Does size matter? The relationship between pond area and biodiversity

Oertli, Beat; Auderset Joye, Dominique; Castella, Emmanuel; Juge, Raphaelle; Cambin, Diana Georgette; Lachavanne, Jean-Bernard

How to cite

OERTLI, Beat et al. Does size matter? The relationship between pond area and biodiversity. In: Biological conservation, 2002, vol. 104, n° 1, p. 59–70. doi: 10.1016/S0006-3207(01)00154-9

This publication URL: https://archive-ouverte.unige.ch/unige:25574

Publication DOI: 10.1016/S0006-3207(01)00154-9

ELSEVIER

Biological Conservation 104 (2002) 59–70

BIOLOGICAL CONSERVATION

www.elsevier.com/locate/biocon

Does size matter? The relationship between pond area and biodiversity

Beat Oertli*, Dominique Auderset Joye, Emmanuel Castella, Raphaëlle Juge, Diana Cambin, Jean-Bernard Lachavanne

Laboratoire d'Ecologie et de Biologie Aquatique, University of Geneva, 18 chemin des Clochettes, CH- 1206 Geneva, Switzerland

Received 23 November 2000; received in revised form 18 June 2001; accepted 20 June 2001

Abstract

Larger areas support more species. To test the application of this biogeographic principle to ponds, we consider the relationship between size and diversity for 80 ponds in Switzerland, using richness (number of species) and conservation value (score for all species present, according to their degree of rarity) of aquatic plants, molluscs (Gastropoda, Sphaeriidae), Coleoptera, Odonata (adults) and Amphibia. Pond size was found to be important only for Odonata and explained 31% of the variability of their species richness. Pond size showed only a feeble relationship with the species richness of all other groups, particularly the Coleoptera and Amphibia. The weakness of this relationship was also indicated by the low *z*-values obtained ($<$ 0.13). The SLOSS analyses showed that a set of ponds of small size has more species and has a higher conservation value than a single large pond of the same total area. But we also show that large ponds harbour species missing in the smaller ponds. Finally, we conclude that in a global conservation policy (protection, restoration, management), all size ranges of ponds should be promoted.

Keywords: Biodiversity conservation; Species richness; Aquatic plants; Gastropoda; Coleoptera; Odonata; Amphibia

1. Introduction

Biogeographical theory has already been put into practice in applied fields including nature conservation (e.g. Gilpin and Diamond, 1980; Lahti and Ranta, 1985; May, 1986; Murphy and Wilcox, 1986; Primack, 1998) and the biogeographical principle that a larger area supports more species has been established for more than a century (see review of Rosenzweig, 1995). This rule offers attractive applications for conservation biology, but the relation between this principle and nature conservation has been more assumed than tested. The biogeographical island (terrestrial or aquatic) has figured repeatedly in studies of size-dependent effects and freshwater examples are prominent in the rich literature on the species–area relationship, which encompasses streams, rivers, pools, ponds, lakes and wetlands (e.g. Lassen, 1975; Broenmark et al., 1984; Broenmark, 1985; Møller and Rørdam, 1985; Hugueny, 1989; Ward and Blaustein, 1994; Benayas et al., 1999).

Ponds are important for biodiversity conservation (Biggs et al., 1994) but have been lost on a large scale during the twentieth century, reaching 40–90% for various northwestern European countries (Hull, 1997). In Switzerland, the proportion of wetlands (including ponds) lost since 1800 has been estimated at 90% (Imboden, 1976). Of the many taxonomic groups with pond-inhabiting species, two flagship groups—Amphibia and Odonata—are strongly associated with these small water bodies. Both groups are highly endangered and in most European countries for which data are available, 20–40% of their species are generally classified as being at least vulnerable. In the absence of more comprehensive data these two groups tend to be used as proxies for entire pond faunas. The assumption is that similar results are likely to be obtained for other taxa as we intensify inventories and species surveys. In North America, a recent analysis has shown that extinction rates among North American freshwater fauna are as high as for the fauna of tropical forests (Ricciardi and Rasmussen, 1999).

* Corresponding author. Tel.: +41-22-701-7101; fax: +41-22-789-4989.

E-mail address: beat.oertli@leba.unige.ch (B. Oertli).

PII: S0006-3207(01)00154-9

Biogeographical theory (e.g. MacArthur and Wilson, 1967) would suggest that pond size should be large ("the bigger the pond, the better"), but the information available about the ecology of ponds and the consequences of their management (Biggs et al., 1994; Gee et al., 1997) is sparse and contradictory. Data are available for lakes, but ponds are a different type of freshwater system (e.g. Boothby, 1998), and it is doubtful that results from lakes apply to ponds. Most published results of investigations conducted in ponds have been based on only one or two biotic groups and comparisons between many taxonomic groups investigated simultaneously are few.

Apart from consideration of the underlying mechanisms generating the species–area relationship (e.g. local or regional factors), we recognise five main questions: (1) Do large ponds support a higher species richness and how much of the variation in species numbers is explained by pond size? (2) Are the results the same if we first score species according to their degree of rarity? We refer to this weighted summation of species as "conservation value". (3) Do the taxonomic groups show the same or different trends? (4) Do individual species exhibit preferences for larger or smaller ponds? (5) Is a single large pond more favourable for biodiversity conservation than several small ponds (SLOSS)?

2. Methods

2.1. Study area

A previous inventory of 8000 ponds (Borgula et al., 1994) from the 60,000 known in Switzerland, provided the baseline data for choosing 80 ponds with a fairly even distribution among size classes (Fig. 1) with a mean area of 8817 m2 and 1.66 m in depth. They are scattered throughout Switzerland (Fig. 2), at altitudes ranging between 210 and 2757 m.a.s.l. Only 31 of these ponds are known to have a natural origin with an age exceeding 4000 years (last glacial retreat). The other 49, with various ages, are artificial, linked to past or present human activities (gravel or clay extraction, fish production, nature conservation, etc.). The main pond characteristics are listed in Table 1 (site details are available on request).

2.2. Survey of flora and fauna

The species richness of six taxonomic groups was investigated in the 80 ponds: aquatic plants, aquatic Gastropoda, Sphaeriidae (Bivalvia), aquatic Coleoptera (larvae and adults), adult Odonata, and Amphibia. All groups were sampled using a standardised survey method, during the summer months between 1996 and 1999 (inclusive), except for the Amphibia, which were inventoried over the 10-year period ending in 1996.

Plants considered here as aquatic are the 254 species listed in the highest humidity class (=5) of Landolt (1977): this includes true aquatics (species submerged or with floating leaves) and most of the emergents. To this "aquatic" species pool, we added a set of 22 species listed by Landolt (1977) under class 4: *Juncus effusus, Carex canescens, Carex flava, Carex lepidocarpa, Carex nigra, Eleocharis acicularis, Eleocharis quinqueflora, Equisetum palustre, Galium palustre, Agrostis stolonifera, Juncus conglomeratus, Scirpus sylvaticus, Juncus filiformis, Juncus inflexus, Lysimachia nummularia, Lythrum salicaria, Lysimachia vulgaris, Mentha longifolia, Myosotis scorpioides, Ranunculus repens, Rorippa palustris, Juncus articulatus.* The Characeae, even when identified to species, were considered as only one taxon. Plant species composition was assessed using quadrat samples (0.5×0.5 m). Quadrats were located in the water every 5 m, along transects perpendicular to the longest axis of each pond. Transects were taken every 5 m for small ponds and every 20 m for large ponds. An average number of 77 quadrats (min 8, max 460) was taken for each pond.

