The Influence of Environmental Heterogeneity on Patterns and Processes in Streams
Author(s): Margaret A. Palmer and N. LeRoy Poff
Source: *Journal of the North American Benthological Society*, Vol. 16, No. 1 (Mar., 1997), pp. 169-173
Published by: The University of Chicago Press on behalf of the Society for Freshwater Science
Stable URL: https://www.jstor.org/stable/1468249
Accessed: 26-08-2019 01:21 UTC

J. N. Am. Benthol. Soc., 1997, 16(1):169–173

HETEROGENEITY IN STREAMS

The influence of environmental heterogeneity on patterns and processes in streams

MARGARET A. PALMER AND N. LEROY POFF

Department of Zoology, University of Maryland, College Park, Maryland 20742 USA

Abstract. This introduction to 9 articles on the influence of heterogeneity on pattern and processes in streams describes why we need to examine heterogeneity and outlines major themes we need to consider. Contributors show that a wide range of lotic patterns and processes may be influenced by physical and biological heterogeneity, including the spatial distribution and persistence of biota, predator-prey interactions, and flux of materials among ecosystem compartments. Authors have relied on both theoretical approaches (e.g., numerical simulation models) and empirical approaches (e.g., manipulative experiments) to garner insights into the causes and consequences of spatial and temporal variability in streams. We outline 6 major themes that emerged from this collection of papers and from the symposium on ecological heterogeneity held at the 1995 meeting of the North American Benthological Society in Keystone, Colorado. These themes encompass much of the nature of heterogeneity, and they have important implications for the study of pattern and process in streams. To elucidate on these themes, we provide specific examples from the papers in this series.

Key words: ecological heterogeneity, temporal and spatial variability, pattern, process, variance, scale.

Stream ecologists have long been aware that lotic systems are amazingly variable across space and time (Hynes 1970). The dynamic nature of streamflow is probably the most obvious form of variability but certainly other factors such as temperature, light, substrate, and resource availability differ seasonally or with position in a stream. Stream ecologists have discussed the notion that variability per se may influence biotic patterns and processes in streams (e.g., Pringle et al. 1988, Downing 1991, Hildrew and Giller 1994) but by far most of the work to date has focused on temporal or position-specific patterns. Recent theoretical and empirical work has suggested that the study of **heterogeneity**, defined as **variability in a process or pattern over space or time**, and of its ecological consequences requires new and more complex conceptual frameworks and empirical approaches (Kolasa and Rollo 1991).

Historically, most ecologists have relied on an equilibrium paradigm to structure their thinking about ecological systems (Wiens 1984, Pickett et al. 1992). Under such a paradigm, systems may be "structured" through biotic coupling, resource limitation, and tight feedback loops. While systems may be structured in a highly predictable way at least for limited time periods (Roughgarden 1989), we are increasingly recognizing that many systems exhibit a combination of deterministic, random, and chaotic behaviors, in part because of the high degree of environmental heterogeneity present in nature (Kolasa and Rollo 1991). This growing recognition suggests that new conceptual frameworks and research methods are necessary to more fully understand the structure and function of ecological systems.

First, we need to de-emphasize the equilibrium paradigm and consider it as a special case (Murdoch 1991), or as a paradigm whose usefulness depends critically on the scale of study (DeAngelis and Waterhouse 1987). Second, we need to de-emphasize simplified field and laboratory approaches that reduce or remove potentially relevant heterogeneity—heterogeneity itself may tell us much about a system and thus be viewed as a factor to *include* in experimental designs (Wiens 1992). Third, we need to accept that biotic and abiotic processes may simultaneously operate to generate biotic patterns, and that both pattern and process may be scale-dependent (Menge and Olson 1990, Levin 1992). Fourth, we need to rethink our empirical approaches so that our measures of heterogeneity have relevance to ecological entities and are not merely absolute and sometimes arbitrary measures that are chosen by convention (sensu **func-**

