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Seasonal and spatial patters in macro-invertebrate assemblage in a heterogeneous landscape

Wilco C.E.P. Verberk[1], Ankie M.T. Brock[1], Gert-Jan A. van Duinen[1], Miranda van Es[1], Jan T. Kuper[1], Theo M.J. Peeters[1], Michel J.A. Smits[1], Liesbet Timan[1] & Hans Esselink[1,2]

[1]Bargerveen Foundation, Department of Environmental Studies, and [2]Animal Ecology and Ecophysiology, University of Nijmegen, POBox 9010, 6500 GL Nijmegen, The Netherlands (wilcov@sci.kun.nl)

There are several possible mechanisms behind the relationship between environmental heterogeneity and species diversity. Species occurrence can be linked to factors operating on different scales. Especially animal species use their surroundings on a broad range in scale levels. We therefore hypothesise that heterogeneity is an especially important factor for animal diversity. To investigate how, and at what scale level, heterogeneity could function, data on aquatic macro-invertebrates were collected in Korenburgerveen, a heterogeneous landscape. Results show seasonal differences which could be linked to decomposition processes winter mortality and population dynamics resulting from differences in lifecycles and dispersion. Results further indicate that the investigated groups of aquatic macro-invertebrates are able to use the landscape on the scale level of the ecological units (~2000 m^2). This provides an important clue that habitat heterogeneity could be important on this scale level. Based on these findings only general recommendations for restoration management can be made which amount to being careful: small scale measures, phased in time and space with a monitoring program to assess starting conditions, flora and fauna assemblage and to observe the changes in biotic and abiotic conditions.

Keywords: aquatic macro-invertebrates, heterogeneity, scale, restoration, assemblage, species diversity

It is well established that in general a high environmental heterogeneity leads to a high species diversity. This relation is described in a number of studies concerning birds (*e.g.* Cody 1968; MacArthur & MacArthur 1961), diatoms (*e.g.* Patrick 1963), and also for aquatic macro-invertebrates (*e.g.* Harper *et al.* 1997; Heino 2000; Ranta 1985). Heterogeneity can be defined in several ways. In this paper heterogeneity is defined in relation to the organisms: the variation in biotopes (used for foraging, reproduction and hibernating) which together constitute the habitat of the species. Species diversity is important for the functioning and resilience of the system (Aarts & Nienhuis 1999). When considering restoration of heterogeneous landscapes, knowledge of the mechanisms behind the relationship between environmental heterogeneity and species diversity is necessary to answer the question how restoration affects fauna species composition and diversity.

The following mechanisms may explain the relation between heterogeneity and species diversity. 1) Additional heterogeneity can imply an additional habitat type, allowing species dependent on this particular habitat type to occur. 2) Additional heterogeneity can also imply a certain arrangement of the different biotopes allowing species which depend on a combination of two or more biotopes to occur (*e.g.* during different life-stages). 3) A heterogeneous landscape could also contain more species when heterogeneity decreases the extinction rate. A lower extinction rate can result in an equilibrium state with a higher diversity (MacArthur 1972). This can arise in two ways. 3a) A heterogeneous spatial arrangement of suitable habitat patches can spread extinction risks for species living in metapopulations (species go extinct only in one habitat patch, which can later be recolonised from other patches). 3b) The presence of different habitat types in a heterogeneous landscape implies that an unpredictable disturbance will not have the same effect on all different habitat types. Therefore species occurring in different habitat types will survive when only a subset of the habitats become (temporarily) inhospitable.

Species occurrence can be linked to factors on different scales (*e.g.* Arscott *et al.* 2000; Li *et al.* 2001) and both temporal and spatial scale components are important (Huston 1994; Magurran, 1998; Lawton 1999; Southwood 1977). The correct (*i.e.* relevant for the organism under study) scale determines for example whether more environmental variation should be seen as more heterogeneity or more fragmentation. The mechanisms described above thus hold for a range of scale levels when applied to different species. In addition, at a small spatial scale level, species in a structurally heterogeneous environment can further partition their resource (*e.g.* specialisation on a spatial structure). Consequently the niche breadth decreases and more species are able to coexist (MacArthur 1972). At larger spatial and temporal scales, differences in regional species pools and regional species filters (Lawton 1999) operate on species diversity. Examples are (historical) dispersion barriers, climatological differences, glaciation and extinction events (Kolasa *et al.*, 1998) and speciation possibilities.

