Biodiversity of aquatic insects: spatial gradients and environmental correlates of assemblage-level measures at large scales

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Abstract

Biodiversity embraces multiple facets of the variability of nature, although most research has dealt separately with population-, species- and assemblage-level measures. This review concentrates on aquatic insect biodiversity and the assemblage-level measures, such as species richness, assemblage compositional variation, taxonomic distinctness and functional diversity. Most studies on aquatic insects have considered biodiversity patterns based on surveys of local assemblages along geographical and environmental gradients, while there is a virtual lack of studies that have considered regional grain sizes (i.e. the size of the observational unit). Latitudinal gradients at both regional and local grain are ambiguous in aquatic insects, as different studies have found either higher or lower local diversity in the tropics than in the temperate zone. Other geographical patterns in aquatic insect diversity may also be relatively weak, as suggested by subtle among-ecoregion differences in both local species richness and assemblage composition. An ecological explanation for the absence of strong geographical gradients is that local environmental features may not necessarily vary with geography, and these factors may override the influences of historical and climatic influences on local diversity. Evidence from large-scale studies suggests, however, that not only various local habitat and ecosystem variables, but also those measured at the watershed, regional and geographical scales are needed to account for variation in the species richness and assemblage composition of aquatic insects. Within regional species pools, species richness and assemblage composition in both lotic and lentic ecosystems vary most strongly along gradients in habitat size and acidity. Knowing how α-, β- and γ-diversity of aquatic insects vary along geographical and environmental gradients has important implications for the conservation of biodiversity in freshwater ecosystems. Such knowledge is not yet well-developed, and two aspects should be considered in future research. First, further survey research on lotic and lentic ecosystems is necessary for improving our understanding of general biodiversity patterns. Second, given that freshwater ecosystems are facing a severe
biodiversity crisis, the implementation of representative networks of freshwater protected areas would certainly benefit from increased understanding of patterns in aquatic insect biodiversity.

Keywords: Assemblage composition; congruence; environmental gradients; functional biodiversity; higher taxon surrogates; lakes; latitudinal gradient; ponds; rivers; species richness; streams.

Introduction

Biodiversity embraces multiple facets of the variability of nature, ranging from genes to species, and from ecosystems to biomes (Gaston & Spicer, 1998). Most research has traditionally been based on populations, species and assemblages (Angermeier & Schlosser, 1995). This review will concentrate on assemblage-level measures of biodiversity using aquatic insects as a model group. Assemblage-level measures in this context include species richness, assemblage composition, taxonomic variability and functional diversity. The approach in this review is general, however, and most consideration will be grounded on general ecological knowledge.

General patterns of biodiversity include diversity–latitude (e.g. Willig et al., 2003), diversity–productivity (e.g. Waide et al., 1999), diversity–disturbance (e.g. Petraitis et al., 1989) and diversity–heterogeneity relationships (e.g. Vinson & Hawkins, 1998). These relationships have been studied across a wide variety of spatial scales. Most of the research on latitudinal gradients has dealt with macro-scales (i.e. wide spatial extents and large-sized grids), and these studies have largely concentrated on terrestrial and marine taxa. Many macro-scale studies on terrestrial and marine taxa show strong latitudinal gradients in species richness (Rosenzweig, 1995; Gaston & Blackburn, 2000; Willig et al., 2003; Hillebrand, 2004). By contrast, few studies have examined freshwater taxa in this respect, and the studies that exist have considered latitudinal variation in local richness (Vinson & Hawkins, 2003; McCreadie et al., 2005). Similarly, although numerous studies in the terrestrial realm have concentrated on macro-scales when examining diversity–productivity and diversity–heterogeneity relationships (Rosenzweig, 1995), freshwater studies have considered these relationships based on surveys of local ecosystems within small regions (Vinson & Hawkins, 1998; Jeppesen et al., 2000).

A decade ago, Vinson & Hawkins (1998) reviewed factors affecting stream insect biodiversity at local, catchment and regional scales. While their review focused on patterns at different scales, especially those at the within-stream scales, large scales received less attention. However, a large number of large-scale studies spanning catchments, ecoregions and countries have emerged since the publication of that paper. One aim of the present paper is thus to update and complement the information provided by the previous reviews on stream insect biodiversity (Vinson & Hawkins, 1998; Meyer et al., 2007; Clarke et al., 2008). The present review concentrates on large-scale patterns across natural environmental gradients, and the reader should consult previous reviews for further insights into small-scale aspects of aquatic insect ecology (Ward, 1992; Allan & Castillo, 2007; Vinson & Hawkins, 1998) and anthropogenic influences on freshwater ecosystems and biodiversity (Malmqvist & Rundle, 2002; Allan, 2004; Dudgeon et al., 2006). The emphasis in this review will be on aquatic insects, because they typically account for more than 80 % of taxa in freshwater macroinvertebrate assemblages (e.g. Sandin, 2003; Briers & Biggs, 2005).

Importance of spatial scale

Spatial scale embraces two components (Wiens, 1989). First, grain refers to the size of the observational unit. In aquatic studies, grain may be related to units sampled by a small sampling device (e.g. Surber sampler), parts of whole ecosystems (e.g. a stream riffle) or whole ecosystems (e.g. a pond). In macroecology, grain sizes are typically much larger than these, and macroecological studies are often based on large-scale grids, regions or countries.
Aquatic insect biodiversity (Gaston & Blackburn, 2000). Second, extent refers to the area over which the sampling units are distributed. In aquatic studies, extent may be a drainage basin, an ecoregion or even a continent. In the present review, emphasis will be given to grain sizes that comprise parts of ecosystems and whole ecosystems and will be directed at extents spanning from single drainage basins and ecoregions to countries and continents.

The importance of considering grain and extent is closely related to the fact that patterns and associated processes typically change with regard to the spatial scales considered (Levin, 1992; Whittaker et al., 2001). For example, the determinants of species richness may differ considerably when streams versus large-scale grids (e.g. 100 km × 100 km) are considered across the same spatial extent (Ricklefs, 1987). In the former case, not only historical and climatic processes determine species richness, but also local-scale factors, such as disturbance, stress and heterogeneity. By contrast, when large-scale grids are considered across the same spatial extent, it is unlikely that ‘mean’ local habitat conditions override the influences of historical and climatic factors on species richness. These scale-dependent differences mainly stem from the fact that local-scale environmental factors are homogenised across large-scale grids. Another reason is that local species richness is pooled over all local assemblages when large-scale grids are considered, yielding a measure of regional species richness. In this vein, it is also important to note that latitudinal gradients are typically stronger when large-scale grids are examined, whereas weaker species richness–latitude relationships may emerge when local ecosystems are considered (Hillebrand, 2004). This pattern may result from different species and species groups responding differently to local-scale environmental factors that do not necessarily co-vary with latitude. More generally, these notions suggest that variation in biodiversity may be best explained by different factors at different grain sizes and geographical extents (Rosenzweig, 1995; Whittaker et al., 2001; Blackburn & Gaston, 2002).

Diversity measured at different scales has typically been expressed as α-, β- and γ-diversity (Whittaker, 1975). Within-habitat diversity has typically been considered as α-diversity, and between-habitat diversity as β-diversity. In this review, the first one refers to the number of species in a local ecosystem, while the latter refers to variation in assemblage composition between local ecosystems. While α-diversity thus reflects the importance of local abiotic and biotic factors, β-diversity is related to the way in which species respond to environmental heterogeneity along ecological gradients. Finally, γ-diversity refers to regional species richness, and is the sum of differences among habitats in species composition. It is thought to be determined primarily by large-scale evolutionary, historical and climatic factors. In this review, γ-diversity refers to the number of species in separate geographical regions, large-scale grids or drainage basins. Another approach to understanding the effects of spatial scale relates to the importance of environmental variables measured at different scales. This approach is closely associated with the idea of environmental filters (Fig. 1) (Tonn, 1990; Poff, 1997) and has been followed in a number of studies on freshwater macroinvertebrate assemblages (Johnson & Goedkoop, 2002; Sandin, 2003; Townsend et al., 2004; Heino et al., 2007a). These studies have generally considered multiple nested scales, with the assumption that factors at different scales are hierarchically structured, and that factors at larger scales determine, at least in part, those at smaller scales (Frissell et al., 1986; Hildrew & Giller, 1994). In this review, both of these approaches will be considered, yet a clear distinction will be made between (i) spatial scale in terms of grain and extent and (ii) variables measured at different spatial scales.

