

## Regional enrichment of predacious water beetles in temporary ponds at opposite east–west ends of the Palearctic

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**Abstract.** Regional and local species richness of temporary pond dytiscid water beetles were compared among three regions within the Palearctic: (1) Sweden in north west Europe, (2) Primorye and (3) Sakhalin Island in the Russian Far East. Both local and regional species richness were highest in Sweden and lowest in Sakhalin. Regional species richness was calculated from literature and collecting data for each region and for nested parts of regions. Local species richness was estimated from standardized net samples from fourteen or fifteen ponds in each region. Two different rarefaction techniques applied to the net-sample data confirmed the observed interregional differences in species richness. Partial least square regression showed that pond area, depth and temperature affected local species richness positively in each region, whereas increasing shade and drought frequency had negative effects. Residuals from the regression analysis were positive in Sweden, negative in Sakhalin, and near zero in Primorye ponds. Consequently,

the local species richness was related positively to regional species richness also when compensated for differences in the local pond environment. This was verified when pond species richness of each region was correlated with principal component scores representing a combination of pond area, depth and temperature. The species' distributions among ponds displayed significantly nested patterns in Sweden and Sakhalin. However, species were significantly sorted along the pond area gradient only in Sweden. It is concluded that the observed interregional differences in local species richness are best explained by the accompanying gradient in regional species richness, lending support to the hypothesis of regional enrichment. Selected historical and ecological explanations for the observed differences in regional species richness are discussed.

**Key words.** Regional diversity, local diversity, regional enrichment, temporary ponds, water beetles, Palearctic.

### INTRODUCTION

The need to study ecological phenomena at many different spatial scales has become evident recently (e.g. Ricklefs & Schluter, 1993). One important issue highlighted in this debate is whether local species richness of small homogeneous habitat patches depends on the number of species present in the regional pool. The traditional view of species saturation has been challenged by the observation that local diversity continues to increase with increasing regional diversity, i.e. regional enrichment. So far, relatively few studies have provided data for unambiguous tests of species saturation versus regional enrichment (see Cornell, 1993 for a review). Basically, such a test should compare the local species richness of selected taxa in two or more regions in which the regional species pools differ in size. For saturation to apply, local species richness would be more or less constant, whereas the regional enrichment hypothesis predicts a positive relationship between observed local and regional richness.

Comparative studies of this kind face the problem of finding local environments that are similar enough to make interregional or intercontinental comparisons meaningful. Similarly, the question of which species are actual or

potential inhabitants of such environments involves some difficult decisions. When compared between regions, local diversity needs to be studied in relation to habitat area and other factors related to the extent of local patches (Westoby, 1993). The wide geographical perspective demanded is often difficult to encompass for practical reasons. Moreover, there are severe problems connected with the delimitation and estimation of both regional and local species richness. Regional diversity estimates depend chiefly on the spatial delimitation of the region and the selection of the taxa to include with respect to taxonomy and habitat preferences.

Temporary ponds represent a habitat of relatively similar physical structure when viewed at a global scale (Williams, 1987). In the boreal region, the local species diversity of insects in temporary ponds is affected positively by pond area, depth and temperature, whereas increasing drought frequency tends to have the opposite effect (Nilsson & Svensson, 1995). Other factors of potential importance for local diversity are the development of vegetation, including moss (Palmer, 1981) and salinity (Colburn, 1988).

Many species of dytiscid water beetles normally occur in temporary ponds, where they often constitute one of the major components of the biota (Wiggins, Mackay & Smith, 1980; Larson, 1985; Nilsson & Svensson, 1995). In north