It is not clear how heterogeneity in a given landscape results in a high species diversity. A higher mobility (Huston 1994), size (Ritchie & Olff 1999) or vision (Magurran 1988) can also influence the effective environment heterogeneity and can lead to stronger species interactions (predators, competitors). As animals differ very much in mobility and size, it is clear that there are large differences between animal species, but also that animal species use the landscape fundamentally different from plant species. Animal species can use the landscape on different scales. Therefore, animal species can be related to heterogeneity by mechanism 1, 2 and 3, whereas plant species can be related to heterogeneity by mechanism 1 and only to a much lesser extent by mechanism 2 and 3. Therefore, we hypothesise that environmental heterogeneity is an especially important factor for animal species diversity, as they are capable of exploiting the heterogeneity of the landscape at a range of scales.

To investigate how, and at what scale level, heterogeneity could function for animal species, a case study is currently being executed in Korenburgerveen. The area has a high variation in water types and earlier studies have shown a high diversity of water beetles (Verberk *et al.* 2001) and other animal species (Biologische Station Zwillbrock 1995). Restoration measures are planned and partly executed. As the restoration measures are hydrological in nature, affecting water quality and water quantity, the aquatic macro-invertebrates were chosen as a study group.

It is yet unknown at what scale macro-invertebrates use the landscape and thus it is hard to give a relevant measure of habitat heterogeneity. Therefore we started the other way round by first trying to link patterns in diversity and community structure to a certain scale level. This provides insight at which scale levels heterogeneity can be important for species diversity. This article focuses on seasonal differences in macro-invertebrate diversity (temporal scale) and macro-invertebrate species assemblage structure at different spatial scales. The investigated spatial scales were 1) local vegetation composition (scale level ~ 50 m^2) and 2) different landscape elements (scale level ~2000 m^2).

MATERIAL AND METHODS

Study area and data collection

Korenburgerveen is an area with a high variation in abiotic conditions, giving rise to different vegetation types. In 1999 and 2000, 35 locations were sampled, with 20 locations sampled both in spring (sample dates ranging from 1 March to 22 May) and autumn (sample dates ranging from 18 September to 29 November). Sample locations were chosen to represent many different water types as determined visually in the field. For each sampling site physical and chemical properties of the water-body and local vegetation composition were measured and described. Samples were collected using a standard pond net of 30 x 20 cm with a mesh size of 0.5 mm. Sample length ranged from 2.5 m to 0.16 m, because in dense *Sphagnum cuspidatum* vegetation large samples were not possible. At each location subsamples were taken to include the different distinghuisable (micro)habitats. In further analysis subsamples are pooled. Verberk *et al.* (2001) gives an extensive description of the research area, sample locations and a list of physical and chemical properties.

Samples were washed and sorted in the laboratory. macro-invertebrates were stored in 70% ethanol, Koenike (Hydrachnella), formaline (Oligochaeta) or identified alive (Tricladia). Numerical counts were made for the different macro-invertebrate groups. Of the collected macro-invertebrates, Araneae, Crustacea, Cylindrotomidae, Tricladia, Odonata larvae, adult Coleoptera, adult Trichoptera and both adult and nymphs of Hemiptera were identified to species level, using Ball & Reynoldson (1981) (Tricladia), Heidemann & Seidenbrusch (1993), Norling & Sahlén (1997), Gerken & Sternberg (1999) (Odonata), Drost *et al.* (1992), Nilsson & Holmen (1995), Angus (1992), van Vondel (1997) (Coleoptera), Wallace *et al.* (1990), Edington & Hildrew (1981),

Table 1. Criteria for the division of species in five groups according to their frequency of occurrence in spring and autumn.

Species group	Criteria
Strict spring (ss-group)	spring frequency ≥ 2 AND autumn frequency = 0
Spring preference (sp-group)	spring frequency ≥ $^3/_2$ * autumn frequency
No preference (np-group)	$^2/_3$ < spring frequency/autumn frequency < $^3/_2$
Autumn preference (ap-group)	autumn frequency ≥ $^3/_2$ * spring frequency
Strict autumn (sa-group)	autumn frequency ≥ 2 AND spring frequency = 0

Higler (unpublished) (Trichoptera), Nieser (1982), Savage (1989), Savage (1999), Andersen (1996) and Jansson (1996) (Hemiptera). Taxonomic groups (*e.g.* Ephemeroptera, Oligochaeta, Diptera) which were not (yet) identified were excluded from further analysis.