Large-scale patterns in species diversity

Geographical patterns in regional diversity

Few studies have considered latitudinal gradients in aquatic insect diversity. Most of the existing studies have been based on surveys of local ecosystems, but a couple of studies have examined patterns across large grain size and considered regional species richness. For example, Boyero (2002) examined the regional species richness of
mayflies and dragonflies in the New World. A general finding was that of the four large regions compared, after region area was accounted for, the regional species richness of mayflies was lowest in tropical South America and highest in Central America. A corresponding analysis of dragonflies showed that Central America was again the most diverse region, whereas North America was home for the lowest number of species. When the area of each region was not taken into account a different pattern emerged. Mayfly diversity was clearly highest in North America and lowest in Central America, whereas dragonfly diversity was by far highest in tropical South America and lowest in temperate South America. The degree to which the four regions comprised too large a grain size for a meaningful analysis is unknown, and more detailed analyses based on smaller grain size would allow more useful insights into the latitudinal patterns of aquatic insect diversity.

A comparison of major aquatic insect groups across Europe shows that there are significantly negative species richness–latitude relationships in mayflies, dragonflies and stoneflies, while other groups do not exhibit significant latitudinal patterns (Table 1). However, most aquatic insect orders attain their highest levels of diversity in France, as opposed to the more southerly countries of Portugal and Greece. Lowest levels of diversity occur in Latvia, the Netherlands, Denmark, Norway and Finland. These among-country differences reflect two potential suites of factors behind geographical gradients in diversity. First, southern and central European countries with major mountain ranges, such as France, Germany, Spain, Italy and Austria, support high diversity, whereas lowland countries, such as the Netherlands, Latvia and Denmark, support low diversity in most aquatic insect groups. This suggests that large altitudinal variation increases the heterogeneity of freshwater habitats and variability of thermal conditions, which has positive effects on diversity. Also, if geographically separated mountain ranges are present, each mountain range may support unique species, contributing to high diversity per country. Second, diversity decreases to the north of Europe, with diversity being clearly higher in the southerly countries, such as Spain and Italy, than in the northerly countries.

Fig. 1. A schematic model of environmental filters affecting local assemblages. The continental species pool is determined by speciation and extinction processes at very large spatial and temporal scales. Filters at the largest scale in this scheme are history (e.g. speciation, extinction, dispersal) and climate (e.g. temperature, precipitation, energy) which determine the structure of regional species pools. Within the limits of regional species pools, there are filters at four levels that eventually determine local assemblages. These are watershed (e.g. vegetation, hydrological regimes), ecosystem (e.g. temperature, water chemistry), macrohabitat (e.g. depositional vs. erosional habitats, macrophyte cover) and microhabitat (e.g. macrophyte structural complexity, substratum particle size) filters. These filters determine diversity, composition, as well as functional and taxonomic variability of assemblages through species traits. Only species with suitable traits are able to overcome the challenges presented by the filters at each scale. For original ideas, see Tonn (1990) and Poff (1997).
Table 1. Numbers of species in major aquatic insect orders in European countries. Data were compiled from [http://www.freshwaterecology.info](http://www.freshwaterecology.info) (web site accessed on December 28, 2007); note that data for some countries and orders may have been updated on the website since. Information for many orders was not available for a number of countries (-). Note that information for the family of non-biting midges (Chironomidae: Diptera) may still be inadequate even in countries for which the numbers of species are given. Spearman rank correlations between species richness and latitude (south latitude of each country) are also shown. Countries are arranged on an approximate north–south gradient.

<table>
<thead>
<tr>
<th>Country</th>
<th>Ephemeroptera</th>
<th>Odonata</th>
<th>Plecoptera</th>
<th>Heteroptera</th>
<th>Coleoptera</th>
<th>Trichoptera</th>
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<td>Dragonflies</td>
<td>Stoneflies</td>
<td>Bugs</td>
<td>Beetles</td>
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* P < 0.05; ** P < 0.01

Note: The number of Odonata species in Finland is actually 54. For comparability purposes, the figure given is that from [http://www.freshwaterecology.info](http://www.freshwaterecology.info).
such as Finland and Norway. This suggests that large-scale historical and climatic factors have some effects on aquatic insect diversity along long geographical gradients. For example, Pleistocene glaciations may have had some effects on the present-day patterns of diversity, with some species having not yet reached all suitable areas. One caveat should be considered in this comparison. Taxonomic and faunistic traditions in each country may affect the degree to which observed diversity reflects clear patterns. For some insect groups, such as non-biting midges, historical faunistic work may differ considerably among countries. This is critical for comprehensive comparisons of aquatic insect diversity between countries and regions.

Latitudinal species richness patterns may vary with the habitat types of the considered taxa. Ribera et al. (2003) found that the diversity of lotic beetles was negatively related to latitude across countries in Europe, whereas lentic beetles did not show a significant latitudinal pattern. The authors interpreted this finding as an indication that the higher historical persistence of lotic than lentic habitats contributed differently to diversity patterns in the two groups of species. Proving the generality of this hypothesis clearly awaits further studies on other aquatic insect groups and geographical regions.

Geographical patterns in local diversity

Patterns detected at regional scales may change when local ecosystems are considered. Based on global literature on local genus richness, Vinson & Hawkins (2003) found no clear linear latitudinal richness trends for stream mayflies, stoneflies and caddisflies. By contrast, the highest levels of genus richness were generally attained at mid-latitudes in North America and South America, although there was much scatter around the relationships. Secondary peaks occurred in the tropics. While these patterns may result partly from inadequate data and taxonomic knowledge in tropical regions, they also suggest that stream insects may deviate from patterns detected for many major terrestrial taxa (Willig et al., 2003). A reason for this discrepancy may be that mayflies, stoneflies and caddisflies contain genera and species showing highly differential temperature preferences, with mid-latitude regions possibly providing a wide range of habitats suitable to various kinds of taxa. However, the fact that other studies have found either higher (Stout & Vandermeer, 1975; Lake et al., 1994; Jacobsen et al., 1997) or lower (Stanford & Ward, 1983; Arthington, 1990; McCreadie et al., 2005) taxa richness in tropical than in temperate streams suggests that more comprehensive studies, especially in tropical streams and spanning several tens of degrees of latitude, are needed to resolve whether stream insects do or do not show clear latitudinal gradients.

At a scale smaller than continents, some studies have examined latitudinal patterns in the local species richness and assemblage composition of freshwater macroinvertebrates. In North Europe, where ecoregional delineations largely follow latitude, there are differences between ecoregions in both species richness (Sandin & Johnson, 2000; Heino et al., 2002) and assemblage composition (Sandin & Johnson, 2000; Heino et al., 2007a). However, these patterns are typically rather weak, and species richness does not show a linear response to latitude from southern to northern ecoregions. Studies that have directly examined species richness–latitude relationships in stream macroinvertebrates in Sweden and Finland have corroborated these findings (Sandin, 2003; Heino, unpublished manuscript). By contrast, it has been found that the species richness of stream macroinvertebrates declines with latitude across Alaska (Wrona et al., 2006). This finding is in accordance with a previous study that found that stream insect genus richness declines linearly from 40°N to 70°N in North America (Vinson & Hawkins, 2003). Similarly to lotic macroinvertebrates, studies of lentic macroinvertebrates have generally found no linear declines in species richness with latitude and ecoregional delineations (Johnson, 2000; Vamosi et al., 2007). By contrast, part of the variability in the assemblage composition of lake macroinvertebrates is related to latitude (Johnson & Goedkoop, 2002; Johnson et al., 2004).