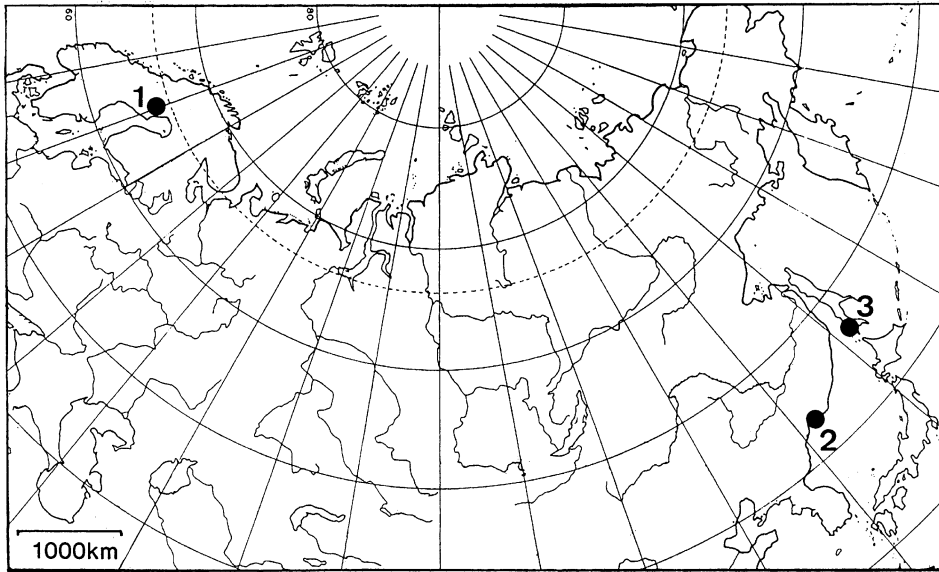


FIG. 1. Map of the Palearctic showing geographical positions of the study areas: (1) N. Sweden, (2) S. Primorye, (3) S. Sakhalin.

Sweden, most of the variation in local diversity of temporary pond Dytiscidae can be explained by a small number of easily measured environmental variables such as pond area, depth and temperature (Nilsson & Svensson, 1995). Once it has been shown that these variables affect local diversity in the same way within the regions being compared, an interregional comparison of local diversity would best be performed if the recorded species richness per pond is compared relative to the combined effects of pond area, depth, temperature and so on. As in most situations, local habitat patches differ in more than their size, and studies of differences in local diversity are related to a multivariate environmental gradient.

Local diversity of temporary pond Dytiscidae in north Sweden is well documented (Nilsson, 1986a; Nilsson & Svensson, 1994, 1995), and hence the seemingly lower local species richness observed during a collecting trip in south Primorye (Far East of Russia), at the opposite end of the Palearctic Region, was striking (Nilsson, unpubl.). Since the literature indicated that a similar difference existed at the regional scale, the system is worthy of a more detailed investigation. To circumvent the limitations inherent in a comparison of only two regions (cf. Tonn *et al.*, 1990), we also included the south part of the Island of Sakhalin that has an even more depauperate fauna (Nilsson & Kholin, 1994).

This study aims to provide an unambiguous test of whether species richness of temporary pond water-beetle faunas in three different parts of the Palearctic supports the hypothesis of saturation or that of regional enrichment.

## STUDY AREAS

The three studied regions were selected to cover the best possible variation in diversity, and were situated at opposite east–west ends of the Palearctic (Fig. 1). After the exclusion of ponds of extreme size and shade, fifteen ponds remained

in each of the two Russian regions, and fourteen ponds in Sweden. In north Sweden, nine ponds were studied in Västerbotten (64°05′–30′N, 19°05′–20°00′E) and five ponds in Norrbotten (66°30′–40′N, 23°10′–21′E) at an elevation of 150–300 m a.s.l. The area comprises Middle Boreal vegetation (Ahti, Hämet-Ahti & Jalas, 1968) of mainly Norway spruce (*Picea abies*) and Scots pine (*Pinus silvestris*). Annual precipitation is 400–500 mm with a maximum in August/September and a minimum in February/March. Snow covers the ground from about early November to late April, with a maximum depth of 0.5–0.7 m. The annual mean temperature is 2–2.5°C; the coldest month of the year is January (–8 to –12°C) and the warmest is July (15–16°C) (Ångström, 1974).

The fifteen ponds studied in south Sakhalin were all situated in the Kholmsk District (47°2′–16′, 141°58′–142°4′E) at an elevation of 1–50 m a.s.l. This area comprises hemiboreal vegetation (Hämet-Ahti, Ahti & Koponen, 1974) with forests formed chiefly by *Picea ajanensis* (Lindl and Gord.) Fisch. ex Carr. and *Abies sachalinensis* Fr. Schmidt. and partly replaced by deciduous forest and elements of the south flora (Tolmachev, 1955). In general the climate of south west Sakhalin is affected by the warm branch of the Tsushima Stream. The climate of this region is typically monsoon, with cold, humid winters and cool, rainy summers. Annual precipitation (around 750 mm) is unimodally distributed, with a maximum in July–September (about 90 mm per month). The snow cover usually reaches 0.5–0.7 m and persists from about early December to early April. The annual mean temperature is 3.9°C; the coldest month of the year is January (–9.6°C) and the warmest is August (17.9°C) (Kholmsk weather station).

