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Rowan, B.

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Nine Years On: Revisiting the Pond Communities of the Lizard Peninsula, UK

Billie Rowan

Project Advisor: David Bilton, School of Marine Science & Engineering, University of Plymouth, Drake Circus, Plymouth, PL4 8AA

Abstract

Ponds contribute in various amounts to freshwater biodiversity and in some regions can be of considerably high biodiversity value compared to other freshwaters. The ecology of pond communities has been studied by numerous authors, yet many of these studies represent only a snapshot in time. This study explored the macroinvertebrate communities of a selection of ponds on the Lizard Peninsula, UK and revisited these ponds after a nine year period, examining changes in composition, environmental variables structuring the communities and their conservation value. Ponds in both years formed distinct groups, based on community similarities. In both years area was an important environmental variable structuring the communities and in the first year visited water chemistry and number of plant species also contributed. Between the two years the number of macroinvertebrate species remained similar, 72 in 2000 and 74 in 2009, but the identity of the species within the pond communities differed. The conservation value of the pond communities between the two years did not significantly differ. With regards to conserving these Lizard ponds, turnover in ponds has not affected their biodiversity value and management should allow for such processes to take place.

Key Words: Macroinvertebrates, community structure, conservation value, turnover

Introduction

Ponds are an important component of the freshwater environment and are known to support rich plant and macroinvertebrate communities (Collinson *et al.* 1995, Nicolet *et al.* 2004) and provide a habitat for a variety of uncommon plant and macroinvertebrate taxa (Collinson *et al.* 1995, Boothby 1997, Nicolet 2001, Nicolet *et al.* 2004, Bilton *et al.* 2009). As a result of this ponds can represent a habitat of considerably high biodiversity value. This value in individual ponds can vary greatly but collectively regional pond biodiversity is generally high and in some instances exceeds that of other lentic and lotic water bodies (Biggs *et al.* 2005, Williams *et al.* 2003, Davies *et al.* 2008a, Davies *et al.* 2008b) although this matter may vary geographically (Ribera *et al.* 2003). The cause behind this high regional biodiversity is attributed to the great variability of ponds locally; community composition can differ significantly over small spatial scales (Kiflawi *et al.* 2003).

Driving the differences between pond community compositions, over various scales, has been attributed to numerous factors. Individual ponds can differ widely in their physical and environmental characteristics and species tolerances to these factors also varies (Williams 1997) therefore environmental and physical factors can influence the species composition of pond communities (Jeffries 2005). Such examples include pH (Nicolet *et al.* 2004), depth, dissolved Oxygen, macrophyte richness (Della Bella *et al.* 2005) and turbidity (Barnes 1983), all environmental factors that have been found responsible for driving the variation between pond communities. In combination the species composition and also number of species and proportion of predators (Bilton *et al.* 2001) in ponds can be influenced by pond size and permanence (Porst & Irvine 2009, Boix *et al.* 2001, Brooks 2000, Della Bella *et al.* 2005, Rundle *et al.* 2002). Size may affect the richness of pond communities by providing increased habitat heterogeneity in larger areas (Della Bella *et al.* 2005) and permanence provides longer time available for colonization, allowing a greater proportion of the regional species pool and wider range of life history traits to occupy the pond (Rundle *et al.* 2002, Bilton *et al.* 2001). The community composition of ponds may also be structured by inter pond processes such as dispersal and isolation (Jeffries 2005). Dispersal ability can be an important component driving the variation in community composition between ponds in actively dispersing taxa such as Coleoptera (Rundle *et al.* 2002) and also for the long term persistence of populations (Svensson 1985). In combination, isolation of ponds may affect the species composition depending on the dispersal ability of taxa (McCauley 2006). In addition, chance events such as stochastic colonization and priority effects can also influence community structure and create communities that differ widely even over small spatial scales (Scheffer *et al.* 2006); such events have been attributed to the variation in community structure of drainage ditches on Somerset levels (Hoskin 2008).

The creation of new ponds in a landscape may therefore enhance its regional biodiversity value by providing habitats for dissimilar ecological communities (Williams *et al.* 2008, Biggs *et al.* 2001) and due to the many processes that can influence community structure a variety of pond types can promote a high value of biodiversity (Williams *et al.* 2008). However many existing ponds are at risk, some of the main threats towards ponds include agricultural practices, land drainage, urban development (Wood *et al.* 2003) and inappropriate management schemes (Williams 1997) leading to outcomes including pollution, acidification, habitat fragmentation and destruction and disruption of natural pond processes. Previously, desiccation of ponds was perceived to also be detrimental, but in recent years authors such as Collinson *et al.* (1995) have highlighted temporary ponds, that dry regularly (Williams 1997), can also be a pond habitat of considerable biodiversity value.

The high biodiversity value that ponds may represent is therefore of considerable importance of conserving. Such efforts to conserve and protect ponds in the UK include the development of a UK Habitat Action Plan for ponds (UK BAP 2007) and numerous local management plans, for example the Dartmoor Biodiversity Action Plan which includes a local action plan for freshwaters, including ponds (Dartmoor Biodiversity Steering Group 2007). Eight freshwater habitats are also outlined as EC Habitats Directive Annex I habitats (Jackson & McLeod 2000). Two such aquatic freshwater habitats of the EC Habitats Directive Annex I habitats are Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp. and Mediterranean temporary ponds (Jackson & McLeod 2000), in the UK a location which contains these two habitats is The Lizard Peninsula (Bilton *et al.* 2009).

