007
	≤1	–	+		
Dispersal strategies	Aquatic	–	+	Arrival probabilities of aquatic dispersers should increase with time; aerial active dispersal strategies favored during the 1st phases of a hydroperiod; aerial passive strategies require more time	Danell and Sjoberg 1982, Bass 1992, Batzer and Wissinger 1996, Bonada et al. 2007
	Aerial active	+	–		
	Aerial passive	–	+		
Feeding strategies	Plant eaters (scrapers + herb. piercers)	+	–	Response to early availability of periphyton and macrophytes	Bonada et al. 2007, Ruhí et al. 2009
	Filter-feeders	+	–	Response to early availability of seston and plankton	Voshell and Simmons 1984
	Shredders	+	–	Response to early availability of macrophytes and large terrestrial litter	Voshell and Simmons 1984
	Fine sediment collectors	–	+	Response to the increase of fine particulate organic matter in the sediments	Bonada et al. 2007
	Predators (engulfers + animal piercers)	–	+	Response to increased abundance of prey; more important than the initial dominance of aerial colonizing predators (e.g., diving beetles and hemipterans)	Batzer and Wissinger 1996, Schneider and Frost 1996, Bloechl et al. 2010
	Parasites	–	+	Response to the increase of the abundance of potential hosts	–

Table 1. (cont.)

Community parameter			
Numerical abundance	– +	Production of the system results in increased numerical abundance of macroinvertebrates with a maximum during advanced successional phase	Margalef 1968, Odum 1971, Gutierrez and Fey 1980, Legendre et al. 1985, Guo 2003
Average taxonomic distinctness	– +	Increased taxonomic diversity and evenness as succession proceeds; arrival of new and taxonomically diverse species should be spread across several taxonomic groups and richness of a few species-rich pioneer groups should decrease over time	Inferred from published faunal lists in: Barnes 1983, Christman and Voshell 1993, Herrmann et al. 2000, Hov and Walseng 2003, Solimini et al. 2003, Lancaster et al. 2004, Ruhí et al. 2009
Variation in taxonomic distinctness	+ –		
Pielou's evenness index	– + –	Evenness and rarefied species richness should attain maximum values during the intermediate phases of succession; arrival of new species should be limited toward an asymptote in a mature community, where a high proportion of the ecological niches are already occupied	Margalef 1968, Batzer and Wissinger 1996, Guo 2003, Milner and Robertson 2010
Rarefied species richness	– + –		
Cumulative species richness	– +		

Materials and methods

Study area

Macroinvertebrate study.—The macroinvertebrate study was carried out at Kalmar Dämme (Fig. 1A, B), which is on the southeastern coast of Sweden. This site consists of a man-made freshwater wetland that was constructed (i.e., excavated and flooded) in late 1996. This freshwater system is fed by the Törneby stream and is situated 2 km from the stream outlet into the Baltic Sea (Fig. 1C). The drainage basin (48 km^2) of the wetland is mainly agricultural, but also includes large forested areas, a few urban areas, and the regional Kalmar Airport. The wetland consists of several connected elongated waterbodies <2 m in depth that are vegetated with belts of common reed (*Phragmites australis*), bullrush (*Typha latifolia*), common water plantain (*Alisma plantago-aquatica*), and branched bur-reed *(Sparganium erectum*). Some submerged plants were planted immediately after construction of the wetland. Initially, the most abundant submerged species were the Canadian waterweed (*Elodea canadensis*) and the spiked Eurasian water milfoil (*Myriophyllum spicatum*). However, both species became less abundant in later years. In addition, several species of fish were present from the time of the initial flooding. The system was designed and built to reduce N levels to 50% of the annual amount of urea-N discharged at the airport. This objective was met by the 2nd y (1998) after construction (based on monthly data from a wetland monitoring program run by the Kalmar Airport authority). A 2nd design objective was to promote aquatic biodiversity (Herrmann et al. 2000).

Coleoptera study.—We did the Coleoptera study in 6 man-made and 10 natural wetlands, which were selected as reference sites (Fig. 1B). To the best of our knowledge, all wetlands were permanent. Three man-made wetlands (Kalmar Dämme, Ljungbyholm, and Resby) were ≥10 y old and 3 (Överstatorp, Rockneby, and Tingby) were 1- to 3-y old at the time of sampling. We chose 10 natural wetlands with different levels of vegetation structure and substratum type from the mainland and the adjacent island of Öland to encompass a broad range of natural variability. The 10 natural wetlands were Arby Dämme, Björkerumsdammen, Bollmossen, Brudhyltetjärn, Glömminge, Igelmossen, Kolboda Hagby, Lenstamossen, Nytorpskärret, and Tyska Bruket. Six of these wetlands were definitely natural in origin, but the origin of Björkerumsdammen, Bollmossen, Igelmossen, and Tyska Bruket was unknown. However, none of the 10 wetlands had been affected by human activity for ≥50 y. See Table 2 for information about the creation of the man-made systems and the characteristics of all 16 study sites.

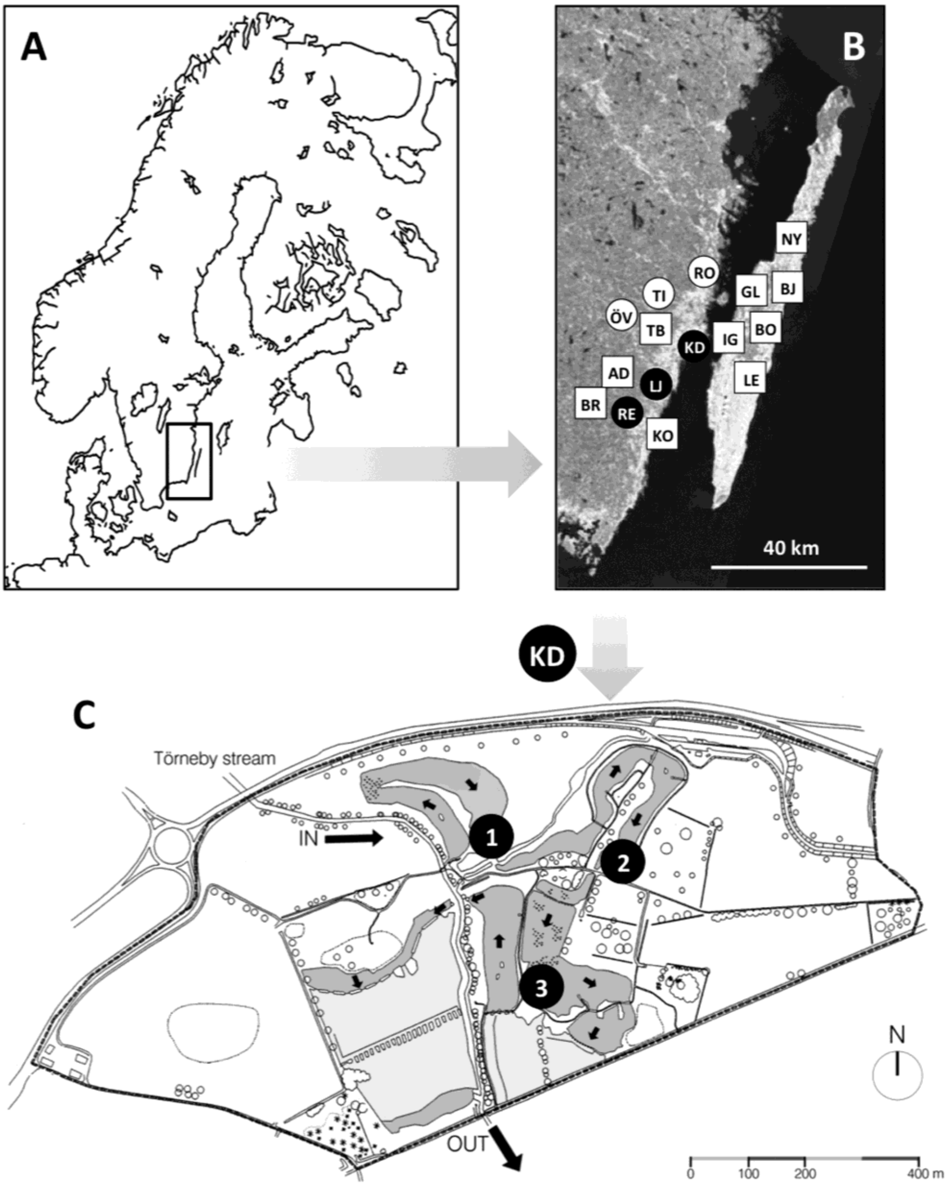

Fig. 1. Study area (A), locations of the study sites (B), and a scheme of water movements and sampling locations (1–3) in Kalmar Dämme (KD) (C). Black circles in (B): Kalmar Dämme (KD) and the 2 man-made wetlands ≥10 y, Ljungbyholm (LJ) and Resby (RE); white circles: man-made wetlands <3 y, Överstatorp (ÖV), Rockneby (RO), and Tingby (TI); squares: selected natural wetlands (>50 y without major human disturbances) Arby Dämme (AD), Björkerumsdammen (BJ), Bollmossen (BO), Brudhyltetjärn (BR), Glömminge (GL), Igelmossen (IG), Kolboda Hagby (KH), Lenstamossen (LE), Nytorpskärret (NY), and Tyska Bruket (TB).

Sampling and sample processing

Macroinvertebrate study.—We visited Kalmar Dämme during 5 periods from early 1997 to late 2009. Period I was the 1st y (1997), Period II the 2nd y (1998), Period III the 3rd y (1999), Period IV the 7th y (2003), and Period V the 13th y (2009) after construction. These 5 periods were intended to represent the progressive development of the changing macroinvertebrate community. In each period, we visited the wetland in spring (March–April), summer (June–July), and autumn (September–October) and sampled macroinvertebrates at 3 fixed sites (Fig. 1B). During each period, personnel from the Kalmar Airport authority did monthly analyses of dissolved inorganic N (DIN = NH_4^+ + NO^{2-} + NO_3^-), and soluble reactive P (SRP = PO_4^{3-}). Monthly meteorological variables were obtained from the Swedish Meteorological and Hydrological Institute. We sampled aquatic macrofauna with a Surber sampler (33 × 33 cm) equipped with an extra 15-cm-high front metal frame and 0.5-mm mesh on both parts. We collected 5 subsamples at each site over a range of depths (10–40 cm). We preserved samples in situ in 70% ethanol. We sorted samples and identified macroinvertebrates in the laboratory. Identification was carried out mostly to species level, except for Oligochaeta and Chironomidae.

Coleoptera study.—We visited each of the 16 wetlands 4 times with ≥1 spring and ≥1 autumn sampling visit over 2–3 consecutive years between 2003 and 2009. We designed the sampling procedure to capture the maximum number of aquatic Coleoptera. We sampled with a dip-net (0.5-mm mesh size). The maximum sampling depth was 1 m and samples covered all microhabitats. We applied a basic sampling effort of 10 min with a sampling rationale to work the site until no new morphospecies were found. We devoted equal effort to recording common and rarer species (Eyre et al. 1986). We passed samples through a 0.5-mm mesh, transferred them to 70% ethanol, and sorted and identified coleopterans species level in the laboratory.

Data analysis

Macroinvertebrate study.—We assessed taxonomic changes over time with analysis of similarities (ANOSIM). This test operates on a resemblance matrix and is similar to a standard univariate analysis of variance (ANOVA), but requires neither normality nor homoscedasticity of data. We compared species abundance matrices among years. The analysis returns a global *R* and a *p*-value expressed as a percentage. When *R* is negative or close to 0, similarities within groups (samples within the same period) and among groups (samples in different periods) are equivalent. In contrast, when *R* values approach 1, samples are more similar within than among groups, and groups of samples from different periods are differentiated (Clarke and Warwick 2001a). We built the distance matrix with the Bray–Curtis similarity measure, based on a sample × species matrix of abundance data, originally standardized and $\sqrt[4]{(x)}$-transformed. We used similarity of percentages analysis (SIMPER) to identify the species that characterized the community of each period. We ordered species from more to less contribution to the total within-period similarity and established a cut-off for a global contribution of 70%. Within the selected species, we considered as typifying those that contributed a large proportion to the total within-period similarity and were found at consistent abundance amongst samples in that period (criterion: mean contribution/SD > 2). A full description of SIMPER analysis is provided by Clarke (1993). We used 2-dimensional nonparametric multidimensional scaling (MDS) to visualize community patterns (99 restarts, 0.01 minimum stress, Kruskal fit scheme 1). We standardized and $\sqrt[4]{(x)}$-transformed abundances and used Bray–Curtis distances. Groups of samples with several thresholds of similarity (12.5%, 25%, 50%) were calculated by means of clustering (complete linkage), and the best threshold was represented over the MDS diagram.

We analyzed 3 categories of biological traits from those put forward by Tachet et al. (2002): reproductive cycles/y, type of dispersion, and feeding strategy. We used affinity scores (Tachet et al. 2002) for each genus to evaluate 11 traits within these categories. Affinity scores ranged from 0 (i.e., no affinity) to 5 (i.e., high affinity). This fuzzy coding technique (Chevenet et al. 1994) allowed us to build a biological traits abundance matrix. We tested for changes in biological traits over time with generalized linear mixed models (GLMMs). We used GLMM to overcome autocorrelation between observations (more similarity is expected among sites within a visit than among different visits) and nested data structures (each period encompassed 3 visits). We built a model in which the response variable was the modality of each biological trait (abundance/sample), the fixed explanatory variable was a nested structure (period factor [year] was fixed and visit factor [visits within each period] was nested within the period), and sampling site was random to overcome spatial pseudoreplication. In mixed models, random effects account for pseudoreplication by modeling the covariance structure introduced in the random part of the model (Crawley 2002). We started with a model without interactions. Validation of the model showed no significant patterns in the residuals, so we followed the current consensus (Zuur et al. 2009) and decided not to include interactions that would have improved the model at the expense of increasing the difficulty of biological interpretation of the results. We applied the Bonferroni procedure to compensate for the effects of multiple tests on Type I errors (adjusted $p = 0.0045$). We used post hoc Scheffé tests to examine pairwise differences among periods.

In addition, we selected 6 measures of community structure for analysis: numerical abundance (N), average taxonomic distinctness (Δ+), variation in taxonomic distinctness (Λ+), Pielou's evenness index (J'), rarefied species richness (S1), and cumulative species richness (S2). Biodiversity analyses are often based on species richness alone, but taxonomic relatedness also should be considered because assemblages composed only of taxonomically related species should be regarded as less diverse than those that host more distantly related species (Warwick and Clarke 1995, Abellán et al. 2006). Average taxonomic distinctness (Δ^+) represents the average path length in the phylogenetic tree connecting 2 random species of those collected, whereas variation in taxonomic distinctness (Λ^+) measures the variance in pairwise lengths between each pair of species and reflects the unevenness of the taxonomic tree (Clarke and Warwick 2001b, Clarke and Gorley 2006). We took into account species, genus, family, order, class, subphylum, and phylum and used the same branch length to weight each taxonomic level. Abundance was variable among samples, so we calculated richness using a rarefaction procedure with the function rarefy deriving from the vegan library (Oksanen et al. 2010). This function, which was inspired by Heck et al. (1975), calculates the estimated species richness for a number of individuals by simulating random draws of a fixed number of individuals based on the least abundant sample. S1 is not an estimate of the total community richness, but it permits an unbiased comparison between samples of unequal abundance. Thus, it can be regarded as a measure of diversity because, for a given number of taxa, it will increase with the evenness of species abundance (Lods-Crozet and Castella 2009). We calculated S2 by considering all species present at least once within each period and accumulating species from one period to the next. We tested community variables for changes over time with GLMM and used the same model design as for biological traits. We explored but did not test S2 statistically because of the lack of replicates. We log(x)-transformed N to ensure a better fit of errors to a normal distribution. For each variable, we used Scheffé post hoc tests to compare values among the 5 periods. We used general linear models (GLMs) with period as a fixed factor to examine differences in environmental variables (air temperature, precipitation, and water-chemistry variables) among periods. Because of the poor taxonomical resolution of Oligochaeta and Chironomidae, we took these groups into account only when their inclusion did not create a bias caused by taxonomic lumping. In the case of biological traits, we included these groups only in the analyses of reproductive cycles per year and dispersal. In the case of community variables, we included these groups only in determination of N.

Coleoptera study.—We analyzed coleopteran assemblages based on a single matrix of 186 species (variables) and 64 samples (16 sites × 4 visits/site). We analyzed 2 factors: 1) wetland type (man-made wetlands <3 y, man-made wetlands ≥10 y, and natural wetlands) and 2) wetland site (each of the 16 wetlands). We used ANOSIM to test for differences in Coleoptera composition across wetland types and sites. We used a 2-way nested layout in which the 2 factors were hierarchic (site factor nested within type factor). We built a rectangular matrix based on originally standardized and posteriorly $\sqrt[4]{(x)}$-transformed data using the Bray–Curtis similarity measure. We used SIMPER with wetland type as factor to detect which species contributed >1% to the similarity of each wetland type. We calculated Coleoptera richness (Sc) by summing all recorded species for each wetland in a given visit. We examined variability in Sc with a GLM with type as a fixed factor. To assess the statistical consequences of the unbalanced design, we ran 5 GLMs in which we selected 3 natural-wetland sites at random. The results of these GLMs were similar to those obtained with the unbalanced design. Therefore, we report the results for the unbalanced models because they included data from more wetlands than the balanced GLMs. We used post hoc Scheffé tests to examine pairwise differences among wetland types. Last, we used 2-dimensional MDS to visualize patterns in coleopteran assemblages among wetland types (99 restarts, 0.01 minimum stress, Kruskal fit scheme 1).