Data analysis

For each location, taxa abundance is expressed as densities to compare the different samples. For comparison of diversity the Shannon index, evenness, the rarefactioned numbers, the Alpha diversity index and the Berger Parker index was calculated (for calculation and discussion of their use see Magurran 1988). Only the Alpha diversity index and the Berger Parker index are shown as they are most sensitive for species numbers and evenness respectively. The Alpha diversity index showed highest correlation with rarefaction results ($R^2=0.851$; $P<0.001$) and is a robust measure of diversity, even when the log-fit is not perfect (Taylor *et al.* 1976)

The criteria used for the division of species in five groups according to their occurrence in spring and autumn are listed in Table 1. For comparisons of different species groups between spring and autumn Hemiptera nymphs and adults were kept separate considering their lifecycle.

Differences in macro-invertebrate assemblage structure were analysed using ordination methods. Sample locations with a similar macro-invertebrate assemblage are plotted close together in an ordination plot. Next, two classifications of sample locations were overlain on this plot to ascertain if there was a relation between these classifications and the macro-invertebrate assemblage structure. Sample locations were classified according to 1) their local vegetation composition as described in the field during sampling and 2) according to their geographical position which was linked to different ecological units. Classification based on local vegetation composition was performed by calculating Jaccard coefficients and using the group average linkage algorithm. This shows a good compromise between clear-cut groups, which are much desired, and the gradual change which approaches reality (Jongman *et al.* 1995). The classification in ecological units was taken from Biologische Station Zwillbrock (1995) and is shown in Fig. 1. Units were distinguished not only on the basis of the vegetation structure, but also by their acidity, nutrient levels, water levels and substrate (this division was made without any prior knowledge of the macro-invertebrate species distribution). It is important to note that although the different units are shown as uniform polygons, they contain much internal variation in vegetation composition, but also in waterbody surface and depth or vegetation structure.

A Principal Component Analysis (PCA) was performed with Canoco for Windows (Ter Braak & Smilauer, 1998) using only species data collected during spring. This was done because using only locations sampled in both periods would reduce the number of sample locations. Furthermore locations contained most species in spring (table 1) so using only spring data would not lead to a large reduction in species numbers. A PCA was chosen because a prior Detrended Correspondence Analysis (DCA) showed that data conformed to a linear response model. In addition a unconstrained analysis was chosen because an unbiased ordination plot was desired in order to relate it to the different classifications.

RESULTS

Seasonal differences

In total 10358 individuals belonging to at least 125 taxa were captured (Table 2). The 125 taxa belong to Coleoptera (67 spp.), Hemiptera (20 spp.), Trichoptera (17 spp.), Odonata (14 spp.), Tricladia (4 spp.) Crustacea (*Asellus aquaticus*), Aranea (*Argyroneta aquatica*), Cylindrotomidae (*Phalacrocera replicata*). The Alpha diversity index differed between spring, autumn and the locations for which both data periods were pooled ($P \leq 0.029$). The evenness did not differ as indicated by the Berger-Parker index for dominance ($P \geq 0.186$). Thus waterbodies have a higher species richness in spring.

When species are grouped according to their seasonal preference there are differences in species number, frequency and density between these species groups (Table 3). The higher species

Table 2. Number of locations, taxa, Alpha diversity index, Berger Parker index for samples in spring and autumn separate, spring and autumn added up (total) and for locations sampled both in spring and autumn (pooled). nc: not calculated (being the average of the indices of spring and autumn)

	number of sample locations	number of taxa	Alpha diversity index	Berger Parker index
spring	33	107	2.69	0.52
autumn	22	67	1.76	0.60
total	55	125	nc	nc
pooled	20	109	3.41	0.51

Table 3. The number of species, frequency and density in autumn and spring for each species group

		Frequency[1]		Density[2]	
	number of species	spring	autumn	spring	autumn
Strict spring (ss-group)	32 (5)[3]	12.5	0.0	59.8	0.0
Spring preference (sp-group)	40 (1)	7.9	1.6	59.9	8.3
No preference (np-group)	22	24.5	22.5	522.6	751.7
Autumn preference (ap-group)	34	4.5	12.6	33.2	190.0
Strict autumn (sa-group)	3	0.0	10.6	0.0	4.4

[1] calculated as the number of occurrences per 100 samples, averaged for all species in a species group.
[2] calculated as the number of individuals per 5 m of sample length, averaged for all species in a species group.
[3] Numbers between brackets are the number of Hemiptera nymphs.