The Lizard Peninsula, UK, is classified as a Special Area of Conservation (JNCC 2009), known for its high density of water bodies that fluctuate in size and permanencies (Bilton *et al.* 2001, Rundle *et al.* 2002, Bilton *et al.* 2009). The origin of these ponds varies from natural depressions, agricultural and conservation based excavations, abandoned mining pits (Rundle *et al.* 2002, Bilton *et al.* 2009) and small ephemeral pools that form along wet track ways and hedgerows and in gateways (Bilton *et al.* 2009). Previous study by Bilton *et al.* (2009) has also highlighted the importance of the Lizard ponds for uncommon taxa, finding four nationally uncommon plant species and fourteen nationally uncommon macroinvertebrates in Lizard ponds. Bilton *et al.* (2009) also found 62% of the ponds studied supported at least one uncommon plant species and 63% at least one uncommon macroinvertebrate. Examples of species of conservation concern found in ponds on the Lizard include *Ranunculus tripartitus*, a plant species classified as vulnerable by IUCN criteria and *Haliplus variegatus*, a macroinvertebrate species classified as endangered by IUCN criteria (Bilton *et al.* 2009).

The aims of this study is to investigate a selection of ponds from the Lizard Peninsula UK. Ponds were previously sampled in 2000 and the same ponds revisited in 2009. This study aims to examine the community composition of the same ponds in both years and investigate what environmental factors are responsible for structuring the pond communities and if the responsible environmental factors have changed between the two years. In combination this study also aims to compare the communities with those sampled nine years previous in the same ponds and examine if there has been any changes in community composition. This will firstly encapsulate all taxa sampled and then be re-examined using only Coleoptera, mostly adult Coleoptera are long lived and not strongly seasonal (Foster 1987) therefore using only Coleoptera will rule out any possible influences of season on changes in community composition as sampling between the two years was undertaken during different seasons. Furthermore this study will also investigate the conservation value of the ponds of the Lizard Peninsula and examine if this has altered between the two years studied.

Methods

The structure, composition and conservation value of pond communities on the Lizard Peninsula, UK had been examined previously by McAbendroth (2004) in 2000. The purpose of the study was to revisit the pond communities and again examine the structure, composition and conservation value and furthermore, using the data collected in 2000 by McAbendroth (2004) and data collected in 2009, examine if any changes in the pond communities had occurred over the nine year period.

Study Site

The study was conducted on the Lizard Peninsula, UK. The area is of importance for nature conservation and many ponds are scattered across the landscape, which are known to support rare invertebrates and plant species (Bilton *et al.* 2009). The ponds on the Lizard Peninsula lie above ultra basic serpentine geology in heathland and grassland (Bilton *et al.* 2009) and have been the subject of some previous studies by Bilton *et al.* (2001), Rundle *et al.* (2002) and Bilton *et al.* (2009).

Sampling

Sampling was undertaken during early July 2009 and had been conducted nine years earlier in a previous study, in 2000, during February/March. Of the sites visited in 2000 fifteen were revisited but three were dry giving a total of twelve ponds for comparison. A map of the ponds visited is provided in Figure 1.

The sampling approach was identical in the two years. Ponds were sampled using a hand net (1mm mesh, 20x25cm dimensions). Each sample consisted of five standardised sweeps, each consisting of approximately ten seconds of back and forth, over 1m, netting in the same area of habitat, distributed between beds with different vegetation composition. At larger sites ten sweeps were used to account for the increase in area. The sweeps were pooled and preserved in 100% Industrial Methylated Spirit (IMS). It has been found that sampling in this manner provides a reliable measure of macroinvertebrate species richness within the pond habitat as it consistently samples between 60-80% of the species pool and therefore allows a robust comparison of macroinvertebrate communities (Foggo *et al.* unpublished data, Rundle *et al.* 2002, Foggo *et al.* 2003, Bilton *et al.* 2009). Sampling in a single season is also sufficient to compare the relative community composition of sites and this method has been adopted in most other pond studies (Nicolet *et al.* 2004, Bilton *et al.* 2006, Bilton *et al.* 2009).

Environmental variables were collected at each pond during sampling using a Solomat 520C probe. Recorded were water temperature, pH, and temperature compensated conductivity. Water samples were also collected in acid washed polypropene bottles for later analysis of nutrient and metal ion content in the laboratory. On both occasions the number of plant species at each pond site was also recorded.

Pond areas were estimated previously in 2000 and derived by using differential GPS (trimble) to map the margin of each pond and calculate the area. These values were also used in 2009 as pond size had not changed (D.T. Bilton, pers. comm.).