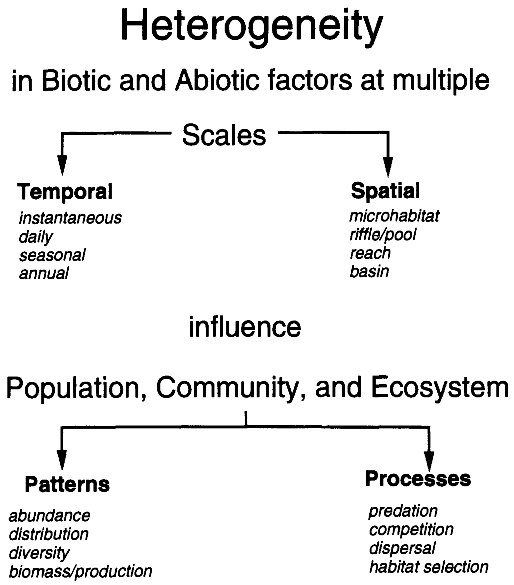

FIG. 1. A schematic illustrating that heterogeneity can occur at multiple spatial and temporal scales for both biotic and abiotic factors and that this heterogeneity influences both pattern and process in ecological systems.

tional vs. measured heterogeneity, Kolasa and Rollo 1991). Fifth, we need to embrace new analytical tools (e.g., fractal analysis, nonlinear modelling) that may open new doors of understanding into how and why heterogeneity is important (Levin 1992).

With these thoughts in mind, we organized a symposium at the NABS 1995 meetings in which participants were asked to consider how we might test for the influence of environmental heterogeneity on pattern and process in streams. This symposium motivated, but did not determine, the collection of papers included in this volume. Because many stream ecologists are working on the role of heterogeneity in streams, we invited contributions from a broad range of scientists with perspectives at the population, community, and ecosystem level. Our goal was to provide a forum for considering how a variety of approaches (theoretical, modelling, empirical) can be used to address a wide range of processes and patterns that may be influenced by many forms of environmental heterogeneity (Fig. 1). These include, for example, the distribution or diversity of biota, predator-prey interactions, community response to disturbance, and ecosystem dynamics.

We specifically hoped contributors would focus on the question of scale, which we believe is embedded in the heterogeneity theme. Large- or small-scale heterogeneity may constrain patterns and processes. For example, predation may be mediated by either local microhabitat heterogeneity within a riffle, by larger reach-scale heterogeneity, or by both. Further, heterogeneity documented at one scale may provide insight into patterns and processes at larger or smaller scales. For example, responses of individuals to resource heterogeneity might inform us about population performance. You will see below that consideration of scale was, indeed, a major focus of this symposium.

Themes in the study of stream heterogeneity

Many themes emerged from the symposium and the discussions that continued after the presentations. Most of these themes are touched on by one or more of the papers in this issue, but all of the themes include research topics that are at the forefront of stream ecology. We summarize 6 of the themes by providing examples from the papers in this issue.

1. Multi-scale analysis

Most of the papers deal either directly or indirectly with scale. Clearly, stream ecology would benefit from the development of a "science" of multi-scale analysis, as is the case for many areas of ecology (e.g., Schneider 1994). In the present collection of papers, Crowl et al. (1997) take a hierarchical approach to nicely demonstrate that predators can control spatial variation in invertebrate abundances in streams. Interestingly though, Downes et al. (1997) present data on streambed disturbance suggesting that it may be dangerous to assume that physical variability at different scales should be viewed as a nested hierarchy (e.g., variability at large scales constrains that at smaller scales but not vice versa). Cooper et al. (1997) support the study of variability at multiple scales as a valuable starting point, but suggest that we can also use alternative and insightful non-hierarchical analyses in the study of stream heterogeneity.

2. Functional perspective

It is far easier to document heterogeneity in physical factors (particularly those easily measured by stream ecologists) than to show that such heterogeneity has biological significance. Despite this, it is imperative that stream ecologists examine heterogeneity from a functional perspective. For us to fully understand how heterogeneity influences ecological patterns and processes in streams, we must identify the mechanisms by which heterogeneity influences individuals, communities, and ecosystems. Valett et al. (1997) suggest that small-scale spatial heterogeneity in biogeochemical processes can be influenced by catchment-scale lithology. The mechanism underlying this link is the constraint lithology imposes on hydrological exchanges across the groundwater–surface water interface. Similarly, Flecker's (1997) work in Andean streams demonstrated that a mechanistic understanding of how fish feed *and* the extent of functional redundancy in guilds of bottom-feeding fish were both necessary to understand the spatial patterns of sediment-accrual in these streams.

