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The evolving legacy of disturbance in stream ecology: concepts, contributions, and coming challenges

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Abstract. We reviewed the development of ideas and empirical understanding about disturbance in lotic ecosystems by providing a pre-1986 historic context and highlighting major themes that have emerged in the 25 y since the inception of *J-NABS*. Disturbance was not well incorporated into stream ecological thinking before 1986, but awareness of its significance began to emerge in the early 1980s, as demonstrated by the publication of several classic papers illustrating the ecological consequences of floods. Broad recognition of disturbance as a fundamental driver in streams was crystallized by Resh et al. (**1988**[4]) in a paper that marked the beginning of a period of intense research on disturbance. We recognized 4 subsequent research themes: 1) definition of terms and concepts and development of tools for quantifying disturbances and ecological responses, 2) the disturbance renaissance, a period during which empirical research increased dramatically, 3) formalization of the significance of disturbance in streams by its incorporation into conceptual models of stream ecosystems, and 4) operationalization of disturbance for management and restoration of streams and rivers. Despite remarkable progress toward understanding disturbance in lotic ecosystems in the past 25 y, opportunities for future research are numerous. Increasing scope and intensity of human activities underscore the need to examine interactions among disturbances and to incorporate ecological principles into management and restoration activities. New insights are likely to arise from recognition of links between geomorphic forms and processes and the ecology of disturbance. Viewing streams in the context of regime shifts should also lead to new advances, particularly for restoration, because disturbances can elicit nonlinear responses. Successes in these efforts should contribute to improved scientific understanding and stewardship of streams and rivers.

Key words: disturbance regime, anthropogenic disturbance, resistance, resilience, regime shift, restoration, stream, river, review.

Determinants of ecological pattern and process can be placed into 3 general categories: biotic interactions, environmental constraints, and disturbance (Urban et al. 1987). Stream ecologists were slow to recognize the role of this final category in shaping population, community, and ecosystem dynamics (Fisher 1983, **Resh et al. 1988** [Fig. 1], **Lake 2000** [Fig. 1]), but in the past 2 decades, disturbance has become a central theme in our discipline. Studies of disturbance have spanned levels of ecological organization from individuals to landscapes and the entire range of spatial and temporal scales considered in lotic research.

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[4] Boldface indicates paper was published in *J-NABS*

Our goal is to provide a broad overview of the development of ideas about disturbance and how these events affect ecological pattern and process in streams. We begin with a brief discussion of the historical foundations of disturbance research in lotic ecosystems for the years before the appearance of *J-NABS* in 1986. Next, we review the development of disturbance concepts, terminology, and empirical knowledge from 1986 to the present, highlighting the role of *J-NABS* in this process. We used the synthesis paper by Resh et al. (**1988**) on the role of disturbance in streams as an important reference point for our analysis. Resh et al. (**1988**) attempted to provide a road map for studying disturbance in streams by suggesting research questions and approaches, and their paper represents the state of the science at the start of the period considered in our review. Therefore, we have used it to mark the progression of our understanding of disturbance over the past 25 y. Our last objective is to look forward and