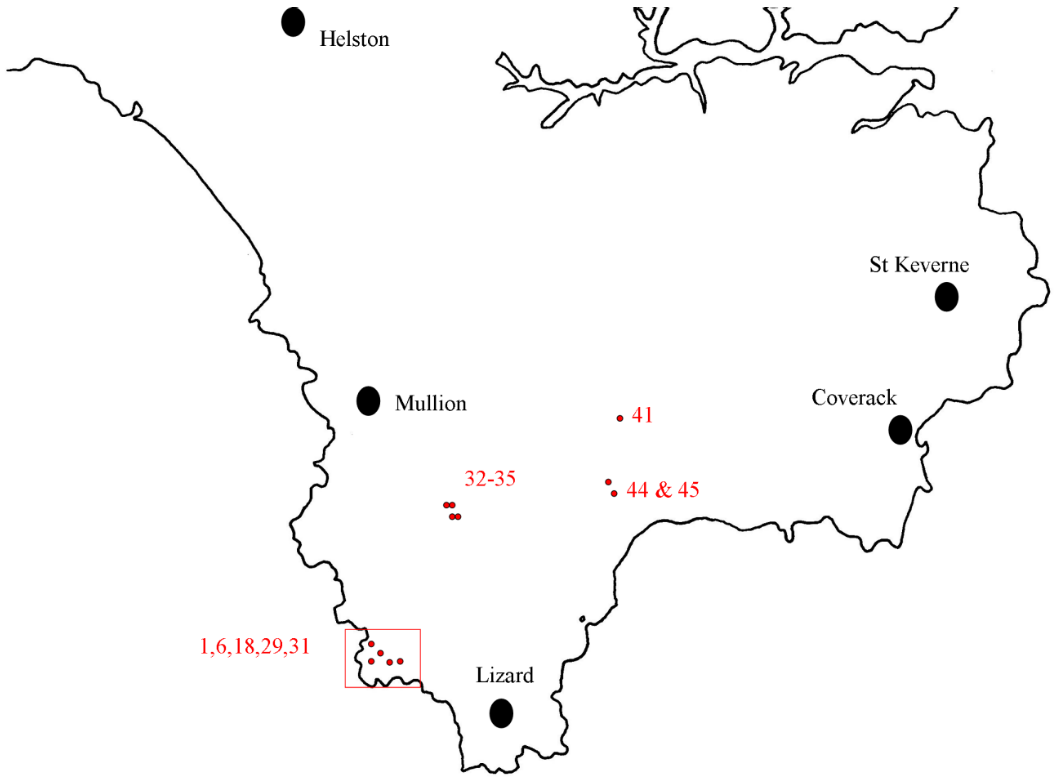

Figure 1 Map of the Lizard ponds sampled in both years, ponds are highlighted by numbers (after McAbendroth 2004).

Laboratory Analysis

In both years Mg, Fe, Cu and Zn were analysed using a SpectrAA 600 flame spectrophotometer and total organic nitrogen measurements (TON) (consisting of nitrate and nitrite) and soluble reactive phosphorus (SRP) were measured using a HacH-BR12000 direct reading spectrophotometer.

Taxon Identification

In the laboratory samples were first washed through a 500µm sieve to remove dirt and debris. Samples were then placed into white plastic sorting trays filled with water. Each tray was systematically sorted through by hand, and macroinvertebrates removed and placed into pots and preserved with 70% IMS for later identification. Using a Kyowa Optical SDZ-PL microscope Coleoptera, Odonata, Hemiptera, Ephemeroptera, Crustacea, Mollusca and Trichoptera were identified to species level and Chironomidae to family. Appendices I and II provide the full data sets for the years 2000 and 2009, respectively, including species abundances, physiochemical data and vegetation presence/absence.

Data Analysis

Firstly both data sets required some species to be amalgamated to ensure both covered the same taxonomic scope. From the 2000 data set all Chironomidae were amalgamated to family level and Trichoptera of *Limnephilus* species were classified as *Limnephilus spp.* to match the 2009 data set and *Sympetrum* species from the 2009 data set amalgamated into *Sympetrum spp*. to match the 2000 data set.

Community Composition in Individual Years
The abundance data gathered from both years was first transformed using a Log(x+1) transformation in PRIMER, this transformation down weights the more abundant species and allows rarer species and those of a mid range to also exert an influence in analysis (Clarke and Warwick 2001). From this a Bray-Curtis similarity matrix (Clarke and Warwick 2001) was generated for each year and non-metric MDS ordinations and group average clusters were created using PRIMER 6. The use of group average cluster was chosen as it is known to most likely produce a realistic pattern of community inter-relationships (Clarke and Warwick 2001). Group average clusters were then used to divide the ponds based on a measure of 50% similarity. To analyse any differences in pond community composition between these groups Analysis of similarities (ANOSIM) was conducted using PRIMER 6 (Clarke and Warwick 2001).

Relationship with Environmental Variables
The relationship between pond community composition and environmental variables was examined using the BIOENV procedure in PRIMER 6 (Clarke and Warwick 2001). For each year a composite variable was created to provide a single measure of water chemistry for metal ion composition using Cu, Zn, Fe, Mg and Ca concentrations in principle component analysis (PCA) within PRIMER 6 (Clarke and Warwick 2001). The results from this are presented in Table 1; PCA axis 1 explaining 95.6% of the variation in metal ion concentration in 2000 and 98% in 2009. PCA 1 scores were then combined with the remaining environmental variables of area, temperature (2009 only), pH, Conductivity, TON, SRP and number of plant species and used in the BIOENV procedure in PRIMER 6 (Clarke and Warwick 2001).

Table 1 Principle Component Analysis (PCA) of metal content (Cu, Zn, Fe, Mg and Ca) of water in (a) 2000 and (b) 2009

(a) 2000									
Eigenvalues				Eigenvectors					
PC	Eigenvalues	%Var	Cum.%Var	Variable	PC1	PC2	PC3	PC4	PC5
1	147	95.6	95.6	Cu mg/L	<0.001	-0.003	-0.071	0.892	-0.447
2	6.82	4.4	100	Zn mg/L	0.001	-0.005	-0.846	-0.292	-0.447
3	1.41E-02	0	100	Fe mg/L	0.094	-0.809	0.311	-0.202	-0.447
4	1.90E-04	0	100	Mg mg/L	-0.75	0.326	0.303	-0.199	-0.447
5	0	0	100	Ca mg/L	0.655	0.489	0.303	-0.199	-0.447
(b) 2009									
Eigenvalues				Eigenvectors					
PC	Eigenvalues	%Var	Cum.%Var	Variable	PC1	PC2	PC3	PC4	PC5
1	139	98	98	Ca mg/L	-0.655	-0.544	-0.177	-0.211	0.447
2	1.86	1.3	99.3	Mg mg/L	0.753	-0.406	-0.156	-0.211	0.447
3	0.945	0.7	100	Zn mg/L	-0.035	0.219	0.839	-0.216	0.447
4	3.30E-03	0	100	Fe mg/L	-0.061	0.701	-0.49	-0.256	0.447
5	0	0	100	Cu mg/L	-0.002	0.03	-0.016	0.894	0.447

Community Comparison between Years

To investigate if any changes were apparent in the pond community between the two years the data from both years were pooled and the abundances first transformed using Log(x+1), as described previously, and also presence absence to investigate if changes in occupancy of species were apparent. Both of these data sets were used to generate Bray-Curtis similarity matrices (Clarke and Warwick 2001) and these used to construct a non-metric MDS ordination and group average cluster for both abundance and presence absence data. To investigate if there were any significant differences in the overall pond community between years both data sets were subject to analysis using ANOSIM in PRIMER 6 (Clarke and Warwick 2001) grouped by year.

