

Invited review

## Linking ecological function, biodiversity and habitat: a mini-review focusing on older ecological literature

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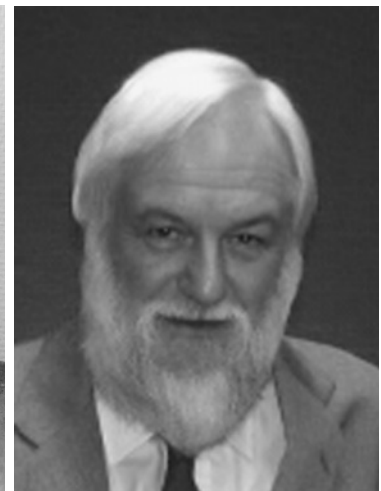
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### Abstract

Current editorial policies of scientific journals in combination with modern technology used for the search of scientific literature intensify the tendency that ecologists lose connections with the knowledge of the past. This is unfortunate because the older ecological literature provides elements for a comparative approach linking ecological function, biodiversity and habitat of large-scale, high-biodiversity systems. Such a comparative approach, seeking common or diverging properties among larger systems, would be a useful complement to current small-scale experimentation, but would require testable hypotheses. Deriving observations, ideas and views from the older ecological literature, we propose such testable hypotheses, linking Ecological processes (EP), Biodiversity (BD), Habitat complexity (HC), Habitat harshness (HH), Habitat extent (HE), Size of organisms (S) and Longevity of organisms (L) in ecosystems through

$$EP \propto BD^{x1} \propto HC^{x2} \propto HH^{-x3} \propto HE^{x4} \propto S^{x5} \propto L^{x6}.$$

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This set of allometric relations represents a sort of null model. We use heterotrophic stream ecosystems as an example to illustrate how these hypotheses could be tested, how observed deviations may improve the mechanistic understanding of a system and how our approach could serve to assess scenarios of biodiversity changes. We also briefly discuss how properties of different ecosystem types could be compared with our approach.

Gegenwärtige Praktiken von Herausgebern wissenschaftlicher Zeitschriften sowie die Nutzung moderner Technologien bei der Beschaffung wissenschaftlicher Literatur verstärken die Tendenz, dass Ökologen älteres Wissen kaum noch beachten. Dies ist bedauerlich, da die ältere ökologische Literatur Elemente für eine vergleichende Methodik enthält, die ökologische Funktion, Biodiversität und Lebensraum von großräumigen, hochdiversen Systemen verknüpft. Solch eine vergleichende Methodik, die gemeinsame oder divergierende Eigenschaften von Systemen zu ergründen sucht, würde eine nützliche Ergänzung zu gegenwärtigen Experimenten mit kleineren Systemen sein. Allerdings benötigte man zur Anwendung dieser vergleichenden Methodik prüfbare Hypothesen. Wir schlagen solch prüfbare Hypothesen vor, die wir aus Beobachtungen, Ideen und Auffassungen der älteren ökologischen Literatur ableiten. Dafür verknüpfen wir ökologische Prozesse (EP), Biodiversität (BD), Lebensraumkomplexität (HC), Lebensraumrauheit (HH), Lebensraumausdehnung (HE), Körpergröße von Organismen (S) und Lebensdauer von Organismen (L) in Ökosystemen durch

$$EP \propto BD^{x1} \propto HC^{x2} \propto HH^{-x3} \propto HE^{x4} \propto S^{x5} \propto L^{x6}.$$

Dieser Satz von allometrischen Beziehungen repräsentiert eine Art von Nullmodell. Am Beispiel heterotropher Fließwasserökosysteme zeigen wir, wie diese Hypothesen geprüft werden könnten, wie abweichende Beobachtungen das mechanistische Verständnis eines Systems verbessern könnten und wie unsere Methodik zur Beurteilung von Szenarien veränderter Biodiversität dienen könnte. Zudem diskutieren wir, wie Eigenschaften verschiedener Ökosystemtypen mit unserer Methodik verglichen werden könnten.