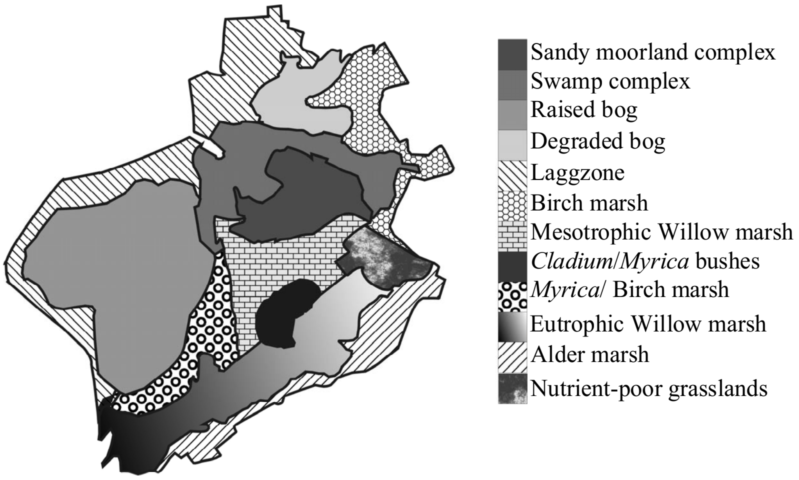

Figure 1. Classification of the Korenburgerveen in ecological units (based on Biologische Station Zwillbrock 1995). Units were classified according to their vegetation, acidity, nutrient levels, water levels and substrate.

richness in spring is mainly caused by the large difference in species numbers between the ss-group (32) and the sa-group (3; *Dugesia polychroa*, *Graptodytes pictus*, *Limnephilus elegans*). The ss-group contained mainly Hydrophilidae, Hydrochidae, *Limnephilus* spp, and Hemiptera adults and nymphs.

Frequency is slightly higher in spring for the np-group (24.5 vs. 22.5). Compared to the sa-group, frequency is also slightly higher in spring for the ss-group (12.5 vs. 10.6). Furthermore, for the sp- and ap-group the relative frequency is also higher in spring (7.9/1.6) compared to autumn (12.6/4.5). Thus species occur in higher frequency in spring.

Highest densities are found in the no-preference group and in the preference for autumn species group. Species which contribute numerically most to density belong to different taxonomic groups (Table 4). Especially *Asellus aquaticus*, *Hesperocorixa sahlbergi* and Odonata larvae contribute to higher numbers in autumn, while beetles (predominantly *Hydroporus* spp.) and *Trichostegia minor* contribute to higher numbers in spring.

Table 4. Species with highest contribution to density differences between spring and autumn. The percentage contribution incorporates relative abundance and relative frequency and is weighted for the total abundance

Species contributing to higher numbers in autumn			
no-preference group		**preference for autumn group**	
name	% contribution	name	% contribution
Asellus aquaticus	72.2	*Ceriagrion tenellum*	41.4
Coenagrion puella/pulchellum	10.1	*Hesperocorixa sahlbergi*	14.5
Leucorrhinia sp.	7.6	*Pyrrhosoma nymphula*	10.2
Argyroneta aquatica	4.4	*Polycelis* sp.	7.0
Hydroporus erythrocephalus	1.6	*Holocentropus stagnalis*	5.1
Triaenodes sp.	1.6	*Plea minutissima*	3.1
Species contributing to higher numbers in spring			
no-preference group			
name	% contribution		
Hydroporus obscurus	51.5		
Hydroporus tristis	28.9		
Hydroporus umbrosus	12.7		
Noterus crassicornis	5.3		
Trichostegia minor	0.7		
Porhydrus lineatus	0.5		

Macro-invertebrate assemblage at different spatial scales

There were large differences between the classification based on local vegetation composition and the classification in ecological units when they were related to the macro-invertebrate assemblage structure in spring (Figs. 2 and 3; Note that the same ordination plot is used in both figures). The polygons of the vegetation groups showed high overlap when plotted on the macro-invertebrate ordination plot (Fig. 2). This means that sample points which have a similar vegetation composition do not necessarily have a similar macro-invertebrate assemblage and the other way round. In contrast, sites within an ecological unit showed almost no overlap in macro-invertebrate assemblage (Fig. 3), indicating that the macro-invertebrate assemblage of the different ecological units is also different. Thus the macro-invertebrate assemblage structure seems to be much better correlated with the type of ecological unit than with local vegetation composition.