To investigate which, if any, species were driving these changes a SIMPER analysis (Clarke and Warwick 2001) was conducted. Following this only data for Coleoptera were compared between years using ANOSIM (Clarke and Warwick 2001).

Conservation Status of Lizard Ponds

The conservation value of the ponds in both years was assessed by first assigning each species a rarity score based upon IUCN categories (Table 2). Total species rarity scores were calculated for 2000 and 2009 data for each of the 12 ponds and a species rarity index (SRI) was produced by dividing the total rarity score by the number of taxa recorded in each pond. Changes in species richness between 2000 and 2009 were analysed by comparing the number of macroinvertebrate species in each pond. Kolmogorov-Smirnov (MINITAB 15) normality tests found the data for both years to be normally distributed for rarity (2000 $p>0.150$; 2009 $p>0.150$) and richness (2000 $p>0.150$; 2009 $p>0.150$) and therefore in both instances two sample T-tests (MINITAB 15) were used for comparison between years.

Table 2 IUCN rarity categories and species rarity scores for calculating Species Rarity Indices (SRI) (after McAbendroth 2004)

IUCN category	Score	Distribution/conservation status
Lower risk least concern (LRlc)	1	>100 hectads
Lower risk nationally scarce (LRnsA/B)	2	species occurring in 16-100 hectads
Lower risk nationally threatened (LRnt) or conservation dependent (LRcd) (Red data book status)	4	species occurring in <16 hectads or the focus of a continuing taxon-specific or habitat-specific conservation programme without which the species would become VU or EN
Vulnerable (VU) (Red data book status)	8	species facing a very high risk of extinction in the wild in the medium-term future
Endangered (EU) (Red data book status)	16	species facing a very high risk of extinction in the wild in the near future

Results

The ponds visited varied in size and vegetation composition and cover. The ponds encountered spanned a range of physiochemical properties (Table 3) and found were a variety of macroinvertebrate taxa, with Coleoptera being dominant. Overall in the twelve ponds studied 72 macroinvertebrate taxa were found in 2000 and 74 in 2009. Similar numbers of taxa have been gained and lost across the years; 30 gained and 28 lost between the two years. The study ponds spanned a range of SRI's and in both years the average of all study ponds was similar; Sri's ranged from 1 to 2.5, with an average of 1.40 in 2000 and from 1 to 2, with an average of 1.29 in 2009.

Table 3 Physiochemical properties of the twelve study ponds on the Lizard peninsula, UK in (a) 2000 and (b) 2009.

	(a) 2000			(b) 2009		
	Min	Mean	Max	Min	Mean	Max
Area	7	2842.2	15005	7	2842.2	15005
Temp (^oC)	n/a	n/a	n/a	16.3	19.0	23.3
pH	5.44	6.49	6.76	5.62	6.96	9.94
Temperature compensated Conductivity (us)	162.3	405.8	731.7	1.2	438.8	919
Total Organic Nitrogen (mg/L)	0.006	0.176	0.542	0.0149	0.0299	0.0925
Soluble Reactive Phosphorus (mg/L)	0.001	0.01	0.027	0.01	0.064	0.35
Ca (mg/L)	0.842	3.198	4.526	4.08	7.023	15.197
Mg (mg/L)	6.125	13.201	33.04	6.602	17.164	39.926
Zn (mg/L)	0.005	0.018	0.069	0.011	0.072	0.407
Fe (mg/L)	0.057	0.337	1.05	0.003	0.179	0.576
Cu (mg/L)	0	0.002	0.006	0	0.009	0.033
No. of plant species	4	13	23	1	6	14
No. of macroinvertebrates	6	19	39	8	21	33

Community Composition in Individual Years

Visual inspection of the MDS of 2000 pond communities (Figure 2A) reveals distinct groupings of the pond macroinvertebrate communities and 7 pond groups are evident from the group average cluster at 50% similarity (Figure 2A). These 7 distinct groups are significantly different from each other (ANOSIM Global R=0.983, p=0.001, pairwise test only significant between groups 6 (ponds 1 and 45) and 7 (ponds 32, 33, 34, 45, 41) p=0.048).

Visual inspection of the MDS of 2009 pond communities (Figure 2B) also reveals distinct groupings of the pond macroinvertebrate communities, and 8 pond groups are evident from the group average cluster at 50% similarity (Figure 2B). These 8 distinct groups are significantly different from each other (ANOSIM Global R=1, p=0.001, although no pairwise tests were significant at $p<0.05$).