The two most probable reasons for the weak relationships between latitude and species richness or assemblage composition are that (i) the local environmental features of freshwater ecosystems do not necessarily
show clear latitudinal variation (e.g. substratum particle size, moss cover, current velocity, gradient), and (ii) local environmental factors override the influences of large-scale historical and climatic factors on local assemblages. This reasoning is undeveloped, however, because single surveys of local assemblages do not typically span large latitudinal gradients. Thus, new large-scale datasets may change our views about the latitudinal diversity patterns shown by freshwater macroinvertebrates.

In addition to patterns along latitudinal gradients, other geographical patterns are also of interest. For example, east-to-west gradients in species richness have been found for stream insects across North Africa (Beauchard et al., 2003). This pattern was explained by a combination of climatic, hydrological and biogeographic factors, with the latter relating to historical dispersal processes. Similar historical influences of dispersal after the last glacial period may also be related to east–west and south–north gradients of stream macroinvertebrate species richness in other regions, although the combination of geographical gradients with local environmental features may be more influential. More complex geographical gradients in species richness and assemblage composition have also been suggested by findings from surveys of streams across ecoregions in New Zealand (Harding et al., 1997), North America (Hawkins & Vinson, 2000) and North Europe (Heino et al., 2002). While stream and lake macroinvertebrate assemblages show some differences between ecoregions, differences are typically rather weak (Hardin et al., 1997; Hawkins et al., 2000; Johnson, 2000; Hawkins & Vinson, 2000). However, even weak relationships suggest that local assemblages are, at least in part, constrained by large-scale climatic and historical factors.

Local–regional species richness relationships

Theoretical considerations and empirical evidence suggest that species richness in local assemblages is constrained not only by local factors, but also by regional species pools (Ricklefs, 1987; Cornell & Lawton, 1992; Griffiths, 1997; Angermeier & Winston, 1998). Much recent interest has been directed to the relationship between local species richness (LSR) and regional species richness (RSR). Two general patterns have been suggested for LSR–RSR plots (Cornell & Lawton, 1992). First, LSR may increase linearly with RSR, suggesting that local factors do not limit LSR, assemblages being mainly under regional control. Second, if LSR attains an asymptote with increasing RSR, then it is suggested that local assemblages are saturated, being mainly under local control. Although the approach in general has been criticised, particularly because highly interactive assemblages may show linear LSR–RSR relationships (Hillebrand, 2005) and because such plots cannot be considered as evidence of competition (He et al., 2005), the examination of LSR–RSR relationships may at least provide hints as to whether regional factors are important at all (Witman et al., 2004; Harrison & Cornell, 2008).

LSR–RSR relationships for freshwater macroinvertebrates have typically been derived using a riffle site as the local arena and a drainage basin as the region. Research on Finnish streams revealed that mean LSR was linearly related to RSR, suggesting that regional species pools limited LSR at least to some degree (Heino et al., 2003a). A similar linear relationship was found for southeastern Australian streams (Marchant et al., 2006). The Australian dataset contained a much larger number of species than the Finnish dataset, suggesting that even at very high levels of LSR and RSR, a linear relationship may prevail. In contrast, based on a much more limited number of species, a strongly asymptotic relationship between LSR and RSR was found for stream blackflies in the New World (McCreadie et al., 2005). A study on Swedish streams and lakes yielded a weakly asymptotic mean LSR to RSR relationship in both habitat types (Stendera & Johnson, 2005). The patterns detected in this study were probably confounded by the fact that RSR estimates for each ecoregion were based on different numbers of streams and lakes, and a correction for the number of sampled sites might have been necessary for valid comparisons of LSR–RSR relationships (Marchant et al., 2006). Finally, a study on Palaearctic predaceous diving beetles showed that LSR was positively related to RSR, even when compensations were made for differences in local pond characteristics (Kholin & Nilsson, 1998). This
finding suggested a regional enrichment of LSR, and that a suite of historical and environmental explanations might be needed to account for variation in the species richness of predaceous water beetles in ponds. The findings from the above studies clearly indicate that there is no single type of LSR–RSR relationship in freshwater macroinvertebrates.

**Relative influences of variables at different scales**

Conceptual models suggest that local assemblages are structured by environmental factors at multiple scales (Fig. 1) (Tonn, 1990; Poff, 1997). These suggestions have been corroborated by empirical evidence. For example, the assemblage composition of both stream and lake macroinvertebrates has been found to be determined by multiple variables, ranging from local habitat and ecosystem features through watershed characteristics to regional climate and geographical factors (Townsend et al., 2003; Johnson et al., 2004; Sandin & Johnson, 2004; Heino et al., 2007a). In general, variables at small scales have been suggested to be the most important, both in terms of explained variability in assemblage composition and in the ecological sense, as small-scale variables are directly associated with the organisms. However, in a study covering a large geographical extent in Europe, geographical position and ecoregion overrode the influences of local factors on stream assemblages (Johnson et al., 2007). Also, species richness in streams has been found to be best explained by models including variables acting at different spatial scales (Sandin, 2003).

**Synthesis and implications**

Aquatic insect biodiversity varies geographically, although present evidence suggests that these patterns are complex. Both species richness and assemblage composition typically show some variability among ecoregions and drainage basins, yet among-site heterogeneity within regions largely masks the influences of climate and history on local assemblages. Such a weak influence of large-scale factors is likely to contribute to weak latitudinal gradients in local diversity. However, proving the predominance of weak latitudinal diversity patterns would necessitate comprehensive surveys of tropical freshwater ecosystems and those that span several tens of degrees of latitude across major biomes. A fruitful approach in this context would be to determine the relative influences of latitude, and of regional, watershed, ecosystem and habitat factors on local aquatic insect diversity, as has been done in studies conducted within smaller geographical extents. Such studies should not only be directed towards lotic systems, for which some data already exist, but also towards lentic systems, for which our knowledge of geographical diversity patterns is more limited. Understanding geographical diversity patterns would be a valuable asset in determining and implementing geographically representative networks of protected areas for the conservation of freshwater biodiversity.

**Species diversity–environment relationships within regions**

The drainage basin is a natural regional unit in lotic ecology (e.g. Frisell et al., 1986), and lake districts have similarly been given considerable recent attention in lentic ecology (e.g. Kratz & Frost, 2000). It is not surprising, therefore, that there have been many within-region surveys of lotic and lentic assemblages. In the following, I will review findings from surveys of aquatic insect assemblages at geographical extents smaller (i.e. single ecoregions, drainage basins and lake districts) than those considered above (i.e. several ecoregions and countries). I will first review research on (i) diversity–disturbance, (ii) diversity–productivity, (ii) diversity–acidity, (iv) diversity–heterogeneity and (v) diversity–habitat size relationships separately in both lotic and lentic ecosystems. I will also consider similarity in the environmental relationships of species richness and assemblage composition. I will end this section by addressing variation in species richness and assemblage composition with regard to the nested subset pattern. Biotic interactions, including predation and competition, will be considered below only if there are shifts in species interactions associated with these major environmental factors.
Aquatic insect biodiversity

gradients. Readers should consult previous reviews for the importance of species interactions at small within-ecosystem scales (Giller & Malmqvist, 1998; Allan & Castillo, 2007).

Species diversity and major environmental gradients in lotic systems

Diversity–disturbance relationships
Floods are major natural causes of disturbance in running waters (Power et al., 1988; Resh et al., 1988; Poff, 1992) and constitute important determinants of diversity (Resh et al., 1988; Lake, 2000). Diversity is typically negatively related to flow disturbance intensity and frequency (Robinson & Minshall, 1986; Death, 2002) and positively related to benthic habitat stability (Death & Winterbourn, 1995; Death, 2002). By contrast, none of the studies reviewed by Vinson & Hawkins (1998) suggested that the intermediate disturbance hypothesis would fit the species diversity patterns of stream macroinvertebrates, although intermediate levels of disturbance may be associated with higher diversity in other systems (Connell, 1978; Petraitis et al., 1989). However, more recent studies have found highest diversity at sites perturbed by intermediate levels of disturbances, leading to a unimodal diversity–disturbance relationship (Townsend et al., 1997). This is due to the fact that high-level disturbances prevent abundant species from attaining a dominant position and competitive advantage (Huston, 1994), yet disturbances of intermediate level do not lead to the exclusion of most disturbance-sensitive species. However, very few studies on lotic macroinvertebrates have examined these relationships across multiple streams (Townsend et al., 1997; Death, 2002), whereas a number of within-stream studies have also examined the effects of disturbance on macroinvertebrate diversity (Matthaei et al. 1999, 2000; McCabe & Gotelli, 2000). These small-scale studies, however, are out of the scope of this review.