3. Dispersal and flux

The study of biotic dispersal and or flux of materials, as a *regional process* that acts to unite or alter heterogeneous systems *locally*, is critical at this juncture in stream ecology. We know far too little about the impact of biotic movements or physical mixing processes on the creation, maintenance, or obliteration of heterogeneity in streams (Palmer et al. 1996). The models of Lancaster and Belyea (1997) reinforce the importance of understanding dispersal dynamics in spatially heterogenous and flow-disturbed streams. Stevenson (1997) stresses that the study of propagule dispersal and nutrient flux may be critical to understanding how habitat heterogeneity influences the structural and functional properties of algal assemblages. Poff and Nelson-Baker's model (1997) suggests that foraging movement of grazers may be dependent on spatial environmental heterogeneity, which in turn affects the spatial distribution and biomass of algae in streams. Finally, Valett et al. (1997) show that the rate and extent of groundwater–surface water fluxes can influence the heterogeneity in interstitial nutrient content in streams.

4. Variance as an ecological metric

Palmer et al. (1997) emphasize why *variance* and not *mean* environmental values may be important in lotic research. The use (and manipulation) of variance as both a dependent and an independent variable may lead to new understandings of how pattern and process are linked in streams. Crowl et al. (1997) and Palmer et al. (1997) use variance expressed as the coefficient of variation (CV) in faunal abundance as a tool to investigate how stream communities respond to both physical and biotic variance (e.g., spatial variability in flow and predation pressure). Cooper et al. (1997) suggest that additional methods that focus on variance (e.g., spatial autocorrelation, spectral analysis, fractal geometry) may also be useful in the study of heterogeneity in streams. Clearly, stream ecologists are only beginning to embrace variance as a factor of ecological significance and to explore various tools (e.g., geostatistical techniques) that can be used to garner ecological insights.

5. Interaction of physical and biotic heterogeneity

Spatial and temporal heterogeneity in the *physical* environment can interact strongly with spatial and temporal heterogeneity in *biotic* abundance, biomass, or processes. For example, Flecker (1997) shows that grazing fish have an effect on resource distribution that varies across space and time and that biotic processes (here, fish foraging) enhance physical heterogeneity (here, distribution of sediments on a streambed). Lancaster and Belyea (1997) demonstrate that population persistence in the face of disturbance is scale-dependent in streams due to spatial habitat heterogeneity (especially with respect to the distribution of flow refugia). Poff and Nelson-Baker's model (1997) suggests that snail grazing creates algal patchiness but does so as a function of spatial heterogeneity in flow. Finally, further examples are provided by Cooper et al. (1997) from their work on the interactive effects of spatial heterogeneity of food resources (whose distributions are influenced by environmental factors) and predator-prey interactions.

6. Emergent properties related to heterogeneity

As the title of the last theme implies, the overall effect of heterogeneity may be greater than the sum of individual heterogeneity components. Emergent or previously unidentified properties of populations, communities, and ecosystems (Allen and Hoekstra 1992) may become apparent when we do not simplify our study systems by removing one or more components of heterogeneity. In streams, this theme is closely related to theme 4 (above) since movement of "materials" is the mechanism that is often responsible for linking pattern and process across scales in streams *and* for linking spatial and temporal heterogeneity in streams (e.g., Lancaster and Belyea 1997). Stevenson (1997) addresses this issue directly by showing that both structural and functional properties of periphyton may be *changed* by heterogeneity (i.e., new properties "emerge" in the presence of heterogeneity). They suggest that stability, biomass, and diversity of algal assemblages may be enhanced by spatial habitat heterogeneity.

In conclusion, this collection of papers demonstrates that physical and biological heterogeneity are now being viewed as "facts of life" in streams—stream ecologists are not shying away from the study of heterogeneity. Many in our scientific community are embracing the challenges presented by the highly variable nature of streams. This collection of papers demonstrates that experimental, modelling, and statistical approaches are being taken to help in understanding the causes and consequences of heterogeneity in lotic ecosystems.

Acknowledgements

We thank the North American Benthological Society and local 1995 organizers, Cathy Tate and Alan Covich, for encouraging us to organize the symposium that motivated these papers, our thoughts, and discussion. We thank Rosemary Mackay for editorial assistance. Finally, we thank the authors whose papers are included in this issue, as well as the following symposium participants and their co-presenters for their insights into the role of heterogeneity in streams: David Hart, Kurt Fausch, Nancy Grimm, Wayne Minshall, Mary Power, Seth Reice, and Colin Townsend.

Literature Cited

ALLEN, T. F. H., AND T. W. HOEKSTRA. 1992. Toward a unified ecology. Columbia University Press, New York.

COOPER, S. D., L. BARMUTA, O. SARNELLE, K. KRATZ, AND S. DIEHL. 1997. Quantifying spatial heterogeneity in streams. Journal of the North American Benthological Society 16:174–188.