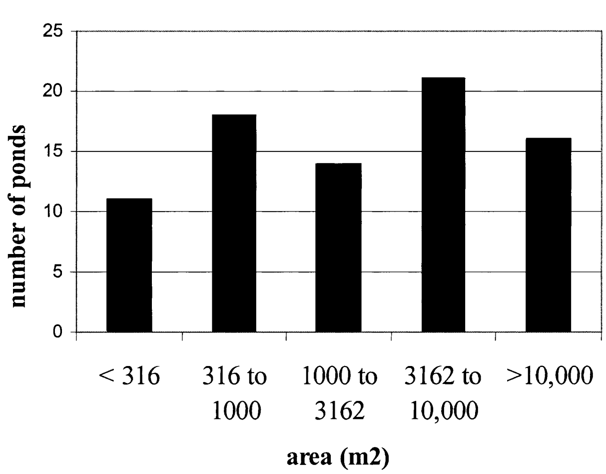

Fig. 1. Distribution of the 80 ponds between five area classes.

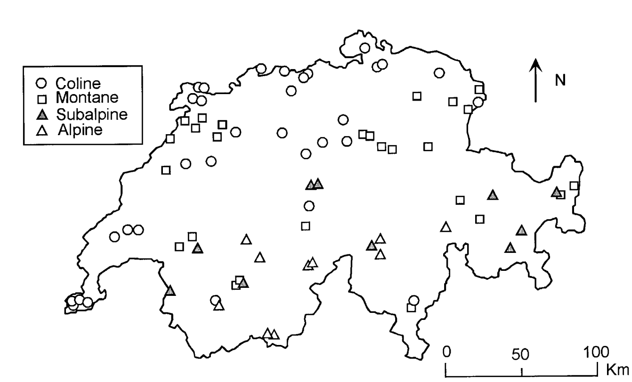

Fig. 2. Location of the 80 ponds studied in Switzerland, showing the altitudinal group to which each pond belongs: Colinar (200–665 m.a.s.l.), Montane (610–1400 m.a.s.l.), Subalpine (1410–2000 m.a.s.l.), Alpine: 1860–2760 m.a.s.l.).

Aquatic invertebrates (Gastropoda, Sphaeriidea, Coleoptera) were collected with a small-framed hand-net (rectangular frame 14×10 cm, mesh size 0.5 mm). The small size of the frame of this net makes it easy to handle among submerged or floating leaves, which are often impenetrable to a larger net. For each sample, the net was swept through the water intensively for 30 s. The number of samples (n) collected at each pond was dependent on pond size (S, in m^2) and calculated as follows:

$$n = 0.885 \times \left(2^{\log(S)}\right)$$

The number of samples taken ranged from 2 to 29 (average: 11.4). Sampling was stratified in the dominant habitats (from the land–water interface to a depth of 2 m): submerged and emergent vegetation, dead organic matter (litter), inorganic substrate (stones, gravel, etc.). When stones or gravel were sampled, they were collected in the net, and washed away from the pond. In all cases, the collected material was preserved in 5% formaldehyde and then comprehensively sorted in the laboratory. Specimens of Gastropoda, Sphaeriidae and Coleoptera were identified to species level and counted.

The diversity of adult Odonata was assessed using a standardised field survey method combining observations from early and late summer (Oertli et al., 2000) and the species richness of Amphibia was obtained from exhaustive inventory data collected over past few years (Borgula et al., 1994) and made available from the Swiss fauna databank (CSCF-KARCH, Neuchâtel, Switzerland).

Richness measured from a non-exhaustive sampling programme is affected by the sampling effort—as area or sample size increases the number of individuals rises consequently and the number of species would also rise (Connor and McCoy, 1979). Except for Amphibia, which were considered complete, and Sphaeriidae, whose numbers of species were too small, this sampling bias was reduced prior to analysis by means of a Jackknife estimator (Burnham and Overton, 1979), calculated with the computer program *Ws2m.exe* (Turner et al., 2000).

2.3. Conservation value of species assemblages

We have employed two criteria as measures of the biodiversity: species richness and conservation value. The conservation value of pond species assemblages was assessed by a procedure similar to those commonly used in the United Kingdom in which every species received a score according to its degree of rarity (Eyre and Rushton, 1989; Foster et al., 1992; Painter, 1999; Linton and

Table 1
Mean values and ranges of selected variables characterising the 80 ponds

Variable	Mean	Minimum	Maximum	Median
Altitude (m.a.s.l.)	999	210	2757	733
Yearly air temperature (Celsius degrees)[a]	6.3	−0.6	12.1	7.2
Maximal depth (m)	3.47	0.40	0.24	2.15
Mean depth (m)	1.66	0.26	8.50	1.15
Area (m^2)	8,817	6	94,346	1,834
Shoreline development[b]	1.47	1.02	3.3	1.34
Shade (percentage of the pond shaded)	1–5	0	100	1–5
Age	–	1	> 4000	100
Coverage by floating vegetation[c]	30	0	100	19
Coverage by submerged vegetation[c]	36	0	100	23
Connectivity[d]	3.2	0	7.7	4.1
Trophic class (total P classes, Wetzel, 1983)	2.4	1 (oligotroph)	4 (hypertroph)	2 (mesotroph)

[a] The yearly air temperature was derived from a long-term mean (1961–1990) based on monthly values from 115 climate stations and a digital terrain model on a 25-m grid.
[b] Ratio of the length of the shoreline to the circumference of a circle of area equal to that of the pond (Wetzel, 1983).
[c] Percentage of the littoral zone (depth $<$ 3 m) covered by this type of vegetation.
[d] Measure of the pond isolation. This measure takes into account the number and size of ponds within a radius of 1000 m and their distance to the studied pond. Large values correspond to low isolation.

Table 2
Species score for each species according to its degree of threat (Swiss national Red List ranking)

	Red List category						
Fauna national Red List	0	1	2	3	4	–	5
Flora national Red List	Ex	E	–	V	R	Attractive	–
IUCN category	Extinct	Endangered	Vulnerable	Vulnerable	Rare	–	–
Species score	32	16	12	8	4	2	1

Goulder, 2000). Swiss species are ranked according to their degree of rarity in Switzerland in the national Red List (Landolt, 1991; Duelli, 1994). For Coleoptera, however, only a partial national Red List exists, covering the Adephaga; therefore the conservation value of non-Adephaga species was arbitrarily assigned to the minimal value (1). The scores assigned to each species are presented in Table 2.