Another form of disturbance affecting stream macroinvertebrates is drought (Lake, 2003). In this regard, some studies have compared intermittent and permanent streams, and found that the former support fewer species than the latter type of streams (Lake et al., 1986; Williams, 1996). This is not surprising, because drying out of streams presents severe challenges to the life history adaptations and physiological performance of aquatic insects. A comprehensive recent review of the effects of drought on stream biota can be found elsewhere (Lake, 2003).

Diversity–productivity relationships
In addition to diversity–disturbance relationships, the effect of productivity on diversity has been studied extensively. Recent reviews have suggested that the diversity–productivity relationship takes many forms, ranging from positive, unimodal and negative to non-significant (Waide et al., 1999; Mittelbach et al., 2001). It is possible that productivity in terms of stream water nutrient concentration or periphyton biomass may also show positive, unimodal or negative relationships to the species richness of stream macroinvertebrates. When productivity ranges from very low to moderate, a positive relationship may occur (Perry & Sheldon, 1986). Such a relationship may also be common in arctic and subarctic streams, which have generally very low to moderately low nutrient levels. When nutrient levels range from very low to very high, a unimodal relationship may be found. Such a relationship may be common in temperate regions with a wide range in stream water nutrient levels. Finally, when nutrients range from moderate to very high levels, a negative relationship may be found. Such a relationship may also be common in temperate regions, where anthropogenic effects have increased nutrient inputs to streams. However, a negative relationship may also occur at relatively low levels of productivity (Malmqvist & Eriksson, 1995). Malmqvist & Eriksson (1995) suggested that the negative relationship resulted, at least in part, from productive lake outlets being dominated by few abundant and competitively dominant species, such as highly aggressive net-spinning caddis larvae (see also Giller & Malmqvist, 1998). It should be emphasised, however, that nutrient levels may not be the sole source of productivity affecting stream insects, although nutrients are most closely associated with autochthonous production in these systems. It should also be noted that the above predictions are largely theoretical
rather than proven correct by empirical evidence. Empirical studies are thus needed to ascertain if the form of the diversity–productivity relationship varies with regard to regional range in potential productivity. These studies should not only consider in-stream productivity, but also the productivity of the riparian zone.

**Interactive effect of disturbance and productivity on diversity**

Disturbance and productivity may act in concert in affecting diversity, and this relationship is typically expressed as the dynamic equilibrium model (Huston, 1994). This model predicts that the unimodal relationship between disturbance and diversity in the intermediate disturbance hypothesis moves in relation to the productivity of a system, producing a contour of decreasing diversity with high disturbance and high productivity. Such patterns of diversity result from two opposing forces: population growth rate and disturbance. First, local processes, such as competition, dominate and reduce diversity under high population growth rates and low disturbances. Second, other local processes, such as extinction, are important at very low levels of growth rate and high disturbance frequencies that thus reduce diversity. Very few studies have tested this model, because it necessitates surveys at large among-stream scales, making experiments unfeasible. However, Death & Zimmerman (2005) tried to overcome this problem, and examined simultaneously the effects of both disturbance and productivity on macroinvertebrate species richness in a set of streams. In general they found weak support for the two above-mentioned diversity models and suggested instead that species richness was a function of time since the last disturbance, this being associated with the recovery of the autotrophic production base for macroinvertebrates (Death & Zimmerman, 2005; see also Death & Winterbourn, 1995; Bond & Downes 2000; Death, 2002).

**Diversity–acidity relationships**

Among the most important stress factors in stream ecosystems is acidity. Species richness–acidity relationships have been studied in regional studies in widely-separated geographical areas, ranging from Sweden (Malmqvist & Hoffsten, 2000) and Britain (Townsend et al., 1983) to the USA (Rosemond et al., 1992) and New Zealand (Collier et al., 1990). Acidity typically leads to a low diversity of stream macroinvertebrates and such patterns have been observed in a number of studies spanning gradients from pH values 4 to 7. In general, considerable reduction in the occurrence and richness of macroinvertebrates is typically seen at pH values below 5.5 (Otto & Svensson, 1983; Townsend et al., 1983; Hämäläinen & Huttunen, 1990; Larsen et al., 1996). However, the findings of general reductions of species richness with acidity have also been challenged (Winterbourn & Collier, 1987; Collier et al., 1990; Dangles et al., 2004; Petrin et al., 2007). These discrepancies may be related to the fact that acidity has both direct and indirect effects through food availability on species richness (Otto & Svensson, 1983), or that species from different regions may possess differing sensitivity to acid stress (Petrin et al., 2007). Furthermore, Petrin et al. (2007) suggested that macroinvertebrate species richness decreases with acidity if it is of anthropogenic origin, while species richness may remain virtually unaltered if acidity is of natural origin. Based on surveys in southern (acidity of anthropogenic origin) and northern Sweden (acidity of natural origin), they showed that the species richness of mayflies decreased with acidity in both regions, whereas the species richness of caddisflies showed a negative response to acidity in the former region. The species richness of stoneflies did not vary along acidity gradients. Thus, the overall species richness–acidity relationships for lotic macroinvertebrates as a whole may be driven by a few taxonomic groups, while others are more or less indifferent with regard to acidity. For example, stoneflies in general may be rather indifferent with regard to acidity, and their species richness typically shows no clear response to acidity (Malmqvist & Hoffsten, 2000). However, despite no effects on species richness, the species composition of stonefly assemblages may, as
in many other insect groups, change along gradients of acidity (Petrin et al., 2007).

**Diversity–heterogeneity relationships**

Habitat heterogeneity has a positive effect on species richness in general (Huston, 1994), and the same is true for stream macroinvertebrates at various spatial scales (Vinson & Hawkins, 1998). Studies conducted at small scales, for example, within streams based on samples of stones, have associated variation in species richness to various measures of habitat heterogeneity, diversity and complexity. For example, species richness is typically positively related to habitat complexity in terms of stone surface features and plant cover at small scales (Hart, 1978; Hart & Horwitz, 1991; Douglas & Lake, 1994; Dudley et al., 1986; Downes et al., 2000; Heino & Korsu, 2008). Positive relationships between stream substratum heterogeneity and species richness have also been found among sites within streams (Cowie, 1985). By contrast, although habitat heterogeneity could be envisaged to account for among-stream variation in species richness, evidence for such relationships is scant (Vinson & Hawkins, 1998). Reasons for the virtual absence of a species richness–habitat heterogeneity relationship at the among-stream scale are unknown, but possibly result from stronger impacts of other physical and chemical factors that override the influences of habitat heterogeneity on species richness. Alternatively, stream ecologists may not have measured heterogeneity at the among-stream scale as perceived by, or is important for, aquatic insects. It is also unknown if habitat heterogeneity is positively related to stream size. It is possible, however, that habitat heterogeneity increases with stream size in small to mid-sized rivers, but larger rivers do not necessarily possess more heterogeneous habitats (see below).