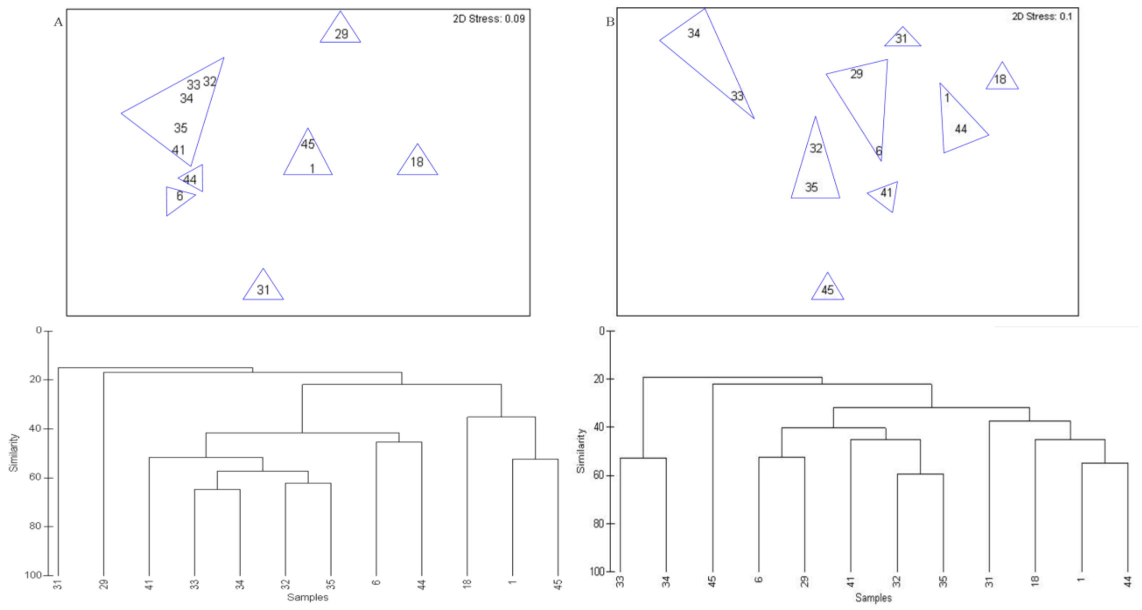

Figure 2 MDS ordination and group average cluster of macroinvertebrate communities from the twelve Lizard ponds in (A) 2000 and (B) 2009. Data transformed using Logx+1 transformation.

Relationship with Environmental Variables

The minimum number of abiotic variables which best provide an explanation for the variation between macroinvertebrate communities in 2000 are area and water chemistry (PCA axis 1) which explain 49.2% of the variation between pond communities (Table 4a). The addition of number of plant species does contribute further to the explanation of variation between communities in 2000, but this is however only a further 0.2% (Table 4a). In 2009, area is the single abiotic variable which best explains the variation between pond communities, explaining 34.9% of the variation (Table 5b).

Table 4 BIOENV analysis of variation in community structure between ponds explained by abiotic variables in (a) 2000 and (b) 2009.

(a) 2000		Best results			(b) 2009		Best results		
Variables		No. Vars	Corr.	Selections	Variables		No. Vars	Corr.	Selections
1	Area	3	0.492	1,6,7	1	Area	1	0.349	1
2	pH	4	0.492	1,5-7	2	Temperature	2	0.349	1,5
3	Conductivity	5	0.492	1,4-7	3	pH	1	0.348	4
4	TON mg/L	4	0.49	1,4,6,7	4	Conductivity	2	0.348	4,5
5	SRP mg/L	2	0.49	1,7	5	TON mg/L	2	0.348	4,6
6	No of plant sp.	3	0.49	1,5,7	6	SRP mg/L	3	0.348	4,5,6
7	PCA 1	3	0.488	1,4,7	7	No of plant sp.	2	0.347	1,6
		4	0.488	1,4,5,7	8	PCA 1	3	0.347	1,5,6
		3	0.486	1,2,6			2	0.344	1,7
		4	0.486	1,2,5,6			3	0.344	1,5,7

Community Composition between Years

Visual inspection of the MDS of pond communities between years (Figures 3A, B) reveals a separation of the pond communities between 2000 and 2009. This separation is apparent in species abundance (Figure 3A) and species occurrence, measured by presence absence data (Figure 3B). Figures 3C,D,E and F also reveal a separation between communities in the same individual ponds in separate years, again apparent in species abundance (Figure 3C,E) and also species occurrence, measured by presence absence data (Figure 3D,F).

The pond communities differed significantly between the two years based not only on abundances (ANOSIM Global R=0.294, p=0.002) but also on the occupancy of ponds based on presence absence data (ANOSIM Global R=0.216, p=0.002).