**Key words:** allometric rules – body size relations – freshwater, marine and terrestrial ecosystems – P/B-ratio – productivity – species loss – stream invertebrates

## Introduction

In 1840, Justus Liebig made perhaps the first scientifically argued link among ecological function, biodiversity and habitat. He showed that, within a given area, plants as different as forest trees, grass, grains and turnips all produce the same quantities of carbon per year, “no matter how endlessly varied the conditions of growth of the plants” (Werner & Holmes 2002, p. 425). These early results were confirmed by a project of the International Biological Program (IBP) in the 1960s, which assessed the productivity of a beech forest (age: 80 yrs), a spruce forest (age: 41 yrs), a fertilized meadow and a fertilized culture of the Italian ryegrass (*Lolium multiflorum* Lam.) in the region Liebig worked in the 1840s. These different types of plant communities had a similar net primary production (range:  $504\text{--}556 \times 10^5 \text{ kcal ha}^{-1} \text{ yr}^{-1}$ ) and efficiency (range of the net primary production efficiency: 1.02–1.30% of the global radiation during the vegetation period) (Runge 1973).

Given that current editorial policies of scientific journals in combination with current technology used for the search of scientific literature intensify the tendency that ecologists lose connections with the past (Statzner et al. 2001), it is not surprising that such

older references are usually not discussed in recent publications on links among ecological function, biodiversity or habitat (e.g., for plants, see Hector et al. 1999, Sankaran & McNaughton 1999, Aarssen 2001, Lundblad & Lindroth 2002, Güsewell & Bollens 2003, Peintinger et al. 2003). This is unfortunate because the older ecological literature still has much to contribute to the current debate on biodiversity and ecosystem function, so we focus this mini-review on older studies and views being relevant for the subject.

A major difference of the ecological approach at the beginning of the last century and today is that the former relied primarily on observations, descriptions and comparisons of large-scale, high-diversity systems (e.g. Warming & Vahl 1909, Thienemann 1918, Hesse 1924, Elton 1927) whereas the latter relies primarily on experiments with small-scale, low-diversity systems (e.g. Naeem et al. 1994, 2000, McGrady-Steed et al. 1997, Petchey et al. 1999, Gessner et al. in press). Thus, the older ecological literature could provide elements for a comparative approach that assesses biodiversity and ecosystem function of large-scale, high-biodiversity systems. Such a comparative approach, seeking common or diverging properties among larger systems, would be a useful complement to current small-scale experimentation, but would require testable hypotheses.

Here, we propose such testable hypotheses, which are derived from four sources: (1) the ideas of pioneers in plant and animal ecology (e.g. Warming & Vahl 1909, Thienemann 1918, Hesse 1924, Elton 1927); (2) the functional assessment of ecosystems and populations, initiated through the trophic-dynamic approach of Lindeman (1942), and considerably advanced during the IBP in the 1960s - 1970s (e.g. Le Cren & Lowe-McConnell 1980); (3) considerations of the ecological implications of body size, which have been a key topic since the beginning of ecology (e.g. Semper 1880, Elton 1927, Peters 1983, Bonner 1988, Niklas & Enquist 2001, Carbone & Gittleman 2002); and (4) some basic principles of fluid dynamics that rule the physical forces acting on organisms (e.g. Von Gelei 1928, Vogel 1994), and thus provide a mechanistic explanation for one of the few universal "laws" in ecology (Lawton 1999). From these four sources, we obtain a set of allometric rules that can be used to predict correlative relationships between ecological function, biodiversity and habitat. This set of allometric rules represents a sort of null or baseline model, resembling "a thought experiment that allows us to explore the range of possible worlds and patterns" (Gotelli & Graves 1996, p. 4).

We use heterotrophic stream ecosystems as an example to illustrate how these hypotheses could be tested, how observed deviations may improve the mechanistic understanding of a system and how our approach could serve to assess scenarios of biodiversity changes. We also briefly discuss how properties of different ecosystem types could be compared with our approach.

### Hypotheses

There are a number of variables that the older ecological literature links to biodiversity and among themselves. A series of relations among these variables can thus be proposed with a background of some rationality. If one of these relations links biodiversity with ecological function and if several variables are used within the set of relations, demonstration of the validity of increasing numbers of relations within the same set of systems would increase the probability that diversity has importance at the large scale. We propose here a theory for testing, using deliberately a low number of variables and briefly suggesting ways in which these may be defined and assessed.