**Diversity–habitat size relationships**

The river continuum concept (RCC) provides a theoretical basis to lotic ecology, for example, by relating river size and longitudinal position to variation in functional feeding group composition and macroinvertebrate species richness (Vannote et al., 1980). The various predictions of the RCC have been summarised several times since its formulation (Minshall et al., 1985a; Hildrew & Townsend, 1987; Allan & Castille, 2007; Cummins, 1996), and suggest that species richness increases from the headwaters (orders 1 to 3) to mid-order rivers (orders 4 to 6) and then declines with increasing river size (orders 7 to 12). These mid-order peaks in species richness have been explained by higher levels of habitat heterogeneity and higher numbers of thermal niches in mid-sized rivers than in smaller or larger rivers (Minshall et al., 1985b). In general, empirical evidence corroborates the prediction of the RCC that the species richness of stream macroinvertebrates increases with stream size up to mid-order rivers. Such patterns have been found in widely-separated geographical regions, including Europe (Malmqvist & Hoffsten, 2000; Céreghino et al., 2003; Arscott et al., 2005), North America (Minshall et al., 1985b; Grubaugh et al., 1996) and South America (Tomanova et al., 2007). However, in studies where only small to mid-sized streams are sampled, species richness may be positively related to stream size (Brönmark et al., 1984; Ward, 1986; Malmqvist & Mäki, 1994; Malmqvist & Eriksson, 1995; Wiberg-Larsen et al., 2000; Paller et al., 2006), although exceptions to these patterns also exist (Winterbourn et al., 1981; Malmqvist & Hoffsten, 2000; Voelz & McArthur, 2000; Heino et al., 2008). When species richness attains an asymptote or decreases in mid-sized rivers, a possible reason for such patterns is that sampling effort has not been sufficient in mid-sized reaches, as opposed to more adequate effort in the headwater reaches (Malmqvist & Hoffsten, 2000; Heino et al., 2008). An alternative explanation is that localised changes in environmental conditions (e.g. substratum particle size, macrophyte cover) disrupt expected species richness–habitat size relationships (Wright & Li, 2002; Heino & Paasivirta, 2008). It should also be emphasised that data from the short and steep catchments in New Zealand and Australian drainage basins do not support the RCC predictions (Winterbourn et al., 1981). Note that habitat size for lotic ecosystems in the above-mentioned studies has been based on a number of measures, including stream order, catchment area, distance to source and stream width. Another important aspect to note is that not all studies have examined a single river continuum, but have been based on surveys of
different-sized streams scattered across a drainage basin or an ecoregion. This may increase the importance of localised environmental influences, causing patterns to differ from the predictions of the RCC.

**Species diversity and major environmental gradients in lentic systems**

**Diversity–disturbance relationships**
Disturbance in terms of hydroperiod has both direct and indirect influences on diversity in lentic littoral and pond ecosystems. Permanent ponds typically support higher numbers of species than temporary ponds, and diversity increases with increasing degree of permanency (Spencer et al., 1999; Urban, 2004; but see Larson, 1985). This is likely to be due to physical limitation on the life history characteristics of various taxa (Schneider & Frost, 1996; Spencer et al., 1999), although the determination of species richness and assemblage composition along the lentic permanency gradient may be more complex (Wellborn et al., 1996). Wellborn et al. (1996) reviewed literature on invertebrate assemblages along this gradient and found that various species occurred in either only temporary habitats, only permanent but fishless habitats, or only permanent fish containing habitats. These patterns were suggested to be driven by the relative roles of: (i) drying that selects for traits allowing rapid development and physiological capacity to cope with disturbance; (ii) winter oxygen stress that eliminates fish; and (iii) types of top predators that vary in different types of lakes, being dragonfly larvae in permanent fishless lakes and fish in least disturbed lakes. The interaction between disturbance and predation should also be manifest in overall assemblage composition and species richness, and different groups of aquatic insects are likely to show differing diversity patterns along the permanency–predation gradient. This freshwater habitat gradient offers interesting possibilities for further studies trying to tease out the effects of disturbance and predation on the species richness and assemblage composition of aquatic insects.

**Diversity–productivity relationships**
Productivity in lentic ecosystems has typically been described by proxy variables, such as nutrient levels and chlorophyll-a concentration (Dodson et al., 2000; Jeppesen et al., 2000; Declerk et al., 2005; Barnett & Beisner, 2007). However, very few studies have directly tested diversity–productivity relationships in lentic macroinvertebrates. Brodersen et al. (1998) found that the species richness and Shannon's diversity index of littoral macroinvertebrates were negatively related to these measures of productivity. Given that the lakes they studied ranged from mesotrophic to highly eutrophic, negative relationships can be easily envisaged. Chase & Leibold (2002) observed two different types of species richness–productivity relationships in pond macroinvertebrates with varying spatial scale. When analysed with ponds as replicates, a unimodal relationship was found in α-diversity. By contrast, when analysed over ponds in a watershed, a positive relationship emerged for γ-diversity. They explained these differing relationships as an indication that, in watersheds with highly productive ponds, β-diversity was higher due to multiple stable states, while β-diversity was lower in low-productivity watersheds. These differences in species turnover contributed to differences in γ-diversity. Despite these rigorous studies, more studies in lentic ecosystems, with macroinvertebrates as the model group, are needed before any general conclusions about the diversity–productivity relationship can be made.

**Diversity–acidity relationships**
Diversity–acidity relationships have been relatively well studied in lentic ecosystems. A typical finding has been that the overall species richness of lentic macroinvertebrates decreases strongly with natural (Bradford et al., 1998) and anthropogenic (Schindler et al., 1989) acidity. However, to my knowledge, no study has tried to determine the actual roles of these two sources of acidity in affecting lentic macroinvertebrates. Decreasing trends between species richness and acidity have been found for both ponds (Friday, 1987) and lakes (McNicol et al., 1995; Hynynen & Meriläinen, 2005; Arnott et al., 2006). These trends are typically driven by the negative responses of...
species in a few taxonomic groups, with mayflies among aquatic insect taxa being generally highly sensitive to acidity in lakes (Meriläinen & Hynynen, 1990; Carbone et al., 1998). However, some taxa may show no significant relationships to acidity (Pollard & Berrill, 1992), and diversity patterns opposite to those of whole assemblages may even be detected due to species benefiting indirectly from acidic conditions (Bendell & McNicol, 1987). These species may not necessarily prefer acidic conditions, but are excluded from neutral lakes due to biotic interactions. For example, fish are often excluded from acidic lakes, this providing an opportunity for macroinvertebrates sensitive to fish predators to thrive in acidic lakes (Eriksson et al., 1980; Bendell & McNicol, 1987; McNicol et al., 1995). Among the most well-known examples in this regard are larval dragonflies, waterstriders and waterboatmen, some species of which may be more frequent and abundant in fishless habitats (Macan, 1965; Bendell & McNicol, 1995; McNicol et al., 1995). Thus, similarly to disturbance, acidity has both direct and indirect effects on species richness and assemblage composition in lentic ecosystems.

Diversity–heterogeneity relationships

Habitat heterogeneity, diversity and complexity are potentially important determinants of diversity in lentic littoral and pond ecosystems (Eadie & Keast, 1984; Rahel, 1984). Similarly to lotic ecosystems, a number of studies have examined diversity–heterogeneity relationships at small within-ecosystem scales. Not surprisingly, these studies have typically found positive relationships between macroinvertebrate diversity, abundance and habitat complexity, including that of macrophyte beds (Carpenter & Lodge, 1986; Brown et al., 1988), although exceptions also exist (Cyr & Downing, 1988; McAbendroth et al., 2005a). Evidence about diversity–heterogeneity relationships based on among-ecosystem surveys is more limited. However, Heino (2000) found that the species richness of littoral macroinvertebrates was strongly related to a composite habitat heterogeneity variable, comprising information about substratum diversity, heterogeneity of organic material distribution, and heterogeneity and diversity of macrophytes. In general, bog lakes with only organic bottoms and sparse cover of macrophytes at best supported much lower species richness than forest lakes with a heterogeneous bottom of both organic and inorganic material, as well as more developed macrophyte beds. This finding is in agreement with a positive relationship between the species richness of diving beetles and macrophyte cover and complexity in lakes (Nilsson et al., 1994; Nilsson & Söderberg, 1996).