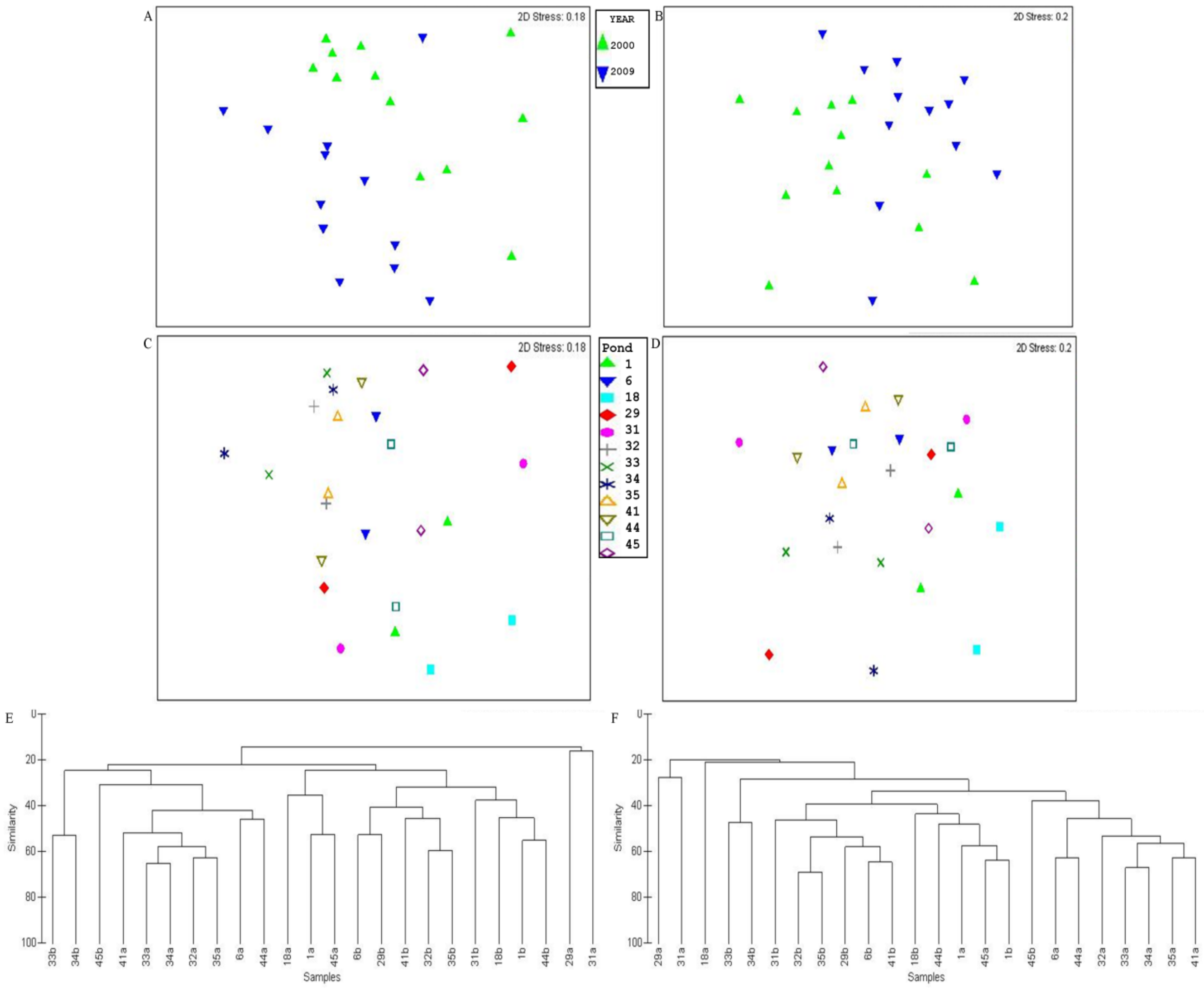

Figure 3 Comparison of pond communities between the two study years. MDS ordinations of pond communities separated by year based on (A) abundance and (B) presence absence, MDS ordinations of individual ponds across years based on (C) abundance and (D) presence absence and group average clusters of individual ponds across years based on (E) abundance and (F) presence absence.

The species driving the dissimilarity between pond communities between years was revealed to be species from across the taxonomic range (Table 5). Members of Trichoptera, Crustacea, Chironomidae, Coleoptera, Odonata, Ephemeroptera and Hemiptera all contributed towards being the main drivers of dissimilarity between years.

Table 5 SIMPER analysis of between year dissimilarity of the macroinvertebrate pond communities on the Lizard Peninsula, UK.

Years 2000 & 2009						
Average dissimilarity = 77.22						
	2000	2009				
Species	Av.Abun	Av.Abun	Av.Diss	Diss/SD	Contrib%	Cum.%
Limnephilus spp.	4.19	1.38	4.68	1.55	6.06	6.06
Asellus aquaticus	2.17	2.49	3.96	1.04	5.13	11.19
Chironomidae	3.06	0.85	3.81	1.42	4.94	16.12
Helophorus brevipalpis	0.51	2.33	3.3	1.14	4.28	20.4
Helophorus minutus	0.85	1.66	2.46	0.95	3.18	23.59
Cloeon dipterum	1.94	0	2.43	1.23	3.15	26.74
Hesperocorixa castanea	0.88	1.24	2.08	0.93	2.69	29.43
Sympetrum spp.	1.2	0.93	2	0.92	2.59	32.02
Anacaena lutescens	0.67	1.49	1.98	1.18	2.56	34.58
Dryops auriculatus	0.6	0.86	1.81	0.73	2.35	36.93
Paracymus scutellaris	0.56	1.13	1.71	1.15	2.21	39.14

Based on Coleoptera alone the pond communities on the Lizard still remained significantly distinct between 2000 and 2009 based on abundance (ANOSIM Global R=0.133, p=0.015) and on occupancy of species measured by presence absence of taxa (ANOSIM Global R=0.141, p=0.012).

The identity of the taxa encountered in the two years did however vary and taxa gained in 2009, (not present in 2000) and lost in 2009 (present in 2000) are listed in Table 6.

Table 6 Taxa gained and lost in the sampled Lizard ponds in 2009. * Taxa gained in 2009 in the sampled ponds but present in 2000 in ponds not revisited. † Taxa found on the site prior to 2000 (D.T. Bilton pers. comm.).

Taxa gained in 2009		Taxa lost in 2009	
Coleoptera	**Trichoptera**	**Coleoptera**	**Trichoptera**
Gyrinus caspius	*Phryganeidae sp.*	*Anacaena globulus*	*Holocentropis picicornis*
Ilybius guttiger	**Hemiptera**	*Berosus signaticollis*	*Agrypnia varia*
Dysticus marginalis†	*Ilycoris cimcoides*	*Enochrus coarctatus*	**Hemiptera**
Stictotarsus duodecimpustulatus	*Hydrometra stagnorum*	*Enochrus affinis*	*Plea leachii*
Hygrobia hermanni	*Gerris laclustris*	*Enochrus melanocephalus*	*Corixa punctata*
Gyrinus urinator	*Notonecta mormorea viridis*	*Haliplus confinis*	*Sigara nigrolineata*
Litodactylus leucogaster	*Gerris thoracicus*	*Haliplus fulvus*	*Arctocorisa germari*
Helochares lividus	*Hesperocorixa moesta*	*Haliplus variegatus*	**Ephemeroptera**
Rhantus grapii	*Sigara scotti*	*Hydrochus angustatus*	*Cloeon dipterum*
Donacia versicolorea†	**Odonata**	*Hydroporus erythrocephalus*	**Plecoptera**
Hydraena riparia	*Lestes sponsa*	*Hydroporus planus*	*Nemoura cinerea*
Prasocuris phellandrii	**Ephemeroptera**	*Hydroporus tesselatus*	**Mollusca**
Coelostoma orbiculare	*Caenis luctuosa*	*Laccobius bipunctatus*	*Potamapyrgus antipodarum*
Cyphon sp.	**Mollusca**	*Laccophilus minutus*	*Lymnaea truncatula*
Bagous collignensis†	*Physa acuta*	*Plateumaris sericea*	*Physa fontinalis*
Dytiscus semisulcatus†			*Pisidium spp.*
*Bagous limosus**			*Crangonyx pseudogracilis*
*Dryops striatellus**			
*Helophorus aequalis**			

Conservation status

The number of macroinvertebrate taxa encountered did not differ significantly between the two years (t=0.06, p>0.05, DF=22) (Figure 4a) and macroinvertebrate SRI did not differ significantly between years (t=0.70, p>0.05, DF=22) (Figure 4b).