In south Primorye, fifteen ponds were confined to the Muravyev Amurski Peninsula (43°14′N, 132°E), north of Vladivostok at an elevation of less than 10 m. This area is in the northern temperate zone (Hämet-Ahti *et al.*, 1974), and covered with mixed broadleaved and coniferous forest

(so called 'blackfir' forest) with needle fir (*Abies holophylla* Maxim.), Korean pine (*Pinus koraiensis* Siabold et Zucc), many different deciduous trees (oak, birch, some maples, linden, hornbeam) and elements of the Far Eastern flora (e.g. the lianes *Vitis amurensis* Rupr., *Schizandra chinensis* (Turcz.) Baill. and *Actinidia* spp.) (Kurentzova, 1968). The species composition of trees is highly variable and depends on local conditions. The climate is cool-temperate monsoon with cold and windy winters affected by the winter continental anticyclone; the early parts of the summers are cool, while the later parts are warm and rainy, depending on the anticyclonic activity upon the Pacific (Shver, 1978). The annual precipitation is about 800 mm, a large part of which falls in August and September with tropical cyclones (taifoons) arriving from the south (mean values are 145 mm and 126 mm, respectively). Snow cover (maximum depth 0.15 m) may occur from early December to early March. The annual mean temperature is 3.4°C. The coldest month of the year is January (−17.1°C) and the warmest is August (20.7°C) (Sad-Gorod weather station, adjacent to study area).

## MATERIAL AND METHODS

### Sampling and measurements

Ponds were visited monthly from May to September or October during 1 year in north Sweden and during 1993 and 1994 in south Primorye. Due to practical problems, the Sakhalin ponds were visited only three times, in June and September 1993, and in August 1994. In Sweden, different sets of ponds were studied in different years between 1987 and 1994. Previous studies suggest that temporal variation in species number is low (Nilsson & Svensson, 1995), and without potential to affect our general results. Depending on the number of total visits in each region in combination with the drought frequency, the numbers of sampling occasions per pond ranged from one to eight and the number of samples collected at each pond from two to thirty-four (Table 1).

Dytiscid larvae and adults were sampled with a small hand-net (frame diameter 150 mm, mesh size 0.6 mm). For

each sample the net was used intensively for 15 s along a distance of 1 m along the pond margin while stirring up the bottom material with one foot. Samples were immediately transferred to a flat bowl with some water, from which the insects were removed. In order to avoid a bias caused by decreasing per-species sampling effort as richness increases (Colwell & Hurtt, 1994), the number of samples taken from a pond depended upon its current size, namely 0.1–0.5 m<sup>2</sup>, one sample; >0.5–2.0 m<sup>2</sup>, two; >2.0–10 m<sup>2</sup>, three; >10–100 m<sup>2</sup>, four; >100 m<sup>2</sup>, five samples. On each sampling occasion, one qualitative sample was taken with a larger net in order to collect the adults of some larger, very mobile species that may have escaped from the smaller net. Species recorded only in qualitative samples were added to the number of species per pond only in the analyses that did not use relative abundance values.

Water temperature was measured 5 cm below the surface in open water when possible. At the same time air temperature was measured (in shade 1 m above ground). For each pond a linear regression model based on all available measurements was used to calculate the predicted water temperature at an air temperature of 20°C. This value was used in the PLS and PCA analyses. Table 1 gives the means and ranges of the measured temperature values for each region.

Pond size is expressed in terms of basin area, defined as the maximum area that can be covered with water before overflow occurs, excluding temporary but including seasonally flooded parts (Cowardin *et al.*, 1979). The depth of each pond was calculated as the maximum depth when the pond basin was full. The proportion of visits when a pond was dry was used as an estimate of the degree of permanence.

The degree of shade experienced by a pond was estimated as the proportion of the pond being shaded by trees, other vegetation or raised ground at midday in June. Ponds were selected to have a maximum of 50% shade. At each visit to a pond, the percentage cover of mosses and emergent vegetation was estimated.