Diversity–habitat size relationships

Species–area relationships have been studied extensively in various systems, and positive relationships have been found in a large number of studies (Rosenzweig, 1995; Gaston & Blackburn, 2000). Habitat size has also been found to be important for the species richness and assemblage composition of aquatic insects in temporary ponds (Nilsson & Svensson, 1995; Kholin & Nilsson, 1996), permanent ponds (Oertli et al., 2002) and lakes (Allen et al., 1999; Heino, 2000). However, non-significant species richness–habitat size relationships have also been found for some groups of aquatic insects in ponds (Larson, 1985; Oertli et al., 2002). For lakes, habitat size and habitat heterogeneity are typically correlated, and a positive relationship between species richness and lake size may thus result from heterogeneity effects. Given that habitat heterogeneity may account for more variation in species richness than lake size, heterogeneity is likely to be behind strong species–area relationships in surveys of lakes. Similarly to species richness, the assemblage composition of lentic macroinvertebrates may vary strongly with lake size and habitat structure (Heino, 2000).

Multiple environmental variables determine diversity

Vinson & Hawkins (1998) called for multi-factor analyses in studies on aquatic insect biodiversity. Since the publication of their review, a number of studies have examined the relative importance of multiple environmental variables on aquatic insect biodiversity. Such studies have been conducted in both lotic (Brosse et al., 2003; Sandin, 2003) and lentic ecosystems (Nilsson & Svensson, 1995;
Heino, 2000). In general, most studies have noted that a comprehensive understanding of variation in the diversity of aquatic insects requires the measurement of multiple environmental variables, including ecosystem-scale (e.g. pH, nutrients, temperature) and habitat-scale variables (e.g. substratum characteristics, current velocity, macrophytes). This reasoning may be true in most cases, but exceptions may occur when one dominant environmental gradient has been surveyed and others are not influential. In such cases, variation in diversity may be explained adequately by a single environmental gradient (Townsend et al., 1983; Wiberg-Larsen et al., 2000). Studies that have not found significant relationships between species richness and environmental features may be complicated by a simultaneous survey of multiple ecosystem types (e.g. springbrooks, headwater streams, large rivers, lake outlets; Malmqvist et al., 1999). Surveys of different ecosystem types, with each harbouring a certain suite of characteristic species, may thus lead to non-significant diversity–environment relationships. Alternatively, if significant diversity–environment relationships have not been detected, it is possible that influential environmental variables were not measured at all. Biodiversity surveys should therefore include a large number of explanatory variables and use multivariate methods to help to identify various factors of potential importance.

Do species richness and assemblage composition vary along the same gradients?

This question is of relevance to conservation, as not only species richness (α-diversity), but also spatial changes in assemblage composition (β-diversity) should be considered in conservation planning. Reports of the environmental relationships of both species richness and assemblage composition have been rather unambiguous. Not surprisingly, both these components of diversity appear to respond similarly to environmental gradients. For example, Townsend et al. (1983) found that pH was the most important variable for both species richness and assemblage composition in southern English streams. Malmqvist & Hoffsten (2000) found that stream size, pH and water colour were the most important variables determining variability in both species richness and assemblage composition of streams in northern Sweden. Wiberg-Larsen et al. (2000) also found that both the species richness and assemblage composition of caddisflies were strongly related to stream size in Denmark. In all of these cases, the environmental gradients were apparently strong enough to modify diversity, and variability in species richness and assemblage composition followed the same gradients. By contrast, in situations where there are several equally strong and uncorrelated environmental gradients, species richness and assemblage composition may vary differently along environmental gradients. This is true in situations where α- and β-diversity vary independently, i.e. showing an anti-nested pattern (see below).

Nestedness

Ecological assemblages within the limits of a regional species pool show a number of generalised patterns (Leibold & Mikkelson, 2002; Heino, 2005a). One such pattern is nestedness. A perfectly nested pattern occurs if species in depauperate assemblages are proper subsets of those in progressively more diverse assemblages, with common species occurring in all assemblages and rare species tending to occur only in diverse assemblages (Patterson & Atmar, 1986). Thus, if a set of assemblages is perfectly nested, the most species-rich site includes all species detected at lower-richness sites. Several studies have found a significant nested subset pattern in various taxa and environments, implying that nestedness is a common pattern in nature (D.H. Wright et al., 1998). However, the virtual ubiquity of nestedness has recently been challenged, and only 10 % to 40 % of the matrices studied by Ulrich & Gotelli (2007) were actually significantly nested. These discrepancies between the two meta-analyses stem from the fact that, in the former study, null models for significance testing were liberal (D.H. Wright et al., 1998), whereas the latter study comprised multiple and typically more conservative null models (Ulrich & Gotelli, 2007). Earlier studies on the nestedness of aquatic insects have typically been based on the liberal null models, such
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as that of the nestedness calculator (Atmar & Patterson, 1993), yet the results have been ambiguous. The published studies on aquatic insects have found either that these assemblages are significantly nested (Nilsson & Svensson, 1995; Malmqvist 1999; Malmqvist & Hofsten, 2000; Baber et al., 2004; Heino, 2005a; McAbendtroth et al., 2005b; Monaghan et al., 2005; Heino et al., 2009) or non-nested (Malmqvist & Eriksson, 1995; Nilsson & Svensson, 1995; Malmqvist et al., 1999; Urban, 2004). However, even when significant nestedness has been found in studies of aquatic insects, it has often been rather weak. Boecklen (1997) noted earlier the same pattern for aquatic invertebrates in general, and suggested that, because these assemblages contain various kinds of organisms many of which possess high colonisation rates, there is only weak nestedness at best. Weak nestedness means that there are somewhat anti-nested patterns, which might mean checkerboard distributions of species pairs and high β-diversity (Gotelli & McCabe, 2002; Heino et al., 2009).

Although a considerable number of studies have assessed the degree of nestedness, very few studies have considered the determinants of this pattern in aquatic insects. McAbendroth et al. (2005b) found that nestedness in pond macroinvertebrates was primarily driven by habitat size, and secondarily by habitat features and isolation. Interestingly, species contributing to perfect nestedness (i.e. nested species) varied in a number of organismal characteristics from species not contributing to nestedness (i.e. idiosyncratic species). Nested species showed stronger spatial structure, weaker dispersal ability and narrower ecological tolerances than idiosyncratic species. These suggestions corroborate well the findings from boreal streams (Heino et al., 2009). In this study, the most important correlate of nestedness in stream insect assemblages was stream size. Furthermore, idiosyncratic species occurred, on average, at more sites than nested species, mirroring the restricted distributions of several nested species that were inclined towards species-rich sites. Idiosyncratic and nested species also differed in niche position and niche breadth, with idiosyncratic species having less marginal niche positions and wider niches than nested species (Heino et al., 2009). Although these environmental and organismal relationships of nestedness could be easily envisaged based on information from terrestrial systems (D.H. Wright et al., 1998) and other aquatic taxa (Soininen, 2008), further studies are required to prove the generality of these findings in aquatic insects.

**Synthesis and implications**

Aquatic insect assemblages within the limits of a regional species pool show many interesting patterns. The relationships of species richness and assemblage composition to major environmental gradients may sometimes be rather predictable, although the explanatory power in statistical models is typically rather low. In general, habitat size and acid stress appear to structure aquatic insect assemblages most strongly in both lotic and lentic ecosystems, although there are some notable differences between streams, rivers, ponds and lakes. Understanding the species richness–environment and assemblage composition–environment relationships has a number of implications for the conservation and management of α-, β-, and γ-diversity. First, conservation of α-diversity benefits from the understanding of species richness–environment relationships, although the degree of nestedness should also be considered (Boecklen, 1997).