DISCUSSION

Differences between spring and autumn can be explained for a number of species by their food ecology. In autumn, decomposition processes dominate and there is an increased input of leaf litter in the waterbodies. This increase in detritus can explain the increase of detritus feeders such as *Asellus aquaticus* (Verdonschot 1990), *Hesperocorixa sahlbergi* (Moller Pillot 1961; Verdonschot 1990) and *Triaenodes* sp (Verdonschot 1990). The detritus feeders can be preyed upon and in turn lead to an increase of predator numbers. For example *Polycelis* sp. which feeds on Oligochaeta and insect larvae (Cuppen 1980), occurred in higher densities in autumn, when also Chironomid larvae reached high densities (data not shown). Differences in lifecycle can also explain part of the observed differences between spring and autumn. Eggs and small stages are more easily missed. The Odonata species which contribute to higher numbers in autumn emerge from May to August. During the adult flight period the eggs are deposited and hatch before autumn. High numbers of juvenile larvae are then found. Due to winter mortality and predation, larval densities are lower in spring. In addition species may hide deep in the substrate such as *Noterus crassicornis* for overwintering, leading to lower catches in (late) autumn. Species which overwinter as adults, such as *H. sahlbergi* and *P. minutissima* (Nieser 1982), may be more susceptible to winter mortality. In contrast, *Trichostegia minor*, contributing to higher numbers in spring, can also overwinter in the egg stage for which it is well adapted (Van der Hoek & Cuppen 1989). *Hydroporus* spp and *Noterus crassicornis* are classified as early spring fauna by Galewski (1971).

In addition to food ecology and lifecycle, during spring most species start the population buildup. For example, Hydrophilidae attach their egg cocoons to plants in springtime (Drost *et al.* 1992). In spring eggs hatch or adult individuals disperse from the wintering habitats to the breeding habitats (Galewski 1971). This dispersion is in agreement with the higher frequencies observed in spring. This can be of special importance for mobile species such as Coleoptera, Hemiptera and Odonata (Van der Hammen 1992), which comprise the bulk of the species under investigation here. In conclusion, the general picture emerging is that the differences in density between spring and autumn can be linked to decomposition processes, winter mortality, lifecycle and dispersion.

How can the differences between the classification based on local vegetation composition and based on ecological units be explained? The vegetation composition at the site reflects the local set of conditions. Part of the variation in fauna assemblage could be related to the local vegetation composition (data not shown) and this was also discussed for Coleoptera (Verberk *et al.* 2001). However, Fig. 2 shows that the local vegetation composition is not very explanatory of the macro-invertebrate assemblage structure. In contrast, ecological units seem to reflect macro-invertebrate assemblage structure rather well (Fig. 3). Although ecological units differ from each other with respect to their vegetation type, within an ecological unit, vegetation is too variable at the different locations to consistently reflect the macro-invertebrate assemblage structure.

How can we interpret these different patterns at the two spatial scale levels? As the classification in ecological units corresponds rather well with the macro-invertebrate assemblage, there seems to be a factor or a combination of factors operating at the scale level of an ecological unit (scale level ~2000 m^2) which explains these differences. Factors which are likely candidates are bottom- and vegetation structure, bottom- and vegetation type, dimensions of the waterbody and water quality. We will argue that, in addition, the distance between the different waterbodies can be an important factor. The ecological units are not fragmented and the sample sites within a unit are located close together. Furthermore, for the analysis, spring data were used, most of the investigated species have a mobile adult life stage and in spring the species seem to have a tendency to disperse as discussed above. Distance cannot be the only factor involved, because some locations in different units are also very closely situated together. Nevertheless, combined with the other factors which differentiate between the units, distance may be an important factor. By dispersing to adjacent waterbodies in spring, the locations which are located close together, become more similar with respect to the macro-invertebrate assemblage. When this is true, it suggests that the investigated species make use of their surroundings at the spatial scale of an ecological unit (scale level ~2000 m^2).

Returning to the issue of habitat heterogeneity, what clues (in relation to heterogeneity and diversity) can be found in these results? When the macro-invertebrates make use of the landscape at the scale level of an ecological unit, they are able to make use of the variation present within an ecological unit (*e.g.* waterbodies which are large-small, temporary-permanent, densely vegetated-scarcely vegetated). The spatial configuration of the *waterbodies* within an ecological unit may thus be important for macro-invertebrate diversity (mechanisms 2 and 3a mentioned in the introduction) as well as the configuration of different *water types* (mechanism 1, 2 and 3b mentioned in the introduction).