Two conservation values were calculated. The conservation value per site of the species assemblage (C) was the sum of the scores of all species present in the site. The mean conservation value per site (Csp) was the value C divided by the number of species present in the site.

3. Results

The sampling of the 80 ponds produced 154 aquatic plant species and 182 species belonging to the five faunal groups selected for study. Among them, 40 plant species and 89 animal species are rated as endangered in Switzerland (Table 3). For all of the taxonomic groups studied, the species collected represent >50% of the regional species pool (Switzerland), apart from the Coleoptera Adephaga (29%). Aquatic plants and Amphibia were present in all the ponds sampled, Gastropoda in 71%, Sphaeriidea in 63%, Coleoptera in 91% and Odonata in 96%. The mean species richness per pond was 11.6 for aquatic plants, 3.2 for Gastropoda, 1.1 for Sphaeriidae, 8.0 for Coleoptera, 8.4 for Odonata and 4.4 for Amphibia.

3.1. Species–area relationship

Prior to analysis of the relation between diversity and area, we investigated the correlation between diversity and other environmental variables. Altitude appeared to be the main factor and accounted, respectively for 12% (aquatic vegetation), 28% (Gastropoda), 45% (Odonata), 27% (Coleoptera), 47% (Amphibia), 57% (faunal species richness) of the variance of the richness. Other pond variables were also involved in driving diversity of some of the taxonomic groups but accounted for a lower proportion of the variance: shade (9%, Odonata), shoreline development (9%, Coleoptera), connectivity (4%, Amphibia), coverage by the submerged vegetation (14%, Coleoptera), coverage by the floating vegetation (9%, Gastropoda), eutrophication (16%, vegetation;

Table 3
Species richness of aquatic plants, Sphaeriidae, Gastropoda, Coleoptera, Odonata, Amphibia, and the five faunal groups pooled, in the 80 ponds. The number of endangered species (classified on the national Red List) is indicated in brackets

Taxonomic group	Total richness (80 ponds)	% of regional species pool (Switzerland)	Per pond		
			Mean	Median	Range
Aquatic plants	153 (40)	53	11.6 (1.2)	10.1 (1)	2–32 (0–5)
Gastropoda	28 (19)	52	3.2 (1.3)	2.0 (0.5)	0–10 (0–6)
Sphaeriidae	9 (2)	47	1.1 (0.25)	1.0 (0)	0–6 (0–2)
Coleoptera:—all	86 (36)	24	8 (0.8)	5.8 (0)	0–32 (0–10)
— only Adephaga	56 (36)	29	4.9 (0.8)	3.9 (0)	0–20 (0–10)
Odonata	44 (19)	58	8.4 (0.7)	8.4 (0)	0–24 (0–7)
Amphibia	15 (13)	83	4.4 (3.5)	4.0 (3)	1–13 (0–11)
Faunal groups pooled	182 (89)	–	25.0 (6.5)	23.0 (5)	3–58 (0–16)

Table 4
Relationship between area ($\log_{10}$ transformed) and richness [$\log_{10}(x+1)$ transformed] for aquatic plants, Sphaeriidae, Gastropoda, Coleoptera, Odonata, Amphibia and the five faunal groups pooled[a]

Taxonomic group	All 80 ponds			Subset of 60 ponds (lower altitude)		
	R^2	P	z value	R^2	P	z value
Aquatic plants	0.066	*	0.071	0.077	*	0.073
Sphaeriidae	0.004	NS	0.017	0.005	NS	0.020
Gastropoda	0.072	*	0.115	0.086	*	0.108
Coleoptera	0.002	NS	−0.018	0.000	NS	0.007
Odonata	0.057	*	0.090	0.312	****	0.129
Amphibia	0.0004	NS	−0.005	0.000	NS	0.0004
Total faunal richness (five groups)	0.023	NS	0.050	0.119	**	0.070

[a] R, correlation associated with the log–log relationship (Fig. 3); z, slope of the relationship; NS, not significant
* $P<0.05$.
** $P<0.01$.
**** $P<0.0001$.