If assemblages are perfectly nested, then the conservation of the most species rich site protects all species. By contrast, if nestedness is weak, as has been found in many studies on aquatic insects, then rare species are not restricted to species rich sites only. In such cases, an alternative conservation strategy should be followed, with interest in both idiosyncratic species and species-rich sites. Second, given the rather predictable assemblage composition–habitat size relationships, different-sized streams and lakes are needed to conserve β-diversity. Thirdly, the protection of sites supporting characteristic assemblage types and sites at different parts of environmental continuums is also important for the conservation of γ-diversity.
Among-taxon congruence in diversity

Understanding the degree to which different taxonomic groups show congruent biodiversity patterns is an important field of study in conservation biology (Gaston, 1996b) and environmental assessment (McGeogh, 1998). However, despite its importance, relatively few studies have examined congruence in the diversity patterns of aquatic organisms in general (Allen et al., 1999; Paavola et al., 2003; Heino et al., 2005) and aquatic insects in particular (Briers & Biggs, 2003; Heino et al., 2003b; Bilton et al., 2006). The studies that have appeared thus far have led to differing conclusions. Heino et al. (2003b) found that the species richness and assemblage composition patterns of stream mayflies, stoneflies, caddisflies and midges were weakly, though sometimes significantly, correlated at the across-ecoregions scale in Finland. Within ecoregions, a few cross-taxon correlations were slightly higher, but even these correlations lacked the predictive power required for them to be useful in practice. These findings generally comply with those for the same four insect groups in a single boreal drainage basin (Heino & Mykrä, 2009). Bilton et al. (2006) also studied among-taxon congruence in species richness and assemblage similarity in several pond macroinvertebrate taxa. They found that, although species richness was weakly correlated among taxonomic groups, assemblage composition patterns showed stronger among-group correlations. Sánchez-Fernández et al. (2006) found that aquatic beetles were relatively good indicators of species richness in various stream macroinvertebrate taxa, with correlations ranging from non-significant for molluscs and mayflies to significant and rather strong for aquatic bugs, stoneflies, caddisflies and total richness of the studied taxonomic groups.

Why should some taxonomic groups show strong correlations in biodiversity? There are four main mechanisms behind strong among-taxon congruence: (i) similar environmental responses; (ii) responses to different, but correlated environmental features; (iii) biotic interactions; and (iv) random draw from the regional species pool (Gaston & Williams, 1996). Bilton et al. (2006) invoked similar environmental responses as the mechanism contributing to co-varying patterns of assemblage composition in pond insects. By contrast, Heino et al. (2003b) stated that, due to differing responses to geographical location and major environmental gradients, stream insect taxa showed weak congruence in biodiversity. Thus, the responses of different taxonomic groups to the same environmental gradients are most likely to be responsible for the degree of congruence. Responses to correlated environmental factors may also contribute to congruence in some situations, whereas biotic interactions and random draw are less likely explanations at the grain of local ecosystems and the extent of single drainage basins. However, random draw from the regional species pool may contribute to strong congruence if local ecosystems are surveyed across long geographical gradients (Heino et al., 2003b). These suggestions are speculative, and given that very few studies on aquatic insects have considered among-taxon congruence, further studies in various regional and environmental settings are needed to resolve this question.

Knowing the degree to which different taxonomic groups show congruent diversity patterns is potentially valuable in the conservation context. In addition to showing strongly congruent patterns with other taxonomic groups, a good biodiversity indicator taxon should possess a number of additional qualities. These include occurrence in various environmental conditions, cost-efficiency, applicability at different scales, and it should be easily sampled, easily identified and ecologically well-known (Noss, 1990; McGeogh, 1998). The concept of biodiversity indicator taxa has only rarely been considered in aquatic insect studies. Briers & Biggs (2003) found that coenagrionid damselflies and limnephilid caddisflies were the most promising groups as indicators of pond biodiversity. Bilton et al. (2006) considered aquatic beetles as the most useful indicator group for pond biodiversity assessment, because they conform best of the studied taxa to the qualities listed above. Similarly, Sánchez-Fernández et al. (2006) also regarded aquatic beetles as a good indicator taxon. However, the degree to which aquatic beetles perform as surrogates in the biodiversity assessment of streams and lakes is uncertain, and recent research on...
boreal bog and forest lakes suggests that aquatic beetles are so sporadically distributed that they cannot be used effectively as an indicator taxon (Heino et al., unpublished). It is thus likely that there is no single, universal indicator taxon among aquatic insect taxa, and that indicator groups need to be adjusted according to regional and environmental settings. This may also mean that indicator groups are unlikely to be useful in most situations.

**Patterns of functional diversity**

Although the functional approach has a long history in ecology (Statzner et al., 2001a), there has been increasing interest in the topic recently due to greater recognition of the importance of functional biodiversity to ecosystem functioning (Kinzig et al., 2002). Early examinations of macroinvertebrate functional feeding groups (Cummins, 1973; Cummins & Klug, 1979) in the context of the river continuum concept provided first glimpses of the utility of the functional approach when studying the longitudinal gradient in lotic ecosystems (Vannote et al., 1980; Minshall et al., 1985a; Minshall, 1988). By contrast, few studies have examined patterns in the functional structure and diversity of freshwater macroinvertebrate assemblages along multiple non-anthropogenic environmental gradients, although the need for such studies has been clearly identified (Poff, 1997; Usseglio-Polatera et al., 2000). Using functional structure, or more generally species traits, as response variables instead of taxonomic composition may increase our understanding of the relationship between freshwater biodiversity and ecosystem functioning. However, although most recent studies have certainly addressed multiple important traits (Gayraud et al., 2003; Lamouroux et al., 2004; Poff et al., 2006), there has typically been rather little division between the traits that are truly functional in terms of ecosystem functioning and those that portray various life history characteristics of stream macroinvertebrates. Yet, directly emphasising the relationships between particular traits and ecosystem functioning might further increase our understanding of freshwater ecosystems.

A few studies have examined functional biodiversity along multiple non-anthropogenic environmental gradients. Finn & Poff (2005) used nine traits for describing variation in the functional structure of stream insect assemblages of mountain streams. They found that functional structure varied primarily with periphyton biomass and particle size, although the longitudinal position was also important. Heino (2005b) concentrated on the macroinvertebrates of boreal lowland streams, and used a combination of functional feeding groups (Cummins, 1973) and habit trait groups (Merritt & Cummins, 1996). Functional feeding groups refer to the feeding modes and approximate food type of macroinvertebrates, whereas information on where food is obtained (e.g. on stones versus within sediments) is used to derive habit trait groups. Functional structure showed both spatially-structured and environmentally-related variation, with pH, stream size and moss cover being among the most important variables. Three measures of functional diversity (functional richness, diversity and evenness) decreased with water acidity, canopy cover and water colour, and increased with moss cover. In a similar study on the functional biodiversity of lake littoral macroinvertebrates, a general finding was that functional structure and diversity varied strongly along gradients in macrophyte cover and lake area (Heino, 2008a). The above findings were somewhat surprising, because some authors have suggested that the trait structure of assemblages varies only little along natural environmental gradients, and virtually no variation is related to geographical location (Charvet et al., 2000; Statzner et al., 2001b). These discrepancies between studies are apparently due to the types of functional traits used and analytical methods. However, despite these methodological differences, theory suggests that functional traits should be strongly related to environmental gradients, be they of natural or anthropogenic origin (Poff, 1997).

A question pertaining to the utility of functional traits in the description of freshwater macroinvertebrate biodiversity has been tackled recently: do functional traits provide more and complementary information to that provided by species? This question is important, because if there are no clear differences in assemblage patterns
between the functional trait and taxonomic approaches, then it may not be necessary to allocate taxa to various functional categories. Recent studies have suggested that both functional groups and taxa show relatively similar assemblage patterns along major environmental gradients (Finn & Poff, 2005; Heino et al., 2007a). Furthermore, diversity measures based on functional groups (e.g. number of functional groups) have been found to be strongly related to similarly derived taxonomic measures (e.g. number of species) in both lentic and lotic macroinvertebrates (Heino, 2008a; Heino et al., 2008).

**Patterns in the taxonomic variability of assemblages**

Species richness and diversity indices have traditionally been used to assess variability in biodiversity across near-pristine and anthropogenically altered ecosystems (Magurran, 2004). However, it has been suggested that biodiversity measures should not only portray variability in species richness and relative abundances, but also take into account the evolutionary relatedness of species (Harper & Hawksworth, 1994). For this purpose, Clarke & Warwick (1998) devised a set of taxonomic distinctness indices that take into account the taxonomic relatedness of species. Thus, an assemblage that harbours distantly-related species from, for example, different phyla is more diverse than an assemblage with the same number of species from just one family. Taxonomic distinctness indices have been widely used in marine studies (Warwick & Clarke, 1998; Rogers et al., 1999; Ellingsen et al., 2005), but research on the taxonomic variability of assemblages has just begun with aquatic insects.

