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Patch dynamics and environmental heterogeneity in lotic ecosystems

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Abstract. We reviewed concepts of patch dynamics and environmental heterogeneity and their applications to the study of fluvial ecosystems, with emphasis on research published in *J-NABS*. We discuss several important papers synthesizing theories and findings on this topic and reports of descriptive and experimental research. A large body of research, much of it published in *J-NABS*, has demonstrated how spatial and temporal variation influences population, community, and ecosystem patterns and processes in fluvial ecosystems. Conceptual models of patch dynamics can be traced to 2 basic approaches: 1) the landscape ecology perspective and 2) the metacommunity perspective. The former focuses on how spatial patterns are created and affect ecological processes over variable scales of space and time, whereas the latter emphasizes the important influence of periodic disturbances, refugia, and dispersal in maintaining nonequilibrium communities within patch mosaics. The origin of the metacommunity Patch Dynamics Concept can be traced to G. Evelyn Hutchinson's ideas about nonequilibrium communities, and a key contribution was Townsend's (**1989**[4]) *J-NABS* review of the Patch Dynamics Concept in stream community ecology. The study of fluvial ecosystem ecology from a patch-dynamics landscape perspective is well represented by empirical studies published in *J-NABS*, but some emerging topics remain little studied, including: 1) experiments designed to test predictions of the Patch Dynamics Concept of metacommunities vs alternative models; 2) empirical documentation of patch dynamics and their effects on ecological processes across longitudinal, lateral, and temporal gradients; 3) the influence of species' life-history attributes on community dynamics in relation to habitat characteristics and aspects of disturbance; and 4) the manner in which landscape patterns, patch dynamics, and metacommunity dynamics affect foodweb patterns and processes.

Key words: dispersal, environmental gradient, habitat heterogeneity, landscape ecology, metacommunity, nonequilibrium dynamics, river continuum.

Rivers and streams are quite obviously spatially and temporally variable in their physical characteristics, biological communities, and ecosystem processes. The role of this spatial heterogeneity and temporal variability in determining biological communities and ecosystem processes has been a central theme of research by stream ecologists over the last few decades (Hynes 1970, Vannote et al. 1980 [Fig. 1], **Minshall 1988**, Junk et al. 1989, **Ward 1989**, Thorp and Delong 1994, Montgomery 1999, Benda et al. 2004, Thorp et al. 2006 [Fig. 1]). The Patch Dynamics Concept incorporates aspects of spatial heterogeneity and temporal variability to describe fluvial ecosystems as dynamic mosaics of interconnected patches of physical conditions or biological communities (**Pringle et al. 1988**, **Townsend 1989**; Fig. 1).

During the middle part of the 20th century, 2 concepts of patch dynamics began to emerge in the ecological literature. We will characterize the 1st

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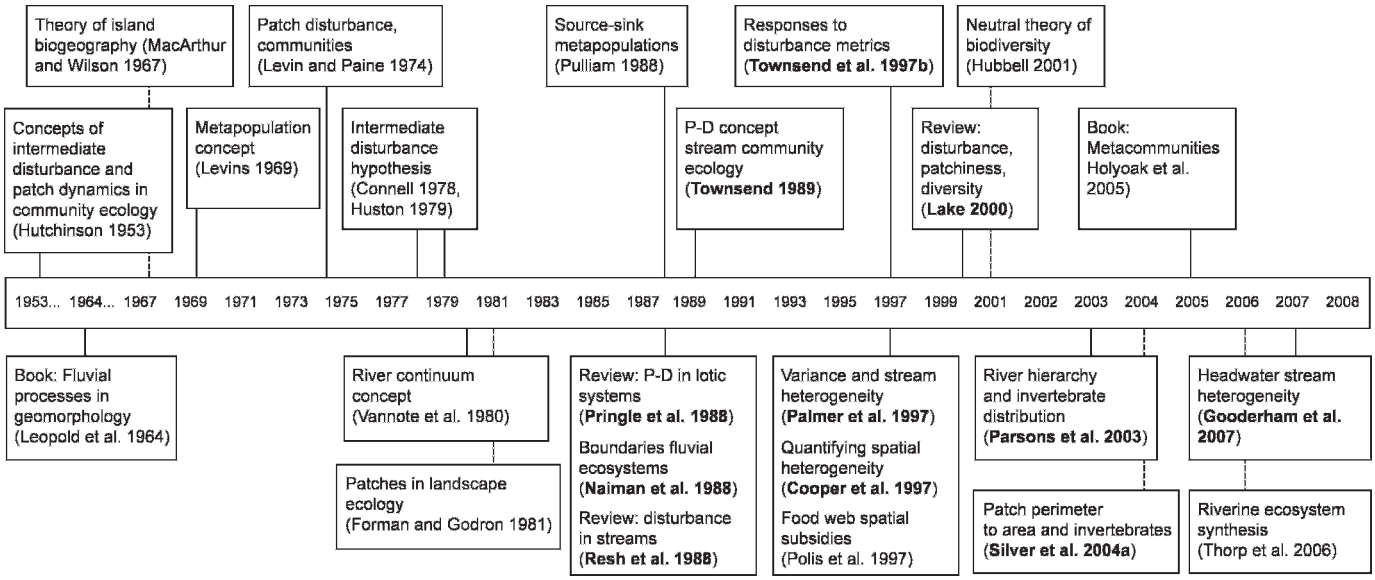


FIG. 1. Timeline of notable papers in the development of patch dynamics concepts and their application to fluvial ecosystems. Papers that emphasize metacommunity perspectives appear above the timeline, and those stressing ideas from landscape ecology are below the timeline. Dashed lines are used for clarity when a connecting line passes behind a box. Boldface indicates papers published in *J-NABS*. P-D = patch dynamics.

concept as the *landscape perspective*, in which environmental factors operating over variable scales of space and time produce patterns of spatiotemporal heterogeneity to form the dynamic habitat template to which organisms and processes respond. The 2nd concept can be referred to as the *metacommunity perspective*. A metacommunity is a set of local communities linked by dispersal of multiple interacting species (Holyoak et al. 2005; Fig. 1), and in the metacommunity perspective, local assemblages, or patches, of coexisting species are seen as being in a nearly perpetual state of disequilibrium (thereby reducing competitive exclusion) and succession following periodic disturbances. These perspectives are not mutually exclusive, and even some of the pioneering ecologists, such as Charles Elton and G. Evelyn Hutchinson, recognized interrelationships between them (Elton 1927, Hutchinson 1941, 1961).