We used PRIMER (version 6.0 for Windows; PRIMER-E, Plymouth, UK) for cluster analysis, ANOSIM, SIMPER, MDS, and calculations of all community variables except for S1 richness. We used PASW (version 18; SPSS, Chicago, Illinois) to run GLMMs, GLMs, and Scheffé post hoc tests.

Results

Macroinvertebrate study

Overview.—No environmental or water-chemistry variables varied significantly among the 5 periods. Across the study, annual mean air temperature varied between 7.3 and 8.2°C ($F_{4,55}$ = 0.324, p = 0.861), annual mean precipitation between 36.8 and 46.6 mm/mo ($F_{4,55}$ = 0.187, p = 0.944), water pH between 7.1 and 7.6 ($F_{4,55}$ = 1.725, p = 0.158), DIN concentration between 4.75 and 6.46 mg/L ($F_{4,55}$ = 0.562, p = 0.691), and SRP concentration between 0.037 and 0.057 mg/L ($F_{4,55}$ = 1.307, p = 0.279).

One hundred taxa were found at Kalmar Dämme. The groups with the highest species richness were: Coleoptera (23), Trichoptera (15), and Heteroptera (14). Six taxonomic groups dominated the community across the 5 periods spanning 13 y (Chironomidae, Asellidae, Corixidae, Baetidae, Oligochaeta, and Planorbidae) and always contributed >80% of the abundance. The relative composition of taxonomic groups was different for each period. For example, periods I and V were dominated by Chironomidae (with secondary groups being Corixidae in period I and Oligochaeta in period V). However, during periods II, III, and IV Baetidae were abundant, the numbers of Asellidae increased, and the numbers of Corixidae declined (Fig. 2A). Eighteen families were present in period I. Eleven new families arrived in period II, 5 in period III, and 2 in period IV, whereas no new families appeared in period V.

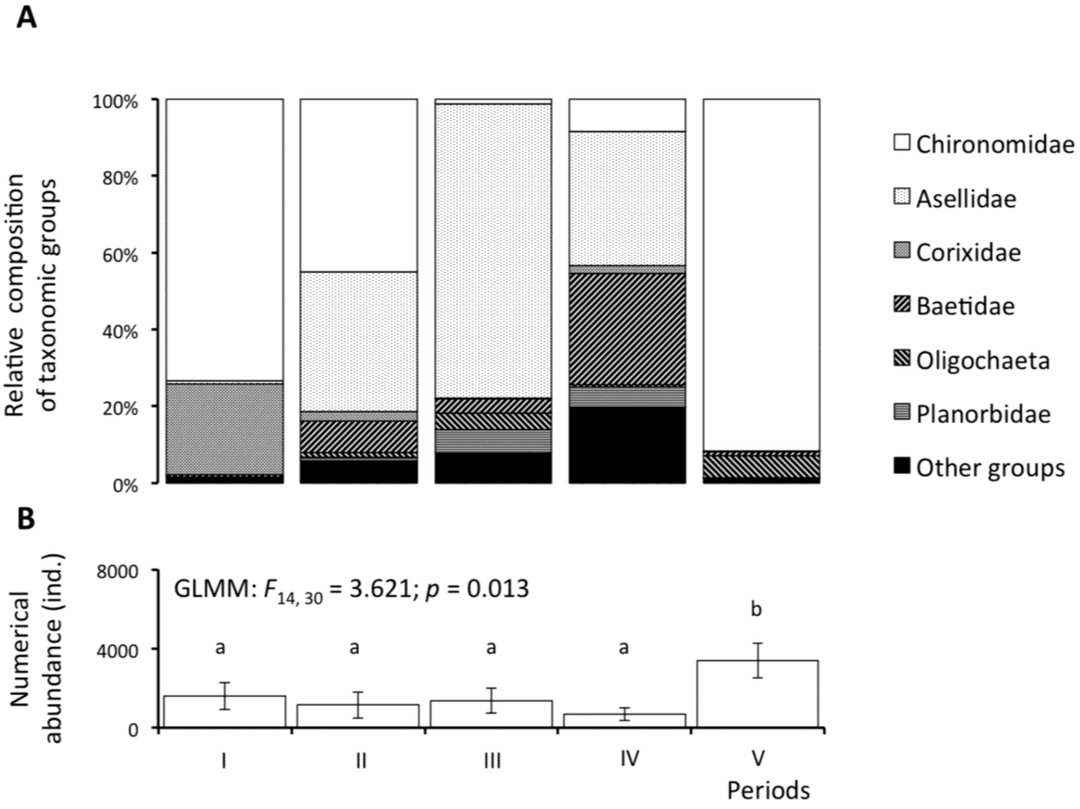

Fig.2. Dominant taxonomic groups (A) and mean (±1 SD) numerical abundance (B) of macroinvertebrates in Kalmar Dämme for each of the 5 study periods. Bars with the same letter are not significantly different (Scheffé post hoc test, $p > 0.05$).

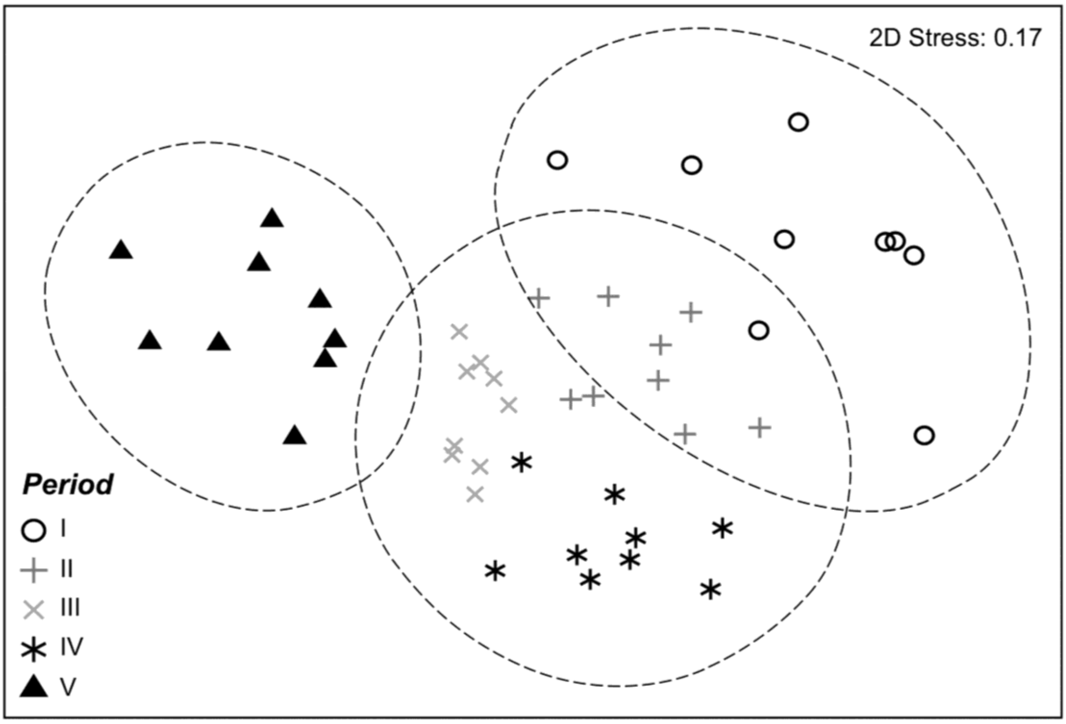

Fig. 3. Plot of sites ordinated by 2-dimensional (2D) nonparametric multidimensional scaling analysis of macroinvertebrate species composition. Circles enclose groups of sites with similarity >12.5% (similarity percentages analysis).

Species composition.—Each of the 5 periods was characterized by a significantly different species composition (ANOSIM global $R = 0.778$, $p = 0.001$; all pairwise $R > 0.600$, $p < 0.05$). MDS and cluster analysis showed that the samples were different in each period and that the samples were distributed along a gradient related to time. The threshold of 12.5% similarity was selected for grouping samples corresponding to: 1) an early phase (period I), (2) an intermediate phase (periods II, III and IV), and (3) an advanced phase (period V) (Fig. 3).

Table 2. Characteristics of wetlands sampled during the Coleoptera study.

Type	Site (abbreviation)	Created	Sampled	Max area (m^2)	Max depth (m)	Emerged vegetation cover	Submerged vegetation cover	Substrate type	Fish
Man-made ≥10 y	Kalmar Dämme (KD)	1996	2006–2008	180,000	1.8	50%	80%	Detritus	Present
	Ljungbyholm (LJ)	1998	2008–2009	300	2.0	20%	20%	Coarse gravel	Absent
	Resby (RE)	1998	2008–2009	5000	1.5	15%	50%	Clay, detritus	Unknown
Man-made <3 y	Överstatorp (ÖV)	2005	2006–2008	20,000	>3.0	25%	25%	Sand	Present
	Rockneby (RO)	2002	2003–2005	160	1.0	70%	70%	Clay, sand	Absent
	Tingby (TI)	2003	2004–2006	1000	>2.5	10%	10%	Sand, detritus	Present
	Arby Dämme (AD)	–	2004–2005	80	2.0	10%	0%	Clay	Absent
	Björkerumsdammen (BJ)	–	2006–2008	100	1.5	10%	50%	Sand, clay	Present
	Bollmossen (BO)	–	2005–2006	5000	2.0	70%	50%	Detritus	Present
	Brudhyltetjärn (BR)	–	2007–2009	3000	>2.0	15%	15%	Peat	Present
Natural >50 y	Glömminge (GL)	–	2007–2009	120	0.5	50%	0%	Clay	Absent
	Igelmossen (IG)	–	2006–2008	10,000	1.5	10%	20%	Sand, gravel	Present
	Kolboda Hagby (KH)	–	2006–2008	2500	0.5	50%	0%	Detritus	Absent
	Lenstamossen (LE)	–	2004–2005	10,000	2.0	70%	20%	Detritus	Present
	Nytorpskärret (NY)	–	2007–2009	2400	0.5	70%	0%	Peat	Absent
	Tyska Bruket (TB)	–	2004–2005	72	0.5	50%	0%	Detritus	Absent

Changes in community composition were further confirmed by SIMPER. Of the 17 species selected by this method, only 8 were categorized as typifying species (Table 3). These typifying species distinguished one period from the next. However, periods II, III, and IV shared the same main species. Thus, the early phase was mainly represented by *Sigara striata*, the intermediate phase by *Asellus aquaticus*, and the advanced phase by *Sialis lutaria*. Period III presented 6 different species that typified the community (instead of a range of 1–3 obtained in the other periods). Also, the mean similarity in composition of each period grew from the lowest level in the early phase (39.98%) to the highest level in the advanced phase (56.43%), with a mean of 51.69% during the intermediate phase.

Biological traits.—Most biological traits presented significant differences across periods, but the relationship between these trends and our hypotheses was not always clear (Table 4). Species with short life-cycles did not differ significantly among periods, whereas species with long life-cycles increased over time (i.e., during periods III, IV, and V) until they became dominant (as expected). Species with aquatic dispersal did not differ significantly among periods. Species with active aerial dispersal were significantly more abundant in period V than in earlier periods (the inverse trend to that expected), and the abundance of passive aerial species increased over time (as expected). The abundance of herbivores did not differ among periods, and filter feeders were most abundant in period V (the inverse trend to that expected). Shredders decreased over time (as expected), whereas the remaining feeding types (fine sediment collectors, predators, and parasites) presented low values during the early periods and became more common over time with high values in period V.

Table 3. Similarity of percentages (SIMPER) analysis of macroinvertebrate community composition in Kalmar Dämme. Values represent the percentage contribution of each species to the within-period similarity (only the most important species contributing globally up to 70% of the within-period similarity are shown). Bold indicates species that consistently typified the community by contributing a large proportion to total within-period similarity and being found at consistent abundance amongst samples in that period (criterion: mean contribution/SD > 2).

Species	**Period**				
	I	**II**	**III**	**IV**	**V**
Average similarity (%)	39.98	50.38	58.00	46.71	56.43
Sigara striata	**38.63***	**8.83***		5.95	
Asellus aquaticus	18.88	**27.11***	**25.29***	**24.20***	
Callicorixa praeusta	13.93				
Cloeon inscriptum		**16.72***	**9.09***	15.81	
Planorbis sp.		9.02	**7.96***		
Erpobdella octoculata			**7.73***		
Glyphotaelius pellucidus			**7.17***		
Ischnura elegans			**5.09***		
Gyraulus sp.			4.83		10.47
Helobdella stagnalis			4.63	3.65	
Phryganea bipunctata				5.56	
Coenagrion puella/pulchellum				5.59	
Brachytron pratense				3.49	
Notonecta glauca				3.37	
Sialis lutaria					**30.71***
Pisidium sp.					15.39
Agrypnia sp.					14.72

Table 4. Differences in abundance of macroinvertebrates biological traits among periods and the results of the respective generalized linear mixed models (GLMMs) (significance was judged at $p \leq 0.0045$ according to Bonferroni correction). For the significant categories, periods with the same letter were not significantly different according to Scheffé post hoc tests ($p > 0.05$): a = low values, b = medium values, and c = high values of the particular trait category at that period. Arrows indicate the direction of difference. sig. = significant, n.s. = nonsignificant.

Biological trait		**Hypothesis through succession**		**GLMM**			**Period**				
		Early →	**Advanced**	$F_{14, 30}$	p	Period effect	I	II	III	IV	V
No. repr. cycles/y	>1	+	–	2.387	0.022	ns	(not performed)				
	≤1	–	+	3.266	0.003	sig	↓a	b	↑c	↑c	↑c
Dispersal strategies	Aquatic	–	+	2.402	0.021	ns	(not performed)				
	Aerial active	+	–	7.552	<0.001	sig	b	b	↓a	b	↑c
	Aerial passive	–	+	18.289	<0.001	sig	↓a	↓a	↓a	↓a	↑c
Feeding strategies	Scrapers + herb. piercers	+	–	2.537	0.017	ns	(not performed)				
	Filter-feeders	+	–	36.934	<0.001	sig	↓a	b	b	b	↑c
	Shredders	+	–	4.451	<0.001	sig	↑c	↑c	↑c	↓a	↓a
	Fine sediment collectors	–	+	14.217	<0.001	sig	↓a	b	b	↑c	↑c
	Engulfers + animal piercers	–	+	6.653	0.001	sig	↓a	↓a	↓a	↑c	↑c
	Parasites	–	+	12.360	<0.001	sig	↓a	↓a	↓a	↓a	↑c

Community variables.—Most community variables changed as hypothesized. GLMMs and post hoc tests showed that N was low during periods I, II, III and IV, and was significantly higher in period V (Fig. 2B). $\Delta+$ and $\Lambda+$ showed that period V contained more taxonomically unrelated taxa than earlier periods, and the tree composition was more even than during preceding periods (Fig. 4A, B). J' was significantly higher in period I than in period III (inverse trend to that expected; Fig. 4C). The highest values for S1 occurred during the intermediate phase and S2 tended toward an asymptote (as expected) that approached 100 species (Fig. 4D).

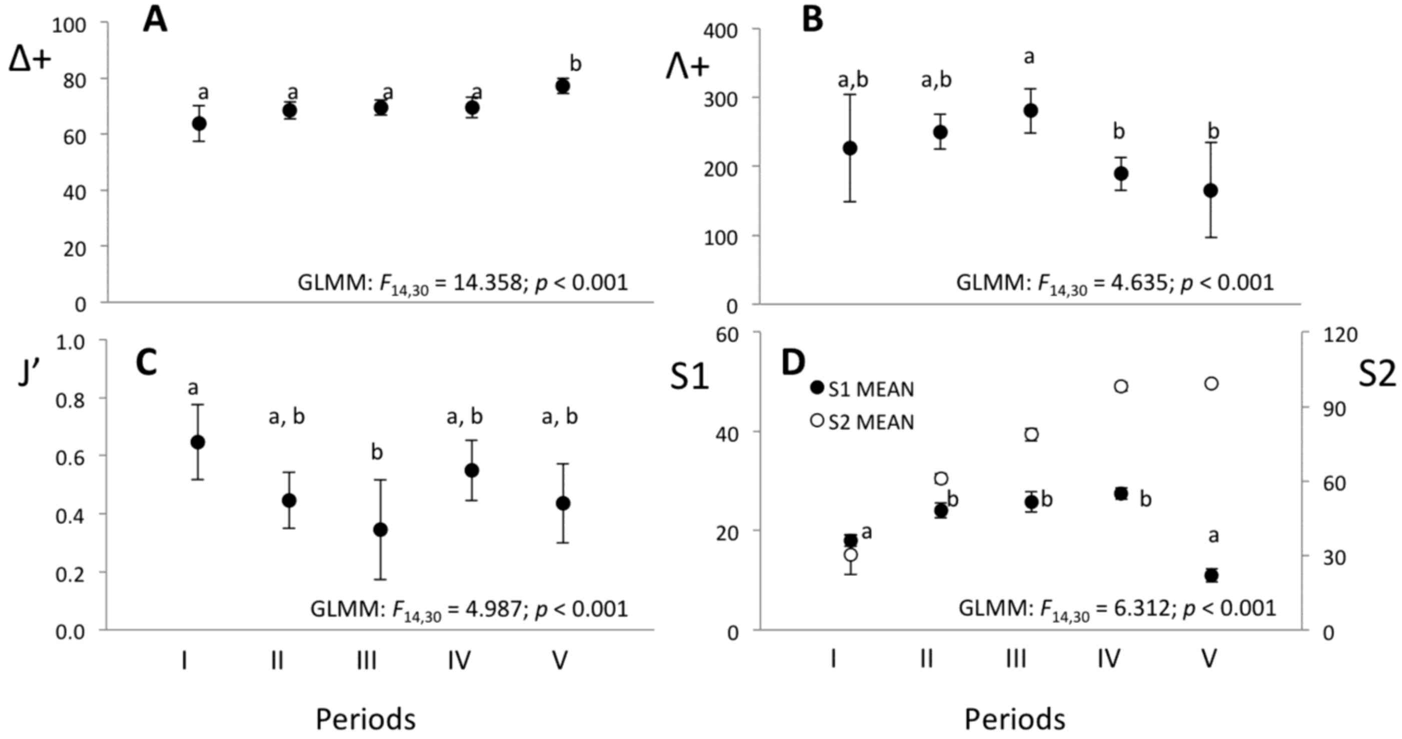

Fig. 4. Mean (±1 SD) taxonomic distinctness (Δ+) (A), variation in taxonomic distinctness (Λ+) (B), Pielou's evenness index (J') (C), and rarefied species richness (S1) and cumulative species richness (S2) (D) of macroinvertebrate communities in Kalmar Dämme across the 5 study periods. Degrees of freedom, *F* statistics and *p*-values from generalized linear mixed models (GLMMs) are also shown. Dots with the same letter are not significantly different (Scheffé post hoc test, $p > 0.05$).