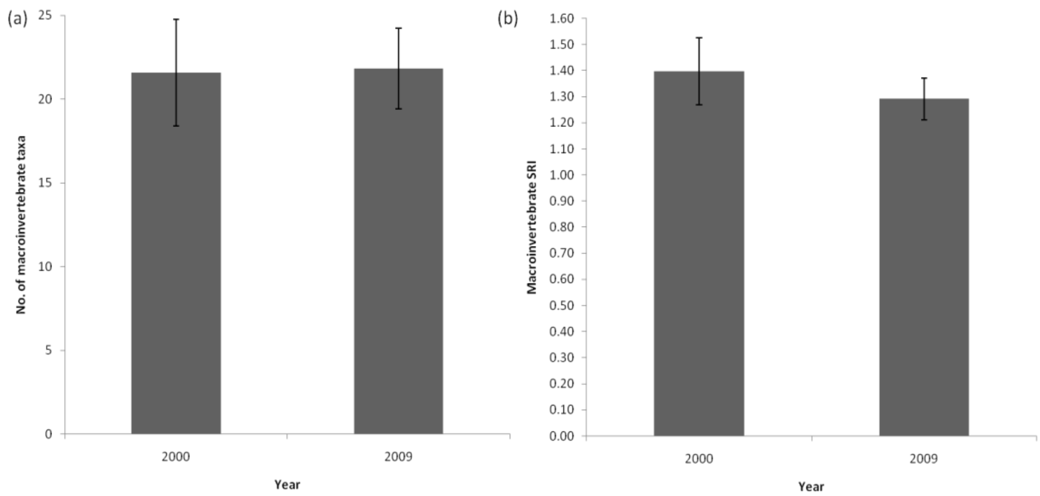

Figure 4 Comparison of (a) macroinvertebrate species richness of the twelve ponds in 2000 and 2009 and (b) macroinvertebrate SRI of the twelve ponds in 2000 and 2009. Histograms display mean values (±SE). Neither was significant at p<0.05.

Discussion

In the separate years distinct pond communities were apparent and the ponds sampled formed a similar number of groups in both years; 8 in 2000 and 9 in 2009. In some groups the identity of ponds remained similar; in 2000 ponds 32-35 and 41 formed a distinct group (Figure 2A) and in 2009 ponds 33 and 34 again remained together within the same group as did ponds 32 and 35 (Figure 2B). However the ponds constituting other groups differed in separate years (Figure 2) and many of the groups consisted of single ponds. Although the identity of ponds within groups differed between years it is interesting that the same abiotic factors play an important role in structuring the pond communities in the separate years. The factor of area was responsible for the variation between pond communities in combination with water chemistry and number of plant species in 2000 and alone in 2009 (Table 4). The fact that area was an important variable in 2009 after finding it to be important in 2000 was not completely unexpected as the area of the ponds had not changed. Area has previously been found to play an important role, in combination with other factors, in explaining the variation in community composition in ponds in Italy (Della Bella *et al.* 2005), farm ponds in France (Céréghino *et al.* 2008a), a selection of small ponds surrounded by an urban landscape (Sanderson *et al.* 2005) and ponds in the New Forest, UK and on the Lizard Peninsula previously (Bilton *et al.* 2009). Pond area is a factor that can be related to the community in a variety of manners. Species may choose to occupy ponds as a direct function of their surface area (Bazzanti *et al.* 1996) and Rundle *et al.* (2002) mentions that some aquatic insects may use physical and chemical cues for site selection. Species occupancy in ponds as a result of their areas may also arise due to indirect associations with other factors; the oviposition preferences of two species of *Notonecta* have been found to influence their contrasting habitat preferences of size, in combination with vegetation cover and substrate (Briers & Warren 2000). Area may also act as a surrogate for habitat availability, which can again influence the composition of the community (Bauer 1989). In addition the possibility of greater environmental heterogeneity provided by larger areas may influence the number of species in the community and may result in a species area relationship, a feature commonly observed in ponds (Fischer *et al.* 2000, Biggs *et al.* 2005, Rundle *et al.* 2002, Céréghino *et al.* 2008a).

In combination, in 2000 water chemistry was also an important factor structuring the pond communities (Table 4a). Species differ in their tolerances to such abiotic factors (Williams 1997) and when such a variable physiochemical environment is encountered, for which small lentic waters are typical (Davies et al 2008*b*), it is likely the community will reflect such tolerances. This is in accordance with the predictions of Poff (1997) in which habitats with differing environmental selective forces, in this case differing water chemistry, are expected to have different species as the species have different attributes to the selective forces.

Also in 2000 although the addition of number of plant species did contribute to explaining further variation between the pond communities, it was very little (Table 4a). The number, structure and cover of vegetation can be another factor that contributes to structuring pond communities alone or in combination with other factors (Sanderson *et al.* 2005, Nicolet *et al.* 2004, Céréghino *et al.* 2008b). A macrophyte richness - macroinvertebrate richness positive correlation is also observed in some ponds (Nicolet *et al.* 2004, Gledhill 1999), possibly as a result of the greater environmental heterogeneity provided by a greater range of macrophyte species. The additions of water chemistry and number of plant species also playing a role in structuring the pond communities could pose an explanation for the identity of ponds within groups of similar community composition, differing between the two years (Figure 2).

In both years the variation between pond communities could not be fully explained by the environmental variables measured; 49.2% in 2000 and 34.9% in 2009 was explained by environmental variables (Table 4). The remaining unexplained variation in both years could possibly be attributed to any factors not measured in this study; permanence for example is widely known to influence community composition and species richness in ponds (Della Bella *et al.* 2005, Boix *et al.* 2001 Rundle *et al.* 2002). In addition, Welborn *et al.* (1996) considers that although the physical environment may determine species that can potentially exist within a habitat, the interplay of this factor with biotic interactions determines the actual species composition. Furthermore processes such as dispersal and inter-pond distance can be responsible for structuring pond communities (Jeffries 2005, McCauley 2006). The feature of chance events and stochastic colonization could also influence community structure as has been observed In Swiss Alpine ponds (Oertli *et al.* 2008), and drainage ditches on the Somerset levels (Hoskin 2008). Therefore factors of both intra-pond quality, for example physiochemistry and biotic interactions and inter-pond dynamics such as dispersal (Jeffries 2005) can all contributes to shaping pond communities.