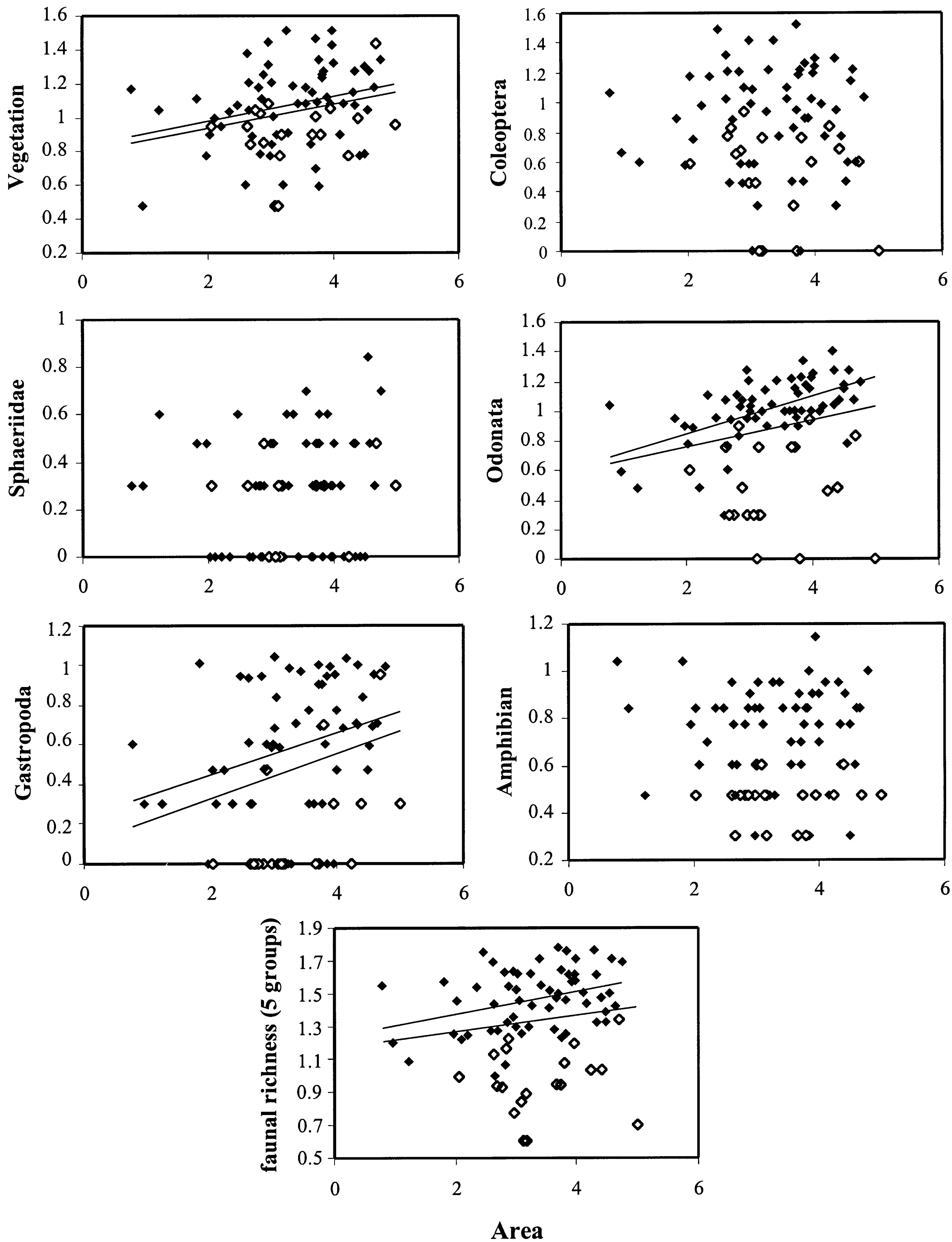

Fig. 3. Relationship between pond area ($\log_{10}$transformed) and species richness ($\log_{10}$transformed) for aquatic vegetation, Gastropoda, Sphaeriidae, Coleoptera, Odonata, Amphibia and all five faunal groups pooled. The solid symbols represent the 60 ponds from lower altitude (colinar and montane belts, altitude $\leqslant$1400 m.a.s.l.), and the open symbols the 20 ponds from higher altitude (subalpine and alpine belts, altitude > 1400 m.a.s.l.). Significant relationships are represented by lines: the upper line represents the relation obtained with all 80 ponds, and the lower line represents the relationship obtained with the subset of 60 ponds.

4% Amphibia) and age (4%, Amphibia). Because of the importance of altitude, in subsequent analyses we have presented the results from the total set of 80 ponds and the subset of the 60 lower altitude ponds (altitude ⩽1400 m.a.s.l.; i.e. excluding alpine and subalpine ponds) as separate sets of figures.

When all ponds were considered, the correlation between richness and pond area (expressed as $\log_{10}$) was positive and significant for the aquatic plants, the Gastropoda, and the Odonata, with area accounting for 7, 7 and 6% of the variance of richness respectively. This relationship was not significant for Sphaeriidae, Coleoptera, Amphibia and total faunal species richness (the five groups pooled; Table 4; Fig. 3). For the 60 low altitude ponds, these values reached 8, 8 and 31%, respectively, and there was a significant value for the five faunal groups pooled (12% of the variance). The correlations were still not significant for the Sphaeriidae, the Coleoptera and the Amphibia.

With the exception of the Odonata, all significant correlation values were relatively low; this indicates that, although these results support the general contention that there is a positive relation between area and richness, there are many other factors influencing this relationship. This is illustrated in Fig. 3, where many ponds fall far from the regression line.

The significant relationships between richness and area all showed low slope (z values): 0.07 (aquatic plants), 0.11 (Gastropoda), 0.09 and 0.13 (Odonata), 0.07 (faunal richness).

3.2. Relation between area and conservation value

For conservation values (total or mean score for all species present), a significant relationship with pond area was only evident in the case of Odonata (Table 5). High conservation values of the assemblages of aquatic plants, Gastropoda, Coleoptera, Amphibia and of faunal groups pooled were found in all sizes of ponds (Fig. 4).

There is thus a lack of correspondence between the significance of pond size, as measured by “species richness “ and “conservation value”. The correlation (r) between these two criteria was relatively high for Amphibia (0.988), Gastropoda (0.890) and Odonata (0.869), but appears weaker for aquatic plants (0.766) and Coleoptera (0.800).

3.3. SLOSS analysis

Cumulative species curves allow estimation of whether or not a single large patch is more favourable than several small patches (e.g. Douglas and Lake, 1994, Honnay et al., 1999). We constructed such curves for both richness and conservation value. For all situations (Fig. 5), the “small to large” curve lies clearly above the “large to small” curve. Thus a set of ponds of small size has more species and has a higher conservation value than a single large pond of the same total area. When comparison is made between taxonomic groups, the magnitude of the space between the two curves highlights the conclusion that “several smaller ponds” are particularly favourable for Coleoptera.

But this result masks the reality that large ponds (like small ponds) can have a distinctive fauna and are also important for conservation. For example, if we remove the largest ponds we loose a part of the global species pool for each taxonomic group, with the exception of Amphibia (Table 6). The same type of process conducted with the smallest ponds leads also to a loss of

Table 5
Relation between pond area ($\log_{10}$) and “conservation value” of species assemblages[a]

		All 80 ponds		Subset of 60 ponds (excluding ponds of altitude)	
		R	*P*	*R*	*P*
Aquatic plants	C	0.189	NS	0.207	NS
	Csp	−0.138	NS	−0.129	NS
Gastropoda	C	0.107	NS	0.128	NS
	Csp	0.123	NS	0.143	NS
Coleoptera	C	0.063	NS	0.107	NS
	Csp	0.109	NS	0.154	NS
Odonata	C	0.318	**	0.414	***
	Csp	0.154	NS	0.258	*
Amphibia	C	−0.060	NS	−0.049	NS
	Csp	−0.171	NS	−0.202	NS
All four faunal groups	C	0.118	NS	0.201	NS
	Csp	0.070	NS	0.095	NS

[a] C, total conservation value; Csp, mean conservation value per species. Sphaeriidae were not included. R, correlation associated with the log–log relationship (Fig. 4); NS, not significant

* $P<0.05$.

** $P<0.01$.

*** $P<0.001$.

species. The removal of medium sized ponds can also induce a loss of species, particularly for Coleoptera whose species pool would be greatly affected.

3.4. Species response to pond size

The occurrence of the 64 most frequent species (plants and animals) was examined in relation to pond size (species occurring in > 16% of the ponds). Among these, about one fifth showed a significant relationship to pond size (non-parametric Mann–Whitney test, $P<0.05$): one Coleoptera species for small ponds, and 11 species (two aquatic plants, two Gastropoda and seven Odonata) for large ponds (Table 7). None of the 64 taxa showed a preference for medium sized ponds.