Table 5. Similarity of percentages (SIMPER) analysis of Coleoptera species composition in 3 wetland types. Values represent percentage contributions of species to each wetland type (only species with >1% contribution to each within-wetland-type similarity are shown). MM = man-made wetland, Nat = natural wetlands.

Species	**MM <3 y**	**MM ≥10 y**	**Nat >50 y**	**Species**	**MM <3 y**	**MM ≥10 y**	**Nat >50 y**	**Species**	**MM <3 y**	**MM ≥10 y**	**Nat >50 y**
Laccophilus minutus	13.0	1.3	–	*Haliplus heydeni*	1.7	5.1	–	*Helophorus minutus*	–	2.0	2.6
Scarodytes halensis	12.9	–	–	*Laccobius minutus*	1.7	1.3	–	*Hydroporus erythrocephalus*	–	2.0	5.4
Nebrioporus canaliculatus	10.6	–	–	*Acilius canaliculatus*	1.5	–	–	*Enochrus testaceus*	–	1.7	–
Hydroglyphus geminus	7.2	2.9	–	*Rhantus suturalis*	1.2	3.2	2.0	*Graptodytes bilineatus*	–	–	6.3
Hydroporus palustris	5.2	2.0	2.3	*Haliplus ruficollis*	–	1.6	–	*Ochthebius minimus*	–	–	4.4
Hygrotus confluens	4.8	–	–	*Noterus clavicornis*	–	6.9	2.0	*Graptodytes granularis*	–	–	4.2
Hygrotus inaequalis	3.8	4.9	3.2	*Helophorus brevipalpis*	–	5.1	3.0	*Hygrotus decoratus*	–	–	4.2
Anacaena lutescens	3.3	8.6	5.2	*Hygrotus impressopunctatus*	–	4.5	–	*Dryops auriculatus*	–	–	4.1
Gyrinus natator	2.6	–	–	*Laccobius bipunctatus*	–	4.0	–	*Dryops similaris*	–	–	3.8
Limnebius truncatellus	2.6	–	–	*Hydroporus umbrosus*	–	3.6	1.0	*Haliplus variegatus*	–	–	3.7
Ilybius fuliginosus	2.3	3.6	–	*Hydrobius fuscipes*	–	3.6	3.1	*Berosus luridus*	–	–	3.6
Agabus bipustulatus	2.2	3.7	2.4	*Hydroporus tristis*	–	3.5	4.4	*Hydroporus gyllenhalii*	–	–	3.1
Agabus nebulosus	2.1	–	–	*Helochares obscurus*	–	2.3	2.9	*Ilybius chalconatus*	–	–	2.3
Agabus sturmii	1.9	4.9	–	*Noterus crassicornis*	–	2.2	–	*Cymbiodyta marginella*	–	–	1.7
Acilius sulcatus	1.9	–	–	*Hydroporus striola*	–	2.9	–	*Copelatus haemorrhodalis*	–	–	1.5

Coleoptera study

The composition of each wetland was distinctive, regardless of wetland type (ANOSIM, $R = 0.912$, $p = 0.001$). Significant compositional differences were obtained when comparing young (<3 y) and old (≥10 y) man-made wetlands ($R = 0.518$, $p = 0.001$) and young man-made wetlands with natural wetlands ($R = 0.324$, $p = 0.001$). In contrast, composition did not differ between old and natural wetlands ($R = –0.150$, $p = 0.986$). In the MDS plot, samples obtained from old man-made wetlands were intermediate between samples from young man-made wetlands and from natural wetlands (Fig. 5). Furthermore, old man-made wetlands shared the highest number of the 45 species selected by SIMPER (56% of total species) with other wetland types, i.e., 17.7% of the 45 species were shared with young man-made wetlands, 23.6% were shared with natural wetlands, and 14.7% were shared with both types of wetlands. Moreover, all species that were common to young man-made wetlands and natural wetlands also were present in old man-made wetlands. Exclusive species occurred more often (48% of species) in natural wetlands than in other wetland types (Table 5).

Sc differed significantly among wetland types ($F_{2,61} = 14.356$, $p < 0.001$). Old man-made wetlands had significantly higher Sc than young man-made or natural wetlands, but Sc did not differ between young man-made and natural wetlands (Fig. 6).

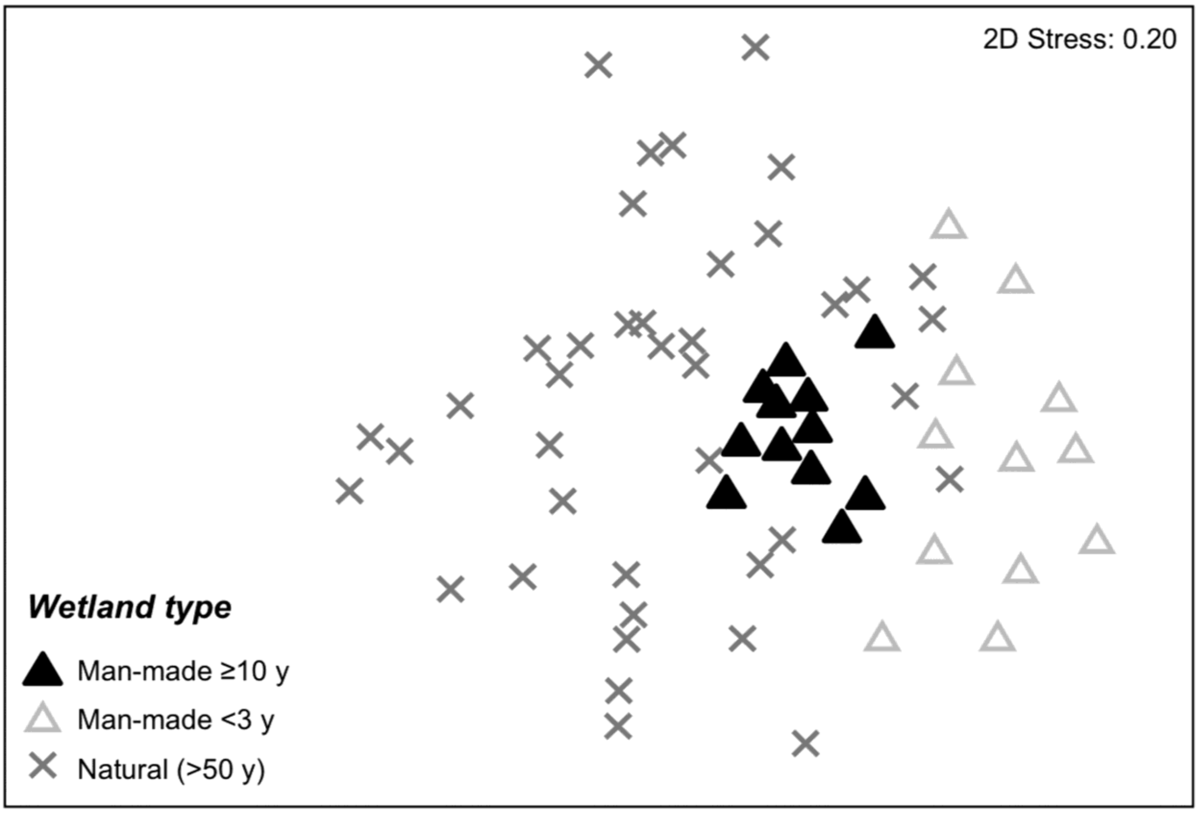

Fig. 5. Plot of sites ordinated by 2-dimensional (2D) nonparametric multidimensional scaling analysis of Coleoptera species composition in 3 wetland types.

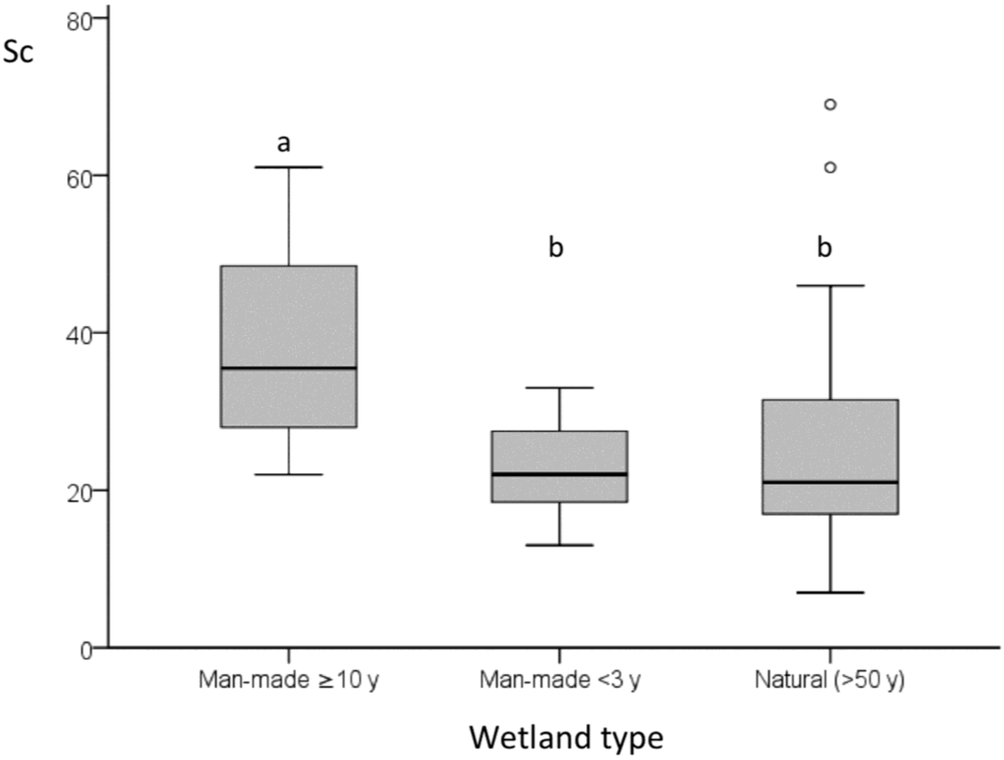

Fig. 6. Box-and-whisker plots of Coleoptera richness (Sc) in 3 wetland types. Bars with the same letter are not significantly different (Scheffé post hoc test, $p > 0.05$). Lines in boxes show medians, box ends show quartiles, whiskers show 95% confidence intervals, circles show outliers.

Discussion

Succession of biological traits

The biological traits and method used (based on fuzzy coding) in our study provided meaningful information about the ecological functioning of this newly created freshwater system despite the unavoidable arbitrariness of assigning species to multiple traits groups (Hooper et al. 2002, Wright et al. 2006). In the macroinvertebrate study, both taxonomic composition and biological traits analyses displayed a 3-phase pattern, and certain life-history strategies were characteristic of the early, intermediate, and advanced phases of succession. As expected, the number of individuals with long life spans and late maturities increased over time. These features are associated with ecological stability rather than environmental stress (Townsend and Hildrew 1994). Also as expected (Batzer and Wissinger 1996), aerial passive dispersal was more common in advanced rather than at early phases of succession. Contrary to expectations, active dispersers also dominated in the advanced successional phase. Initial dominance of this strategy is expected when dispersal distances can be covered efficiently by flight (Barnes 1983, Velasco et al. 1993b, Bloechl et al. 2010). The high abundance of chironomids (active dispersers) in the advanced successional phase in our study wetlands might explain the lack of support for this hypothesis.

The abundances of most functional feeding groups increased over time. The results supported our predictions for fine sediment collectors, predators, and parasites, but contradicted our predictions for filter-feeders, which were expected to decrease. Hydrological conditions of man-made wetlands strongly affect the resultant communities (Mitsch and Wilson 1996). The unexpectedly high abundance of filter-feeders in the late successional phase might have been a consequence of the continuous input of nutrient-rich water, which may have sustained individuals in this guild throughout the study period (Gallardo et al. 2009). As expected based on their dependence on macrophytes and large terrestrial litter (Voshell and Simmons 1984), shredders dominated at the early rather than at the advanced successional phase. Plant cover strongly influences macroinvertebrate communities (De Szalay and Resh 2000), and submerged macrophytes (mainly *Elodea*) covered large areas of the wetland during the early successional stage and into the intermediate stage but declined mid-way through our study. Predators are an important component of macroinvertebrate communities in the initial phases of succession in both temporary and newly created water bodies (e.g., Layton and Voshell 1991, Boix et al. 2006). Moreover, predator abundance increases over time as wetlands undergo succession (Batzer and Wissinger 1996). Thus, predation is an important mechanism in creating community structure in freshwater habitats (reviewed by Wellborn et al. 1996).

Community structure

In the macroinvertebrate study, maximum N was recorded at the advanced phase, as expected (Gutierrez and Fey 1980, Legendre et al. 1985). However, this increase was mainly explained by the dominance of chironomids. Thus, the hypothesized accompanying increase in evenness was not supported. Community structure was clearer under the prism of taxonomic distinctness indices than when viewed in terms of diversity. On the one hand, the initial low values of $\Delta+$ and Λ^{+} showed that only a few taxonomic groups colonized the wetland, a pattern that has been observed frequently in other systems (Velasco et al. 1993a, Heino et al. 2005, Ruhí et al. 2009). On the other hand, despite a decline in S1, the increase in $\Delta+$ near the end of the study showed that the accumulation of species during succession (S2) contributed to a more taxonomically diverse community at the advanced phase. Moreover, the decrease in

Λ^+ demonstrated that the taxonomic structure of the community became more complex and more even in the advanced successional phase. The arrival of new and taxonomically unrelated species took place in several taxonomic groups and largely compensated for the loss of species from the few species-rich pioneer groups. Overall, the uneven community structure with low taxonomic distinction in the early phase developed progressively into a richer, more even, and regular structure. Maximum S1 was attained during the intermediate period, and increases in S2 showed that new species continued to colonize the area, trends that were expected (Margalef 1968, Batzer and Wissinger 1996, Guo 2003, Milner and Robertson 2010). However, the rate of colonization declined over time until it was almost negligible between periods IV and V, >10 y after creation of the wetland.

Man-made wetlands vs natural wetlands

Use of surrogate or model groups with biodiversity metrics often has raised the criticism that the surrogate group might not be representative of other groups within the community of interest (Bonn and Gaston 2005, Rodrigues and Brooks 2007). However, aquatic Coleoptera have been identified as potential biodiversity indicators in continental ecosystems (Foster et al. 1989, Sánchez-Fernández et al. 2006). Moreover, this group is particularly species rich in northern Europe (Nilsson 1984, Lundkvist et al. 2001, Thiere et al. 2009). Therefore, it is a useful surrogate. We were unable to determine whether the total macroinvertebrate community in the advanced phase truly resembled a community that would be present in a natural wetland. The Coleoptera study provided interesting evidence to address this question because Coleoptera usually require a long time to form mature assemblages (Valladares et al. 1994). Taxonomic similarity develops only after specialist taxa, which require environmental stability and arrive after pioneer generalist colonizers, can settle in the man-made wetland

(Barnes 1983, Fairchild et al. 2000). Under the prism of composition (ANOSIM), 10 y of succession seemed sufficient for Coleoptera assemblages in the studied man-made wetlands to become similar to those found in natural wetlands.

The significant differences in macroinvertebrate community composition found among wetlands of similar type may be attributed to several factors. Idiosyncratic responses of species to different temporal and patch-specific factors is the most plausible explanation. Eventual critical episodes (e.g., an unexpected dry period or the growth of different plant species) may strongly influence the final composition of the community (Jeffries 2003). Thus, similar wetlands in close proximity to one another may differ in habitat heterogeneity, which affects the potential maximum number of coexisting taxa (Savage et al. 1998, Della Bella et al. 2005). Differences in vegetation structure between natural and older man-made wetlands also may explain differences in macroinvertebrate species richness within a wetland type (Nilsson and Söderberg 1996).