The variables proposed are as follows:

(a) *Ecological processes*, (EP), a measure of ecological function that could be an absolute rate such as the amount of carbon processed per unit time or per unit area. Alternatively, it could be a specific rate such as

the amount of carbon processed per unit biomass, per unit of energy input or per unit of nutrient resource. We separate absolute and specific rates as they may respond differently to other variables used here; this point will be re-considered when we examine patterns observed in heterotrophic stream ecosystems.

(b) *Biodiversity*, (BD), which might be measured as species richness, equitability, number of functional groups, number of trophic levels, number of species within a functional group or trophic level or even number of genetic strains.

(c) *Size*, (S), of organisms within a system, using mean, median or maximum body size or size frequency distributions of organisms in populations or the whole assemblage. Obviously, this variable is difficult to define for modular organisms. Despite of this problem, size has been frequently considered as a key variable for two reasons. First, it is known since about hundred years that size has tremendous implications for various ecological functions. For example, in 1880 Semper argued that about 10% of the biomass is transferred between trophic levels (from plants to herbivores as well as from herbivores to carnivores), and in 1927 Elton concluded that animal size increases but animal numbers decrease along herbivore-carnivore food chains. In other terms, small animals are more abundant and produce more organic matter than larger ones, or the longer a food chain, the larger the animals in the top level are and the more of the organic matter produced by plants is mineralised by animals. Second, size largely interferes with the forces experienced by an organism living in a moving fluid such as air or water. The first who treated this subject in a comprehensive physical context was Von Gelei (1928), who corresponded with the famous hydrodynamicist Prandtl. This early work introduced elements from fluid dynamics into a debate about body size and shape of aquatic organisms in relation to flow constraints.

(d) *Longevity*, (L), of organisms within a system, using mean, median or maximum age or mortality rates of organisms in populations or the whole assemblage, or the frequency distribution of age or mortality. Again, this variable is difficult to define for modular organisms. Despite of this problem, work done in the IBP demonstrated that longevity, mean age and mortality rates have major implications for ecological processes such as the production-biomass ratio (e.g. Lévêque et al. 1977). In addition, longevity, age and mortality rates indicate the potential vulnerability of organisms to disturbances.

(e) *Habitat complexity*, (HC), measured as number of recognisable patches or number of recognisable "subhabitats", or as random samples of habitat variables. Analysing the latter with multivariate tech-

niques, such measures can be used to assess overall habitat complexity (e.g. Cellot et al. 1994).

(f) *Habitat extent*, (HE), measured as size of the physical habitat structure. This will be simpler for a pond or fragmented terrestrial landscapes than for more continuous land- and waterscapes. For the latter, analyses of measured habitat variables with multivariate techniques can be used to detect the extent of similar spatial structures (e.g. Thioulouse et al. 1995).

(g) *Habitat harshness*, (HH), measured either as mean or minimum/maximum of abiotic variables such as wind or water current, or as degree of unpredictability of such abiotic variables over time (e.g. as coefficient of variation). This simple approach is appropriate for the assessment of a single variable. However, it might require some re-scaling when working across a major gradient of habitat harshness (e.g. very cold habitats may provide a similar degree of harshness as very hot habitats, i.e. minimum and maximum temperature would score "1" for HH, whereas optimum temperature would score "0"). If several variables have to be considered simultaneously, multivariate techniques can provide a synthetic measure for HH (e.g. Cellot et al. 1994).

With seven variables there are 21 possible paired relations ( $7 \times 6/2$ ). Addition of more variables would increase the rigour of the hypotheses, and demonstration, within a set of systems, of the validity of an increasing number of these relations increases the probability that all are true, or conversely, false. To link these seven variables, we use the six most reasonable (in our view) relations of the 21 possible pairs and express them in form of proportionalities to power terms, because such variables often scale non-linearly as allometric relations (e.g. Peters 1983, Niklas & Enquist 2001). However, using allometric relations is no judgement of the precise nature of the relation, because hump-shaped response curves may be more realistic in some cases (as discussed below). The six relations are as follows:

$$EP \propto BD^x. \quad (i)$$

According to the current ecological debate, the ultimate hypothesis to be tested is that BD enhances EP and vice versa. For example, does increasing species richness enhance productivity at a given level of nutrient availability (e.g. Schmid 2002)? Already the older ecological literature produced equivocal support for this hypothesis. Results of Liebig (1840) and later Runge (1973) that illustrated similar productivity in very different plant communities suggest to reject it, whereas the views of Semper (1880) and Elton (1927) that longer herbivore-carnivore food chains mineralise more of the organic matter produced by plants suggest to accept it.