Interestingly between the two years studied the ANOSIM revealed significant differences between the pond communities and Figure 3 illustrates this separation. Table 6 further highlights that a number of taxa have been gained and lost between the two years. The pond habitat is one characteristic of high turnover and therefore of high colonization and extinction rates (Oertli *et al.* 2008, Briers & Warren 2000, Welborn *et al.* 1996, Scheffer *et al.* 2006, Svensson 1985), amongst taxa these colonization and extinction rates do however vary (Jeffries 1994). Overall this may result in pond communities which see a variation in the identity of taxa that occupy ponds and alterations in species distributions over time. The distinction between the pond communities between the two years (Figure 3) illustrates that not only the abundance of species has altered between the two years (Figures 3A,C,E) but the identity of the species in the pond communities has also changed between the two years (Figure 3B,D,F). In addition, in 2009 *Bagous limosus*, *Dryops striatellus* and *Helophorus aequalis* were recorded in the study ponds, in 2000 these taxa were recorded in ponds on the Lizard Peninsula but not the twelve revisited (Table 6) highlighting that changes in distribution have occurred at the site.

Between the two years similar numbers of taxa have been gained and lost (Table 6). The previous data collection, in 2000, was extensive over the study area and likely to have encapsulated a large proportion of the taxa at site. As a result the taxa gained in 2009 are likely to have colonized regionally, however some taxa considered to have regionally colonized, *Dysticus marginalis* for example, are not necessarily new to the Lizard as they have been recorded at the site prior to the study in 2000 (D.T. Bilton pers. comm.). The taxa that are regarded as lost (Table 6) however are likely to have gone extinct only locally as only a proportion of the ponds sampled in 2000 were revisited in 2009.

The temporal changes in distribution of taxa have been attributed in some instances to the varying responses of taxa to environmental conditions (Scheffer *et al.* 2006), with community composition tending to track such conditions as water regime (Jeffries 1994), hydroperiod (Welborn *et al.* 1996) and habitat conditions and hydrology (Jeffries 2005); a possible explanation for the changes in community composition observed in this study. However driving the dynamics and distributions of species between years may also be the factor of chance. Chance colonisation and extinction events can be important factors affecting the assembly and dynamics of ecological communities (Hubbell 2001). Such chance events have been observed responsible for the turnover of pond communities of *Notonecta* (Briers & Warren 2000). Chance events have been proposed to be of importance in macroinvertebrate communities with regards to colonization of the habitat (Brier & Warren 2000, Jeffries 2005) and deterministic factors such as habitat suitability possibly play a more prominent feature with regards to extinction within communities (Briers and Warren 2000, Jeffries 2005). In the current study possible chance events could be attributed to the presence of *Strictotarsus duodecimpustulatus* and *Gyrinus urinator* as these are both running water species (Friday 1988) and their presence is likely to be a result of chance colonization.

Upon SIMPER analysis it was revealed that species from across the taxonomic range were responsible for the dissimilarity in the pond communities between years (Table 5). Species at the forefront of this dissimilarity are invertebrates for which the difference in sampling season may have possibly influenced the results by the exclusion of or encountering species in lower abundances. Taxa such as *Limnephilus spp.* are one such example; they were of greater responsibility than other taxa for the dissimilarity between years (Table 5), but most larvae of *Limnephilus spp.* metamorphose into adults during spring (Wallace *et al.* 2003 pp.131) and would be best sampled between March and May (Wallace *et al.* 2003 pp. 10). This suggests that the difference in sampling season may be responsible for between year dissimilarity. However, upon the removal of taxa other than Coleoptera significant differences still remained between the years, revealed by ANOSIM. Mostly adult Coleoptera are long lived and not strongly seasonal (Foster 1987) ruling out possible seasonal influences driving between year dissimilarity. Therefore it remains that there has been a significant change in the pond communities between years.

Although changes in the pond communities were apparent in this study interestingly there was no significant change in species richness or SRI of the ponds at the study site (Figure 4). This suggests that between the two study years there has been dynamic turnover in the pond communities but this has not affected the conservation value of the studied Lizard ponds.

The Lizard Peninsula is an important area for conservation and its pond communities have considerable biodiversity value; ponds on the Lizard have been found to support more rare species on average than those from a wider UK comparison (Bilton *et al.* 2009). Uncommon taxa found within this study also highlight the ponds to be of particular conservation interest; *Bagous collignensis* is a species considered as nationally threatened and has been recorded from only a small number of sites in the UK since 1960 (D.T. Bilton pers. comm.).

The changes in pond community composition but no change in conservation value of the studied ponds highlights that conserving the biodiversity of the Lizard ponds needs to allow for the turnover of communities over time. In combination although area plays an important role structuring the communities, highlighting that a variety of different sized ponds would be beneficial for biodiversity, other factors can also be important for structuring communities, as was observed in 2000, and therefore with regards to conserving the ponds this supports the suggestions of numerous authors in that a variety of ponds of differing characteristics are needed to maintain the biodiversity of ponds (Collinson *et al.* 1995, Wood *et al.* 2003, Jeffries 2005, Williams *et al.* 2008, Bilton *et al.* 2009). In combination to protect species that alter in their abundance and distribution conservation effort should be aimed at regional scales (Bilton *et al.* 2009) to encapsulate the surrounding terrestrial habitat important for species dispersal between ponds and support the dynamics between pond communities that may contribute to changes in composition. In addition management and study at the longer term scale as suggested by Jeffries (2005) would assist understand and support the temporal dynamics of pond communities.

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