Natural and old man-made wetlands were similar in terms of Coleoptera composition and structure, but young wetlands hosted an important proportion of characteristic species (many of them from the family Dytiscidae). Some of these characteristic species (e.g., *Scarodytes halensis, Nebrioporus canaliculatus, Hygrotus confluens*) showed the pioneering nature of the assemblage (Ruhí et al. 2009, Bloechl et al. 2010) and were absent from older wetlands. Other species (e.g., *Laccophilus minutus, Hydroglyphus geminus, Hydroporus palustris*) remained until later in the successional process and contributed to the community present in old wetlands. Thus, a substantial core group of taxa may explain the similarity of communities in old man-made wetlands. Moreover, after enough time has passed for the establishment of a viable and sustainable community, old man-made wetlands may, in some cases, support higher levels of biodiversity than natural wetlands (Mitsch and Wilson 1996). However, this conclusion should be treated with caution because the number of species found exclusively in natural wetlands was high in our study. Moreover, many Coleoptera species are rare and only occur in nonimpacted or natural sites (Nilsson and Söderberg 1996, Lundkvist et al. 2002).

Conclusions

We observed 3 distinct phases of succession, during which taxonomic composition and some measures of community structure changed according to our hypotheses. A 3-phase pattern has been presented previously as a theoretical framework within which to describe secondary succession in temporary water bodies (Lake et al. 1989, Bazzanti et al. 1996, Boix et al. 2004b). These phases were described as initial allogenic, middle autogenic, and final allogenic. We propose that the early successional phase in Kalmar Dämme was allogenic as a direct consequence of the creation of the wetland. However, the important community changes that occurred in Kalmar Dämme during the intermediate and advanced phases were not related to shifts in environmental variables, which were stable during our study. Instead, we suggest that competitive exclusion led to a more stable community in the advanced successional phase (Guo 2003). In a temporary water body, successional changes in the final phase have been described as allogenic because the water body is drying. However, the advanced successional phase of a community in a man-made wetland would not be allogenic but autogenic because of ongoing primary succession, as long as the system remains stable. Our results suggest that a community in a stage of advanced succession might be more taxonomically robust and biodiverse and would also provide the ecosystem with higher functionality than a community in an earlier successional stage (Hooper et al. 2005, Graham et al. 2006). Higher multifunctionality in an ecosystem has been related to higher levels of stability (Chapin et al. 2000, Hector and Bagchi 2007). Therefore, we suggest that primary succession dynamics in a newly created wetland may be regarded as a process with successive increasing thresholds of community complexity and stability.

Acknowledgements

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CHAPTER 5. Man-made Mediterranean Temporary Ponds as a tool for amphibian conservation

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Abstract

Mediterranean temporary ponds (MTPs) are crucial breeding sites for local amphibians, a faunal group in decline mainly due to wetland destruction in the Mediterranean. Although the disappearance of lentic habitats in other regions of the world has been ameliorated by the creation and restoration of wetlands, these tactics remain untested in Mediterranean wetlands. To evaluate the amphibian colonization dynamics of artificial MTPs in the north-eastern Iberian Peninsula, we monitored two artificial MTPs (one located in a high diversity area and the other in a low diversity area) over two years, as well as several reference wetlands. We aimed to (i) determine which amphibians could colonize artificial MTPs within a short-term period; (ii) compare the community established in the man-made MTP to that of nearby reference wetlands; and (iii) study the colonization dynamics and reproductive success of a species of conservation concern, the natterjack toad *Bufo calamita*, in the newly created MTP. We found that, beginning in the first year, artificial MTPs were a valuable habitat for regional amphibian fauna. Using a drift fence equipped with pit-fall traps, we measured the abundance of *Bufo calamita* reproductive adults entering the pond and post-metamorphic individuals exiting the pond. Using mark-recapture methods, we analysed the time and energy costs associated with reproduction in the artificial MTPs. We observed a highly variable colonization dynamics between sites, between hydroperiods, and within hydroperiods, and these dynamics often depended on meteorological factors. Our results suggest that even at a short timescale, native amphibian species such as *B. calamita* can benefit from wetland creation in the Mediterranean region.

Introduction

Amphibians have suffered a recent serious global decline (Houlahan et al. 2000, Stuart et al. 2004, Beebee and Griffiths 2005), and due to habitat reduction, pollution, pathogens, and introduced predators, native amphibian species are facing a potential mass extinction (Wake and Vredenburg 2008). In the Mediterranean region, wetland destruction is the main cause for amphibian decline, as 89% of the endangered species have suffered habitat loss (Cox et al. 2006). In this context, temporary ponds represent neglected habitats of vast biological value in the Mediterranean region (Boix et al. 2001, Grillas et al. 2004), providing essential breeding sites for amphibians (Jakob et al. 2003, Díaz-Paniagua et al. 2010). Although the maintenance of Mediterranean temporary ponds (MTPs) as priority habitats is encouraged by the 92/43/CEE European Commission Habitats Directive, continuing increases in agriculture and urban development make MTP long-term preservation critical (Zacharias et al. 2007).

The global-scale process of assisting the recovery of degraded and damaged ecosystems (aka ecological restoration) has been identified as one of the grand challenges to the Earth in the twenty-first century (Comín 2010). In the United States of America, the 1989 federal goal of achieving “no overall net loss” of wetlands (Brown and Lant 1999) partially addressed the progressive disappearance of lentic habitats through wetland creation and restoration. To evaluate how to lessen the effects of wetland loss on amphibian populations, studies have monitored both short-term (e.g. Perry et al. 1996, Lehtinen and Galatowitsch 2001, Balcombe et al. 2005, Barry et al. 2008) and long-term (e.g. Pechmann et al. 2001, Petranka et al. 2003, Vasconcelos and Calhoun 2006) colonization patterns and restoration effects. These studies revealed that the timescale of operation for the newly created or restored wetland is critical, as temporal population responses and environmental stressors determine which species are likely to benefit from the wetlands (Petranka et al. 2007).

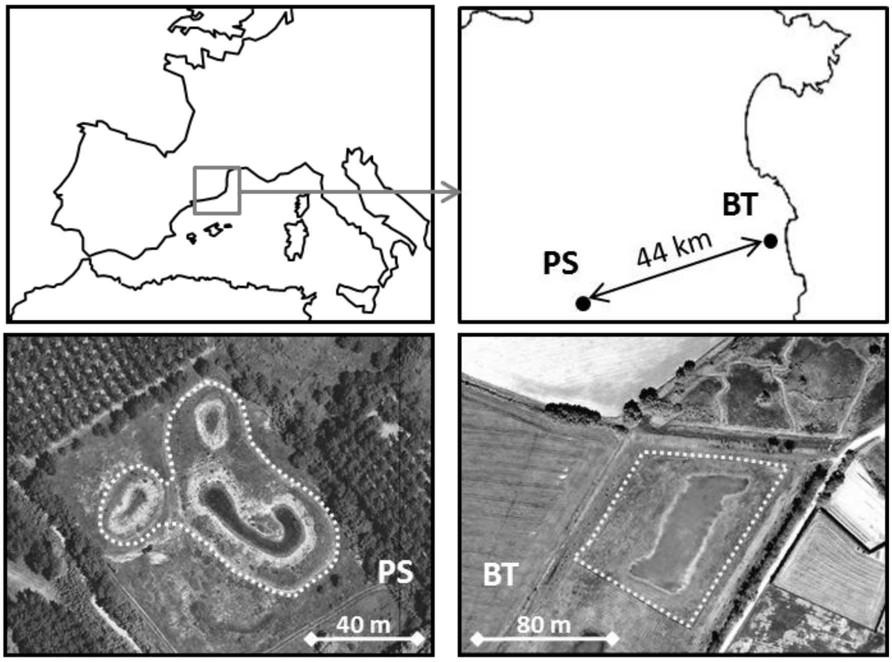
Many European studies have also demonstrated the conservation value of temporary wetlands (Oertli et al. 2005), particularly for amphibians (Laan and Verboom 1990, Jeffries 1991, Joly and Grolet 1996, Beebee 1997, Stumpel and van der Voet 1998, Baker and Halliday 1999, Rannap et al. 2009, Lesbarrères et al. 2010). However, the creation and restoration of MTPs in the Mediterranean region is still very rare. Although there is some information about invertebrate colonization of these restored wetlands (e.g. Ruhí et al. 2009), there are few data that describe amphibian colonization of newly created MTPs. New wetlands are often designed to replace natural wetlands within short time periods, (i.e. Pechmann et al. 2001, Lesbarrères et al. 2010) despite associated controversy (Mitsch and Wilson 1996). Therefore, it will be crucial to determine if species of high conservation concern can colonize artificial MTPs within these brief periods. Moreover, quantifying the productivity of these MTPs will provide an estimate of how well creating new aquatic habitats maintains local biodiversity (Gibbons et al. 2006). Here, we investigated amphibian colonization and reproduction in two artificial MTPs over a two-year period. Specifically, we (i) determined which amphibians could colonize artificial MTPs within a short-term period; (ii) compared the community established in the man-made MTP to that of nearby reference wetlands; and (iii) studied the colonization dynamics and assessed the reproductive success of a species of conservation concern, the natterjack toad *Bufo calamita* (Laurenti 1768), in the newly created MTP.

Materials and methods

Study sites

The artificial MTPs are located in two lowland areas of the NE Iberian Peninsula: Baix Ter and Plana de la Selva (Figure 1). In the summer of 2006, arable lands at these sites were transformed into human-made wetlands (BT and PS, respectively), which were flooded in September 2006. Both newly created wetlands were excavated from lacustrine silty clays.

Fig. 1 Map of the study sites. Dashed lines represent the drift fences at each site



Both wetlands covered < 0.5 ha and were < 1 m deep. BT was < 200 m from the *Ter Vell* wetlands, a pond-marsh-pond system under marine influence, and PS was < 200 m from the *Esplet* temporary stream and some natural temporary and permanent ponds. For both sites there already existed some information about amphibian assemblages, being BT a low diversity area, with 5 species, and PS a high diversity area, with 11 (Pleguezuelos et al. 2002, Boix et al. 2004a).

At both sites, nearby riparian vegetation was dominated by alders (*Alnus glutinosa*), poplars (*Populus nigra*), willows (*Salix alba*), ashes (*Fraxinus angustifolia*), and elms (*Ulmus minor*). Aquatic vegetation was not planted within the wetlands, but within the first year of the study, charophytes had colonized both wetlands. By the second year, macrophytes, such as the common reed (*Phragmites australis*), bullrush (*Typha latifolia*) and water plantain (*Alisma plantago-aquatica*), had also appeared in both wetlands. The ECELS index (Sala et al. 2004), which characterizes the conservation status of a wetland in terms of (1) basin littoral morphology, (2) human activity, (3) water characteristics, (4) emergent vegetation, and (5) hydrophytic vegetation, provided high punctuations for most of the components in both sites (PS, 97 out of 100 points; BT, 79 out of 100 points). Human activity in BT lowered the value of the index, mainly due to influence of intensive agriculture. In order to gather information about the local amphibian community, 10 existing reference wetlands were selected, 5 in each area (Figure 1, Table 1). These wetlands were located within a 3 km range of the respective man-made MTPs. Different types of reference wetlands were selected in order to encompass the natural variability of the existing waterbodies. Thus, at each site, 1 out of the 5 was a semipermanent (hydroperiod ≥ 10 months) naturalised man-made wetland, 3 were natural MTP's similar to the man-made ones (hydroperiod 4 – 9 months) and 1 was an ephemeral pool (hydroperiod ≤ 3 months).

Table 1 Study sites characteristics.

Site	*Type*	*Origin*	*Coordinates*	*Water permanence*	*Mean size (m^2)*	*Max. depth (cm)*	*Surrounding vegetation*
BT	Man-made	Artificial	42° 02' 43" N 3° 11' 04" E	Temporary (4 – 9 mo)	4500	100	Riparian forest
BT_REF1	Reference	Natural	42° 02' 36" N 3° 10' 56" E	Temporary (4 – 9 mo)	20.000	100	Riparian forest
BT_REF2	Reference	Natural	42° 02' 09" N 3° 11' 32" E	Temporary (4 – 9 mo)	3000	60	Glasswort swamp
BT_REF3	Reference	Natural	42° 01' 33" N 3° 11' 29" E	Ephemeral (≤ 3 mo)	120	40	Sedgelands and rushlands
BT_REF4	Reference	Man-made, naturalised	42° 00' 45" N 3° 11' 03" E	Semipermanent (≥ 10 mo)	430	150	Riparian forest, rice fields
BT_REF5	Reference	Natural	42° 00' 17" N 3° 10' 09" E	Temporary (4 – 9 mo)	12.000	80	Riparian forest, rice fields
PS	Man-made	Artificial	41° 49' 45" N 2° 43' 04" E	Temporary (4 – 9 mo)	2600	100	Riparian forest
PS_REF1	Reference	Natural	41° 48' 55" N 2° 43' 01" E	Temporary (4 – 9 mo)	250	200	Riparian forest
PS_REF2	Reference	Natural	41° 49' 09" N 2° 42' 34" E	Temporary (4 – 9 mo)	5000	250	Riparian forest
PS_REF3	Reference	Man-made, naturalised	41° 49' 22" N 2° 41' 31" E	Semipermanent (≥ 10 mo)	20	60	Wet grasslands
PS_REF4	Reference	Natural	41° 50' 02" N 2° 40' 44" E	Temporary (4 – 9 mo)	30	80	Dry meadows
PS_REF5	Reference	Natural	41° 50' 15" N 2° 40' 32" E	Ephemeral (≤ 3 mo)	15	30	Dry meadows

Sampling and sample processing

Man-made MTPs

In BT and PS, every month from September 2006 to September 2008 we measured water conductivity using a Crison 524 conductivity meter, dissolved oxygen using a Hach HQ10 Portable LDO meter, and water level using a graduated gauge. On each sampling visit, water samples were collected, filtered through GF/C Whatman filters, and frozen in the laboratory. We analyzed the dissolved inorganic nutrient content (ammonium, NH_4^+; nitrite, NO_2^-; nitrate, NO_3^-; and soluble reactive phosphorus, PO_4^{3+}) of the filtered samples according to Grasshof et al. (1983).

Amphibian larvae were sampled monthly using a dip net (250 µm mesh; 20 cm in diameter). To capture all types of the macrofaunal community, we swept the dip net twenty times in rapid sequence, covering all different microhabitats. Amphibian larvae were sorted, identified, and measured in the laboratory.

Within the two hydroperiods (September 2006 to August 2007 and September 2007 to August 2008) we surveyed post-metamorphic and adult amphibians during two intervals (Figure 2): interval 1 was from 03/29/2007 to 06/12/2007 and interval 2 was from 03/12/2008 to 06/28/2008. For these surveys, 10 cm of a 50-cm tall plastic drift fence was buried, completely encircling the pond. Outside and inside of the fence, pitfall traps (30 cm in diameter and 40 cm deep) were located every 15 m. Each trap was equipped with a funnel to prevent trapped climbing species from escaping. To avoid desiccation in the trap, a lid above the entrance reduced insolation, and a wet sponge inside the trap reduced dryness. Traps were checked every other day, being from both sites visited on the same day. From 04/11/2007 to 04/28/2007, area floods decreased the trapping efficiency in BT. For each capture we recorded species, sex, weight (± 0.01 g), length (SVL ± 0.1 mm) and released the animal on the opposite side of the fence. Additionally, in interval 2 we individually marked *B. calamita* adults using a toe-clipping technique (Donnelly et al. 1994). For each marked individual, we measured the number of times it entered and exited the wetland within the interval, the time (in days) that it spent inside the wetland, and the amount of weight lost during reproduction. During interval 1 and interval 2, precipitation and minimum and maximum daily temperature data were collected from nearby Catalan Meteorological Service (SMC-Meteocat) stations.

Table 2 Water and meteorological variables for BT and PS sites during two hydroperiods. For water variables, mean values (in bold) and standard deviation (in italics) are shown. Water variables: Ox. = dissolved oxygen saturation; Cond. = conductivity, Depth = average depth of the water column; DIN = concentration of dissolved inorganic nitrogen; SRP = concentration of soluble reactive phosphorus. For meteorological variables, cumulative precipitation during the study (in bold) and the range of monthly average minimum – maximum values (in italics) are shown. The average temperature during the study (in bold) and the range of monthly average minimum – maximum values (in italics) are shown. Meteorological variables: Rain = cumulative precipitation and monthly average minimum – maximum values; T = average temperature and monthly average minimum – maximum values.