3.5. Relationship between faunal and floral diversity

Besides the relationship between diversity and area, it is also important to know if the faunal diversity (species richness and conservation value) was correlated with floral diversity (species richness). This relationship is impossible to test directly, because floral diversity is linked to area and altitude and could, in consequence, act as a surrogate of area and altitude in the mathematical relationship. To overcome this problem, we calculated

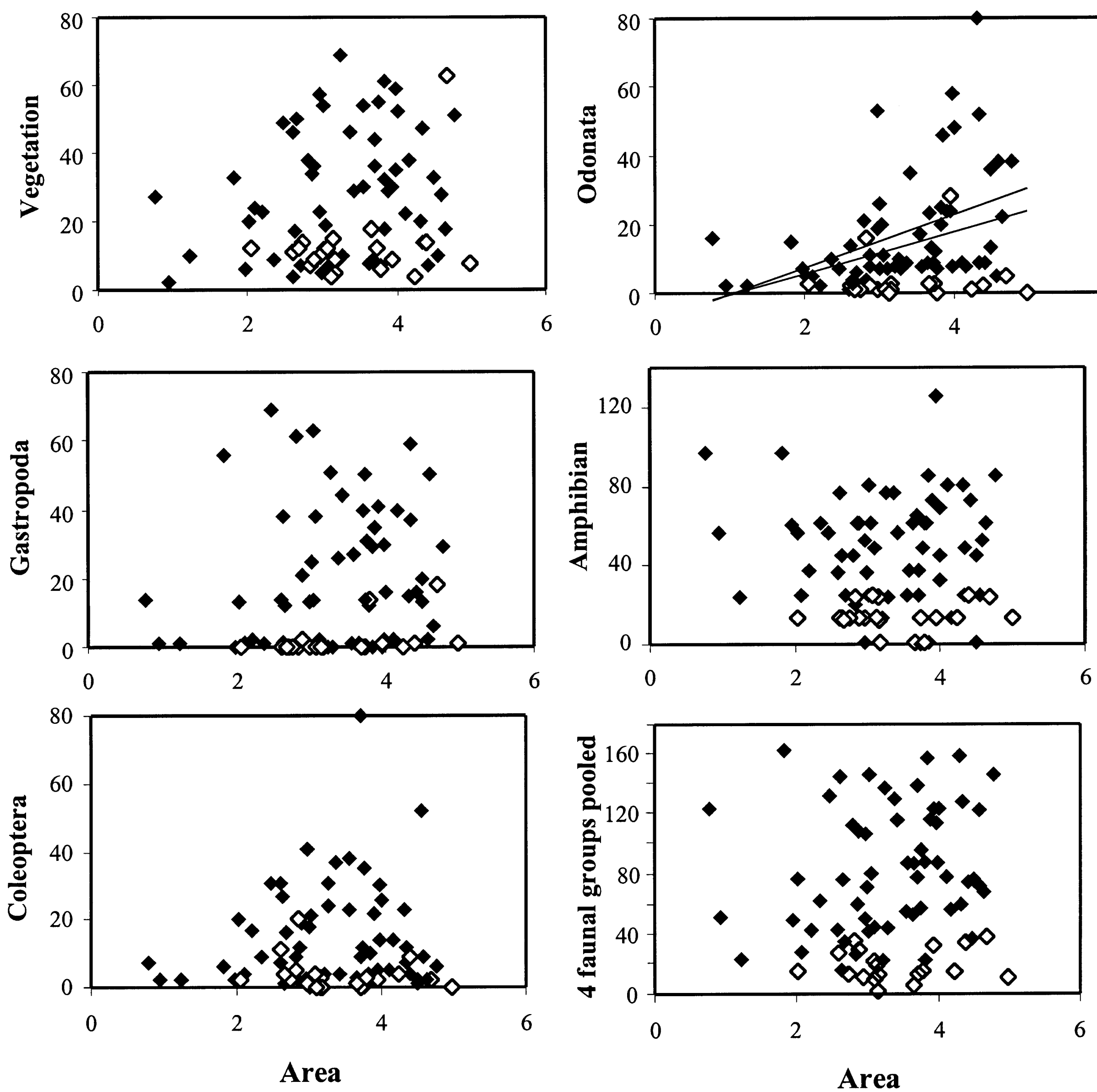

Fig. 4. Relationship between "conservation value" and pond area ($\log_{10}$transformed) for aquatic vegetation, Gastropoda, Coleoptera, Odonata, Amphibia and all four faunal groups pooled. The solid symbols represent the 60 ponds from lower altitude (colinar and montane altitudinal belts), and the open symbols the 20 ponds from higher altitude (subalpine and alpine belts). The significant relationships are represented by lines: the upper line represents the relation obtained with all 80 ponds, and the lower line represents the relationship obtained with the subset of 60 ponds.

Table 6
Species loss in the global species pool (80 studied ponds) by the removal of a set (10 or 15 ponds) of the smallest, medium sized, or largest ponds[a]

Ponds removed	Species loss per taxonomic group				
	Aquatic plants (SP = 160)	Gastropoda (SP = 29)	Coleoptera (SP = 86)	Odonata (SP = 45)	Amphibia (SP = 15)
10 smallest (6–223 m^2)	12	1	1	2	0
15 smallest (6–434 m^2)	14	2	4	3	0
10 medium sized (1400–3600 m^2)	2	0	6	0	1
15 medium sized (1200–4600 m^2)	4	0	7	0	1
10 largest (24,000–96,000 m^2)	10	1	3	2	0
15 largest (14,000–96,000 m^2)	14	2	5	3	0

[a] SP, species pool (number of species).

Table 7
Relationship between the 64 most frequent taxa and pond area. *P* values (Mann–Whitney test)[a]

Species associated with the smallest ponds	
Coleoptera	*Agabus bipustulatus* *
Species associated with the largest ponds	
Flora	*Carex elata* ***, *Phragmites australis* **
Gastropoda	*Gyraulus albus* **, *Radix auricularia* **
Odonata	*Aeshna grandis* **, *Anax imperator* **, *Cordulia aenea* **, *Enallagma cyathigerum* ***, *Ischnura elegans* *, *Orthetrum cancellatum* ****, *Somatochlora metallica* **
Species whose occurrence showed no significant relationship to pond size	
Flora	*Caltha palustris*, *Carex acutiformis*, *Carex nigra*, *Carex rostrata*, *Carex vesicaria*, *Equisetum fluviatile*, *Galium palustre*, *Iris pseudacorus*, *Juncus articulatus*, *Lemna minor*, *Lythrum salicaria*, *Menyanthes trifoliata*, *Potamogeton natans*, *Potamogeton pusillus*, *Ranunculus trichophyllus*, *Schoenoplectus lacustris*, *Typha latifolia*
Gastropoda	*Gyraulus crista*, *Hippeutis complanatus*, *Lymnaea stagnalis*, *Planorbis carinatus*, *Radix ovata*, *Radix peregra*
Sphaeriidae	*Musculium lacustre*, *Pisidium casertanum*, *Sphaerium corneum*
Coleoptera	*Anacaena lutescens*, *Haliplus ruficollis*, *Hydroporus palustris*, *Hyphydrus ovatus*, *Noterus clavicornis*
Odonata	*Aeshna cyanea*, *Aeshna juncea*, *Aeshna mixta*, *Coenagrion puella*, *Lestes viridis*, *Libellula depressa*, *Libellula quadrimaculata*, *Sympetrum sanguineum*, *Sympetrum striolatum*, *Sympetrum vulgatum*[a]
Amphibia	*Alytes obstetricans*[a], *Bombina variegata*, *Bufo bufo*, *Hyla arborea*, *Rana esculenta*, *Rana temporaria*, *Triturus alpestris*, *Triturus cristatus*, *Triturus helveticus*, *Triturus vulgaris*

[a] #$P<0.10$; *: $P<0.05$; **: $P<0.01$; ***: $P<0.001$; ***: $P<0.0001$

first the amount of variability of faunal diversity explained by the two variables “area” and “altitude”. The third variable “floral diversity” was then added to see if this increased the proportion of the variability of the faunal diversity explained. This analysis showed clearly that for Gastropoda, Coleoptera, Odonata and the four faunal groups pooled, species richness and conservation value “C” (total score of all species) were related to floral diversity (Fig. 6), but with weak relations. For the Amphibia, there was obviously no relation. In the case of conservation value Csp (mean score per species), only the Odonata (and to a much lower extent the Coleoptera) seem to be affected by the floral diversity.