CROWL, T. A., C. R. TOWNSEND, N. BOUWES, AND H. THOMAS. 1997. Scales and causes of patchiness in stream invertebrate assemblages: top–down predator effects. Journal of the North American Benthological Society 16:277–285.

DEANGELIS, D. L., AND J. C. WATERHOUSE. 1987. Equilibrium and nonequilibrium concepts in ecological models. Ecological Monographs 57:1–21.

DOWNES, B. J., A. GLAISTER, AND P. S. LAKE. 1997. Spatial variation in the force required to initiate rock movement in 4 upland streams: implications for estimating disturbance frequencies. Journal of the North American Benthological Society 16: 203–220.

DOWNING, J. A. 1991. Biological heterogeneity in aquatic ecosystems. Pages 160–180 *in* J. Kolasa and S.T.A. Pickett (editors). Ecological heterogeneity. Springer-Verlag, New York.

FLECKER, A. S. 1997. Habitat modification by tropical fishes: environmental heterogeneity and the variability of interaction strength. Journal of the North American Benthological Society 16:286–295.

HILDREW, A. G., AND P. S. GILLER. 1994. Patchiness, species interactions and disturbance in stream benthos. Pages 21–61 *in* P.S. Giller, A.G. Hildrew, and D.G. Rafaelli (editors). Aquatic ecology: scale, pattern and process. Blackwell Scientific Publications, London.

HYNES, H. B. N. 1970. The ecology of running waters. University of Liverpool Press, Liverpool.

KOLASA, J., AND C. D. ROLLO. 1991. Introduction: the heterogeneity of heterogeneity: a glossary. Pages 1–23 *in* J. Kolasa, and S.T.A. Pickett (editors). Ecological heterogeneity. Springer-Verlag, New York.

LANCASTER, J., AND L. R. BELYEA. 1997. Nested hierarchies and scale-dependence of mechanisms of flow refugium use. Journal of the North American Benthological Society 16:221–238.

LEVIN, S. C. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

MENGE, B. A., AND A. M. OLSON. 1990. Role of scale and environmental factors in regulation of community structure. Trends in Ecology and Evolution 5:52–57.

MURDOCH, W. W. 1991. Equilibrium and non-equilibrium paradigms. Bulletin of the Ecological Society of America 71:49–51.

PALMER, M. A., J. D. ALLAN, AND C. A. BUTMAN. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. Trends in Ecology and Evolution 11:322–326.

PALMER, M. A., C. C. HAKENKAMP, AND K. NELSON-

BAKER. 1997. Ecological heterogeneity in streams: why variance matters. Journal of the North American Benthological Society 16:189–202.

PICKETT, S. T. A., V. T. PARKER, AND P. L. FIEDLER. 1992. The new paradigm in ecology: implications for conservation biology above the species level. Chapman and Hall, New York.

POFF, N. L., AND K. NELSON-BAKER. 1997. Habitat heterogeneity and algal–grazer interactions in streams: explorations with a spatially explicit model. Journal of the North American Benthological Society 16:263–276.

PRINGLE, C. M., R. J. NAIMAN, G. BRETSCHKO, J. R. KARR, M. W. OSWOOD, J. R. WEBSTER, R. L. WELCOMME, AND M. J. WINTERBOURN. 1988. Patch dynamics in lotic systems: the stream as a mosaic. Journal of the North American Benthological Society 7:503–524.

ROUGHGARDEN, J. 1989. The structure and assembly of communities. Pages 203–226 *in* J. Roughgarden, R.M. May, and S.A. Levin (editors). Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey.

SCHNEIDER, D. C. 1994. Quantitative ecology: spatial and temporal scaling. Academic Press, San Diego, California.

STEVENSON, R. J. 1997. Scale-dependent determinants and consequences of benthic algal heterogeneity. Journal of the North American Benthological Society 16:248–262.

VALETT, H. M., C. N. DAHM, M. E. CAMPANA, J. A. MORRICE, M. A. BAKER, AND C. S. FELLOWS. 1997. Hydrologic influences on groundwater–surface water ecotones: heterogeneity in nutrient composition and retention. Journal of the North American Benthological Society 16:239–247.

WIENS, J. A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. Pages 439–457 *in* D.R. Strong, D. Simberloff, L.G. Abele, and A.B. Thistle (editors). Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey.

WIENS, J. A. 1992. Ecology 2000: an essay on future directions in ecology. Ecological Society of America Bulletin 73:165–169.