Site	**Hydroperiod**	***Water variables***					***Meteorological variables***	
		Ox. (%)	***Cond. (µS/cm)***	***Depth (cm)***	***DIN (mg/l)***	***SRP (mg/l)***	***Rain (mm)***	***T (ºC)***
BT	1	**92.7**	**2005.9**	**19.3**	**0.084**	**0.011**	**164**	**15.7**
		18.6	*497.1*	*15.7*	*0.139*	*0.042*	*2 – 93*	*9.0 – 24.9*
	2	**85.9**	**3742.5**	**11.7**	**0.103**	**0.002**	**149**	**14.4**
		13.1	*2489.0*	*12.2*	*0.087*	*0.002*	*13 – 54*	*8.9 – 24.2*
PS	1	**77.2**	**143.1**	**23.2**	**0.100**	**0.007**	**302**	**14.2**
		21.2	*200.9*	*19.0*	*0.067*	*0.011*	*23 – 101*	*1.7 – 26.6*
	2	**87.1**	**114.9**	**12.0**	**0.067**	**0.009**	**420**	**14.0**
		11.4	*74.7*	*16.5*	*0.023*	*0.005*	*61 – 169*	*2.2 – 25.7*

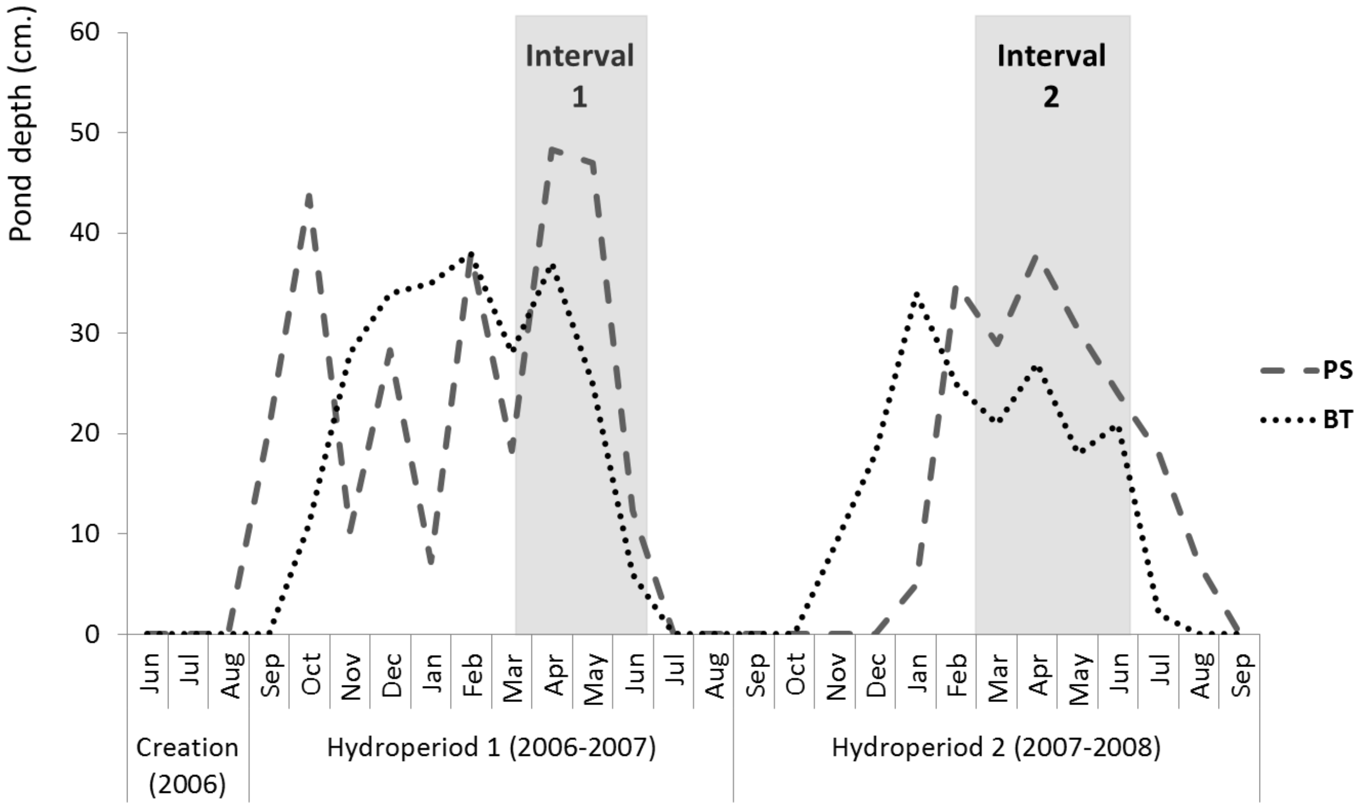


Fig. 2 Hydrological regime of BT and PS. The water levels are shown by dotted and dashed lines. The intervals for the pit-fall experiments are shown in gray.

Reference wetlands

In order to know the local amphibian community, all reference wetlands were surveyed during the year previous to the study. They received 4 visits, 2 in autumn (September-November) and 2 in spring (March-May). At each visit, two sampling procedures were applied. On one hand, larvae were captured dip-netting, using the same sampling methodology as in man-made MTPs. On the other hand, nocturnal transects (sensu Pearman et al. 1995) provided data on singing adults that would have been hardly detected otherwise.

Data analysis

In order to compare the extent to which the man-made MTP community of the first and second hydroperiod was similar to the amphibian community inhabiting the reference wetlands at each site, we performed an ANOSIM (analysis of similarities) test. This type of test operates on a resemblance matrix and is similar to a standard univariate ANOVA, but requires neither the normality nor homoscedasticity of data. *Wetland type* was selected as factor in the simple layout of this test, using the species presence/absence matrix. The distance matrix was built with the Bray-Curtis similarity measure, and the results showed a global R and *p*-value expressed as a percentage. Besides, a similarity of percentages analysis (SIMPER) identified those species which characterized the community of each wetland type, ordering the species from more to less contribution to the total within-type similarity (cut-off for low contributions at 70%). A full description of SIMPER analysis is provided by Clarke (1993).

Spearman non-parametric correlation tests allowed analysing if the daily number of *B. calamita* adults entering the wetlands or the daily number of post-metamorphic individuals exiting the wetlands were correlated to meteorological data (precipitation, maximum daily temperature, and minimum daily temperature). To account for the every other day sampling pattern, precipitation data was given as the cumulative precipitation over the two days, and temperature data were averaged over the two days. Using a Generalized Linear Mixed Model (GLMM), we set the response variable as the number of *captured individuals per day*, the tested factors were *site* (BT vs. PS), *interval* (interval 1 vs. interval 2), and *week* (1 to 16), set out as fixed effects, and *sampling day* was set as a random factor to account for temporal pseudoreplication. In mixed models, random effects deal with pseudoreplication by modelling the covariance structure introduced in the random part of the model (Crawley 2002).We started with a model without interactions. We started with a model without interactions. Since the validation of the model showed no significant patterns in the residuals, interactions were not included. All matrices were log-transformed for a better fit of errors to a normal distribution. Using ANOVA, we tested for site and sex effects on mobility (number of recaptures), time (number of days spent in the wetland), and reproduction cost (pre- and post-reproduction difference in weight).

ANOSIM and SIMPER routines were performed using Primer (v. 6.0 for Windows, PRIMER-E, Plymouth); Spearman correlation tests, GLMM, and ANOVA were performed using the software package PASW (v. 18, SPSS Inc., Chicago).

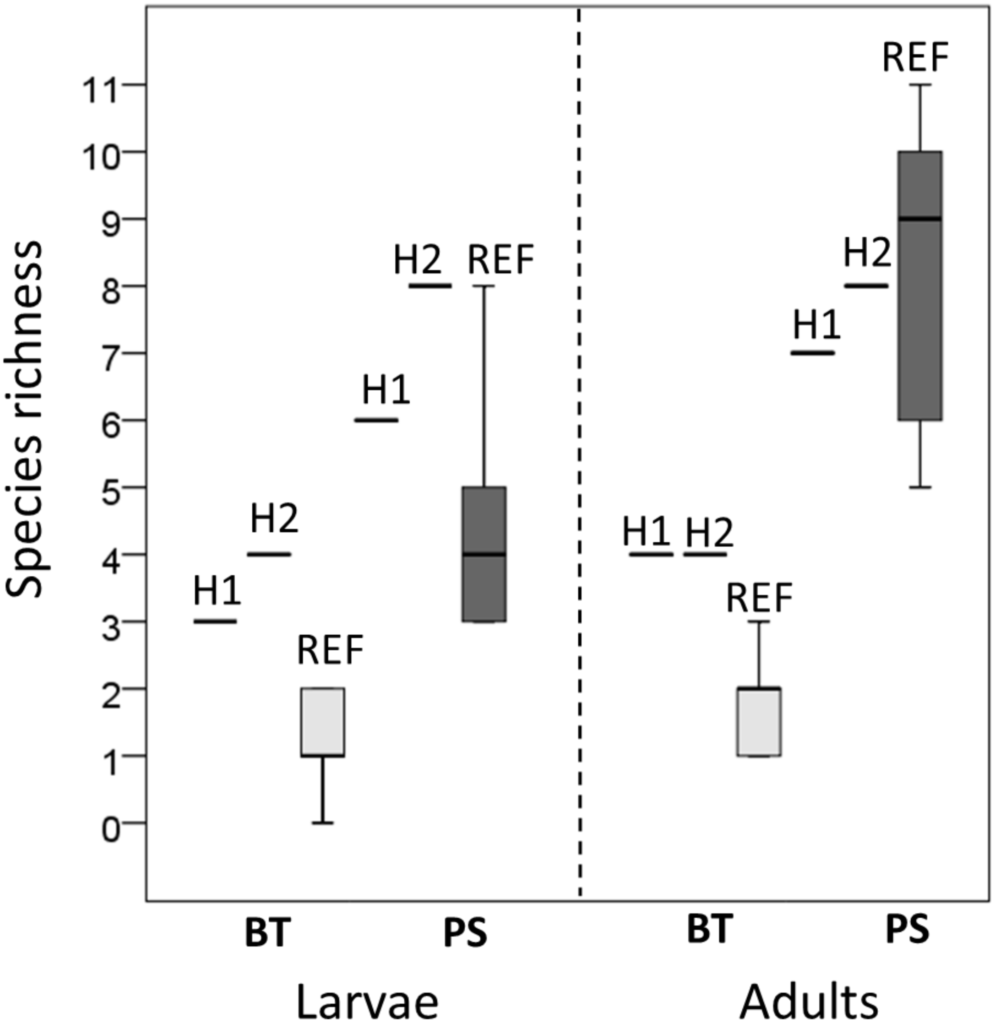
Results

Characterization of BT and PS

BT and PS had similar average temperatures, but PS had a wider temperature range (Table 2). Average precipitation was higher in PS. The hydrological regime was similar, with both sites exhibiting level oscillations despite the shallow mean depth (11.7 cm for BT and 23.2 cm for PS) and hydroperiods of 7 to 9 months (Figure 2).

On the other hand, the surveys in the reference wetlands provided information on the local existing amphibian communities. Five species were detected in BT reference wetlands (*Discoglossus pictus*, *Bufo calamita*, *Hyla meridionalis*, *Pelophylax perezi* and *Pelobates cultripes*), whereas PS reference wetlands community consisted of these five species and six additional species (*Salamandra salamandra, Lissotriton helveticus, Triturus marmoratus, Alytes obstetricans*, *Pelodytes punctatus*, and *B. bufo*).

Fig. 3 Comparison of the species richness detected in the studied man-made MTPs (BT and PS) and the reference wetlands. H1 = 1st hydroperiod of the studied man-made MTPs; H2 = 2nd hydroperiod of the studied man-made MTPs; REF = Reference wetlands at each site.



Man-made MTPs – reference wetlands community comparison

The ANOSIM test showed a global significant effect of *wetland type* over the amphibian community (R = 0.458, $p \leq 0.01$), with significantly different compositions between BT and PS reference wetlands (R = 0.718, $p \leq 0.01$). In both sites the respective man-made MTP community was similar to that inhabiting the reference wetlands, both during the first hydroperiod (BT: R = 0.12, $p \geq 0.05$; PS: R = -0.12, $p \geq 0.05$) and the second one (BT: R = 0.12, $p \geq 0.05$; PS: R = -0.02, $p \geq 0.05$). The SIMPER routine identified 5 species characterizing PS reference communities (*B. calamita, D. pictus, H. meridionalis, P. punctatus and P. perezi*), whereas only 1 species was identified in reference communities of BT (*B. calamita*). Higher species richness levels were achieved in man-made MTPs in BT than in the reference wetlands, both for larvae and adults and during both hydroperiods. Contrarily, species richness levels in PS fell within the reference wetlands margins, both for larvae and adults, throughout the study (Figure 3).

Colonization of the man-made MTPs

In both sites, all species that were detected in hydroperiod 1 were also present during hydroperiod 2, being the most abundant *B. calamita* (95% of the total captures in BT, 74% in PS). In BT, three of the five local amphibian species were successfully reproducing in the new wetland during hydroperiod 1. The fourth local species, *H. meridionalis*, arrived at hydroperiod 1 but did not reproduce until hydroperiod 2, and *P. cultripes* was never recorded (Table 3). Besides, in PS six of the eleven local amphibian species reproduced in the wetland during hydroperiod 1. In addition, two extra species reproduced there during hydroperiod 2: *T. marmoratus* arrived to PS as an adult at hydroperiod 1 but did not reproduce there until hydroperiod 2, and *L. helveticus* was detected and reproduced during hydroperiod 2.

Although *B. bufo* adults were caught at PS during both hydroperiods, there was no evidence that they reproduced. *P.perezi* and *P. cultripes* were never detected in PS (Table 3).

Table 3 Life cycle stage of amphibians captured at BT and PS during the study. L = larvae; M = individuals in post-metamorphic stage; A = adults.

Species	***BT***							***PS***						
	Locally present	***Hyd. 1***			***Hyd. 2***			***Locally present***	***Hyd. 1***			***Hyd. 2***		
		L	***M***	***A***	***L***	***M***	***A***		***L***	***M***	***A***	***L***	***M***	***A***
Salamandra salamandra	-	-	-	-	-	-	-	Yes	0	19	5	0	3	5
Lissotriton helveticus	-	-	-	-	-	-	-	Yes	0	0	0	0	1	1
Triturus marmoratus	-	-	-	-	-	-	-	Yes	0	0	2	0	1	1
Discoglossus pictus	Yes	0	29	4	0	85	9	Yes	2	4	16	124	309	48
Alytes obstetricans	-	-	-	-	-	-	-	Yes	0	6	3	0	1	0
Pelodytes punctatus	-	-	-	-	-	-	-	Yes	0	2	1	0	1	3
Bufo bufo	-	-	-	-	-	-	-	Yes	0	0	4	0	0	2
Bufo calamita	Yes	0	2629	14	6	234	509	Yes	127	10	780	102	316	432
Hyla meridionalis	Yes	0	0	1	14	0	3	Yes	5	0	0	20	18	2
Pelophylax perezi	Yes	0	2	13	0	2	2	Yes	0	0	0	0	0	0
Pelobates cultripes	Yes	0	0	0	0	0	0	Yes	0	0	0	0	0	0

Table 4 Spearman non-parametric correlations (ρ) between the colonization variables of *B. calamita* (number of adults entering and number of post-metamorphic individuals exiting the wetland) and rain or temperature data. (Rain, two days cumulative precipitation; Tmin, minimum daily temperature; Tmax, maximum daily temperature). ns, $p > 0.05$; *, $p < 0.01$.