4. Discussion

4.1. Does a larger area support more species?

The biogeographic principle that larger areas support more species seems to have limitations in its application to ponds. In the set of ponds studied here, this principle was relevant for Odonata and to a lesser extent for Gastropoda and the total species richness of the five faunal groups. This was not the case for the three other taxonomic groups investigated, the Coleoptera, Sphaeriidae and Amphibia. This result also underlines the reality that different taxonomic groups can show different trends.

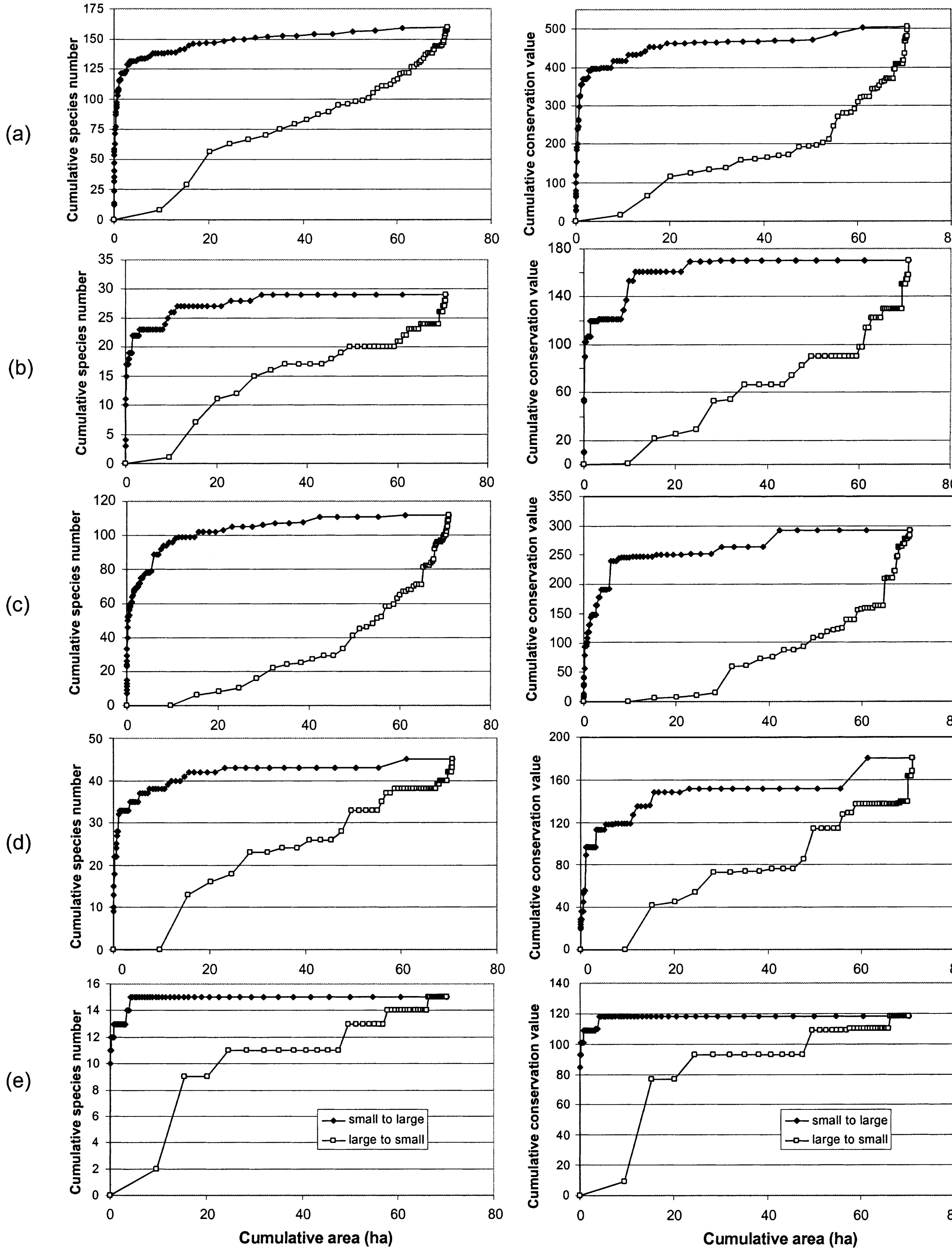

Fig. 5. SLOSS analysis. Relationships between cumulative area and (left side) cumulative species number and (right side) cumulative conservation value for (a) aquatic plants, (b) Gastropoda, (c) Coleoptera, (d) Odonata and (e) Amphibia. The 80 ponds are ranked from the smallest to the largest and from the largest to the smallest.

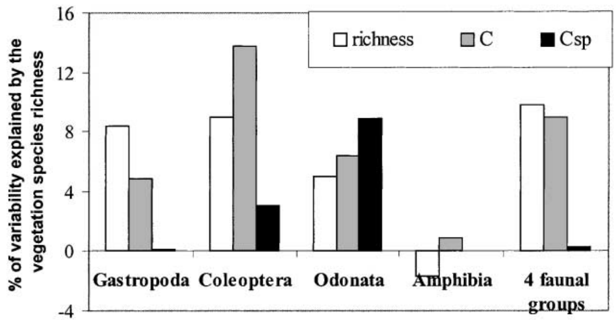

Fig. 6. Percentage of the variability of faunal diversity explained by the species richness of the vegetation. Faunal diversity is represented here by three components: the species richness, the conservation value C (total score of all species) and Csp (mean score per specie). The percentage of variability value was obtained by subtraction of (1) the percent of variability of faunal diversity explained by the two variables altitude and area, from (2) the percent of variability of faunal diversity explained by the three variables altitude, area and species richness of vegetation. The percentage of variability corresponds with the R^2 from the multiple regression linking faunal diversity to the other variables.

For aquatic plants, a positive relationship between pond size and species richness could be a valid generalisation. The same positive relationship was also shown in the studies of Møller and Rørdam (1985), Gee et al. (1997), Jeffries (1998) Pond Action (1994), although the works of Friday (1987) and Linton and Goulder (2000) provide exceptions. Further, the same positive trends have been shown for lakes (Rorslett, 1991; Lachavanne et al., 1986).