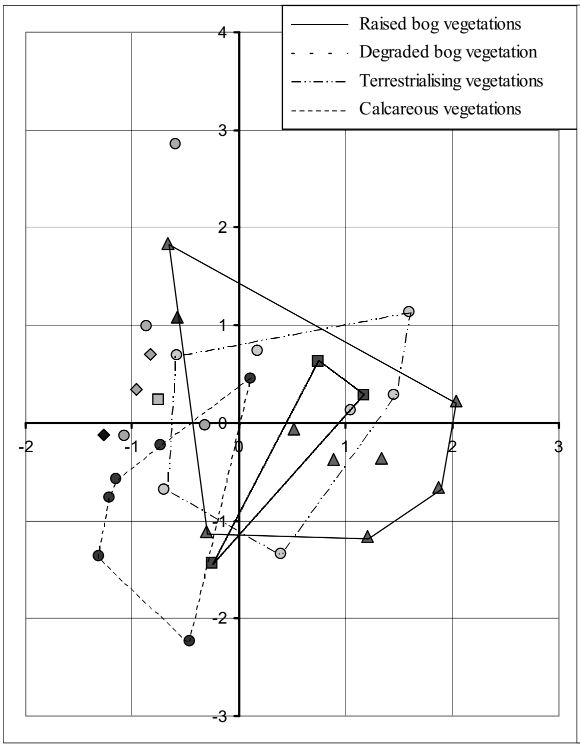

Figure 2. Ordination plot (PCA) based on faunal assemblage. Samples belonging to the same vegetation group have identical symbols. Classification based on local vegetation composition is overlain (polygons). Only the four groups containing most samples are outlined.

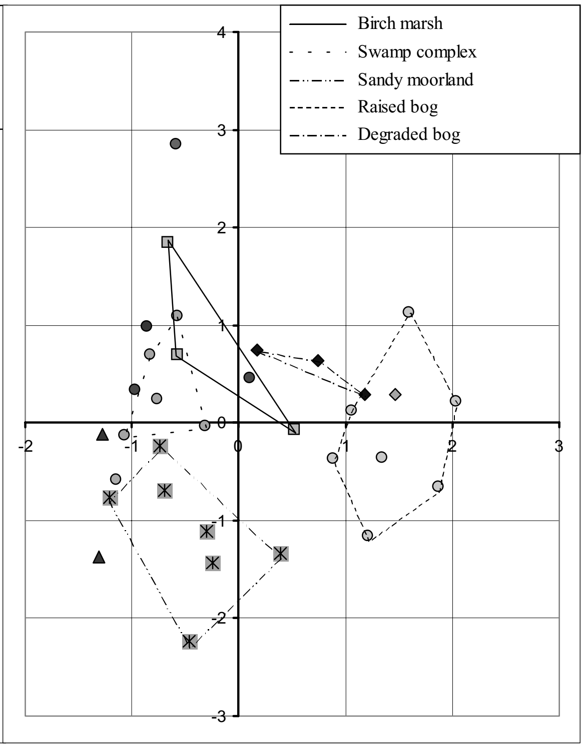

Figure 3. Ordination plot (PCA) based on faunal assemblage. Samples belonging to the same ecological unit have identical symbols. Classification based on ecological units is overlain (polygons). Only the five units containing most samples are outlined.

Considering these clues, for the conservation and restoration of aquatic macro-invertebrates, size and configuration of the different ecological units must be taken into account. Measures must be executed carefully to avoid loss of too many water types or fast shifts in the spatial configuration. The problem is that the words ‘fast’ and ‘too’ cannot be precisely quantified. Which water types harbour important breeding habitats and which waterbodies represent important stepping stones for which species? Until there is more detailed knowledge, the general advise is to phase measures (in space and time) and if possible not to execute large scale measures. Measures should be preceded by a description of the situation at the start (to determine the best course of action) and followed by a thorough monitoring program to ascertain the effects of the measures. This will allow local populations to recover from disturbance by recolonisation and allow species to gradually shift along with the changes as a result of the restoration measures.

Conclusion

In conclusion, the seasonal differences can be linked to decomposition processes leading to changes in the food availability (detritus, detritivores) from which certain species can profit, winter mortality and the natural population dynamics resulting from differences in lifecycles and dispersion in spring.