$$BD \propto HC^x. \quad (ii)$$

There is abundant evidence in the older ecological literature that a more complex habitat has more species than a simple one (e.g. Thienemann 1918, Hesse 1924).

$$BD \propto HH^{-x}. \quad (iii)$$

Another rule repeatedly addressed by the older ecological literature is that species richness decreases with increasing habitat harshness (e.g. Thienemann 1918, Hesse 1924). Thus, habitats with unpredictable, extreme (minimum or maximum) abiotic conditions (e.g. wind exposed sand dunes, wave exposed shores) have fewer species than equable ones (e.g. tropical forests, calm bays). Likewise, habitats with predictable, extreme abiotic conditions (e.g. hot springs) have fewer species than less extreme ones (e.g. cool springs).

$$HC \propto HE^x. \quad (iv)$$

Almost by definition, the complexity of a habitat increases as it gets bigger, and early ecologists described this phenomenon when discussing related biodiversity patterns (e.g. on islands, see Hesse 1924).

$$S \propto HE^x. \quad (v)$$

Larger habitats provide the space required by larger organisms, which is another relation discovered in the pioneer age of ecology (e.g. Semper 1880, Elton 1927).

$$L \propto S^x. \quad (vi)$$

Early observations that longevity of organisms increases with their size (e.g. Levander 1900, cited after Hesse 1924, Warming & Vahl 1909) were generally supported by subsequent work of ecological pioneers, although they questioned this relation when analysing a smaller size range of organisms (e.g. cicindelid beetles, see Pearse 1926). Thus, to apply eq. (vi), the size range of the organisms included into the analysis should be as great as possible.

As a result of these six relations, the overall link among all our seven variables becomes

$$EP \propto BD^{x1} \propto HC^{x2} \propto HH^{-x3} \propto HE^{x4} \propto S^{x5} \propto L^{x6}. \quad (vii)$$

Thus, the six initial relations used by us produced others such as harsher habitats (1) will support smaller organisms than more benign habitats; (2) will support organisms with shorter longevity and thus lower vulnerability to disturbance than more benign habitats; (3) will be simpler in their structural complexity, etc. These indirectly derived relations also correspond to early discoveries in ecology (e.g. Buxton 1923, Hesse 1924).

However, older views and evidence in ecology suggest that our previously developed construct may not apply to systems that are too small. For such smaller subsystems, both the theory of succession and the intermediate disturbance hypothesis link biodiversity patterns to ecological functions along gradients of succession or disturbance (Odum 1971, Connell 1978).

Biodiversity responds with a hump-shaped curve, and lower diversity in an early successional stage (or frequently disturbed system) is associated with high turnover rates, whereas lower diversity in a late successional stage (or a rarely disturbed system) is associated with maintenance (see Aarssen 2001, for a recent review of alternative hypotheses of the hump-shaped species richness response curve). Thus, for smaller subsystems, our eq. (i) and (iii), and consequently also eq. (vii), may only apply to systems that are in the range of early to intermediate succession respectively frequent to intermediate disturbance. In contrast, these equations should consistently apply to big systems, because the latter include patches of early successional stages (e.g. tree gaps in a forest) or local disturbance (e.g. fire patches in a prairie). Therefore, big systems integrate across local patchiness in biodiversity and ecological processes, and our hypotheses focus on the overall properties of such big systems.

Evidently, testing of the relations suggested by eq. (vii) could be quite complex. First, with six “chained” hypotheses between seven variables, error propagation as well as confounding indirect effects could become a problem in practical applications (see Peters 1991). Second, testing of these relations could not be done on laboratory, solely microbial, systems because the size components (of the organisms and the habitat) would be too narrow. It would also be difficult on real systems (stream-estuary-coastal zone or stream-wetland-pelagic) because of the amount of work involved in handling say five different systems with adequate replication of each. One compromise would be to do it on a stream order sequence, in a set of streams with varying impact of acid precipitation, in a group of small lakes differentially impacted by eutrophication, in mesocosms containing at least microorganisms and invertebrates and impacted by nutrients, temperature or toxins, in a set of natural ponds including some that are permanent and some that dry up, or in a set of hot and cool springs, to create the complexity and include locations that provide the harshness.