The size of the regional species pool was estimated from Nilsson & Persson (1989, 1993) in Sweden, and from Nilsson & Kholin (1994) in Sakhalin. Information about south

TABLE 1. Means and ranges of selected environmental variables used to characterize the studied ponds, and the numbers of samples taken and species recorded per pond in each region.

Variable	N. Sweden		S. Primorye		S. Sakhalin	
	Mean	Range	Mean	Range	Mean	Range
Area, m <sup>2</sup>	85.1	0.6–600	41.5	0.5–240	71.0	1–432
Depth, m	0.41	0.11–1.50	0.47	0.10–1.30	0.3	0.07–1.00
Water temperature	10.8	3.9–20.2	19.7	6.5–31.0	19.4	13.5–26.5
Frequency of drying, %	49.0	20–60	31.9	12–62	50.0	33–67
Shade, %	22.9	10–50	20.7	0–50	4.0	0–20
Moss, % cover	44.3	5–100	1.7	0–20	7.8	0–40
Emergent vegetation, % cover	30.0	0–80	45.3	0–90	42.0	0–90
No. of samples × pond <sup>−1</sup>	13.2	7–24	20.6	6–34	8.0	2–15
No. of species × pond <sup>−1</sup>	11.6	7–22	9.4	1–17	6.1	3–12

TABLE 2. Size of regional species pool of Dytiscidae calculated for different geographical levels in the three studied regions. Separate values are given for total number of species and for lentic species only.

Territory	Area (km <sup>2</sup> )	Number of species	
		Total	Lentic
<b>Sweden</b>	449,750	149	131
N. Sweden	272,506	125	111
Västerbotten & Norrbotten Districts	41,753	104	92
Studied ponds		39	39
<b>Primorye</b>	168,000	63	54
S. Primorye	72,000	56	52
Vladivostok District	700	32	32
Studied ponds		28	28
<b>Sakhalin</b>	76,400	36	31
S. Sakhalin	13,000	34	29
Kholmsk District	2,000	22	18
Studied ponds		17	17

Primorye Dytiscidae was compiled from Lafer (1989) in combination with our own observations and study of museum collections (Nilsson, unpubl.). For each region, the size of the regional species pool was given for selected geographical levels from which faunistic data were available (Table 2). Species lists from all three regions are available from the junior author on request.

### Analyses

Because the number of sampling occasions and subsamples per pond differed between regions, two statistical approaches were used to compare the regional species richness. First rarefaction curves were calculated for each region (expected number of species) from the total number of individuals collected of each species using the program RAREFACT (Krebs, 1989). Secondly, the relationship between the number of sampling occasions (sampling in one pond at one date: north Sweden fifty-one, south Primorye ninety, and south Sakhalin thirty-one occasions) and the number of species were examined with a simulation procedure. In each step of this procedure, a sampling occasion was chosen randomly (without replacement) from the total set of occasions, and all species present on this occasion were recorded. In each following step only species not already present were added to the cumulative list. Ninety-nine cumulative curves were generated for each regional set of samples and then the mean of the expected number of species in each step of the accumulation was calculated. With these methods it is possible to estimate the sampling effort, i.e. did the estimation of regional species richness reach its ceiling?

The predictive powers of different environmental variables with respect to the total number of dytiscid species collected in each pond were analysed using partial least square regression (PLS) (Martens & Naes, 1989). With PLS, a large number of correlated variables are replaced by a smaller number latent variables or components. The

dependent variable (the number of species) is then regressed upon these new components. The significance of each component is tested by least-square fit using cross-validation. In this analysis arcsine-transformation was used for proportional variables, and all other variables were log-transformed in order to increase the normality of the variables and the linearity of the relationships among them (Zar, 1984). PLS was also used to obtain residual values of the number of species per pond in the three different regions, providing a way to compare local diversity values after the effects of the local environmental factors had been removed. All studied ponds were included in the same regression model in which the number of species were entered without transformation.

Principal component analysis (PCA) was used to reduce the dimensions of the positively correlated variables pond area, depth and temperature. This analysis was run on the correlation matrix of the log-transformed variables. In the ANCOVA analyses, homogeneity of variances were tested with Levene's test and log-transformation applied when the latter test result was significant. The Newman-Keuls test was used for *post-hoc* tests.