Relations between the faunal communities on the one hand and vegetation composition and ecological units on the other indicate that the investigated groups of aquatic macro-invertebrates are able to use the landscape on the scale of the ecological units. This provides an important clue that the spatial arrangements of water types within an ecological unit can be important. In more general terms this means that habitat heterogeneity could be important on this scale level.

No precise information is available on the exact dimensions of units and ranges of dispersion to allow for precise recommendations for restoration management. Only general recommendations can therefore be made which amount to being careful: small scale measures, phased in time and space with a monitoring program to assess starting conditions, flora and fauna assemblage and to observe the changes in biotic and abiotic conditions.

Further research

The results raise some interesting new directions for future research. The observed patterns are mostly based on the mobile species. It would be interesting to make a clear distinction between mobile and less mobile taxa and see in what respect the patterns differ from each other. Also it has been discussed that in spring, species have a tendency to disperse. It would be interesting to compare the spatial patterns in macro-invertebrate assemblage structure between spring data and autumn data. The present data do not indicate how species make use of the variation within an ecological unit. Future research could focus on a selection of units and examine these and their interaction in more detail. These and other questions we hope to answer in future research in order to gain a more complete understanding of the role of heterogeneity in relation to species diversity.

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REFERENCES

Aarts, B.G.W & P.H. Nienhuis, 1999. Ecological sustainability and biodiversity. Intern. J. Sust. Dev. World Ecol. 1-29.

Andersen, N.M., 1996. Heteroptera Gerromorpha, semiaquatic bugs. pp. 77-90. In: Nilsson, A. (ed.) Aquatic Insects of North Europe. A Taxonomic Handbook. Vol. 1. Apollo Books, Stenstrup.

Angus, R., 1992. Insecta: Coleoptera: Hydrophilidae: Helophorinae. Süβwasserfauna von Mitteleuropa-Gustav Fischer Verlag.

Arscott, D.B., K. Tockner & J.V. Ward, 2000. Aquatic habitat diversity along the corridor of an Alpine floodplain river. Archiv für Hydrobiol. 149(4): 679-704.

Biologische Station Zwillbrock, 1995. Beheersvisie Korenburgerveen. Eigen uitgave Station Zwillbrock, Vreden.

Cody, M.L., 1968. On the methods of resource division in grassland bird communities. Am. Nat. 102: 107-147.

Cuppen, H.P.J.J., 1980. De Macrofauna in een aantal droogvallende- en permanente stilstaande wateren in het ruil-verkavelingsgebied Brummen-Voorst. Regionale milieu-raad Oost-Veluwe.

Drost, M.B.P., H.P.J.J. Cuppen, E.J. van Nieukerken & M. Schreijer (eds.), 1992. De waterkevers van Nederland. Uitgeverij KNNV, Utrecht.

Edington, J.M. & A.G. Hildrew, 1981. A key to the caseless caddis larvae of the British Isles with notes on their ecology. Freshwater Biological Association. Scientific Publication no. 43.

Galewski, K., 1971. A study on morphobiotic adaptaions of European species of the Dytiscidae (Coleoptera). Polski Pismo entomologiczne 41: 487-702.

Gerken, B. & K. Sternberg, 1999. Die Exuvien Europäischer Libellen (Insecta Odonata). Arnika & Eisvogel. Höxter und Jena.

Harper, D., J. Mekotova, S. Hulme, J. White & J. Hall, 1997. Habitat heterogeneity and aquatic macro-invertebrate diversity in floodplain forests. Global Ecol. Biogeogr. Lett. 6: 275-285

Heidemann, H. & R. Seidenbrusch, 1993. Die Libellenlarven Deutschlands und Frankreichs. Handbuch für Exuviensammler. Verlag Erna Bauer. Keltern.

Heino, J., 2000. Lentic macro-invertebrate assemblage structure along gradients in spatial heterogeneity, habitat size and chemistry. Hydrobiologia 418: 229-242.

Higler, B., Kokerjufferlarven van Nederland (Trichoptera). Voorlopige tabel. (Unpublished).

Huston, M.A., 1994. Biological Diversity – The coexistence of species on changing landscapes. Cambridge University Press, Cambridge.

Jansson, A., 1996. Heteroptera Nepomorpha, aquatic Bugs. p. 91-104. In: Nilsson, A. (ed.). Aquatic Insects of North Europe. A Taxonomic Handbook. Vol. 1. Apollo Books, Stenstrup.

Jongman, R.H.G., C.J.F. ter Braak & O.F.R. van Tongeren, 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge.