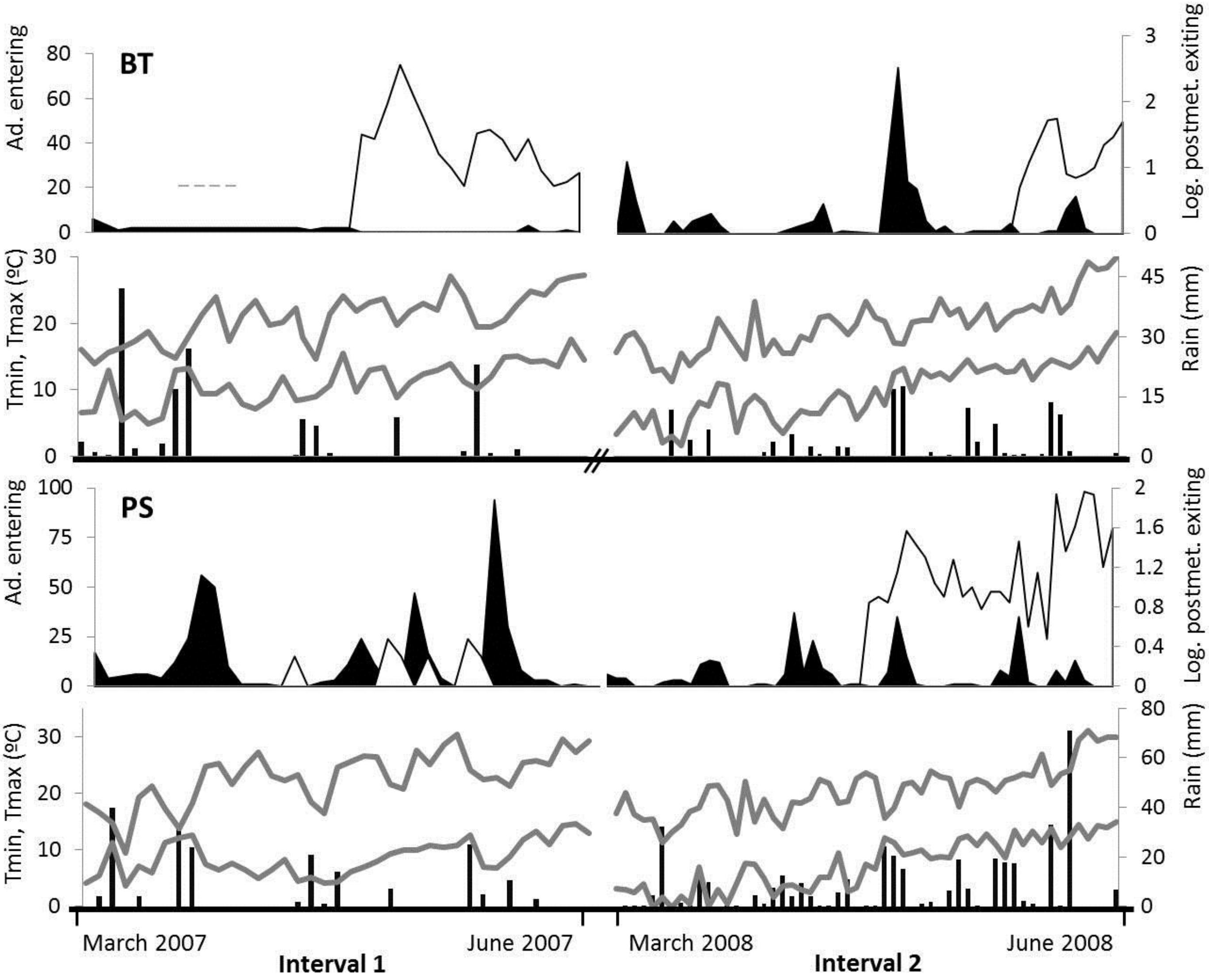
	BT		***PS***	
	Ad. entering	***Post-met. exiting***	***Ad. entering***	***Post-met. exiting***
Rain	+ 0.457 (*)	- 0.095 (ns)	+ 0.182 (*)	+ 0.040 (ns)
Tmin	+ 0.051 (ns)	+ 0.567 (*)	+ 0.168 (*)	+ 0.440 (*)
Tmax	- 0.291 (*)	+ 0.600 (*)	+ 0.042 (ns)	+ 0.313 (*)

Colonization dynamics and reproductive success of *B. calamita* in man-made MTP's

During both intervals the number of adult of *B. calamita* individuals entering the wetland and post-metamorphic individuals exiting the wetland were correlated to meteorological variables (Figure 4). At the beginning of both intervals, adults were already being captured in an irregular pattern that generally followed rain events. For both BT and PS, there was a positive significant correlation between the number of adults entering the wetland and the cumulative precipitation (Table 4). Minimum daily temperature had a positive significant correlation with the number of entering adults only in PS. By contrast, maximum daily temperature had a negative significant correlation with the number of entering adults in BT. Post-metamorphic individuals appeared for the first time during weeks 7 to 9 and dominated the second half of both intervals at both sites. While the number of post-metamorphic individuals exiting the wetland was not significantly affected by precipitation at either site, both minimum daily temperature and maximum daily temperature had significant positive correlations to the number of post-metamorphic individuals exiting the wetland in both sites (Table 4).

GLMM confirmed that the number of *B. calamita* adults varied significantly between sites ($F_{1,3} = 3.993$, $p < 0.05$), intervals ($F_{1,3} = 75.841$, $p < 0.001$), and weeks ($F_{14,16} = 35.165$, $p < 0.001$; Figure 5). Although the number of adults entering the wetland was higher in PS than in BT, the number of post-metamorphic individuals exiting the wetland was higher in BT than in PS ($F_{1,42} = 5179.71$, $p < 0.001$). In both sites, there was a higher number of post-metamorphic individuals caught in the traps in interval 1 compared to interval 2 ($F_{1,42} = 7.392$, $p < 0.01$). Adults had irregular movements throughout the intervals. By contrast, post-metamorphic individuals consistently exited the wetlands beginning at the seventh week ($F_{9,50} = 7998.84$, $p < 0.001$).

Fig 4 Colonization dynamics of *B. calamita* and weather data. For the first and third panels, the number of adults entering the wetlands (Ad. entering) is shown in black, and the log of the number of post-metamorphic individuals exiting the wetlands (Log. post-met. exiting) is shown in white. For the second and fourth panels cumulative precipitation (Rain) is shown in black columns, and the minimum daily temperature (Tmin) and maximum daily temperature (Tmax) are shown by gray lines. During the dashed interval in BT (04/11/2007-04/28/2007), the pit-fall traps were only partially functional due to flooding.



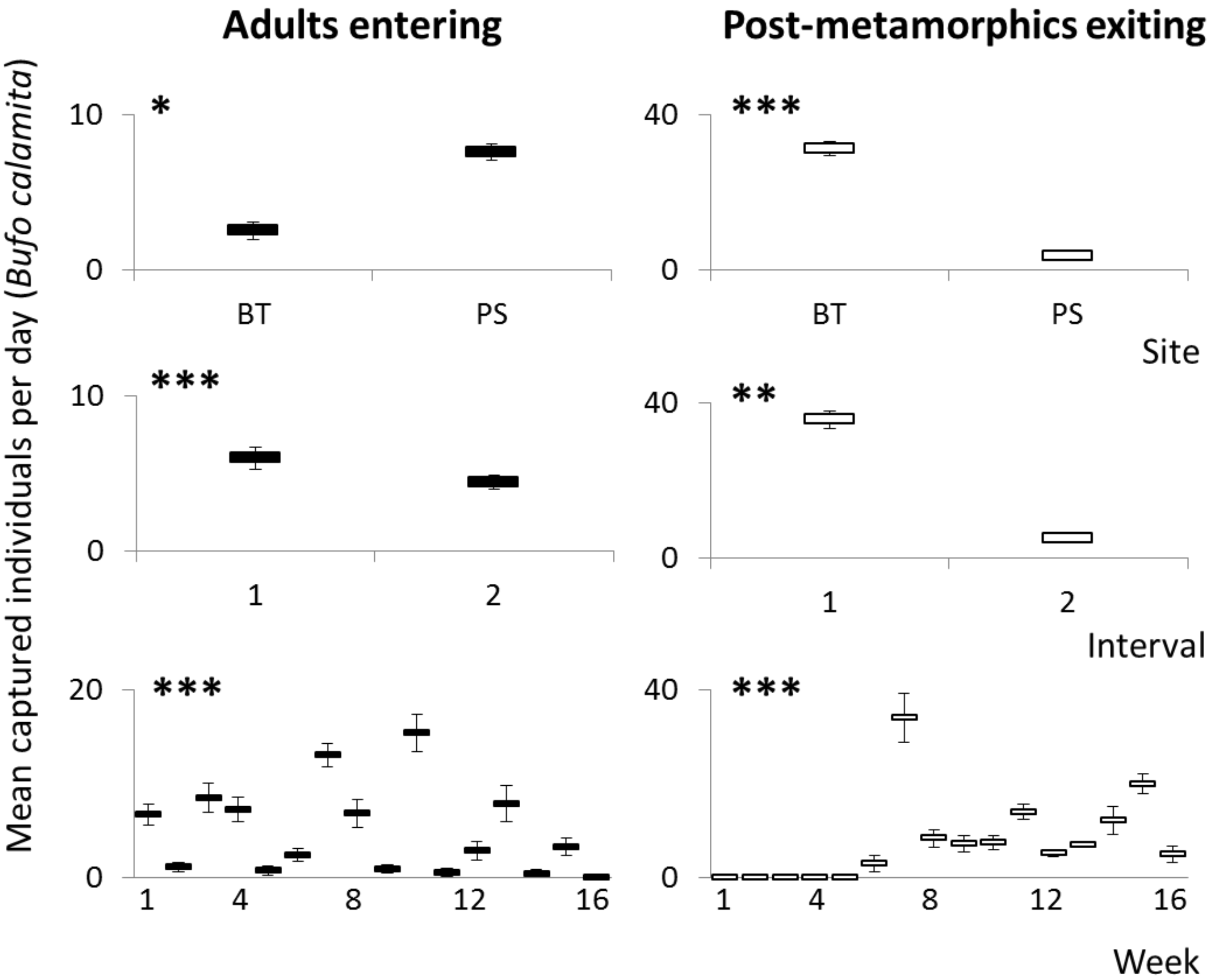


Fig 5 GLMM results of the spatial and temporal variability of *B. calamita* colonization. *Site*, *interval* and *week* were fixed effects, whereas *sampling day* was set as a random factor. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Using toe clips, we marked 186 *B. calamita* in BT and 359 in PS (Table 5). In both sites, males were significantly more likely to be recaptured than females. Additionally, the maximum number of times that an individual was recaptured was higher for males than for females. Males spent approximately twice as much time in the wetland compared to females. In spite of the shorter time in the wetland, females lost a higher proportion of weight (15-18% of their pre-reproductive weight) during breeding compared to males (4-5% of their pre-reproductive weight).

Table 5 Sex and site effect on the mean recapture rate per adult, the maximum recapture rate for adults, the mean number of days spent in the wetland, and the mean reproductive cost. These 3 parameters were tested by means of ANOVA, both by site (BT / PS) and by sex (males / females) factors. ns, p > 0.05; *, p < 0.05; **, p < 0.01; ***, p < 0.001.

	BT		*Sex effect*		*PS*		*Sex effect*		*Site effect*	
	Males	*Females*			*Males*	*Females*				
Ind. marked / recaptured	118 104	68 52	*F*	*p*	131 110	228 178	*F*	*p*	*F*	*p*
Mean recapt. (max.)	1.41 (6)	1.21 (3)	15.03	***	2.12 (8)	1.40 (3)	85.82	***	3.54	ns
Mean days in the wetland ± SE	19.43 ± 2.7	9.17 ± 2.4	5.23	*	23.02 ± 2.4	11.50 ± 1.4	21.27	***	0.019	ns
Mean weight % when exiting ± SE	96.12 ±1.3	81.63 ± 2.3	32.93	***	94.95 ± 2.9	85.45 ± 1.8	9.34	***	1.22	ns

Discussion

Local amphibian diversity and colonization of man-made wetlands

Local diversity levels differed between BT and PS areas, a result coherent with previous studies in both areas (Pleguezuelos et al. 2002, Boix et al. 2004a). Strong anthropogenic influences such as intensive agriculture have been associated with habitat fragmentation, which in turn controls the viability of regional amphibian populations (Lehtinen et al. 1999, Beja and Alcazar 2003, Cushman 2006, Fischer and Lindenmayer 2007). This could have caused in BT the absence of urodeles, a group with low dispersion rates and short maximal dispersal distances (Smith and Green 2005). Furthermore, cultivation and nutrient enrichment has probably affected the natural wetlands in BT watershed, as observed in other regions of the Iberian Peninsula (García-Muñoz et al. 2010). Negative effects of agricultural intensification on micro and macrofaunal assemblages have already been described (Beja and Alcazar 2003, Rohr and Crumrine 2005, Peltzer et al. 2006). Particularly, the impact of pesticides to water quality has been confirmed both regionally (e.g., Hildebrandt et al. 2008) and locally, at nearby wetlands (e.g., López-Flores et al. 2003, Salvadó et al. 2006). Hence, despite having no data from the studied natural and reference wetlands, we believe this fact could explain why in BT some species were using the man-made MTPs, rainwater-fed, instead of the natural ones, which were often connected to managed ecosystems such as rice fields.

Key factors that influence the colonization of a new or restored pond include the regional amphibian community and the size and isolation of the pond (e.g. Laan and Verboom 1990, Lehtinen and Galatowitsch 2001, Oertli et al. 2002). In our case, high connectivity to other local bodies of water led to the high proportion of local species that arrived to the new wetlands during the first hydroperiod. Compared to amphibian colonization and reproduction in new wetlands in Europe (Table 6), PS had not only the highest regional diversity for potential colonization (11 species) but also a remarkably high percentage of successful colonization (82 %). Moreover, most of the species in both sites also reproduced in the new wetlands within the first (60% in BT, 55% in PS) or second (80% in BT, 73% in PS) year. This proportion will likely evolve in subsequent years, yet it is remarkably high compared to other short-term colonization studies in Europe (Laan and Verboom 1990, Lesbarrères et al. 2010). These studies have found little or no reproduction in new or restored wetlands, whereas other studies have found colonization and reproduction rates similar to what we show here by studying older wetlands (Beebee 1997, Baker and Halliday 1999) or by including many more (> 100) bodies of water (Stumpel and van der Voet 1998, Rannap et al. 2009). Accordingly, amphibian colonization studies of North American new or restored wetlands have shown similar results for a wide range of potential colonizing species (Table 6), supporting our finding that important colonizers arrive at the new or restored wetland within the first two years (e.g. Perry et al. 1996, Lehtinen and Galatowitsch 2001, Pechmann et al. 2001, Stevens et al. 2002). Unlike what we found, however, only one case of North American colonization detected more than 50% of these local species reproducing by the second year (Vasconcelos and Calhoun 2006).

Although the colonization of the new wetlands included individuals from most local species of the amphibian community, many species were present in low numbers (< 50 individuals). These low numbers might be related to limited dispersal abilities of some species (Smith and Green 2005 and references therein) and a high site fidelity (e.g. Cushman 2006). Also, low counts could be biased by our capture methods, that probably underestimate the abundance of climbing species such as *H. meridionalis* (Dodd 1992). The two most abundant species, *D. pictus* and *B. calamita*, are known to be pioneering and opportunistic and to have wide dispersal ranges (Sinsch 1988, Miaud et al. 2000, Boix et al. 2004b, Montori et al. 2007), which appear to have helped them to take advantage of temporary newly created wetlands.

Colonization dynamics and reproductive success of *B. calamita*

The annual biological cycle of *B. calamita* is characteristically discontinuous, with peaks in activity related to the weather (Tejedo and Reques 1997, Brooke et al. 2000). Here, we confirmed the known role of temperature and precipitation on the breeding phenology of *B. calamita* (Banks and Beebee 1986, Sinsch 1988). In BT, where the average rainfall was lower than in PS, the movement of adult *B. calamita* had a stronger correlation with rain events.

Low minimum temperatures and high maximum temperatures led to a reduction in adult movement. In BT, a sea-regulated microclimate, the temperature range was narrow. Due to inactivity on hot days, maximum temperature was inversely correlated with adult movement. By contrast, without the sea-regulated microclimate, PS exhibited much lower minimum temperatures, which led to reduced adult activity. The activity of exiting post-metamorphic individuals was correlated with both the minimum and maximum temperatures, likely due to the rapid larval development of *B. calamita* (e.g. Álvarez and Salvador 1984, Boomsma and Arntzen 1985) and the quick-response effect of water temperature on the metamorphosing larvae. Evaporation of these shallow wetlands increases the density and the intraspecific competition, leading to the acceleration of metamorphosis (Tejedo and Reques 1994, Newman 1998).

It generally takes two to five years for *B. calamita* individuals to reach sexual maturity (Denton and Beebee 1993, García-París et al. 2004). Although stressed populations can show secondary sexual characteristics during the first year of life, which would lead to faster reproduction (unpublished data on *B. calamita* populations of the Cantabrican Coast, Spain), we did not observe such early reproduction in either BT or PS. Consistent with other studies (Pough et al. 1992, Joly and Grolet 1996), the reproductive investment for females was much higher than for males. *B. calamita* males invested more time in the wetland and exhibited more movement into and out of the wetland, both of which have been related to male mating success (i.e. Arak 1988). *B. calamita* population variability has also been described in long-term studies of natural systems (Bragg 1960). In this study, this natural variability could be mixed with effects such as the changing invertebrate community of newly created wetlands (Ruhí et al. 2009) and the hydrological unpredictability of Mediterranean ecosystems (Álvarez-Cobelas et al. 2005, Gascón et al. 2007), also observed in these man-made MTPs.

Table 6: Amphibian colonization studies (published since 1990) concerning newly created or restored wetlands in the Holarctic region. The location of the new created or restored wetland, as well as the habitat type, is shown. [For 'Duration and frequency of the study', more than 20 visits of a single water body, or a continuous pit-fall trap monitoring, was classified under 'many visits'. For 'Monitored water bodies', created and restored wetlands were taken into account but reference sites were left apart. For 'Wetland age', when the monitoring involved more than one year, it is shown the age range from the youngest wetland at the beginning of the monitoring until the oldest, at the end. Moreover, when the original data was detailed enough wetland age groups were made. 'Spp in modified sites' refers to the maximum number of amphibian species found (a) in a particular wetland (when available), or (b) in the wetland age-group. In brackets, the species fraction that successfully bred, with clutches, tadpoles or froglets evidence; when not enough data was available for this parameter, it was indicated by "(-)". 'Spp in reference sites' refers to the number of species present at nearby wetlands (in parentheses, the species fraction that successfully bred). When the study did not encompass the monitoring of natural/reference sites, the cumulative richness is shown in italics.]