In a perfectly nested series, the species present in a given fauna are also present in all larger faunas. Species absent from a given fauna are absent from all smaller fauna. Deviations from perfect nestedness were estimated with the nestedness index ( $N'$ ), calculated with the method described by Patterson & Atmar (1986): (1) for each species, the smallest fauna in which it occurs is located, (2) all larger faunas lacking this species are tallied, and (3) tallies are summed for all species. The departure of observed nestedness from randomness was assessed using the program RANDOM1 with 1000 randomizations and a probability distribution weighted by the actual range occurrences of species (Patterson & Atmar, 1986).

To investigate how pond area may have affected the distribution of individual species, we analysed distribution patterns by the occurrence-sequence method (Schoener & Schoener, 1983). For each region, we ranked ponds along sequences of increasing area and analysed patterns of occurrence of species along the sequences for ordered or haphazard distributions via Mann-Whitney  $U$ -tests.

Beta-diversity or between-habitat diversity was calculated with the method described by Wilson & Shmida (1984). The numbers of species gained and lost along the pond-size gradient of each region were summed and divided by the doubled mean number of species per pond.

### RESULTS

When the faunas of the three studied regions were compared, the total numbers of species of Dytiscidae were lowest in south Sakhalin and highest in north Sweden (Table 2). The proportions were similar when the species richness of parts of these regions were compared, as well as when the number of species collected in the studied ponds were compared (Table 2). The exclusion of lotic species did not change this pattern. The mean number of species recorded per pond was highest in north Sweden and lowest in south Sakhalin (Table 1).

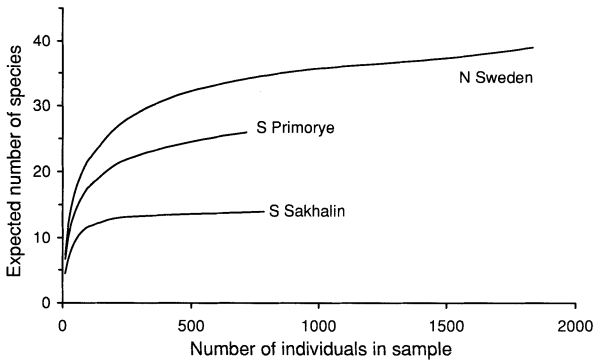


FIG. 2. Rarefaction curves showing the expected number of dytiscid species as a function of sample size in the three studied regions.

The differences in species richness between regions recurred when rarefaction was applied to the total numbers of individuals collected in the studied ponds in each region (Fig. 2). The alternative method to produce rarefaction curves based on the presence or absence of species on separate sampling occasions produced a similar pattern (Fig. 3). In both methods, the curves reached a plateau, indicating that more sampling would increase the species richness very slowly or not at all. This is supported by the fact that the second year of sampling in south Primorye and south Sakhalin did not add more than one or no species to those found already in the first year.

In each region, the predictive power of selected environmental variables for local species richness of temporary pond Dytiscidae were studied with PLS regressions (Fig. 4). Variables with strong positive correlations with species richness were pond area, depth, temperature and cover of emergent vegetation (Table 1). Whereas the correlations with moss cover varied between regions, the correlations with the degree of shade and the drought frequency were negative in all regions. The first significant PLS component explained 72.9 % of the total variance in species richness in the north Swedish ponds, whereas the corresponding values for south Sakhalin and south Primorye were 70.5 and 72.0%, respectively. In addition to the development of the moss cover, these results showed that local species richness was affected by the studied

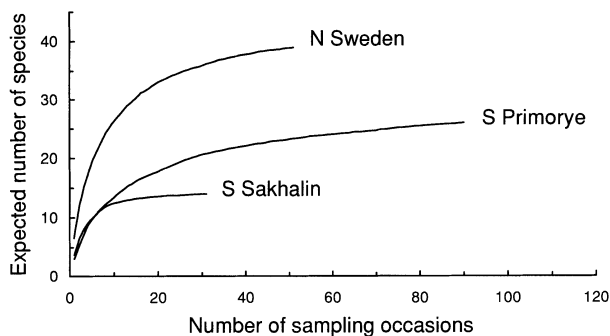


FIG. 3. Relationship between the number of sampling occasions and the simulated accumulated number of dytiscid species in the three studied regions.