Landscape patch-dynamics perspectives on rivers and streams came initially from the fluvial geomorphologists who emphasized physical patterns and their changes, especially in response to flow variation (Leopold et al. 1964; Fig. 1). With the exception of riparian vegetation influences on erosional patterns, biotic components of lotic ecosystems received little attention from the early fluvial geomorphologists. Among the early studies emphasizing patchy ecological dynamics was Reice's (1974) demonstration of the effects of substrate composition and patch size on leaf litter decomposition in a North American stream. Numerous studies in the 1970s examined nutrient dynamics and decomposition of organic material in lotic ecosystems, and this body of work gave rise to 2 highly influential conceptual models: nutrient spiralling (Newbold et al. 1981, **Mulholland and Webster 2010**) and the River Continuum Concept (Vannote et al. 1980).

The metacommunity patch-dynamics model has a long history, with some ecologists citing Connell (1978; Fig. 1) as the originator of the idea that often has been equated with the Intermediate Disturbance Hypothesis (Wilson 1994). Early models of population dynamics and species interactions, such as the familiar Lotka–Volterra models, were linear and yielded equilibrium solutions. These models and associated experimental investigations, such as those performed by Gause (1934), led to the idea of competitive exclusion among species with the same ecological requirements. Hutchinson, upon contemplating the coexistence of species in patchy environments subject to disturbance, first described the core idea of interactions within and among nonequilibrium communities in patches (Hutchinson 1951, 1953 [Fig. 1]). Hutchinson's idea was that disturbances open new habitat patches for colonization by inferior competitors before they can be completely excluded from the landscape by superior competitors.

Subsequent theoretical developments related to the Patch Dynamics Concept include Levins' (1969; Fig. 1) metapopulation model; Levin and Paine's (1974; Fig. 1) model of interactions between disturbance,

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patch formation, and community structure; and the Intermediate Disturbance Hypothesis (Connell 1978, Huston 1979 [Fig. 1]). Reice (1994) summarized evidence for nonequilibrium community dynamics, including many examples from stream ecology. The Patch Dynamics Concept is now considered to represent just one of at least 4 distinct models of metacommunity dynamics (Leibold et al. 2004; see discussion below). Figure 1 illustrates some of the key contributions to the Patch Dynamics Concept in lotic ecology. Papers that emphasize metacommunity perspectives appear above the timeline, and those stressing landscape ecology are positioned below the timeline.

Here we review concepts of patch dynamics and heterogeneity, and their application to river and stream ecosystems, with an emphasis on contributions in *J-NABS*. Of course this topic is quite broad and contains multiple components, each of which could provide rich material for in-depth discussion. *J-NABS* has published some highly cited works that have elucidated the value of a patch dynamics framework for the study of running waters (**Naiman et al. 1988** [Fig. 1], **Pringle et al. 1988**, **Townsend 1989**, **Lake 2000** [Fig. 1]). We will compare and contrast their conclusions, and then focus attention on more recent research. Disturbance is a key component of patch dynamics, but we discuss it only briefly because it is the focus of an accompanying paper in this *J-NABS* anniversary issue (**Stanley et al. 2010**; see also Lepori and Hjerdt 2006).

What is a Patch?

To understand the conceptual development of patch dynamics, one must have a clear sense of what is meant by a *patch*. The definition of patches and patch dynamics has largely occurred in a broader literature outside of benthic ecology. A straightforward definition provided by Forman (1995) is ''a relatively homogeneous non-linear area that differs from its surroundings'' (see Forman and Godron 1981 [Fig. 1] for an alternative description of patch types as communities or species assemblages surrounded by a matrix of differing composition or structure). Pringle et al. (**1988**) offered a definition that emphasized the importance of defining a patch within the context of spatial and temporal scales appropriate for the organism of study and the question being asked. Thus, the appropriate scale of patches varies tremendously, ranging from microns to tens of kilometers or more because patches can represent such disparate entities as clumps of algal cells on sand grains to large geomorphic landscape features (**Pringle et al. 1988**, Thorp et al. 2006). A variety of statistical techniques from the landscape ecology literature have been used in the study of stream heterogeneity (O'Neill et al. 1988, Li and Reynolds 1994, 1995, Ganio et al. 2005). A review by Cooper et al. (**1997**; Fig. 1) covered geostatistical methods, such as semivariogram analyses, for estimating patch sizes and other spatial patterns.

Influential Papers and Reviews Appear in *J-NABS* (1986–2000)

The landscape perspective: patchy lotic ecosystems

Two important review papers published in *J-NABS* summarized and interpreted stream ecological research from the landscape perspective of spatial heterogeneity (**Naiman et al. 1988**, **Pringle et al. 1988**). Perspectives expressed in these reviews were influenced by advances in the field of landscape ecology (reviewed by Turner 1989, Wu and Loucks 1995). Pringle et al. (**1988**) described how environmental heterogeneity influences the dynamics of virtually all ecological processes within streams, including nutrient spiralling, periphyton communities, leaf litter decomposition, and benthic foodweb dynamics. They also discussed patch dynamics at large spatial scales involving beaver-induced changes within drainage networks and river–floodplain exchanges. Pringle et al. (**1988**) emphasized that, until that time, most research had compared environmental conditions or communities within and between patches, and relatively little research had examined how interactive processes among patches can determine patterns and dynamics within the stream patch mosaic. Their review provided many examples of stream heterogeneity and physical transport or organism movement between patches at variable spatial scales ranging from millimeters for lithophytic algae to many kilometers for migratory fishes. The nutrient environment of streams can be extremely patchy because of combined influences of subterranean flow, surface runoff, and instream nutrient dynamics, and this patchiness greatly influences periphyton dynamics (**Larned 2010**). In addition, riparian canopy coverage and the light environment in streams tend to be patchy.