Location	*Habitat type*	*Duration and frequency of the study*	*Monitored water bodies*		*Wetland age*	*Spp in modified sites*	*Spp in reference sites*	*Source*
Catalonia	Created Mediterranean Temporary Ponds	2 years (many visits)	2	BT	1 year	4 (3) [a]	5 (5)	This study
					2 years	4 (4) [a]		
				PS	1 year	8 (6) [a]	11 (11)	
					2 years	9 (8) [a]		
France (Maine & Loire)	Created replacement ponds	4 years (many visits)	4		0 to 4 years	5 (4) [b]	6 (-)	Lesbarrères et al. (2010)
UK (E. England)	Created ponds	1 year (1 visit)	78		1 to 20 years	3 (3) [a]	4 (4)	Baker & Halliday (1999)
UK (S. England)	Created dewponds	2 years (1 visit)	10		≥ 6 years	4 (4) [b]	5 (5)	Beebee (1997)
The Netherlands (Limburg)	Created pools	1 year (6 visits)	39		≤ 5 years	8 (-) [b]	*8 (-)*	Laan & Verboom (1990)
The Netherlands (across the country)	Created ponds	1 year (2 visits)	133	5	0 years	1 (1) [a]	*9 (9)*	Stumpel & Van der Voet (1998)
				18	1 year	2 (2) [a]		
				34	2 years	4 (4) [a]		
				35	3 to 5 years	6 (5) [a]		
				30	6 to 10 years	5 (4) [a]		
				11	11 to 34 ears	5 (3) [a]		
Estonia (Haanja and Otepää)	Created and restored ponds	3 years (3 visits)	230 (208 created, 22 restored)		1 years	7 (7) [b]	8 (8)	Rannap et al .(2009)
					2 years	7 (7) [b]		
					3 years	7 (7) [b]		

Location	***Habitat type***	***Duration and frequency of the study***	***Monitored water bodies***	***Wetland age***	***Spp in created or restored sites***	***Spp in natural or reference sites***	***Source***
USA (South Carolina)	Created replacement ponds	8 years (many visits)	3	1 year	16 (1) [b]	19 (8)	Pechmann et al. (2001)
				2 years	12 (5) [b]		
				3 years	14 (8) [b]		
				4 to 8 years	13 (9) [b]		
USA (West Virginia)	Constructed pools	2 years (18 visits)	22	0 to 2 years	3 (3) [a]	*6 (4)*	Barry et al. (2008)
USA (West Virginia)	Constructed and partially restored wetlands	2 years (6 visits)	11	4 to 22 years	7 (-) [b]	7 (-)	Balcombe et al. (2005)
USA (Missouri)	Constructed wetlands	1 year (3 visits)	49	(-)	16 (-) [b]	22 (22)	Shulse et al. (2010)
USA (Ohio)	Constructed mine-water wetland	3 years (18 visits)	1	3 to 5 years	9 (-) [b]	9 (-)	Lacki et al. (1992)
USA (Minnesota)	Restored wetlands	0.5 years (5 visits)	7	0 to 2 years	8 (4) [b]	12 (8)	Lehtinen & Galatowisch (2001)
USA (Illinois)	Restored wetlands	4 years (many visits)	1	0 to 3 years	8 (-) [b]	8 (-)	Mierzwa (2000)
USA (Maryland)	Suburban stormwater ponds	2 years (many visits)	16	(-)	6 (6) [b]	1 (0)	Brand & Snodgrass (2010)
	Suburban artificial wetlands		21	(-)	4 (4) [b]	1 (0)	
	Forested artificial wetlands		5	(-)	6 (3) [b]	0 (0)	
USA (Maryland)	Created forested wetland	2 years (many visits)	1	1 year	10 (-) [a]	10 (-)	Perry et al. (1996)
				2 years	10 (-) [a]		
USA (Maine)	Created pools	6 years (many visits)	3	0 years	2 (2) [a]	*5 (4)*	Vasconcelos & Calhoun (2006)
				1 year	4 (3) [a]		
				2 year	4 (3) [a]		
				3 to 6 years	5 (4) [a]		
Canada (Prince Edward Is.)	Restored wetlands	2 years (3 visits)	22	2 to 8 years	5 (-)	5 (-)	Stevens et al. (2002)

Conservation interest of man-made MTPs

It is well accepted that newly created wetlands should be assessed with deep, qualitative, and long-term studies (Zedler and Callaway 1999, Pechmann et al. 2001, Petranka et al. 2003, Vasconcelos and Calhoun 2006, Petranka et al. 2007). However, this study provided evidence of the benefits of artificial MTPs for amphibian conservation already within a short-term period. Other short-term studies in recovered wetlands have shown that anuran densities can be similar to or even higher than the densities in natural wetlands (e.g. Balcombe et al. 2005, Brand and Snodgrass 2010). Hence, in such situations artificial wetlands may help recover declining populations of threatened species (Rannap et al. 2009).

B. calamita is a species protected by Spanish and European laws that has lately suffered a population decline (Beja et al. 2008). The creation of these and other MTPs would likely benefit *B. calamita* populations in the Mediterranean region, as has already been observed in the United Kingdom (Denton et al. 1997). In a broader sense, although we show that artificial MTPs created new habitat mainly for local amphibian pioneering or opportunistic species, our results imply that effects of man-made MTPs need to be further evaluated. We suggest there is enough evidence to regard these man-made systems as a key tool for aquatic biodiversity conservation even in short-term perspectives, a fact which could partly compensate for the loss of natural temporary ponds in the Mediterranean region.

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GENERAL DISCUSSION

Successional phases and temporal scales

The results obtained throughout this thesis suggest the existence of three successional phases related to wetland age and characterized by the different processes that occur in each. The characteristic features of the first successional phase are those derived from the colonization process, mainly (i) a rapid increase in species richness; (ii) an important dominance of some pioneer active dispersal species, highly shared with communities of nearby natural wetlands; and (iii) the absence of any structural changes in assemblage parameters within this period other than those related to seasonality, such as biomass shifts. Several previous studies on temporary waters have described different faunal compositions at the beginning of hydroperiods, e.g., in the playa lakes of the southwest US (Sublette and Sublette 1967, Moorhead et al. 1998), ephemeral pans, tropical pools and temporary ponds in Africa (Rzóska 1961, Meintjes 1996, Lahr et al. 1999), or temporary ponds in the Mediterranean region (Bazzanti et al. 1996, Boix et al. 2004b). Whether the phases observed in temporary wetlands (secondary succession) coincided or not with those occurring in man-made wetlands (primary succession) has remained untested to date. According to our results in man-made wetlands *(chapter 1)*, we suggest that the main features of this initial allogenic phase (called flooding phase by Lake et al. 1989) are shared between man-made and temporary aquatic ecosystems, since the constant increase of species richness and the dominance of aerial colonizers have proved to be characteristic of both primary and secondary succession. Higher species richness values have been found as hydroperiods became longer within this first successional phase at a nearby Mediterranean temporary pond (6 different hydroperiod lengths; Boix et al. 2004b). Furthermore, in studies of man-made aquatic systems, rapid and constant increases in richness have been described in newly created streams or channels (Malmqvist et al. 1991), experimentally flooded lakes and wetlands (Herrmann et al. 2000), and impounded reservoirs (Bass 1992). Thus, in our case, the high increase that we obtained (after 1-2 months, 50% of the species that would arrive within the 1st year had already colonized the Catalan man-made wetlands; *chapter 1*) had already been anticipated. However, we believe our short-term approach has made an important contribution in showing the lack of assemblage parameters and composition tendencies within the first year, hinting at the independence between rapid colonization and structure changes.

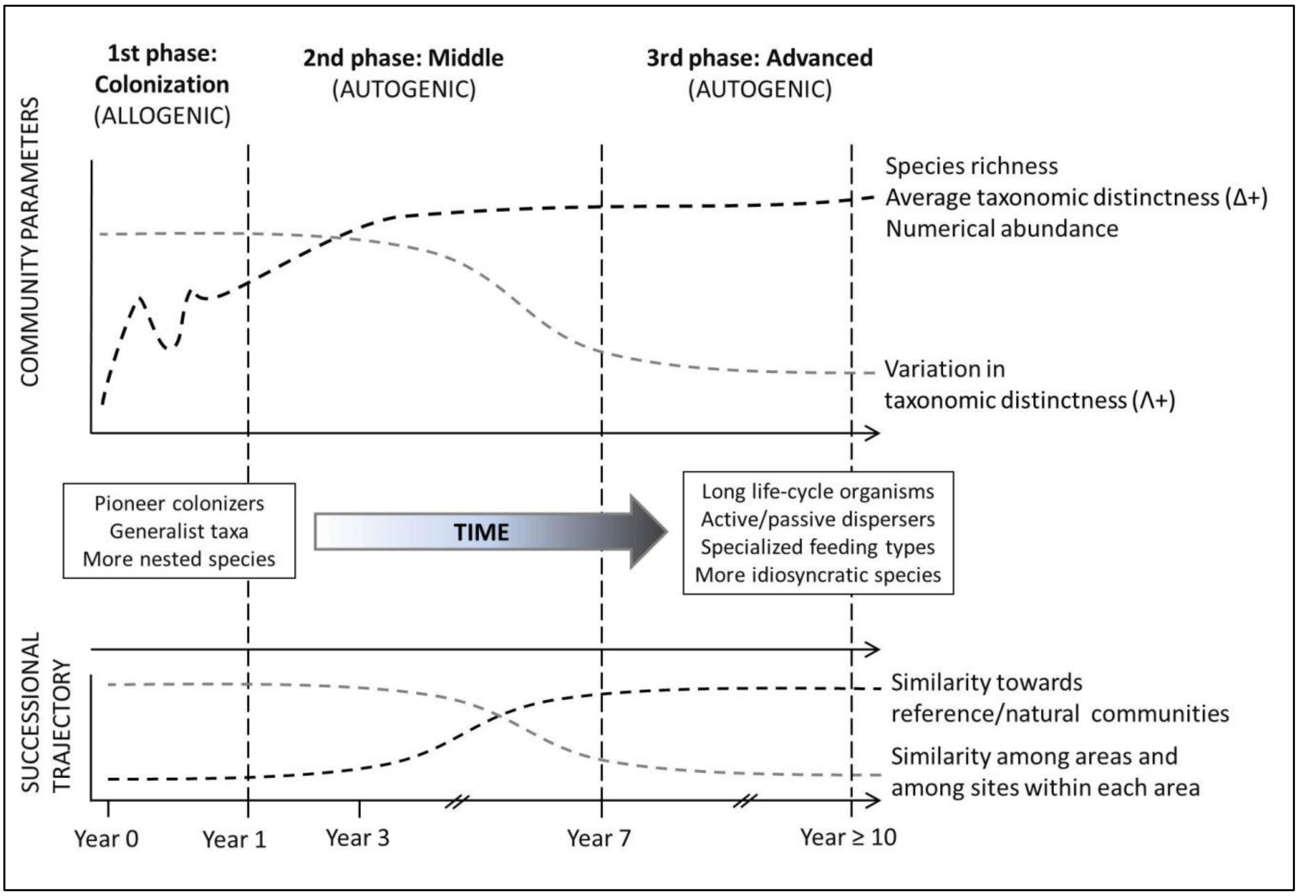

Figure D1. Synthesis of the obtained temporal changes of community parameters, biological traits and successional trajectories through time.

As well as colonization, we have observed two other distinct successional phases (Figure D1). First, the autogenic *middle* phase described in temporary ponds (Lake et al. 1989) was also found throughout this thesis, in the mid-term *(chapters 2 & 3)* and especially in the long-term approaches *(chapter 4)*. It has been characterized by the arrival of low dispersers contributing to idiosyncrasy among areas; and by structural alterations that can be properly assessed by means of changes in average (Δ+) and variation (Λ+) in taxonomic distinctness. Second, the phase we have called *advanced* (> 10 years from creation) and which we have detected only in our long-term approach *(chapter 4)* is characterized by higher values of Δ+ and lower of Λ+; decreases in instant-, and asymptotes in, cumulative-species richness. It is also characterized by the dominance of animals with longer life-cycle durations, aerial dispersal strategies, and certain feeding types (i.e., filter feeders, fine sediment collectors, predators, and parasites). Both the *middle* and *advanced* phases drive the community towards higher levels of taxonomic robustness and biodiversity, although it is at the *advanced* phase when some community parameters (e.g., species richness) reach a certain plateau. An interesting finding is the fact that the older man-made communities may host a higher number of macroinvertebrate species than young man-made and natural wetlands, while presenting virtually indistinct communities, in terms of composition, from the latter *(chapter 4)*. Although this idea had already been defended by Mitsch and Wilson (1996), we need to point out that, even in these cases, some rarer species may only occur in natural sites (Fairchild et al. 2000, Lundkvist et al. 2002). Overall, assessing succession from a longer perspective than usual has demonstrated, on one hand, the need to assess structural, taxonomic and functional changes across different temporal scales sensu Guo (2003), since only the combination of short-, mid- and long-term perspectives allows us to observe the whole picture in a successional process. On the other hand, it has shown that the advanced successional phase provides the ecosystem with higher taxonomic robustness and, consequently, functionality, than communities in earlier successional stages (Hooper et al. 2005, Graham et al. 2006).

Assembling mechanisms and spatial factors affecting successional trajectories

The study of succession has generated highly debated theories on the mechanisms by which communities assemble (Connell and Slatyer 1977). Since under ideal conditions no remnants of the previous biotic community should remain when primary succession starts (Gore and Milner 1990), how communities are assembled from the very first moment may condition subsequent communities. On the one hand, an important part of the debate has recently focused on the relative role of deterministic vs. stochastic variables in the process of community assembly (Lepori and Malmqvist 2009, Milner and Robertson 2010). Whereas deterministic communities follow predictable directional trajectories, stochastic communities are formed by chance colonization and extinction and do not follow any particular direction. Although many authors have traditionally defended stochastic views of community organization in aquatic systems (Fisher 1983, Townsend 1989, Reice 1994), much of this work has been carried out in streams and there is very little evidence of assembling mechanisms in wetlands through primary succession (but see Matthews and Spyreas 2010, Jeffries 2011). Our latitudinal comparison has shown random compositions from the regional pool of recruiters during the very first stages of colonization in Mediterranean wetlands, as anticipated *(chapter 3).* In contrast, non-random assemblages start the successional process in the cold temperate wetlands, as seen in successional pathways in the initial development stages of postglacial streams (Milner and Robertson 2010). Thus, our results contradict authors who defend community assembling as always being entirely stochastic (Fisher 1983, Townsend 1989, Reice 1994), and agree with the theory that overriding large scale effects (such as climate, sensu Poff 1997) may facilitate/hinder certain fauna under unfavorable conditions (Flory and Milner 2000, Milner et al. 2008, Milner and Robertson 2010).

On the other hand, we have observed that successional trajectories are influenced by regional communities *(chapter 2)*. Connell and Slatyer (1977) put forward three possibilities for successional processes: (1) facilitation, where early species modify the environment to make it more suitable for later colonizers; (2) tolerance, where a progressive tolerance of invading species occurs in the changing environment; and (3) inhibition, where early colonizers restrict the invasion of later colonizers. More modern approaches have analyzed the process from the perspective of successional trajectories. However, because successional case studies failed to support deterministic predictions (del Moral 2007), the traditional term of *climax* community has been progressively substituted by *reference* community. To this effect, the model recently proposed by Matthews and Spyreas (2010) has been valuable in allowing us to put forward a proposal based on their two key ideas from succession theory (convergence vs. divergence in species composition successional sites; and progression towards vs. deviation from a desired reference state) and on the recent concept of nested distributions (McAbendroth et al. 2005), particularly useful in the case of faunal succession because differential colonization between active and passive dispersers produces this kind of pattern (Wissinger et al. 2008, Florencio et al. 2011). Hence, we aimed to incorporate the spatial component to the model by Matthews and Spyreas (2010) in order to relate temporal variations of nestedness to eventual divergent successional trajectories. A nested colonization combined with divergent successional trajectories was observed, as it had been in several flora (Pineda et al. 1981, Christensen and Peet 1984, Seabloom and Van Der Valk 2003, del Moral 2007) and fauna studies (Chase 2007, Jeffries 2011). In our case, despite decreasing progressively through time, the highly nested pattern prevented wetland areas from diverging enough to compensate for, on a local level, the regional loss of pioneering taxa. Overall, the decline of species gain combined with constant species losses described through succession (Anderson 2007, Santos et al. 2011) was related, in our study, to the highly nested situation *(chapter 2).*

In our study, the main local factor influencing man-made communities was the permanent/temporary nature of wetlands *(chapters 1 & 2).* Although in some cases the ecological constraint attributed to temporary waters has been reflected in a smaller number of taxa than found in permanent ponds (Della Bella et al. 2005), the idea of low biodiversity in temporary environments has called for a revision (Williams 2006). In some studies comparing species richness of temporary and permanent environments, water permanence has not appeared to present a relevant effect on species richness (Boix et al. 2008), and other authors have pointed out that habitats with an intermediate hydroperiod can present a higher species richness than more temporary or permanent ones (Frisch et al. 2006). Temporality had a double effect: on one hand, this disturbance caused primary succession effects to be entangled with the secondary succession ones observed, for instance, in the high nestedness values and the presence of a permanent pioneering community in the temporary wetlands area. On the other, it limited the presence of some particular taxa, among which were the main exotic invasive species of the region, the red swamp crawfish and the mosquitofish (Geiger et al. 2005, Rodríguez et al. 2005, Gherardi and Acquistapace 2007, Vilà and García-Berthou 2010). Moreover, the hydrological variability factor achieved global significance when comparing Mediterranean wetlands to those of the cold temperate region *(chapter 3).* We related the high hydrological variability of Mediterranean man-made wetlands (chapter 5; Álvarez-Cobelas et al. 2005, Beklioglu et al. 2007) to the lack of clear seasonal and successional patterns in the mid-term. In regards to structural and functional adaptations between aquatic ecosystems in the Mediterranean and temperate regions, evidence observed in streams and rivers was mostly corroborated in man-made wetlands (Townsend and Hildrew 1994, Bonada et al. 2007). In the Mediterranean, communities are characterized by traits favoring resilience and resistance to disturbances, in contrast to the lack of necessary strategies for overcoming such ecological bottlenecks in the temperate region (Bêche et al. 2006, Bonada et al. 2007).