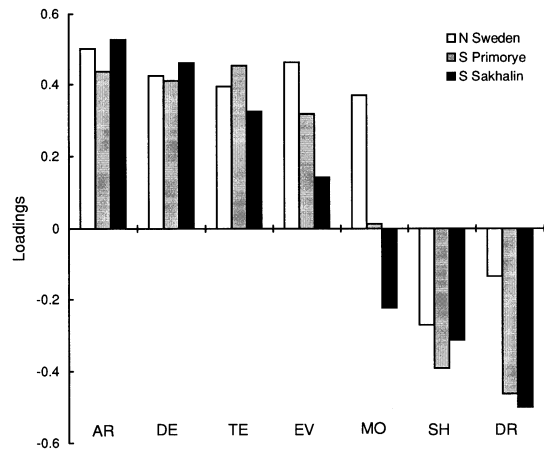


FIG. 4. Loadings of seven variables on the first component of PLS analysis with the number of dytiscid species as dependent variable in comparison between the three studied regions. Variables coded as: (AR) pond area, (DE) pond depth, (TE) water temperature, (EV) emergent vegetation cover, (MO) moss cover, (SH) degree of shade and (DR) drought frequency.

environmental variables in the same way in the three regions. Excluding moss cover, untransformed values of local species richness were used in a PLS regression including all forty-four ponds and the six remaining environmental variables. This model produced a first significant component that explained 42.1% of the total variance in species richness. The mean values of the residuals of the number of species per pond showed an increase with the regional species richness of each region (Fig. 5), supporting the regional enrichment view. There was a significant effect of region on the residuals (Kruskal–Wallis,  $H_{2,44} = 17.97, P < 0.001$ ).

Since local species richness was strongly and positively correlated with a combination of increasing pond area, depth and temperature, PCA was used to find a single vector for the regression of local species richness. The first

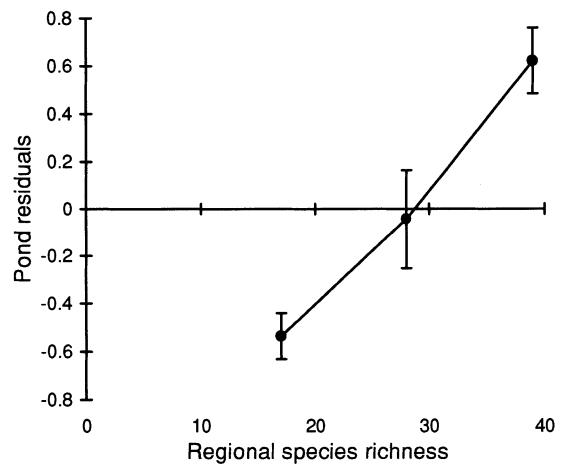


FIG. 5. Relation between regional species richness and mean residuals of the number of species per pond from a PLS regression including all forty-four studied ponds and the following environmental variables: pond area, pond depth, water temperature, emergent vegetation cover, degree of shade and drought frequency.

TABLE 3. Loadings from PC analysis of three abiotic variables in temporary ponds in the three studied regions. All variables log-transformed.

Variable	Region		
	N. Sweden	S. Primorye	S. Sakhalin
Area	0.647	0.658	0.583
Depth	0.574	0.636	0.614
Temperature	0.502	0.403	0.532
Variance explained %	68.6	64.0	78.9

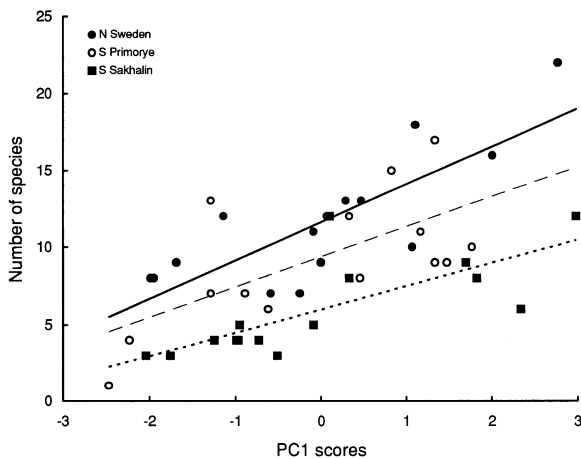


FIG. 6. Relation in each studied region between pond scores of first PCA component (from analysis of pond area, depth and temperature) and the recorded number of species.

principal component (PC1) from an analysis of pond area, depth and temperature had strong positive loadings for all three variables in all three regions (Table 3).