Naiman et al. (**1988**) described how boundaries between patches in fluvial ecosystems fundamentally influence many ecological processes. They proposed a chaos dynamics perspective to argue that boundaries can impart resistance or resilience to disturbances experienced by adjacent patches, e.g., on a lateral gradient from channel to floodplain and upland habitats. Boundaries themselves can be created or maintained by internal factors or external events (e.g., disturbance). They extended their thinking to the influence of boundaries, or ecotones, on biodiversity, with highest levels of biodiversity expected at

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intermediate frequencies of ecotones on the landscape. This prediction results from observations regarding edge effects whereby, to remain viable as populations, some species require large unbroken habitat patches, whereas others exploit the interface between patches. Habitats that are too patchy or insufficiently patchy will be detrimental to one or the other type of species.

Patch dynamics is premised on the notion that ecosystems are fundamentally heterogeneous. Documenting patterns of environmental heterogeneity, defined as variability of pattern or process in space or time, and understanding its consequences have been central themes of research by benthic ecologists. As part of a special issue in *J-NABS* on ''Environmental Heterogeneity in Streams'' (volume 16, issue 1), Palmer and Poff (**1997**) described 6 emerging themes: 1) multiscale analysis, 2) a functional perspective identifying mechanisms by which heterogeneity influences stream organisms and ecosystems, 3) biotic dispersal and material fluxes as regional processes that alter local heterogeneity, 4) the importance of variance as an ecological metric, 5) interactions of physical and biotic heterogeneity, and 6) emergent properties in which the overall effects of heterogeneity are greater than individual heterogeneity components.

Two major challenges for research on lotic-system patch dynamics from the landscape ecology perspective have received increasing attention in recent years: improved quantitative methods, and integration of species traits with analysis of abundance patterns at the scale of watershed or drainage basin. Studies of stream heterogeneity must use new quantitative methods to identify objectively and precisely patches and the scales at which patterns and processes operate (**Cooper et al. 1997**). According to Palmer et al. (**1997**; Fig. 1), greater attention must be paid to variance measures recorded over space and time to understand better the causes and effects of ecological patterns and processes. They proposed a 3-step process: 1) documentation of a pattern with respect to variance, 2) examination of empirical data to explore causes for the pattern, and 3) manipulation of the variances of factors as independent variables in experiments. Identification of the correct spatial scales for the variables under study is critically important because the spatial scale at which population processes are modeled greatly influences equilibrium dynamics (DeAngelis and Waterhouse 1987, Kolasa and Pickett 1991).

The metacommunity perspective: disequilibrium community dynamics

In an influential review published in *J-NABS*, Townsend (**1989**) examined patch dynamics in streams from a community ecology perspective. He contrasted the traditional niche-controlled, equilibrium model of community structure with 3 nonequilibrium models founded in patch dynamics: dominance controlled, founder controlled, and relict controlled. A dominance-controlled community follows the classic Patch Dynamics Concept of Hutchinson (1953), whereby patch disturbance allows competitively inferior species to colonize patches and occupy them for variable periods before competitively dominant species eventually exclude them from a patch. In contrast, a founder-controlled community is one in which there is no functional dominance among species so that relative abundances on a patch largely reflect the sequence of colonization. In a relict-controlled community, disturbances selectively remove species from patches, and the relative abundances during the interval between disturbances are a function of the initial abundances of remnant populations plus colonists. Each of these patch dynamics models is likely to apply to a variety of benthic stream organisms. In headwater streams, spates scour the bed and selectively remove attached algal taxa, which results in relict control of the community (e.g., Fisher et al. 1982). For benthic macroinvertebrates on and around rocks, flash floods can completely empty certain patches, and the ensuing community development might conform to either founder control (e.g., when certain taxa recolonize rapidly because they have a major refuge nearby or possess superior dispersal ability) or dominance control (taxa colonize in a more or less stochastic sequence, but with some species functionally dominant).

Townsend (**1989**) examined the application of Chesson's (1986) competitive lottery model to stream communities. According to this model (see also Hutchinson 1948), competitive hierarchies arise when species have different responses to the range of environmental conditions so that the colonization sequence yields different patterns of deterministic succession on different patches. Studies of benthic algae and macroinvertebrate assemblages in North American streams were cited in support of the competitive lottery model (Hemphill and Cooper 1983, Power and Stewart 1987). Townsend (**1989**) also highlighted the potential for life-history traits to buffer local populations against unfavorable conditions as an important factor in community patch dynamics. The ability of a population to resist unfavorable conditions, including disturbances, and extended periods of low recruitment has been termed the storage effect (Warner and Chesson 1985). Townsend (**1989**) also discussed the role of grazers as biological disturbance agents for communities of attached algae and sedentary invertebrates (Power et al. 1985).