Biodiversity benefits of wetland creation

The way in which the *success* of created or restored wetlands is measured, and the ability to achieve this success, are two issues currently debated by wetland scientists and managers (Mitsch and Wilson 1996, Mitsch and Gosselink 2007). The species similarity between a restored or newly created ecosystem and one or more reference sites, rather than univariate indicators based on single species or parameters, should be regarded as the parameter of restoration progress (Matthews and Endress 2008, Matthews et al. 2009, Meyer et al. 2010). Thus, fair comparisons of success may be made with communities of reference/natural wetlands, or eventually with the communities existing in the previous wetland in the case of mitigation purposes. Therefore, we believe two aspects are crucial: the temporal scale over which newly created wetlands are intended to work and the final goal, or beneficiary target group.

The temporal scale of most creation/restoration projects is less than five years (Zedler and Kercher 2005). The fact that new wetlands are often designed to replace, within very short time periods, natural ones (Pechmann et al. 2001) is a problem both for the biodiversity values the wetland may achieve within that period and for a correct evaluation of success, as shown in our long-term approach. In this sense, we have observed a significant contribution to biodiversity, reflected into no compositional differences towards reference wetlands, only when comparing communities of man-made wetlands $\geq$ 10 years with those of natural ones. This observation, which corroborates the findings of other authors (e.g., Fairchild et al. 2000), may demonstrate the self-design and time needs of an ecosystem through succession, and thus the difficulty of artificially accelerating this process (Mitsch and Gosselink 2007). In contrast, the study of MTPs created for amphibian conservation, showed they provided a remarkably valuable habitat from a short-term perspective (1-2 years), taking into account the proportion of species that colonized and bred effectively in the area compared to other European studies (Laan and Verboom 1990, Lesbarrères et al. 2010). Temporary ponds provide major breeding sites for amphibians in the Mediterranean region thanks mainly to low predation pressures in these habitats (Jakob et al. 2003, Díaz-Paniagua et al. 2010). Therefore, we believe creating these habitats in the Mediterranean area may help amphibians in general, and the less mobile species in particular, since the viability of regional amphibian populations is threatened by habitat fragmentation (Lehtinen et al. 1999, Cushman 2006, Fischer and Lindenmayer 2007). Thiere et al. (2009) observed that catchment-scale wetland creation for simultaneous retention and diversity purposes benefited the biodiversity of agricultural landscapes, particularly if the density of aquatic habitats is increased by at least 30%. Other authors have claimed that both biodiversity conservation and nutrient retention in agricultural areas can be achieved simultaneously (Hansson et al. 2005). When creating wetlands for aquatic biodiversity enhancement, we believe the main goal to be the consideration that a single water body can serve more than one purpose. As new wetlands are often created without much knowledge (Williams et al. 2008), we propose that any action for wetland creation should first consider the wetland density and connectivity goals, favorable morphology and characteristics of the target groups, as well as the temporal framework to compensate/produce biodiversity benefits.

CONCLUSIONS

1) In the short term (1st year from creation), only colonization is found in Mediterranean man-made wetlands. No structural, taxonomic or functional changes take place, despite a rapid and constant species richness increase that hints at the independence between colonization and community structure changes.

2) In the mid-term (2 to 7 years from creation) succession signs are conspicuous (i.e., patterns of taxonomic distinctness parameters), but it is not until later ($\geq$ 10 years) when parameters such as species richness reach an asymptote. This asymptote is located in high taxonomic robustness and functionality levels. Moreover, some biological traits are favored towards this advanced phase of succession, namely longer life-cycle durations and certain feeding types (i.e., filter-feeders, fine sediment collectors, predators, and parasites).

3) The regional scale on which primary succession takes place influences the nature of the assembling mechanisms, favoring random initial compositions in Mediterranean man-made wetlands and deterministic compositions in cold temperate ones. This factor also plays a “filtering” role of taxa and biological traits, which conditions both the early and mid-term colonizer communities when comparing Mediterranean vs. cold temperate wetland communities: Mediterranean communities are characterized by traits favoring resilience and resistance to disturbances, in contrast to the lack of necessary strategies to overcome such ecological bottlenecks in the temperate region.

4) Temporal changes of nested patterns in macrofaunal succession are explained by the differential colonization between active and passive dispersers. This phenomenon plays an important role in the assembling mechanism of the early colonizer community of Mediterranean man-made wetlands, since the more nested a local community is, the higher the influence it receives from the regional pool of recruiters. From a mid-term perspective, divergent successional trajectories among areas may not always imply higher regional diversities, since local communities are still too nested within the regional reference ones to make relevant net contributions to global richness.

5) Water permanence/temporality can have a significant effect on the successional dynamics and composition of a Mediterranean man-made wetland community from a mid-term perspective. In temporary man-made habitats, primary and secondary succession effects are entangled and their communities suffer higher nestedness, and lower idiosyncrasy levels, than permanent ones.

6) Ten years can be enough for a man-made wetland to achieve a similar invertebrate community, in terms of structure and composition, to that of surrounding natural wetlands. In turn, these older man-made wetlands (≥ 10 years from creation) can be as rich, or even richer, than both young man-made and natural wetlands.

7) Man-made Mediterranean temporary ponds (MTPs) may enhance amphibian populations within the 1st year from creation, both in high and low amphibian-diversity areas.

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APPENDIX 1: PICTURES OF THE MAN-MADE WETLANDS

1

2

From top to bottom and left to right (next page): wetlands at PS area being constructed (Spring-Summer 2006) (1, 2); collecting samples during the first Winter after construction (3); a view of the wetland after c. 2 years, during Spring 2008 (4, 5).
[pictures 1 and 2 are courtesy of *Fundació Emys*]

3

4

5


Espai Esplet
Espai destinat a la creació de la zona humida de l'Esplet
Projecte de recuperació de l'hàbitat de la població de tortuga d'estany i d'altres espècies i hàbitats d'interès comunitari
Diputació de Girona

6

7

8

From top to bottom: wetlands at PE area just after the first flooding (Autumn 2006) (6, 7) and after c. 1 year, in Spring 2007 (8).

9

10

11

From top to bottom: wetlands at BT area just after the first flooding (Autumn 2006) (9), the first Spring (10) and after c. 3 years from creation, during Spring 2009 (11).

12

13

14

From top to bottom: wetlands in KD (Sweden) c. 3 years from creation (12,13) and after 13 years, during Summer 2009 [pictures 12 and 13 are courtesy of Dr. Jan Herrmann]

15

16

17

18

19

From top to bottom: sequence of the setting up of the drift fences in BT (pictures 15 to 18) and in PS areas (19) for the amphibian monitoring (chapter 5) during early Spring 2007. [picture 19 is courtesy of *Fundació Emys*]

APPENDIX 2: FAUNAL LIST

Phylum	Class	Order	Family	Taxa	KD	BT	PE	PS
Cnidaria	Leptolida	Capitata	Hydridae	*Hydra* sp.			+	
Annelida	Oligochaeta			Oligochaeta indet.	+			
		Lumbriculida	Lumbriculidae	Lumbriculidae indet.			+	
		Tubificida	Enchytraeidae	Enchytraeidae indet.			+	+
			Naididae	Naididae indet.		+		
			Tubificidae	Tubificidae indet.		+	+	+
	Hirudinea	Arhynchobdellida	Erpobdellidae	*Dina lineata*	+			
				Erpobdella octoculata	+			
				Erpobdella testacea	+			
		Rhynchobdellida	Glossiphonidae	*Helobdella stagnalis*	+			
				Hemiclepsis marginata	+			
				Theromyzon tessulatum	+			
Platyheliminthes	Turbellaria	Seriata	Dendrocoelidae	*Dendrocoelum lacteum*	+			
			Dugesiidae	*Dugesia* sp.	+			
Mollusca	Gastropoda	Pulmonata	Lymnaeidae	*Galba truncatula*	+			
				Radix sp.	+			
			Physidae	*Physella acuta*		+	+	
				Physa fontinalis	+			
			Planorbidae	*Ferrissia* sp.			+	
				Gyraulus sp.	+			
				Planorbis sp.	+			
	Bivalvia	Veneroidea	Sphaeriidae	*Pisidium* sp.	+		+	
Arthropoda	Malacostraca	Isopoda	Asellidae	*Asellus aquaticus*	+			
				Proasellus coxalis		+		
		Decapoda	Atydae	*Atyaephyra desmarestii*			+	
			Cambaridae	*Procambarus clarkii*		+	+	
	Aracnida	Prostigmata		Hydrachnidia indet.	+			
			Arrenuridae	*Arrenurus (Megaluracarus)* sp.			+	+
			Hydrachnidae	*Hydrachna globosa*			+	+

Arthropoda	Aracnida	Prostigmata	Hydrachnidae	*Hydrachna (Hydrachna)* sp.			+	
			Hydrodromidae	*Hydrodroma despiciens*		+	+	+
			Hydryphantidae	*Hydryphantes ruber*			+	
			Pionidae	*Piona* sp.			+	
	Insecta	Ephemeroptera	Baetidae	*Cloeon inscriptum*	+	+	+	+
				Centroptilum luteolum	+			
			Caenidae	*Caenis luctuosa*	+	+	+	+
				Caenis horaria	+			
			Ephemeridae	*Ephemera glauca*			+	
			Leptophlebiidae	*Leptophlebia* sp.	+			
		Odonata	Aeshnidae	*Brachytron pratense*	+			
				Aeshna cyanea		+	+	+
				Anax imperator		+	+	+
				Boyeria irene				+
			Coenagrionidae	*Coenagrion puella/pulchellum*	+			
				Coenagrion mercuriale				+
				Ischnura elegans	+	+	+	+
			Lestidae	*Lestes sponsa/dryas*	+			
				Lestes viridis			+	
			Libellulidae	*Leucorrhinia pectoralis*	+			
				Libellula quadrimaculata	+			+
				Orthetrum cancellatum	+		+	+
				Sympetrum striolatum/sanguineum	+			
				Sympetrum fonscolombii		+	+	+
		Heteroptera	Corixidae	*Callicorixa praeusta*	+			
				Corixa punctata	+			
				Corixa afinis			+	+
				Cymatia rogenhoferi			+	
				Hesperocorixa linnaei	+			
				Hesperocorixa sahlbergi	+			
				Micronecta scholtzi		+	+	
				Paracorixa concinna	+	+	+	
				Sigara falleni	+		+	

Arthropoda	Insecta	Heteroptera	Corixidae	*Sigara lateralis*		+	+	+
				Sigara limitata		+	+	+
				Sigara cf. *nigrolineata*	+	+	+	+
				Sigara semistriata	+			
				Sigara scripta				+
				Sigara selecta				+
				Sigara striata	+	+		
			Gerridae	*Gerris lacustris*	+	+	+	+
				Gerris odontogaster	+			
				Gerris argentatus		+	+	
				Gerris lateralis		+	+	+
				Aquarius paludum		+	+	+
			Hydrometridae	*Hydrometra stagnorum*				+
			Nepidae	*Ranatra linearis*	+			+
			Notonectidae	*Anisops sardeus*		+	+	+
				Notonecta glauca	+			
				Notonecta maculata		+		+
			Pleidae	*Plea minutissima*			+	
			Velidae	*Microvelia pygmaea*		+	+	
				Velia caprai	+			
		Coleoptera	Dryopidae	*Dryops algiricus*		+	+	+
			Dytiscidae	*Agabus* sp.	+			
				Agabus nebulosus			+	+
				Agabus bipustulatus			+	+
				Colymbetes sp.	+			
				Dytiscus sp.	+			
				Eretes griseus		+	+	+
				Hydroglyphus geminus		+	+	+
				Hydroporus palustris	+			
				Hygrotus confluens				+
				Hygrotus inaequalis	+			
				Hyphydrus ovatus	+			
				Ilybius sp.	+			

Arthropoda	Insecta	Coleoptera	Dytiscidae	*Laccophilus hyalinus*			+	+
				Laccophilus minutus	+		+	
				Nebrioporus depressus	+			
				Porhydrus lineatus	+			
				Rhantus exoletus	+			
				Rhantus suturalis		+		+
				Scarodytes halensis	+			
				Yola bicarinata				+
			Gyrinidae	*Gyrinus dejeani*			+	
				Gyrinus distinctus			+	
				Gyrinus urinator		+		
				Gyrinus aeratus	+			
				Gyrinus marinus	+			
			Haliplidae	*Haliplus flavicollis*	+			
				Haliplus fulvus	+			
				Haliplus ruficollis	+			
			Helophoridae	*Helophorus alternans*		+		+
				Helophorus asturiensis		+	+	
				Helophorus minutus		+		
				Helophorus obscurus				+
				Helophorus cf. *lapponicus*		+	+	
			Hydraenidae	*Aulacochthebius exaratus*				+
				Hydraena sp.	+			
				*Ochthebius (*cf. *Asiobates)* sp.			+	
				Ochthebius dilatatus		+		
				Ochthebius minutus		+	+	+
			Hydrophilidae	*Berosus* sp.	+			+
				Enochrus bicolor		+	+	
				Enochrus ochropterus	+			
				Enochrus testaceus	+			
				Helochares lividus		+	+	+
				Limnoxenus sp.				+
			Noteridae	*Noterus clavicornis*	+		+	

Arthropoda	Insecta	Coleoptera	Noteridae	*Noterus crassicornis*	+			
		Megaloptera	Sialidae	*Sialis lutaria*	+			
		Trichoptera	Ecnomidae	*Ecnomus* sp.			+	
			Leptoceridae	*Oecetis ochracea*	+			
				Trianodes bicolor	+			
			Limnephilidae	*Glyphotaelius pellucidus*	+			
				Grammotaulius nigropunctatus	+			
				Limnephilus affinis/incisus	+			
				Limnephilus flavicornis	+			
				Limnephilus cf. *fuscicornis*	+			
				Limnephilus griseus	+			
				Limnephilus marmoratus	+			
				Limnephilus rhombicus	+			
				Limnephilus vittatus	+			
				Nemotaulius punctatolineatus	+			
			Phryganidae	*Agrypnia* sp.	+			
				Phryganea bipunctata	+			
			Polycentropodidae	*Holocentropus stagnalis*	+			
		Diptera	Ceratopogonidae	Ceratopogonidae indet.	+			
				Bezzia sp.		+	+	+
				Culicoides sp.		+	+	+
			Chaoboridae	Chaoboridae indet.	+			
				Chaoborus flavicans			+	+
			Chironomidae	Chironomidae indet.	+			
				Ablabesmyia sp.		+	+	
				Chironomus/Einfeldia sp.			+	
				Cladopelma sp.			+	
				Cladotanytarsus sp.		+	+	
				Corynoneura sp.			+	
				Cricotopus sylvestris		+	+	+
				Cryptochironomus sp.			+	
				Endochironomus sp.			+	
				Kiefferulus tendipediformis		+	+	+

Arthropoda	Insecta	Diptera	Chironomidae	*Labrundinia neopilosella*			+	
				Meropelopia sp.			+	
				Microchironomus sp.			+	
				Parachironomus sp.			+	
				Paramerina sp.			+	
				Paratanytarsus sp.		+	+	+
				Polypedilum nubifer		+	+	+
				Polypedilum scalaenum		+		
				Procladius choreus		+	+	+
				Psectrocladius gr. *sordidellus*		+	+	+
				Tanytarsus cf. *mendax*		+	+	
			Culicidae	Culicidae indet.	+			
				Aedes vexans		+		
				Anopheles gr. *maculipennis*		+	+	+
				Culex pipiens			+	
				Culex theileri		+	+	
			Dixidae	Dixidae indet.	+			
			Dolichopodidae	Dolichopodidae indet.	+			
			Empididae	Empididae indet.	+			
			Ephydridae	Ephydridae indet.	+			
				Scatella sp.		+	+	
			Limoniidae	Limoniidae indet.	+		+	
			Ptychopteridae	Ptychopteridae indet.	+			
			Stratyomidae	Stratyomidae indet.	+			
				Stratyomis sp.				+
			Syrphidae	Syrphidae indet.	+		+	
			Tabanidae	Tabanidae indet.	+			
			Tipulidae	Tipulidae indet.	+			
Chordata	Osteichtyes	Cypriniformes	Cyprinidae	*Barbus meridionalis*			+	
				Squalius laietanus			+	
		Cyprinodontiformes	Poeciliidae	*Gambusia holbrooki*		+	+	
	Amphibia	Anura	Alytidae	*Alytes obstetricans*				+
			Bufonidae	*Bufo bufo*				+

Chordata	Amphibia	Anura	Bufonidae	*Bufo calamita*	+	+	+
			Discoglossidae	*Discoglossus pictus*	+	+	+
			Hylidae	*Hyla meridionalis*	+	+	+
			Pelodytidae	*Pelodytes punctatus*		+	+
			Ranidae	*Pelophylax perezi*	+	+	
		Urodela	Salamandridae	*Lissotriton helveticus*			+
			Salamandridae	*Salamandra salamandra*			+
			Salamandridae	*Triturus marmoratus*			+