Local pond species richness was positively correlated with the scores of PC1 (Fig. 6;  $r=0.798$  for north Sweden, 0.649 for south Primorye, and 0.746 for south Sakhalin;  $P<0.01$ ). When plotted in the same diagram, the regression lines for the three regions displayed the same orders as the differences in the regional species richness with north Sweden highest and south Sakhalin lowest (Fig. 6). The significances of these differences were studied with one-way ANCOVA, using the scores from PC1 as covariate. There was a strong positive effect of region (Table 4), and the *post-hoc* tests showed significant differences between all regions ( $P<0.05$ ).

TABLE 4. ANCOVA model for the effect of region on the number of dytiscid species in temporary ponds in N. Sweden, S. Primorye and S. Sakhalin. Scores from PC1 of pool area, depth and temperature were used as covariate.

Source	MS	d.f.	F	p
Region	117.396	2	15.251	<0.001
PC1 scores	326.918	1	42.471	<0.001
Error	7.697	40		

TABLE 5. Result of occurrence–sequence test relating the distribution of individual species to the pond area gradient in each region. Significance level of Z was  $P<0.05$ .

No. of species	N. Sweden	S. Primorye	S. Sakhalin
Recorded from 2 or more ponds	28	20	14
Significantly positive Z values	10	3	4
Significantly negative Z values	5	0	0
Total	39	28	17

In other words, ponds with the same combination of area, depth and temperature, were inhabited by more species in north Sweden than in the two other regions, and by more species in south Primorye than in south Sakhalin ponds.

Significant nested patterns in species distributions among ponds were found in north Sweden and south Sakhalin ( $N=139$  and 56, respectively,  $P<0.001$ ), whereas the south Primorye pattern was not significantly different from random ( $N=116$ ).

The results of the occurrence–sequence analysis with respect to pond area showed that most species in south Primorye and south Sakhalin were not sorted along this gradient (Table 5). In the north Swedish ponds, a substantial number of species had distributions which were positively or negatively affected by pond area.

The beta diversity along the gradient of increasing pond size was highest in south Primorye (2.45), lowest in south Sakhalin (1.48) and intermediate in north Sweden (2.28).

## DISCUSSION

That north Sweden had a higher regional diversity of water beetles than south Primorye was unexpected for two reasons. First, more recently glaciated areas are generally believed to have depauperate biotas (e.g. Brown & Gibson, 1983), for example the lower diversity of temperate tree species in Europe than in East Asia (Latham & Ricklefs, 1993). Secondly, the results contradict the general trend of decreasing diversity with increasing latitude in the northern hemisphere (e.g. Brown & Gibson, 1983; Cushman, Lawton & Manly, 1993). In spite of the fact that the Scandinavian climate is much warmer than in areas of corresponding latitude in the Far East, our comparison included boreal conditions in Sweden with hemiboreal or temperate conditions in the Far East. In Sweden, the temperate dytiscid fauna is more diverse than the boreal one, and least-square fittings of the species richness of grid squares as a function of longitudinal and latitudinal grid positions display a decreasing diversity from south to north (Nilsson & Persson, 1989; Nilsson, unpubl.). If a similar pattern exists in the Far East, it further stresses the exceptionality of these results.

Explanations for the lower than expected regional diversity of south Primorye Dytiscidae pertain either to ecological or historical settings. The frequency of suitable

pond habitats in the landscape represents a potential ecological explanation with historical causes. Based on experience, the frequency of temporary ponds is markedly lower in south Primorye than in north Sweden. A large part of south Primorye is mountainous, where ponds are normally rare on mountain slopes. Instead, ponds are accumulated in river valleys and are often of a more permanent character including vertebrate predators like fish. In Scandinavia, the recent glaciations have probably increased the frequency of the temporary pond habitat due to effects of ice-movements on local topography. Moreover, the normally thick snow-cover of north Sweden provides a reliable source of water to fill all morainic depressions in the spring. In the Vladivostok region, most precipitation falls as rain in August and September, chiefly during taifoons, whereas little or no snow accumulates in winter (Shver, 1978). This seasonal occurrence of water may result in difficulties for the boreal temporary pond fauna, which seems to have life histories adapted to wet springs and early summers, when the larval development is passed (Nilsson, 1986b).