Ketelaar, R., in press. Een overzicht van de huidige vliegplaatsen in Nederland van de Speerwaterjuffer *Coenagrion hastulatum*, een karakteristieke soort van weinig aangetaste vennen. Faunistische Mededelingen.

Kolasa, J., Hewitt, C.L. & Drake, J.A., 1998. Rapoport's rule: an explanation or a byporduct of latitudinal gradient in species richness? Biodiv. Conserv. 7: 1447-1455.

Lawton, J.H., 1999. Are there general laws in ecology? Oikos 84: 177-192.

Li, J., A. Herlihy, W. Gerth, P. Kaufmann, S. Gregory, S. Urquhart & D.P. Larsen, 2001. Variability in stream macro-invertebrates at multiple spatial scales. Freshwater Biology 46: 87-97.

MacArthur, R. & J. MacArthur, 1961. On bird species diversity. Ecology 42: 594-598.

MacArthur, R.H., 1972. Geographical Ecology – Patterns in the Distribution of Species. Harper & Row, Publishers, Inc., New York.

Magurran, A.E., 1988. Ecological diversity and its measurement. University Press, Cambridge.

Moller Pillot, H.K.M., 1961. De waterwantsen en andere insekten van het Leersumse veld. De Levende natuur 64: 146-155.

Nieser, N., 1982. De Nederlandse water- en oppervlaktewantsen (Heteroptera: Nepomorpha en Gerromorpha). Wetenschappelijke Mededelingen van de KNNV 155: 1-103.

Nilsson, A.N. & M. Holmen, 1995. The aquatic Adephaga (Coleoptera) of Fennoscandia and Denmark. II. Dytiscidae. Fauna Entomologica Scandinavica, vol. 32.

Norling, U. & G. Sahlén, 1997. Odonata, Dragonflies and Damselflies. pp. 13-65. In: Nilson, A. (ed.). Aquatic insects of North Europe, a taxonomic handbook.Vol. 2. Odonata-Diptera. Apollo Books, Stenstrup.

Patrick, R., 1963. The structure of diatom communities under varying ecological conditions. Ann. NY Acad. Sci. 108: 353-358.

Ranta, E., 1985. Communities of waterbeetles in different kinds of waters in Finland. Proc. Acad. Nat. Sci. Phil. 137: 33-45.

Ritchie, M.E. & H. Olff, 1999. Spatial scaling laws yield a synthetic theory of biodiversity. Nature 400: 557-560.

Savage, A.A., 1989. Adults of the British aquatic Hemiptera Heteroptera: a key with ecological notes. Scientific Publications of the Freshwater Biological Association 50: 1-173.

Savage, A.A., 1999. Keys to the larvae of British Corixidae. Publications of the Freshwater Biological Association 57: 1-56.

Southwood, T.R.E., 1977. Habitat, the templet for ecological strategies? J. Anim. Ecol. 46: 377-365.

Taylor, L.R., R.A. Kempton & I.P. Woiwod, 1976. Diversity statistics and the log-series model. J. Anim. Ecol. 45: 255-272.

Ter Braak, C.J.F. & P. Smilauer, 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (v. 4). Microcomputer power (Ithaca, New York, USA).

Van der Hammen, H., 1992. De macrofauna van het oppervlaktewater van Noord-Holland. Provincie Noord-Holland; Dienst Ruimte & Groen, Haarlem.

Van der Hoek, W.F. & J.G.M. Cuppen, 1989. Life cycle and growth of *Trichostegia minor* (Curtis) in temporary woodland pools (Trichoptera: Phryganeidae). Hydrobiol. Bull. 23(2):161-168.

Van Vondel, B.J., 1997. Insecta: Coleoptera: Haliplidae. Süβwasserfauna von Mitteleuropa. Gustav Fischer Verlag.

Verberk, W.C.E.P., G.A. van Duinen, T.M.J. Peeters & H. Esselink, 2001. Importance of variation in water-types for water beetle fauna (Coleoptera) in Korenburgerveen, a bog remnant in the Netherlands. Proc. Exp. Appl. Entomol. 12: 121-128.

Verdonschot, P.F.M., 1990. Ecologische karakterisering van oppervlaktewateren in Overijssel. Provincie Overijssel, Zwolle; Rijksinstituut voor natuurbeheer, Leersum.

Wallace, I.D., B. Wallace & G.N. Philipson, 1990. A key to the case-bearing caddis larvae of Britain and Ireland. Freshwater Biological Association. Scientific Publication no. 51.

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