For the fauna the published data are more heterogeneous. As we observed for Odonata and Gastropoda, a positive relation between area and richness is evident for Crustacea (Fryer, 1985), for Dytiscidae (Nilsson and Svensson, 1995) and for Gastropoda (Lassen, 1975; Broenmark, 1985). Such trends were also observed in lakes for Gastropoda (Aho, 1978; Browne, 1981) or macroinvertebrates in general (Allen et al., 1999). Absence of significant relationship, as we observed for Sphaeriidae, Coleoptera and Amphibia, has also been reported by other authors for macroinvertebrates (Friday, 1987; Pond Action, 1994; Gee et al., 1997) and for Amphibia (Hecnar and McCloskey, 1998). It must also be emphasised that most of the cited studies did not remove the sampling effort effect. Many of the positive relationships found could be a consequence of this, and so possibly cannot be relied upon.

As z-values illustrate the strength of the effect of area on species number (Murphy and Wilcox, 1986), the low values we observed (from 0.07 to 0.13) demonstrate the weakness of the relationship. In other relationships between species richness and area (mainly from terrestrial habitats), z-values obtained are typically around 0.25, with a range from 0.20 to 0.40 (Connor and McCoy, 1979). For water bodies, it appears from the published values that z is often smaller. Low values of z were reported for pond snails (0.114; Broenmark, 1985), for small lakes Gastropods (0.16; Aho, 1978), for pond macrophytes (0.13; Gee et al., 1997; 0.129; Broenmark, 1985; 0.189 and 0.182; Jeffries, 1998), for stream macroinvertebrates (0.19; Broenmark et al., 1984), for vascular plants from small lakes (0.13; from data in Virola et al., 1999), for fish from lakes (0.15; Barbour and Brown, 1974). Some higher values have been reported for pond vascular plants (0.27–0.32; Møller and Rørdam, 1985), for snails from small eutrophic ponds (0.37; Lassen, 1975) or from lakes (0.23; Browne, 1981). The low z-values observed in the Swiss ponds, and the non-significant relations between area and richness, give two bases for argument that area may be of only secondary importance in determining pond biodiversity.

The vegetation itself was expected to play a direct role in driving faunal diversity: a higher flora diversity can be an indicator of higher habitat diversity, and as Rosenzweig (1995) recalled it, "The greater the habitat variety, the greater the species diversity". Nevertheless, only a weak relationship was observed and it did not apply at all to Amphibia.

4.2. Does a larger area support a higher conservation value?

Weighting individual species according to their rarity reduced rather than increased the statistical relationship with pond area. In other words, even small ponds could contain important groups of species for conservation. Similar results were obtained by Pond Action (1994) in Oxfordshire and by Linton and Goulder (2000) in East Yorkshire.

Differences between the information provided by species richness and conservation value in the case of vegetation and Gastropoda demonstrates that richness cannot act as a surrogate for conservation value. The low level of correspondence between these two parameters was also observed in other situations, for example in Irish water beetle assemblages, where some assemblages with relatively few species had high species-quality scores (Foster et al., 1992). This is also true on a larger geographic scale, where conservation of species-rich sites is not synonymous with effective conservation of rare species (Prendergast, 1993).

4.3. Many small or a few large?

In our study, a set of ponds of small size had more species and had a higher conservation value than a single large pond of the same total area. Helliwell (1983) also observed such a pattern for plant species. Nevertheless, large ponds cannot be ignored in conservation policy, since our study shows that they can harbour species missing in the smaller ponds. Furthermore, many species occur in both large and small ponds, and larger populations will live in larger ponds and will be less sensitive to extinction.

At the species level, while one fifth of the species showed a preference for large ponds, only one species (*Agabus bipustulatus*, Coleoptera) appeared to be more frequently associated with smaller ponds in this study. However, Fryer (1985), for example, found that some species of Crustacea appeared to be more frequently associated with smaller ponds.

Our results demonstrate that, in relation to promoting species richness and/or richness of endangered species in ponds, pond size is a prominent parameter only for selected taxa or groups. Contrary to what would be expected from biogeographic theory, a pond does not necessarily have to be large to have a high value. In terms of their conservation (protection, restoration and management), there is a need to promote conservation of all ponds, regardless of their area. Since the creation of small ponds is a relatively easy task, such an undertaking should be recommended to people with an interest in ponds (farmers, local authorities, nature conservation organisations, schools, etc.) and could have a beneficial impact on conservation of freshwater biodiversity. Suitable advice on "appropriately designed" pond creation can be found in the "Pond book" (Williams et al., 1999).

Acknowledgements

We thank our collaborators C. Antoine, C. Ilg, J. Müller, C. Pulfer, T. Rohmig, M. Saam, H. Humbert-Droz for help in the field work. We are very grateful to M.L. Rosenzweig for valuable advice on methods to reduce the sampling bias when estimating diversity, and for the computer program *Ws2m.exe* (Turner et al. 2000) realising such procedure. Thanks to F. Kienast (*Swiss Federal Institute of Forests, Snow and Landscape*) for climatic data, to the KARCH for Amphibia data, to the CRSF and CSCF for the access to the Swiss databanks on respectively flora and fauna. Help in identification was provided by A. Badstuber and P. Richoux (Coleoptera), N. Thew (Sphaeriidae), G. Falkner and P. Stücki (Gastropoda), C. Cook (Ranunculaceae), E. Landolt (Lemnaceae), M.-A. Thiébaud (*Eleocharis*), P. Charlier and C. Schneider (other aquatic plants).

Thanks to M.C.D. Speight for improving the English style and for comments on the manuscript. The authors appreciate also the constructive comments from B.N.K. Davis and two anonymous reviewers.

This paper was realised with the data collected in a study financially supported by the "*Swiss Agency for the Environment, Forests and Landscape*".

References

Aho, J., 1978. Freshwater snail populations and the theory of island biogeography. I. A case study in southern Finland. Annales zoologici Fennici 15, 146–154.

Allen, A.P., Whittier, T.R., Kaufmann, P.R., Larsen, D.P., OConnor, R.J., Hughes, R.M., Stemberger, R.S., Dixit, S.S., Brinkhurst, R.O., Herlihy, A.T., Paulsen, S.G., 1999. Concordance of taxonomic richness patterns across multiple assemblages in lakes of the northeastern United States. Canadian Journal of Fisheries and Aquatic Sciences 56, 739–747.

Barbour, C.D., Brown, J.H., 1974. Fish species diversity in lakes. American Naturalist 108, 473–489.

Benayas, J., Colomer, M., Levassor, C., 1999. Effects of area, environmental status and environmental variation on species richness per unit area in Mediterranean wetlands. Journal of Vegetation Science 10, 275–280.

Biggs, J., Corfield, A., Walker, D., Whitfield, M., Williams, P., 1994. New approaches to the management of ponds. British Wildlife 5, 273–287.

Boothby, J. (Ed), 1998. Ponds and pond landscapes of Europe. Proceedings, International Conference of the Pond Life Project. Maastricht.

Borgula, A., Fallot, P., Ryser, J., 1994. Inventaire des sites de Reproduction de Batraciens d'importance Nationale. OFEFP, Bern.

Broenmark, C., 1985. Freshwater snail diversity: effects of pond area, habitat heterogeneity and isolation. Oecologia 67, 127–131.