This habitat density hypothesis gains support from a comparison with running water insects. The available data suggest a markedly higher diversity of this fauna in south Primorye than in north Sweden (Levanidova, 1982), at least in the orders Ephemeroptera, Plecoptera and Trichoptera. Based on field experience and map studies, stream habitats are more abundant in south Primorye than in north Sweden. A reversed latitudinal gradient in species richness has been documented among Fennoscandian wader birds (Järvinen & Väisänen, 1978), and attributed to the increased availability of different habitats in the north.

A possible historical explanation is connected with recent climatic change. In the absence of glaciations, south Primorye has experienced other strong and more recent climatic disturbances, as reflected by vegetational history (Frenzel, 1968; Krasnov, 1988). During the Holocene the climatic fluctuations have been considerable with fast changes from warm to cold periods (Golubeva & Karaulova, 1983; Elias, 1994). Furthermore, modern spore-pollen data suggest that lowland forest was more or less absent from south Primorye some 800–1200 years ago, indicating drier conditions (Verkhovskaya, 1990).

Both south Primorye and south Sakhalin belong to the Manchurian (Ussurian/Japanese) fauna subregion, which is characterized by its high proportion of endemic and relict species (Kurentzov, 1965). Freshwater biogeographers tend to include this subregion in the Sino-Indian Region (e.g. Banarescu, 1991), whereas divisions based on the terrestrial fauna assign it to the Palearctic (e.g. Lattin, 1967). This situation indicates that biogeographically, the Far East study areas belong to a transitional zone, however, without the expected enrichment of the studied part of the fauna due to mixing of biotas.

The different sizes of the regional species pools of the three studied regions were positively related to the area of the regions (Table 2) since the smallest area, south Sakhalin had the fewest species, and vice versa. Comparing areas of more similar sizes, the differences remain significant when only the Västerbotten plus Norrbotten Districts are

compared with south Primorye and south Sakhalin, or if the Vladivostok District is compared with all of Sakhalin (Table 2). Moreover, the rarefaction curves (Figs 1–2) also showed the same direction of differences in regional diversity, independent of sample size.

Because the north Swedish ponds were more widely distributed (max distance *ca.* 300 km) than in the two other regions, their higher total number of species (Table 2) could be an effect of a higher beta diversity. This was apparently not the case, however, as only one of the species collected in the north Swedish ponds is known only from one of the two studied districts, i.e. *Laccornis oblongus* (Stephens) in Norrbotten. The five additional species collected in Norrbotten but not in Västerbotten ponds reflect chiefly the different size distributions of ponds in the two districts (smaller in Norrbotten). Calculated values of beta diversity show that north Sweden was intermediate. Moreover, as values were highest for south Primorye, they showed a negative relation with the investigated area of each region.

Nilsson & Svensson (1995) found strong nested patterns of temporary pond Dytiscidae, and suggested that species may have different minimum thresholds for pond size with reference to colonization. The present datasets showed significantly nested patterns in north Sweden and south Sakhalin, but not in south Primorye. The lack of nestedness in one of the regions may reflect the larger size gradient as some species confined to smaller and colder ponds were absent from larger ponds. However, as many species occurred only in larger ponds, the size of the regional species pool (if more narrowly defined) appears to increase with pond size. This view is only partly supported by the result of the occurrence–sequence test which showed that species were only sorted along the pond area gradient in north Sweden (Table 5).

South Primorye or Ussuriland is generally viewed as having a rich fauna characterized by its mixture of Chinese and Siberian elements (e.g. Kurentzov, 1965; Knystautas, 1987). The few available studies comparing species richness between Europe and the Far East are contradictory. Whereas papilionoid butterflies are about twice as diverse in Primorye than in north Fennoscandia (Kostrowicki, 1969), aquatic and semiaquatic bugs (Jaczewski & Kostrowicki, 1968) conform with the water-beetle results. As these examples are too few to support any general conclusions one can only note that different insect taxa show different diversity gradients and that more interregional studies are needed.

The observed differences in temporary pond dytiscid species richness were best explained by a combination of local and regional factors. The effects of the local factors were the same in all studied regions, namely positive of pond area, depth and temperature, and negative of increasing shade and drought frequency. The species richness of ponds of a given combination of local factors but situated in different regions depended on the size of the regional species pool. This supports the theory of regional enrichment, and suggests that explanations of local diversity differences are best sought at the regional level. Regional diversity in turn depends mainly on the history of the region in terms of habitat density, disturbance and isolation, in

combination with the history and properties of the group of organisms studied.

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