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Townsend (**1989**) emphasized the important roles of disturbance refugia (e.g., hydraulic refugia, bed interstices, floodplain areas) and dispersal via the water column and hyporheos for patch dynamics. Some of the rare species in stream benthic communities are maintained essentially as early colonists that exploit ephemeral patches created by disturbance, the classic idea of the *fugitive species* (Hutchinson 1951). Townsend (**1989**) pointed out that, even in a fairly homogeneous environment, greater temporal variation will tend to increase species coexistence under the niche-control model, with different species dominating during different periods (see also Hutchinson 1941, 1961). Last, Townsend (**1989**) observed that scales of patchiness and the nature of disturbances are different in headwater vs downstream segments of longitudinal gradients. Some local populations probably persist only because of the mass effect—the continuous or periodic influx of individuals from adjacent or distant (e.g., via drift) habitats. According to Townsend (**1989**), the Patch Dynamics Concept might provide a more general foundation for understanding community structure and dynamics in lotic ecosystems than the River Continuum Concept.

The value of patches as refugia depends upon their size, arrangement (Lancaster 2000), and frequency of disturbance (**Silver et al. 2004b**), and the quality of refugia affects recolonization (**Matthaei et al. 2000**, **Gjerløv et al. 2003**). Lancaster and Belyea (**1997**) described 4 classes of mechanisms of refuge use across spatial and temporal scales in streams. At large scales (>1 generation, >1 habitat patch), disturbance might effectively remove all individuals from a patch, but local populations persist through time because of recruitment from outside sources. This recruitment might be the result of use of ''refugia through complex life-cycles,'' such as desiccation-resistant life stages in temporary streams, or ''between habitat refugia'' where individuals from undisturbed patches colonize patches depleted by disturbance (e.g., via long-distance drift or dispersal of winged adults). The 2 other classes of mechanisms operate at smaller scales (<1 generation, $\leq$1 habitat patch) and are related to behaviors of taxa as ''refugia through changes in habitude'' and use of ''within-habitat refugia'' that allow individuals to survive disturbance within the patch. Refugia through changes in habitude include such behaviors as dormancy or diapause in sediments or the hyporheic zone, ontogenetic shifts in microhabitat use, and changes in net-building behavior or use of silken draglines in macroinvertebrates. Within-habitat refugia operate via 4 mechanisms that passively or actively affect survival within the patch. These mechanisms include proportional persistence in a homogeneous patch, and effects of microhabitat heterogeneity on source–sink dynamics, undirected flux of individuals among potentially erosive microhabitats and refugia, and directional flux of individuals from erosive microhabitats to refugia (**Lancaster and Belyea 1997**). Effects of within-habitat refugia on resistance to disturbance have received the most attention in stream studies.

Lake (**2000**) examined community resistance and resilience in relation to severity of disturbance, particularly from floods (see also review by Death 2008). Lake (**2000**) discovered that most studies found negative correlations between diversity and flood severity, and few studies observed unimodal diversity curves consistent with predictions from the Intermediate Disturbance Hypothesis (e.g., Townsend et al. 1997a). Lake (**2000**) suggested that the type of relationship might be related to spatial scale, with unimodal responses more likely when separate river systems are compared, whereas streams within the same river system might show negative correlations between diversity and flood severity. Lake (**2000**) reinforced Townsend's (**1989**) observations concerning the critical role of refugia, including those that buffer populations from the effects of floods and others that buffer from drought (see also Magoulick and Kobza 2003). In an earlier review of disturbance in stream ecology, Resh et al. (**1988**; Fig. 1) emphasized relationships between disturbance intensity, frequency, and predictability with population responses as influenced by species life-history traits (see also reviews of hydraulic habitat by **Statzner et al. 1988** and disturbance by **Stanley et al. 2010**). The classic Patch Dynamics Concept of Hutchinson (1953) requires a fundamental tradeoff between colonizing ability and competitive ability; without this feature, species that are both superior colonizers and competitors will dominate the system and reduce species diversity. Patch disturbance, local depletion/extinction, and recolonization will not promote species coexistence if species can disperse among different patches at rates vastly greater than the rate of patch disturbance. This caveat might explain why relatively immobile benthic organisms, such as attached algae, immature aquatic insects, and riffle-dwelling fishes, have provided good support for the model. For example, Matthaei and Townsend (2000) and Effenberger et al. (2006, 2008) found long-term effects of local disturbance on stream invertebrate communities.

Recent Theoretical Refinements and Empirical Tests (2000–present)

Processes within and among patches

Recent efforts to integrate patch dynamics, geomorphology, and river landscape ecology (Wiens 2002,

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Lowe et al. 2006) have resulted in shifts away from the paradigm of river systems as a gradational continuum of physical conditions. Instead, several frameworks have been proposed that challenge the assumption of longitudinal gradients central to the River Continuum Concept (Thorp et al. 2006, **Stanley et al. 2010**). For example, Montgomery (1999) proposed the Process Domain Concept as an alternative to the River Continuum Concept and emphasized the importance of spatial variability in geomorphic processes in governing temporal patterns of disturbance that drive ecosystem structure and dynamics. The Process Domain Concept highlights the significance of patch-forming geomorphic processes resulting in different process domains within a watershed. Likewise, Poole (2002) provided a Hierarchical Patch Dynamics framework for understanding interactions between structure and function in fluvial landscapes. The Hierarchical Patch Dynamics perspective focused on rivers forming a patchy discontinuum from headwaters to mouth, with a hierarchy of patch mosaics at different scales linked by interactions and feedbacks between patches both within and across scales. This landscape approach emphasizing heterogeneity and hierarchical scaling of patches was developed further in the Network Dynamics Hypothesis (Benda et al. 2004), which made an explicit set of predictions about the degree and spatial distribution of heterogeneity in river systems in relation to general features of branching river networks. Gooderham et al. (**2007**; Fig. 1) provided a similar perspective for headwater streams in which ecological patterns and processes are strongly influenced by high ratios of structural component size to stream width. Thorp et al. (2006) presented a heuristic framework, which they called the Riverine Ecosystem Synthesis, for understanding ecological patterns in river networks across broad spatiotemporal scales. They integrated hierarchical models of patch dynamics and fluvial geomorphology in their framework, which characterizes functional process zones associated with different types of hydrogeomorphic patches. For example, the relative importance of C sources used by aquatic communities might differ in different hydrogeomorphic patches. Landscape-scale foodweb studies conducted recently in the Paraná River Basin (Hoeinghaus et al. 2007a, 2008) support the functional process zone concept.