#### Patterns in benthic stream invertebrates

Given that the previous hypotheses were derived *a priori* from the older ecological literature, we briefly assess them here, using existing knowledge on benthic stream invertebrates as an example. Our hypotheses try to circumvent the problem of species/taxa identity by including body size as a key variable to assess and predict ecological function (see Morin 1997, for a similar approach using stream invertebrates), so we begin with invertebrate size.

Assessments of the size distribution of species are difficult and often biased (e.g. Peters 1983), particularly

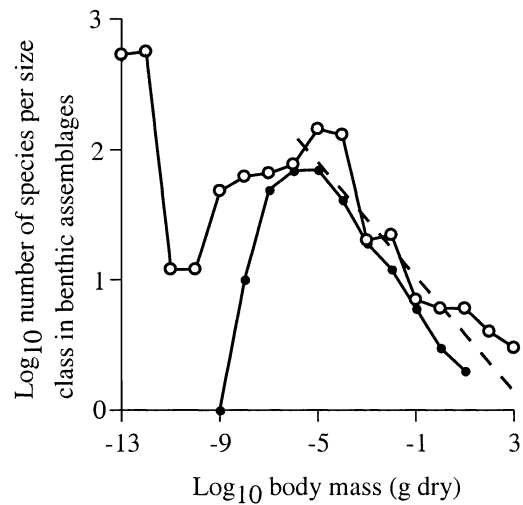


Fig. 1. Typical, hypothesized body size distribution of species in a benthic freshwater assemblage (open circles, redrawn after Palmer et al. 1997) and a benthic stream invertebrate assemblage (solid circles, after data in Statzner 1979 and Schmid et al. 2000). The broken line has a slope of  $\approx -0.2$ .

towards the smaller sizes. An approximate, hypothesized distribution in a “typical” freshwater sediment ecosystem (Palmer et al. 1997) shows that the distribution does not monotonously increase towards smaller size classes (Fig. 1). Likewise, the curve showing the size distribution of benthic stream invertebrates does not monotonously increase towards smaller size classes (Fig. 1). This latter curve combines data from a study that sampled relatively small areas with a small mesh size in the UK (Schmid et al. 2000) with that from a study sampling intermediate to very large areas with intermediate to large mesh sizes in Germany (Statzner 1979). Thus, the invertebrate curve includes protozoa (Testacea) as well as large mussels (Unionidae). Despite the small mesh size used in the UK, it is obvious that mesh effects should bias towards a falling distribution curve at smaller size classes if body size becomes smaller than the mesh size. On the other hand, the fall of the curve towards the larger size classes ( $w > 10^{-5}$  g) should reflect an unbiased pattern. It links the biodiversity per size class (BDs) to specific body mass ( $w$ , g dry mass) by

$$BD_s \propto w^{-0.2}. \quad (1)$$

The UK stream studied by Schmid et al. (2000) had 260 invertebrate species, for which the relation of mean annual population densities ( $D$ , individuals  $m^{-2}$ ) and  $w$  were compared with that of 448 species in an Austrian stream. For both streams, this relation is

$$D \propto w^{-0.7}. \quad (2)$$

The exponent of this relation varies considerably among different taxonomic groups (range:  $-1.0$  in Turbellaria to  $-0.2$  in Hydracarina). In contrast, densi-

ty changes similarly with body mass if the populations are re-grouped to compare detritivorous vs. predatory/omnivorous species, species from stream 1 vs. stream 2, or species common to both streams vs. species typical for each stream. The species richness of these groupings ranges from 50–448, i.e. eq. (2) should be relatively stable across richness gradients of different streams. This view is supported by the relative stability of density-weight relations observed for Canadian stream invertebrate assemblages that differ clearly in their taxonomic composition (Bourassa & Morin 1995). However, a world-wide analysis of 670 stream invertebrate taxa (Morin 1997) provides a greater exponent ( $-0.5$ ) than that in our eq. (2), perhaps because these world-wide data consider the size spectrum across populations and not in real assemblages. Despite this deviation, eq. (2) provides a fundamental relation for our subsequent reasoning.