Three recent studies on aquatic insects have addressed taxonomic variability based on the taxonomic distinctness indices. These studies have not only considered variability in near-pristine ecosystems, but have also examined biodiversity along anthropogenic gradients. Campbell & Novelo-Gutierrez (2007) studied the response of taxonomic distinctness of odonate assemblages to dam impoundment and detected reduced values after the construction of hydroelectric impoundment. Abellán et al. (2006) found that the taxonomic distinctness of aquatic beetle assemblages responded more weakly than species richness to anthropogenic alteration of inland waters in Spain. This finding is, in part, in accordance with those from Finland, where neither taxonomic distinctness nor species diversity indices varied between near-pristine and anthropogenically altered streams (Heino et al., 2007b). However, because taxonomic distinctness and species diversity indices were at best weakly correlated, both groups of indices should be used in biodiversity assessment. By contrast, Marchant (2007) found that taxonomic distinctness values of stream insect assemblages from anthropogenically altered sites were often below expectations of random draws of species from the species pools (see also Clarke & Warwick, 1998), and taxonomic distinctness was also negatively correlated with a water quality gradient that described variation in turbidity and total phosphorus. Thus, it was suggested that, due to a high number of species and taxonomic variability in the dataset, a taxonomic distinctness index was able to separate near-pristine and anthropogenically altered sites (Marchant, 2007). Accordingly, taxonomic distinctness indices in the other two studies on aquatic insect assemblages may not have performed well due to a more limited number of species or higher taxa. Given that measures of taxonomic variability of assemblages are important in biodiversity assessment, not only environmental researchers but also biodiversity researchers should include taxonomic distinctness indices in their toolbox.

**Higher taxon surrogates for species-level patterns**

The higher taxon approach in biodiversity research has usually been directed at examining genus and family richness as surrogates for species richness. These studies have generally concluded that the numbers of higher taxa are typically strongly correlated with species richness (Williams & Gaston, 1994; Balmford et al., 2000; Gaston, 2000). By contrast, very few studies have directly examined cross-taxonomic level patterns in assemblage composition, so it is uncertain if patterns in assemblage composition are similarly strongly congruent between taxonomic levels as
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with taxon richness patterns. It has been suggested that assemblage patterns between different taxonomic levels are strongly congruent in regions where there are low species-to-genus and species-to-family ratios, whereas congruence diminishes in regions with high species diversity, resulting from high degrees of adaptive radiation (Hawkins & Norris, 2000). These suggestions remain to be studied rigorously with aquatic insects.

Freshwater research has traditionally concentrated on examining the importance of taxonomic resolution in bioassessment, whereas few biodiversity studies have addressed higher taxa as surrogates of species-level diversity. A number of lessons can be drawn from bioassessment studies. First, species richness has often been found to be correlated with genus and family richness (Guerold, 2000; Hill et al., 2001; Marshall et al., 2006). Also, patterns of assemblage composition of different taxonomic levels are typically strongly correlated (Bowman & Bailey, 1997; Marshall et al., 2006; Heino, 2008b). Second, higher taxa often respond similarly to species to major environmental gradients (Furse et al., 1984; Marchant et al., 1995; Feio et al., 2006). Third, although genus- and family-level identifications of stream macroinvertebrates are less expensive and time-consuming than species-level identifications (Marshall et al., 2006), the latter are necessary when the interest is in community ecology and species distribution for conservation purposes (Furse et al., 1984; Bailey et al., 2001; Lenat & Resh, 2001). Studies addressing the higher taxon approach for biodiversity and conservation purposes have generally corroborated the findings from bioassessment research, with patterns in taxonomic richness and assemblage composition being highly similar at species, genus and family levels (J.F. Wright et al., 1998; Heino & Soininen, 2007). Thus, because higher taxa show patterns similar to those of species, they can be used in rapid biodiversity assessments, the goal of which is to assess and rank a large number of sites according to their relative biodiversity value. Such approaches may be the only option for studies in tropical regions lacking taxonomic information at the species level, and higher taxon surrogates have thus been used as estimates of species-level biodiversity patterns (Jacobsen et al., 1997; Jacobsen, 2004).

Conclusions

Biodiversity patterns exhibited by aquatic insect assemblages are complex. This complexity is seen in the environmental relationships of both species richness and assemblage composition. In general, multiple environmental variables are needed to understand variation in the diversity of aquatic insects. Although a few major environmental gradients, such as habitat size and acidity, typically account for a modest amount of variability in aquatic insect assemblages, other minor factors are also often required to understand variation in diversity. This is especially true in cases where there is no single dominant environmental gradient which has an overriding effect on biodiversity. Knowing assemblage–environment relationships is valuable for conservation planning, and generally sites along different parts of major environmental gradients should be protected to conserve α-, β- and γ-diversity of aquatic insect assemblages (Clarke et al., 2008).

However, our knowledge of various aspects of aquatic insect biodiversity is woefully incomplete. For example, understanding one of the oldest patterns in ecology, the latitudinal diversity gradient (Hawkins, 2001), is severely hindered by the lack of both distributional data at broad scales and comprehensive surveys of aquatic insect assemblages across long south–north gradients. A challenge to future studies is thus to survey local assemblages along latitudinal gradients. More than that, researchers should aim at comparing the relative importance of geographical position, regional factors, watershed characteristics, and ecosystem and habitat variables for aquatic insect diversity across large geographical extents. There are emerging possibilities for such studies in Europe, and recent research on streams has already touched this topic (Johnson et al., 2007). However, there are severe problems in studies of local ecosystems across large geographical extents. One such problem relates to the species-level identification of the aquatic larval stages of insects. Given that taxonomic knowledge is unevenly distributed among countries, large-scale surveys in poorly known areas could utilise higher taxa as surrogates for local species-level diversity.
patterns at least in the early phases of inquiry into large-scale patterns (Jacobsen, 2004). Such surrogates have proved promising in previous environmental assessment and biodiversity studies (J.F. Wright et al., 1998).

In addition to species richness and assemblage composition, other measures of biodiversity should be given more attention in research on aquatic insect assemblages. For example, it is still a largely unsettled question as to whether measures of the taxonomic variability of assemblages are useful in assessing environmental degradation of biodiversity in freshwater ecosystems. Both negative and positive results have emerged from studies that have used this approach (Heino et al., 2007b; Marchant, 2007). However, even though measures of taxonomic variability of assemblages would not perform well in determining anthropogenic degradation of freshwater ecosystems, the fact that they are at best weakly correlated with various other measures of biodiversity suggests that they should be utilised more widely in studies on aquatic insect assemblages (Heino et al., 2008).

Functional biodiversity should also be given more attention in the freshwater realm. This attention should not only be directed at comparing functional measures between near-pristine and anthropogenically altered ecosystems (Statzner et al., 2001b), but also for the interest of general ecological research. Further attention should thus be given to variation in functional biodiversity across natural environmental gradients, and a simultaneous examination would be of interest into how different functional groups and functional diversity contribute to ecosystem functioning at different parts of environmental gradients (Jonsson et al., 2001). This information is not only of basic ecological interest, but also a prerequisite for separating out variation in functional biodiversity that is accounted for by natural environmental gradients, as opposed to influences of anthropogenic factors on ecosystem functioning.

Finally, because more survey research on freshwater ecosystems and aquatic insect biodiversity has been directed at (i) streams than rivers, (ii) ponds than lakes and (iii) large than small lakes, a challenge for entomologists, ecologists and conservation biologists is to increase our knowledge of biodiversity patterns in large rivers and headwater lakes. Streams and ponds have been used as arenas for testing ecological theory for a long time, and given the easier sampling of small than large freshwater ecosystems, this emphasis on streams and ponds is likely to continue. However, because freshwater biodiversity is in severe crisis (Dudgeon et al., 2006), we should have no excuse for neglecting surveys of large rivers and headwater lakes across extensive regions. Only by knowing biodiversity patterns in various types of freshwater ecosystems, will we be able to predict, conserve and manage aquatic insect biodiversity effectively enough.

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