Environmental heterogeneity in streams is the result of multiple interacting factors, and research aimed at understanding the major drivers of heterogeneity is important from both metacommunity and landscape perspectives. Studies documenting heterogeneity and its causes in running waters have been published in a wide variety of outlets, and publications in *J-NABS* have made important contributions. In recent years, a substantial number of studies published in *J-NABS* have revealed patterns of spatial and temporal heterogeneity generated by a diverse array of interacting abiotic factors, including hydrologic disturbance and streambed stability (**Downes et al. 1997**, **Lancaster and Belyea 1997**, **Stevenson 1997**, **Suren and Duncan 1999**, **Lake 2000**, **Matthaei et al. 2000**, **Kilbane and Holomuzki 2004**, **Riseng et al. 2004**, **Barquín and Death 2006**), stream hydraulics (**Statzner et al. 1988**, **Doisy and Rabeni 2001**), habitat connectivity (**Bonada et al. 2006**), microtopographic location (**Kobayashi and Kagaya 2004**), surface–subsurface exchanges (**Valett et al. 1997**, **Dent et al. 2001**, **Henry and Fisher 2003**, **Wright et al. 2005**), microhabitat distributions (**Fairchild and Holomuzki 2002**), substrate grain size and shape (**Holomuzki and Biggs 2003**), and channel units (**Halwas et al. 2005**).

Consumers also can play an important role in influencing patterns of heterogeneity (Hildrew and Giller 1994, Flecker and Taylor 2004). For example, a number of *J-NABS* papers have discussed the role of benthic herbivores in generating spatial heterogeneity and patchiness of benthic resources (**Steinman et al. 1987**, **Pringle et al. 1988**, **Cooper et al. 1997**, **Flecker 1997**, **Poff and Nelson-Baker 1997**). Clearly, grazer foraging behavior is influenced by the quality and dispersion of algal patches (Kohler 1984, 1985, Hoffman et al. 2006). Likewise, predators can produce a patchy distribution of invertebrates (**Crowl et al. 1997**, McIntosh et al. 2004). By modifying the behavior or densities of grazing invertebrates, predators can indirectly influence the heterogeneity of algal resources (McIntosh et al. 2004). Research exploring interactions between consumers and resource heterogeneity has focused on a very limited set of consumers, resources, and spatial scales, in particular algal–herbivore interactions. A rich area of research lies ahead if we are to tease apart the role of consumers in generating heterogeneity in river systems.

The effect of disturbance (especially spates) on biota in heterogeneous stream environments has received considerable recent attention. Experimental studies published in *J-NABS* by Holomuzki and Biggs (**2000**, **2003**) demonstrated that biotic responses to patch disturbance in a stream were a function of substrate characteristics (e.g., stability, heterogeneity, grain size) and species-specific traits (**Townsend et al. 1997b** [Fig. 1], Olsen et al. 2007). Population responses to floods might differ between micro- and macrohabitat scales and interact with patch type (**Kilbane and Holomuzki 2004**). In larger rivers, seasonal floodplain inundation, a pulse disturbance according to Lake (**2000**), might affect communities quite differently than the manner in which short-duration

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spates affect streams. With increasing water levels, macroinvertebrates might move from deeper habitats into the shifting littoral zone, which serves as a flood refuge because of the presence of slower moving water and more stable substrates (**Rempel et al. 1999**). Arrington and Winemiller (**2006**) found that fish and macroinvertebrate assemblages in littoral habitat patches of a tropical floodplain river disassembled and reassembled according to both stochastic and deterministic processes as the land–water interface moved across the landscape. The interstitial spaces below stones might serve as a refuge from drought for some macroinvertebrate species because sufficient humidity might remain during short droughts (**Lake 2000**). The hyporheic zone might not be as effective a refuge to extended drought conditions as suggested for floods (**del Rosario and Resh 2000**, **Lake 2000**, **Dewson et al. 2007**). Macrohabitats (e.g., riffles, runs, pools) might differ in their value as drought refugia among species and size classes within species, depending in part on relative predation risk and conditions for growth (Magalhaes et al. 2002), and connectivity among such macrohabitats during drought might affect assemblage structure (**Bonada et al. 2006**).

Although much of the literature on patch dynamics and heterogeneity in streams focuses on patterns, underlying mechanisms, and consequences of variation in structural properties of running waters, stream functional processing rates also are strikingly variable (Thorp et al. 2006). For example, Reice (1974, 1977, 1980) described the spatial heterogeneity of litter breakdown in streams as occurring among patches with variable rates of decomposition associated with different substrates and patch sizes. The heterogeneous nature of instream processing is a central feature of the Telescoping Ecosystem Model (Fisher et al. 1998), which characterized stream ecosystems as analogous to a telescope with a series of concentrically arranged components (stream, hyporheic, parafluvial, and riparian zones). Processing rates and retention can differ widely among subsystems and among types of materials. In addition, processing lengths vary temporally as they elongate with disturbance and contract during postdisturbance recovery (Fisher et al. 1998).

McClain et al. (2003) discussed how rates of biogeochemical processes vary in space and time to produce what they termed ''biogeochemical hot spots'' and ''hot moments,'' which are patches or time periods of disproportionately high biogeochemical reaction rates. Hot spots and hot moments should be particularly prevalent at terrestrial–aquatic interfaces, areas where hydrological flow paths converge and episodic hydrological flow events mobilize reactants. Consistent with the idea of biogeochemical hot spots, Henry and Fisher (**2003**) described large differences in the abundance of N-fixing cyanobacteria and N retention by algal mats growing in outwelling compared to inwelling edges of sandbars in Sycamore Creek, Arizona.