Broenmark, C., Herrmann, J., Malmqvist, B., Otto, C., Sjoerstroem, P., 1984. Animal community structure as a function of stream size. Hydrobiologia 112, 73–79.

Browne, R.A., 1981. Lakes as islands: biogeographic distribution, turnover rates, and species composition in the lakes of central New York. Journal of Biogeography 8, 75–83.

Burnham, K.P., Overton, W.S., 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology 60, 927–936.

Connor, E.F., McCoy, E.D., 1979. The statistics and biology of the species–area relationship. American Naturalist 113, 791–833.

Douglas, M., Lake, P.S., 1994. Species richness of stream stones: an investigation of the mechanisms generating the species-area relationship. Oikos 69, 387–396.

Duelli, P., 1994. Listes Rouges des Espèces Animales Menacées de Suisse. OFEFP, Bern.

Eyre, M.D., Rushton, S.P., 1989. Quantification of conservation criteria using invertebrates. Journal of Applied Ecology 26, 159–172.

Foster, G.N., Nelson, B.H., Bilton, D.T., Lott, D.A., Merritt, R., Weyl, R.S., Eyre, M.D., 1992. A classification and evaluation of Irish water beetle assemblages. Aquatic Conservation: Marine and Freshwater Ecosystems 2, 185–208.

Friday, L.E., 1987. The diversity of macroinvertebrate and macrophyte communities in ponds. Freshwater Biology 18, 87–104.

Fryer, G., 1985. Crustacean diversity in relation to the size of water bodies: some facts and problems. Freshwater Biology 15, 347–361.

Gee, J.H.R., Smith, B.D., Lee, K.M., Griffiths, S.W., 1997. The ecological basis of freshwater pond management for biodiversity. Aquatic Conservation Marine and Freshwater Ecosystems 7, 91–104.

Gilpin, M.E., Diamond, J.M., 1980. Subdivision of nature reserves and the maintenance of species diversity. Nature 285, 567–568.

Hecnar, S.J., McCloskey, R.T.M., 1998. Species richness patterns of amphibians in southwestern Ontario ponds. Journal of Biogeography 25, 763–772.

Helliwell, D.R., 1983. The conservation value of areas of different sizes: Worcestershire ponds. Journal of Environmental Management 17, 179–184.

Honnay, O., Hermy, M., Coppin, P., 1999. Effect of area, age and diversity of forest patches in Belgium on plant species richness, and implications for conservation and reforestation. Biological conservation 87, 73–84.

Hugueny, B., 1989. West African rivers as biogeographic islands: species richness of fish communities. Oecologia 79, 236–243.

Hull, A., 1997. The pond *life* project: a model for conservation and sustainability. In: Boothby, J. (Ed.), British Pond Landscape, Proceedings from the UK conference of the Pond *Life* Project. Pond Life Project, Liverpool, pp. 101–109.

Imboden, C., 1976. Eaux vivantes—Initiation à la biologie des zones humides. LSPN, Basel.
Jeffries, M.J., 1998. Pond macrophyte assemblages, biodisparity and spatial distribution of ponds in the Northumberland coastal plain, UK. Aquatic Conservation: Marine and Freshwater Ecosystems 8, 657–667.
Lachavanne, J.-B., Perfetta, J., Noetzlin, A., Juge, R., Lods-Crozet, B., 1986. Etude Chorologique et Écologique des Macrophytes des Lacs Suisses en Fonction de leur Altitude et de leurs Niveau Trophique. FNRS, University of Geneva.
Lahti, T., Ranta, E., 1985. The SLOSS principle and conservation practice: an example. Oïkos 44, 369–370.
Landolt, E., 1977. Ökologische Zeigerwerte zur Schweizer Flora. Veröffentlichungen des Geobotanischen Institutes der ETH Stiftung Rübel (Zürich) 64, 1–208.
Landolt, E., 1991. Plantes Vasculaires Menacées en Suisse: Listes Rouges Nationale et Régionales. OFEFP, Bern.
Lassen, H.H., 1975. The diversity of freshwater snails in view of the equilibrium theory of island biogeography. Oecologia 19, 1–8.
Linton, S., Goulder, R., 2000. Botanical conservation value related to origin and management of ponds. Aquatic Conservation: Marine and Freshwater Ecosystems 10, 77–91.
MacArthur, R., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey.
May, R.M., 1986. The search for patterns in the balance of nature: advances and retreats. Ecology 67, 1115–1126.
Møller, T.R., Rørdam, C.P., 1985. Species numbers of vascular plants in relation to area, isolation and age of ponds in Denmark. Oikos 45, 8–16.
Murphy, D.D., Wilcox, B.A., 1986. On island biogeography and conservation. Oikos 47, 385–389.
Nilsson, A.N., Svensson, B.W., 1995. Assemblages of dytiscid predators and culicid prey in relation of environmental factors in natural and clear-cut boreal swamp forest pools. Hydrobiologia 308, 183–196.
Oertli, B., Auderset Joye, D., Castella, E., Juge, R., Cambin, D., Lachavanne, J.-B., 2000. Diversité Biologique et Typologie écologique des Étangs et Petits Lacs de Suisse. OFEFP, University of Geneva, Geneva.
Painter, D., 1999. Macroinvertebrate distributions and the conservation value of aquatic Coleoptera, Mollusca and Odonata in the ditches of traditionally managed and grazing fen at Wicken Fen, UK. Journal of Applied Ecology 36, 33–48.
Pond Action (Eds.), 1994. The Oxfordshire Pond Survey. A report to the World Wide Fund for Nature (WWF-UK). Oxford Brookes University, Oxford.
Prendergast, J.R., 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature 365, 335–337.
Primack, R.B., 1998. Essentials of Conservation Biology. Sinauer Associates, Sunderland.
Ricciardi, A., Rasmussen, J.B., 1999. Extinction rates of north American freshwater fauna. Conservation Biology 13, 1220–1222.
Rorslett, B., 1991. Principal determinants of aquatic macrophyte richness in northern European lakes. Aquatic Botany 39, 173–193.
Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge.
Turner, W., Leitner, W.A., Rosenzweig, M.L., 2000. *Ws2m.exe*. Software for the measurement and analysis of species diversity. Available at: http://eebweb.arizona.edu/diversity/.
Virola, T., Kaitala, V., Kuitunen, M., Lammi, A., Siikamaki, P., Suhonen, J., Virolainen, K., 1999. Species immigration, extinction and turnover of vascular plants in boreal lakes. Ecography 22, 240–245.
Ward, D.W., Blaustein, L., 1994. The overriding influence of flash floods on species–area curves in ephemeral Negev Desert pools: a consideration of the value of island biogeography theory. Journal of Biogeography 21, 595–603.
Wetzel, R.G., 1983. Limnology. Saunders, Philadelphia.
Williams, P., Biggs, J., Whitfield, M., Thorne, A., Bryant, S., Fox, G., Nicolet, P., 1999. The Pond Book: A Guide to the Management and Creation of Ponds. Ponds Conservation Trust, Oxford.