For aquatic ecosystems that differ considerably in size (ranging from microcosms to the world oceans), the maximum body size observed in the assemblages increases with ecosystem area (Kamenir et al. 1999). To scale such relations between body size and habitat extent, Peters (1983) used mammals, birds and lizards as examples. He argued that the space needed by the individuals of different species should be related to the inverse of the density-weight relation in eq. (2), the so-called individual area ( $A_i$ ,  $m^2$  individual $^{-1}$ ), which would be for stream invertebrates

$$A_i \propto w^{0.7}. \quad (3)$$

Thus, from eq. (1) and (3) we obtain, for the larger body size classes,

$$BD_s \propto w^{-0.2} \propto A_i^{-0.3}, \quad (4)$$

which is a quantitative relation between biodiversity, body size and habitat extent if  $w > 10^{-5}$  g. It tells us that smaller invertebrates have more species that need less space than larger invertebrates. Thus, if habitat extent increases, invertebrate assemblages would have larger species added (though at a decreasing rate) so that biodiversity would increase, and the mean body mass of the assemblages would also increase; these patterns support eq. (vii). However, if  $w < 10^{-5}$  g, eq. (4) cannot be applied, perhaps because smaller invertebrates were not quantitatively sampled with the used mesh size (see above) or because benthic invertebrates are not representative for the entire size-spectrum of organisms in stream systems (see Fig. 1).

Habitat extent of running water sections of identical length is indicated by channel width (proportional to space in  $m^2$ ), which is approximately proportional to the discharge  $Q$  (in  $m^3 s^{-1}$ ; see Leopold et al. 1964) by

$$\text{width} \propto Q^{0.2}. \quad (5)$$

Therefore, an ecological process such as annual tissue weight production ( $P$ , g dry mass  $m^{-2} yr^{-1}$ ), which is an absolute process rate, should increase with the discharge in a section (see eq. vii). Based on production estimates for 31 invertebrate assemblages (Benke 1993), this is the case for primary invertebrate consumers if the mean annual discharge is  $>0.02 m^3 s^{-1}$ , because, approximately (re-estimated from a polynomial equation in Benke 1993),

$$P \propto Q^{0.3}, \quad (6)$$

and thus

$$P \propto \text{width}^{1.5}. \quad (7)$$

Thus, productivity per unit area increases with habitat extent, but only above a discharge threshold of  $0.02 m^3 s^{-1}$ , whereas below this value, productivity decreases with habitat extent. These different trends at lower and higher discharge levels may be related to three complications caused by longitudinal (i.e. along increasing discharge) patterns prevailing in running water systems, which illustrates how confounding effects can interfere with the testing of eq. (vii).

First, mean habitat harshness caused by the near-bed flow does not monotonously decrease with increasing habitat extent along running waters. Along a gradient of increasing mean annual discharge in running water sections, mean annual shear stress and thus shear velocity ( $U_*$ ) near the bed increases towards intermediate discharge levels, and then monotonously decreases with further increasing discharge (Statzner et al. 1988). Putting the complex relations (see Vogel 1994) among flow forces, body size and near-bed flow into a nutshell, it is reasonable to assume that the drag and lift force experienced by an invertebrate individual at a given near-bed velocity increases with its body size. Therefore, with increasing near-bed velocity ( $U_*$ ,  $cm s^{-1}$ ), mean body size (i.e.  $w$ ) in invertebrate assemblages should follow

$$w \propto U_*^{-x}, \quad (8)$$

i.e. body size decreases with increasing mean habitat harshness (indicated by  $U_*$ ), which supports eq. (vii). However, as  $U_*$  does not monotonously decrease with increasing habitat extent in running waters, eq. (vii) is difficult to apply to entire running water systems and support of it provided by eq. (7) is limited to sections with elevated discharge.

Second, the ecologically relevant habitat extent along running waters is not equally described through mean annual discharge or channel width, because the relative importance of local riparian influences on local processes in a section decreases on a downstream gradient (e.g. Minshall et al. 1983). Thus, in comparison to larger streams and rivers, discharge or channel width of smaller headwater streams (e.g. with a dis-

charge  $<0.02 \text{ m}^3 \text{ s}^{-1}$ ) may be not sufficient to characterize the ecologically relevant habitat extent (i.e. the properties of the relevant, bigger system).