Spatial heterogeneity in processing rates also can be created by biota. For example, Caraco and Cole (2002) found that macrophyte beds in the Hudson River caused measurable differences in dissolved (DO) concentrations, as a result of respiration and the degree to which photosynthetically produced O_2 was vented by macrophytes directly into the atmosphere or water column. Macrophyte beds dominated by the invasive Eurasian water chestnut (*Trapa natans*), which vents O_2 into the atmosphere, had consistently lower DO, whereas beds dominated by the native macrophyte *Vallisneria*, which vents O_2 into the water column, displayed substantially greater DO than the adjoining open channel. These patchy DO concentrations have important implications for biogeochemical reactions and the suitability of macrophyte beds as habitat for taxa, such as fish.

Consumers also can create hot spots of nutrient regeneration. McIntyre et al. (2008) measured rates of nutrient regeneration by fishes in a Neotropical stream and found that community-wide N and P excretion varied by an order of magnitude among a set of 49 contiguous channel units distributed along a >2.5-km stream segment. N regeneration by fishes appeared to meet ecosystem demand in some channel units, whereas nutrient uptake in other channel units exceeded measured excretion rates. Thus, the stream can be viewed as a mosaic of interacting patches of regeneration and uptake, a perspective often not incorporated into models of nutrient spiraling. Few works in *J-NABS* have addressed the heterogeneity of functional processing rates, and this area is ripe for future research.

Models of community dynamics with a spatial framework

In reviews of metacommunity concepts, Leibold et al. (2004) and Holyoak et al. (2005) proposed 4 fundamental models: patch dynamics, species sorting, mass effects, and neutral (Table 1). Holyoak et al. (2005) pointed out that the familiar island biogeography model of MacArthur and Wilson (1967; Fig. 1) is actually a patch dynamics model, with the only difference being that the source pool for patch colonization is a single large patch (the mainland) rather than multiple units within a habitat mosaic. Thus, following the island biogeography model, communities on the island patches are in a dynamic equilibrium for species richness (actually a nonequilibrium community in terms of species composition)

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TABLE 1. Summary of key features of 4 metacommunity models (adapted from Holyoak et al. 2005) and examples of studies published in *J-NABS* consistent with the models.

Characteristic	Patch dynamics	Species sorting	Mass effects	Neutral
Patch similarity	High	Low	Low	High
Interpatch movement	Variable[a]	Not specified	High	Variable
Species similarity	Variable	Low	Low	High
Tradeoffs among traits	Yes	Yes	Yes	No
Local species composition	Variable	Constant	Constant	Variable
Regional species composition	Constant	Constant	Constant	Variable
Spatial synchrony	Some	Not specified	High	Not specified
Local equilibrium dynamics	No	Yes	Depends on dispersal rates	No
J-NABS studies supporting model	Casas and Langton 2008	Palmer et al. 1991 Brunke and Gonser 1999 Suren and Duncan 1999 Kobayashi and Kagaya 2004 Arrington and Winemiller 2006	Englund 1991 Matthaei et al. 2000 Gjerløv et al. 2003 Silver et al. 2004a Tronstad et al. 2007	?

[a] According to Townsend (**1989**), dispersal between patches often can be rapid in stream community patch dynamics, whereas Holyoak et al. (2005) contend that interpatch movement is relatively low under the patch dynamics metacommunity model.

as a result of local extinctions and colonization from a single source patch. An important difference between Hutchinson's (1953) patch dynamics model and the island biogeography model is that the former was focused on a community of competing species, such as plants, whereas the latter was applied broadly to communities containing diverse trophic niches (implying that multiple kinds of species interactions can cause local extinctions). Applications of island biogeography theory to colonization dynamics in streams represent some of the earliest patch dynamics studies (Stout and Vandermeer 1975, Sheldon 1977, Minshall et al. 1985).

The mass effects metacommunity model (Schmida and Wilson 1985) proposes source–sink metapopulation dynamics (sensu Pulliam 1988; Fig. 1), whereby sink subpopulations are subsidized by subpopulations in adjacent patches. This model essentially is the supply-side idea promoted by Roughgarden et al. (1987) and applied to intertidal invertebrate (Menge et al. 2003) and coral reef fish (Sale et al. 1984) assemblages. With local densities elevated by immigration from more favorable patches, competitively inferior species might assume greater potential to influence local foodweb dynamics as prey, predators, or ecosystem engineers than they otherwise would. Townsend (**1989**) discussed this model briefly, but, to date, it appears not to have been tested experimentally in lotic ecosystems.

The species sorting model assumes differential resource-use efficiencies and competitive hierarchies among species occupying local patches that span a range of environmental conditions. This model assumes that a local population can reach its equilibrium in a patch before the next major perturbation. Colonization must be sufficiently frequent to allow local assemblages to reach their endpoint trajectories, but not so frequent that immigrants to a patch overwhelm the equilibrium state according to the dynamics of the mass effects model. The species that persist on patches are those that encounter appropriate physical environmental conditions, resources, and biotic environments where they are capable of competing or avoiding predation. Species sorting in response to environmental requirements has been invoked as a potential explanation for distribution patterns in numerous studies of lotic assemblages, including algae (Rosemond et al. 2000), meiofauna (**Brunke and Gonser 1999**), macroinvertebrates (**Palmer et al. 1991**), and fishes (Winemiller et al. 2000, Taylor and Warren 2001, Arrington et al. 2005, Zeug et al. 2005, **Arrington and Winemiller 2006**, Hoeinghaus et al. 2007b). Nevertheless, experiments designed specifically to test predictions of the species sorting model relative to those of other metacommunity models have not been done in streams.

A neutral model of metacommunity dynamics was formalized by Hubbell (2001; Fig. 1) who intended it to serve as a null model that generates patterns derived from chance and history, which can then be compared with patterns from real communities. The neutral model assumes all species have equivalent competitive abilities (i.e., no niche differentiation), dispersal is stochastic on a patchy landscape, and that local extinctions follow a random walk. These assumptions of Hubbell's (2001) neutral model clearly do not apply to very many natural communities, but

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the model generates null statistical distributions that could be useful for comparing empirical data from streams. Moreover, the model has key variables (e.g., average rates of extinction, speciation, and dispersal) and assumptions (e.g., equivalent species niches, stochastic dispersal) that can be manipulated for comparisons with real stream communities.

Each of these metacommunity concepts is associated with a different combination of factors, including patch similarity, dispersal between patches, species similarity, local and regional species composition, spatial synchrony, and equilibrium dynamics of local communities (Table 1). How do organisms occupying patches at various spatiotemporal scales within fluvial systems conform to these model characteristics? Some patches in streams will have very similar conditions (e.g., beds of cobble or gravel in riffles of high-gradient streams), whereas others will have very divergent abiotic and biotic environmental conditions (e.g., isolated floodplain pools with different geomorphologies and histories of connectivity). Interpatch movement might be very high, as in the case of drifting aquatic insects, or very low when habitat patches are disconnected over extended time intervals (e.g., isolated channel pools in arid regions or isolated oxbow lakes in floodplains). Species might have similar ecological niches (e.g., many diatoms, meiofaunal elements, chironomid larvae, mussels) or highly divergent attributes. *J-NABS* has been a prominent outlet for studies examining habitat heterogeneity and community dynamics, particularly with respect to streams of moderate to high gradient with rocky or gravelly beds subject to movement during high flow events. Studies of community ecology in large rivers, including examination of heterogeneity in the lateral dimension, have been less common in *J-NABS* (e.g., **Holland-Bartels 1990**, **Strayer and Ralley 1993**, **Arrington and Winemiller 2006**, **Paillex et al. 2007**). In general, more studies of lotic systems published in *J-NABS* have had results consistent with the species sorting and mass effects models of metacommunities than with the patch dynamics model (Table 1). However, none of these studies was designed specifically to falsify multiple competing hypotheses.

Patch dynamics and foodweb ecology

Appreciation for the manner in which the flow of nutrients, detritus, and organisms across habitat boundaries affects trophic dynamics within local communities has increased in recent years. Polis et al. (1997; Fig. 1) drew attention to the effect of spatial subsidies on foodweb processes and patterns, such as enhanced top–down control and trophic cascades. When exchanges occur between patches with different levels of productivity, the less-productive patch generally experiences donor control, i.e., a foodweb subsidy. Some of the best examples of subsidized food webs are from research on stream ecosystems (Wallace et al. 1997, Nakano et al. 1999, Nakano and Murakami 2001, Naiman et al. 2002, Sabo and Power 2002a, b, Baxter et al. 2004, 2005, Power et al. 2004, Winemiller and Jepsen 2004, Marczak et al. 2007, Janetski et al. 2009). However, the significance of subsidies on foodweb dynamics depends on many factors. For example, the influence of spawning salmon on stream productivity is not spatially or temporally uniform but varies greatly among sites because of heterogeneity in a host of factors, including spawning salmon density, light attenuation, background water chemistry, and stream temperature (Chaloner et al. 2004, 2007). Wallace et al. (1997) conducted an ecosystem-scale, litter exclusion experiment over a 3-y period, and traced habitat-specific responses of different trophic levels to terrestrial organic matter subsidy. Strong bottom-up effects of riparian detritus inputs propagated through multiple trophic levels on the predominant mixed substrate habitat, but few changes were observed in patches of moss-covered bedrock habitat (also see **Reice 1991,** who found little response of invertebrates to CPOM loading). These results suggest that the nature of foodweb exchanges among patches can contrast sharply, even when patches are separated by only a few meters.

In general, theoretical research on spatially heterogeneous food webs, little of which has been published in *J-NABS*, has outpaced empirical research. For example, Huxel and McCann (1998) created a tritrophic food chain model that demonstrated how mass effects sometimes can stabilize interactions within a habitat patch. Real food webs contain hundreds of interactive components, and dynamic models with high dimensionality often produce complex behavior. Empirical studies have contributed to a greater appreciation of the context-dependent nature of foodweb interactions in streams. On this empirical front, papers published in *J-NABS* have made a more visible contribution. Studies in *J-NABS* (**Flecker 1997**, **McNeely et al. 2006**, **Alvarez and Pardo 2007**) and other journals (Power 1992, McNeely and Power 2007) have revealed substantial variability in the strength of species interactions that can depend on the characteristics of habitat patches. For example, Flecker (**1997**) found habitat-specific variation in pools vs riffles in the ability of a large detritivorous fish, *Prochilodus mariae*, to influence patterns of organic matter accrual. Likewise, Alvarez and Pardo's (**2007**) research in a Mediterranean karstic stream revealed that levels of calcareous deposition over substratum

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surfaces influence colonization by grazers, which in turn, affects periphyton accrual. A comparative experimental approach used at different spatial scales (varying from patches within streams to among catchments) showed that different environmental characteristics greatly influence the effect of consumers on algal abundance in streams (Power 1992, Power et al. 2008, McNeely and Power 2007). In addition, several studies have examined the context-dependent interaction between the efficacy of grazing by stream insects and physical factors. These studies reveal differential effects of herbivores that vary according to flow regimes (Poff and Ward 1992, Wellnitz and Poff 2006) and light availability (Wellnitz and Ward 2000). Experiments examining top-down effects under different nutrient regimes have shown strong interactions between grazers and nutrients (**McCormick and Stevenson 1989**, Rosemond et al. 1993, Flecker et al. 2002, Riley et al. 2004). Understanding the context dependency of interactions remains a fundamental challenge for stream ecologists, and a great need exists for careful study of foodweb ecology within a patch-dynamics framework (Townsend et al. 1998, Thompson and Townsend 2005).