Third, physical habitat harshness in terms of rapidity and height of flood responses to rainfall in a running water section decreases with increasing catchment size (Gordon et al. 1992). This pattern corresponds to the predicted relation between habitat harshness and habitat extent in eq. (vii); the observed invertebrate productivity, however, does not consistently increase with increasing mean annual discharge (and thus catchment size). Thus, it seems that habitat harshness in terms of rapidity and height of flood responses to rainfall has less impact on invertebrate productivity patterns than the two previously discussed factors.

For a last check of eq. (vii), we assess body size relations with a specific process rate and longevity. A universal measure that describes the functional efficiency (at an annual rate) of a population is the ratio of annual tissue weight production (P,  $\text{g m}^{-2} \text{ yr}^{-1}$ ) per unit of mean annual biomass (B,  $\text{g m}^{-2} \text{ yr}^{-1}$ ) (Peters 1983). Based on world-wide studies of >1500 populations of stream invertebrates (Benke 1993), the annual P/B-ratio relates to the maximum individual weight (w) reached by the specimens in these populations by

$$P/B \propto w^{-0.25}. \quad (9)$$

Concerning longevity (L, yr) in lotic invertebrate populations of two streams, it increases almost linearly with the maximum body mass (w) (see Statzner 1987), i.e.

$$L \propto w^{1.0}. \quad (10)$$

Thus, using longevity as an indicator of vulnerability (see hypotheses), larger species would have a greater probability of experiencing a disturbance event and, because of their longer life cycles, would have a lower potential to recover from such an event than smaller species. This assumption needs clarification: even if mammals or birds are considered, there is no consistent answer to how vulnerability, or risk of extinction, relates to the maximum body mass of a species (Gaston & Blackburn 2000).

Combining eq. (9) and (10) with the previously described invertebrate patterns implies that, if invertebrates have a body mass  $>10^{-5} \text{ g}$  and discharge is not too low, an increase of habitat extent would increase biodiversity through the addition of larger species (at a decreasing rate) to the assemblages. Mean body mass, mean longevity and the absolute process rate annual productivity per unit area of habitat of the assemblages would increase, but the mean specific process rate P/B of the assemblages, i.e. a function provided per unit biomass, would *decrease*. This example sug-

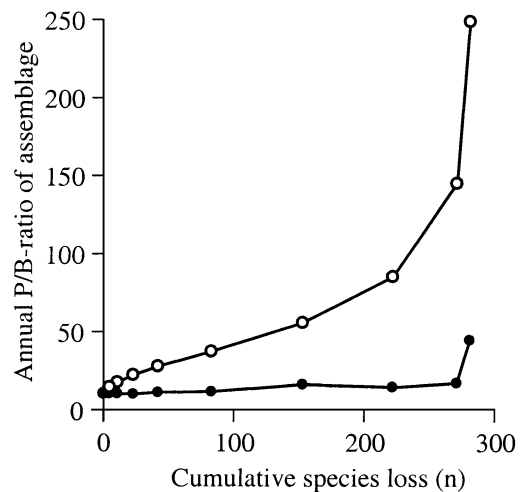


Fig. 2. Annual Production/Biomass-ratio (P/B) of simulated stream invertebrate assemblages for 2 scenarios of species loss (open circles: all species of a given body size class [see Fig. 1] subsequently disappear from large to small size; solid circles: at each loss event of the previous scenario, the same number of species disappears, but species are lost at random [i.e. independently of body size]). See text for further details.

gests that eq. (vii) may be difficult to apply for both absolute and specific process rates. Nevertheless, our exercise on stream invertebrates illustrates ways how the hypotheses of our approach could be tested and how observed deviations from the hypotheses may lead to better mechanistic understanding.

If improved by solid tests, the types of relations in our hypotheses may provide considerable insights into the functional consequences of biodiversity changes, which we demonstrate through a simple example here. The relation between P/B and body size (eq. 9) is in principle caused by physiological factors (larger stream invertebrates use more energy for respiration and thus maintenance and less energy for tissue production than smaller ones; Statzner 1987) and should be independent of the biodiversity itself. Likewise, eq. (2) seems to be relatively stable across richness gradients (see above).