Future Prospects for Research on Patch Dynamics in Fluvial Ecosystems

Ten years have passed since *J-NABS* published a collection of review and synthesis papers dealing with stream heterogeneity and patch dynamics (**Palmer and Poff 1997**). Since that time, many findings from empirical research, both descriptive and experimental, have increased our overall knowledge of stream ecology when viewed across variable scales of space and time. Thus, many of the insights and recommendations that were offered in the 1997 special issue appear to have been embraced. Rivers and streams are outstanding systems for examining patch dynamics, both from the landscape ecology and metacommunity perspectives, because they are spatially heterogeneous and dynamic in response to flow variation. Here we provide a few suggestions for future research on fluvial ecosystems from a patch dynamics perspective.

The Patch Dynamics Concept of community dynamics appears to apply to benthic algae and aquatic invertebrates, small organisms that respond quickly to disturbances and heterogeneity at small spatial scales (**Townsend 1989**), but studies designed to test the model critically appear scarce (Matthaei and Townsend 2000, Effenberger et al. 2006, 2008). Taxa, such as fishes and riparian plants, that have longer generation times and a greater demographic storage effect might conform to alternative models. Experimental manipulations are needed to discriminate between metacommunity models, and these manipulations must be done in various habitat types over variable scales of space and time (e.g., microhabitats in response to spates to functional process zones in response to annual flow variation). A tenet of hierarchy theory is that assumptions that hold at a given spatial or temporal scale might not apply when examined at a different scale. Lotic community and ecosystem ecologists also should evaluate nonlinear models that yield alternate states and the manner in which their projections might be changed by abiotic inputs, such as hydraulic disturbances and nutrient influx from adjacent patches.

Future research should test models by comparing natural patterns or conducting manipulative experiments across multiple scales in a hierarchical manner, from small habitat patches to subwatersheds within river basins (e.g., **Peckarsky et al. 1997**, Vinson and Hawkins 1998, **Lamouroux et al. 2004**). This suggestion does not imply that the size of measured or manipulated patches has to increase, but rather that study designs should include spatial and temporal scales of response variables as independent variables in the analysis (e.g., **Parsons et al. 2003**; Fig. 1). Montoya et al. (**2006**) showed how biomass of both sestonic and benthic algae varied in a tropical floodplain river landscape at multiple spatial scales in relation to abiotic variables during different periods of the annual flood cycle. Values of water variables and algal biomass were similar in the river channel and floodplain lagoons during the annual flood period. In contrast, these values differed between river and lagoon sites during the low-water period. Benthic algal biomass was relatively uniform at small spatial scales and significantly heterogeneous at larger spatial scales. A similar finding was obtained by a recent study published by Doi and Katano (**2008**) in which densities of periphyton and herbivorous caddisflies varied more predictably among stream riffles than at smaller (micohabitats) or larger (reaches) spatial scales.

Patch dynamics theories appear to be outpacing empirical research designed to test them. Knowledge of the role of disturbance in stream ecosystems would be enhanced by research quantifying multiple aspects of disturbances (e.g., intensity and duration) and responses by abiotic (e.g., habitat quality, patch isolation) and biotic (e.g., measures of individual fitness, population abundance, and assemblage composition and structure) variables over extended periods and multiple patches. Essential characteristics of habitat patches (e.g. quality, size, arrangement, stability) and species also should be quantified (**Silver**

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et al. 2004a; Fig. 1). In an innovative study, Townsend et al. (**1997b**) revealed relationships between taxonomic and functional composition of benthic macroinvertebrate assemblages and variables associated with bed disturbance, flow variation, and overall stream channel stability. Disturbance measured in the form of bed-movement metrics predicted patterns of species richness and distributions of functional traits, but variables related to flow variation generally did not. Several studies have identified stream refugia used by a variety of taxa during disturbances, but few have quantified differential refuge use or relative importance of alternative refugia for various taxa or functional groups. This information is critical because, in highly variable ecosystems like streams, refugia strongly affect biotic responses to disturbance and the maintenance of species diversity.

The evolutionary aspects of stream heterogeneity and metacommunity dynamics have scarcely been investigated from an empirical standpoint. Adaptation is a response to selection imposed by local abiotic and biotic environments, but population gene pools are regional because of dispersal at the landscape level. Some recent theoretical models have examined the equilibrium dynamics of this interaction (Holt and Gomulkiewicz 1997, Gomulkiewicz et al. 1999, Bolnick and Nosil 2007), and an empirical study examined this question in stickleback populations (Hendry et al. 2002). Investigations of the population genetics consequences of interpatch dispersal are rare among studies published in *J-NABS* to date (e.g., **Schmidt et al. 1995**).

Last, we must gain better understanding of habitat and metacommunity dynamics in lotic systems for practical applications, including restoration of damaged ecosystems (Matthaei et al. 2004). Freshwater mussels rank high among the world's most imperiled freshwater taxa, and a recent review by Newton et al. (**2008**) presented evidence and arguments for how a landscape ecology perspective could improve mussel research and conservation. Water resource management and regulations in North America and many regions of the world now rely upon indices of biotic integrity and reference conditions for biomonitoring (**Dolédec and Statzner 2010**, **Hawkins et al. 2010**). Indicators of biotic integrity and reference sites essentially assume that lotic communities respond to spatial variation according to the species sorting model of metacommunity dynamics. Moreover, often little or no consideration is given to temporal dynamics involving abiotic and biotic disturbances (Effenberger et al. 2008), dispersal, and biotic interactions causing community trajectories. Greater knowledge of community patterns over multiple spatial scales, ranging from microhabitats to watersheds, and the mechanisms that create them will enable refinement of these important tools for conservation of lotic ecosystems.

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