Therefore, we use these relations (plus additional information provided by Benke 1993 and Schmid et al. 2000, e.g. about temperature effects on P/B) to illustrate, for two scenarios of species loss, how P/B (at a mean annual water temperature of  $10 \text{ }^\circ\text{C}$ ) would change for an assemblage with a similar initial species number-body size distribution of benthic invertebrates to that given in Fig. 1. Scenario 1 assumes that all species of a given size class subsequently disappear in sequence from large to small size during repeated loss events, whereas scenario 2 assumes that, at each loss event, an identical number of species is lost to that in scenario 1, but this time the species are lost at random.

Given that larger species are less numerous than species of intermediate size (see Fig. 1), the loss of a large size class in scenario 1 has only minor effects on the overall species richness of the assemblage and causes only a minor increase of the assemblage P/B (Fig. 2). However, if intermediate size classes subsequently disappear in scenario 1, the cumulative species loss and the P/B of the assemblage rapidly increase (Fig. 2). With further losses of size classes, the P/B increases towards values that are an order of magnitude greater than that of the initial, entire assemblage. In contrast, in scenario 2, the P/B remains relatively stable with increasing cumulative species loss, i.e. it does not dramatically increase until a single species remains (Fig. 2).

These two simple scenarios illustrate the outstanding importance of size in any consideration of species loss and function. Thus, the above equations, all established for benthic stream invertebrates, do not only provide examples for specific tests of our hypotheses: they also enable the identification of issues that require particular research efforts.

#### Distinctiveness of ecosystem types

Stream invertebrates served as an example to show how our hypotheses can be assessed in field tests. It is evident that other systems have to be considered in the context of the forces that drive their function.

For example, the many IBP studies have shown that, on a global scale, the benthic secondary production of lake invertebrates increases with phytoplankton production (Morgan et al. 1980). Because phytoplankton production is almost non-existent in smaller streams, it cannot have a similar importance for the benthic secondary production of stream invertebrates. Likewise, the density-body size relation in eq. (2) has a considerable greater exponent in the lake zoobenthos ( $-0.4$  instead of  $-0.7$ ; see Strayer 1994), i.e. in lakes density decreases less rapidly with body size than in streams. One reason for this difference could be that the lake zoobenthos is released from size-related physical flow constraints that prevail in streams (eq. 8). On the other hand, if only dominant lake species of the phytoplankton, zooplankton, zoobenthos and fish are included, the exponent varies among lakes between  $-1.1$  and  $-0.7$ , suggesting that there is much more variation in the density-body size relation when more complete assemblages are considered, and that this variation is related to local habitat conditions (Cyr et al. 1997). Furthermore, the size distribution pattern of benthic invertebrate species in streams (Fig. 1) differs considerably from that in marine systems (see Fig. 2 in Strayer 1991), and marine and lacustrine benthic invertebrate assemblages differ also in their size structures (Strayer 1991, but see Mercier et al. 1999, for similar size struc-

tures of benthic assemblages [including both algae and invertebrates] from streams, lakes and marine littoral zones).

In contrast to stream invertebrates, the species number of terrestrial animals falls more rapidly with increasing size [exponent  $-0.7$  instead of  $-0.2$ , see eq. (1)] along the upper tail of the distribution (Peters 1983). On the other hand, the annual P/B-ratio of terrestrial vertebrates (i.e. those animals near the upper tail of the species richness-size distribution) scales to weight as in the stream invertebrates [exponent  $-0.23$  instead of  $-0.25$ , see eq. (8)] (Peters 1983). Finally, the density-body size relation has a greater exponent in stream invertebrates [ $-0.7$ ; eq. (2)] than in terrestrial plants and in marine phytoplankton ( $-0.8$ ; Belgrano et al. 2002) or carnivorous mammals ( $-0.9$ ; Carbone & Gittleman 2002).

Thus, the effects of size in relation to biodiversity or species loss and ecological function should vary among ecosystem types, i.e. the loss of a given number of large species in one type may have a different consequence for the ecosystem function than the loss of the same number of large species in a second type. Despite these differences, however, the general framework set by our hypotheses should enable appropriate field tests in, as well as comparisons among, all of these different ecosystem types.

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