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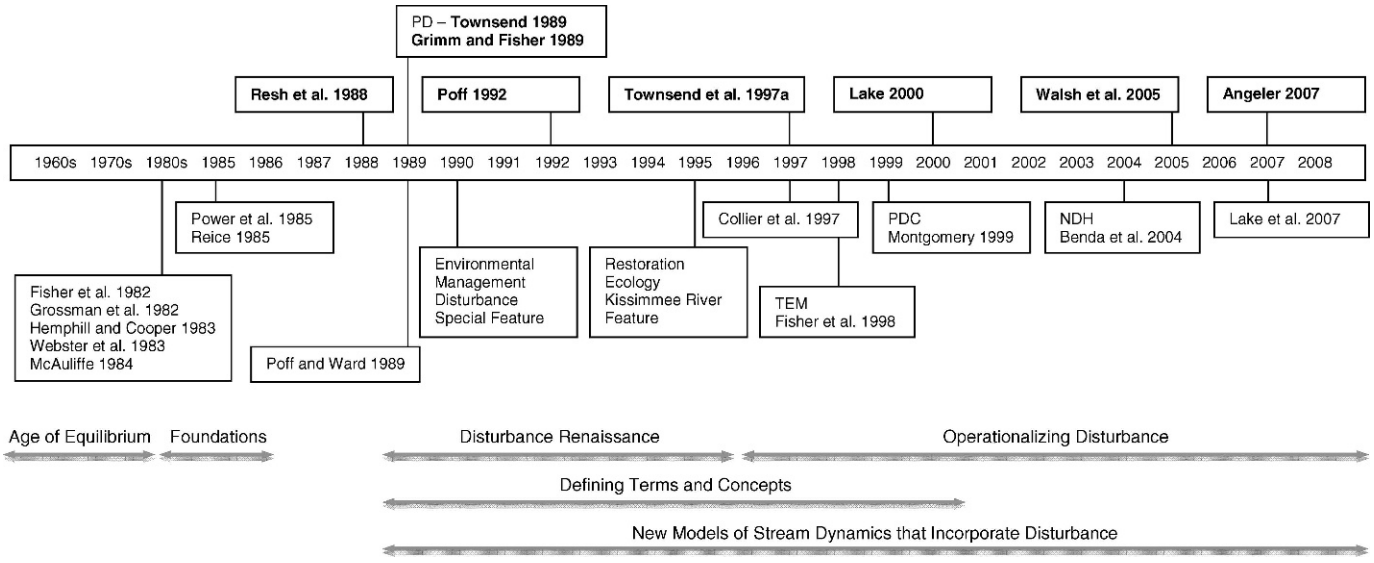


FIG. 1. Timeline of landmark publications and phases of development in the study of disturbance in stream ecology. Major conceptual papers that incorporated disturbance are indicated by the abbreviations: PD = patch dynamics, PDC = process domain concept, TEM = telescoping ecosystem model, NDH = network dynamics hypothesis. Boldface indicates papers published in *J-NABS*.

to identify emerging questions and challenges involving disturbance in lotic ecosystems.

We caution readers against interpreting our paper as an exhaustive review. Our efforts focused on the task of encapsulating broad themes in research and idea development using representative contributions. Supporting citations are, in most cases, a subset of examples from a larger collection of studies demonstrating a particular point, and we have inevitably excluded many excellent publications. Because the literature on disturbance is substantial, we also limited our consideration to the aquatic realm and did not include studies that considered disturbance effects in riparian and floodplain environments.

The task of distilling the vast body of research on disturbances in streams and rivers into a comprehensive synthesis presented a remarkable challenge. A simple keyword search of ''disturbance* and stream* or disturbance* and river*'' using Web of Science® produced no articles before 1982, followed by a sudden, sharp, and sustained increase in publications beginning in 1990 (Fig. 2). The maturation of disturbance-related research is chronicled by multiple review articles about major taxonomic groups (Detenbeck et al. 1992, Mackay 1992, Peterson 1996, Magoulick and Kobza 2003), specific disturbance types (Scrimgeour et al. 1994, Lake 2003, **Dewson et al. 2007**, Bond et al. 2008), disturbance-driven (Gasith and Resh 1999, Brasher 2003, Dodds et al. 2004) and disturbed (e.g., Paul and Meyer 2001, Allan 2004) ecosystems; special issues in journals (e.g., ''Recovery of Lotic Communities and Ecosystems following Disturbance: Theory and Application'' Yount and Niemi 1990a [Fig. 1]; ''Drought and Aquatic Ecosystems,'' Humphries and Baldwin 2003); and steady production of empirical and conceptual articles. Over the past 25 y, the pendulum has swung the other way. For better or worse, we have moved from failing to recognize the importance of disturbance as a driving force in streams to seeing it nearly everywhere and excluding little in our use of the term. The question is: how or why did this shift happen, and is the broad interest in disturbance likely to continue over the next 25 y?

Pre-1986: The Age of Equilibrium

Historically, stream ecology embraced a strange contradiction by recognizing the importance of floods (and occasionally, drying) on one hand, but having an equilibrium view of communities and ecosystems on the other (**Lake 2000**). Before the mid-1980s, studies of disturbances, particularly those other than floods, were extremely rare, and applications of disturbance-oriented concepts, such as succession, were even scarcer (Fisher 1983). Fisher suggested that one reason for this early lack of emphasis reflected the geographical distribution of stream ecologists; that is, researchers lived and worked in areas where streams did not have flashy hydrographs, and thus, were not organized by disturbance.

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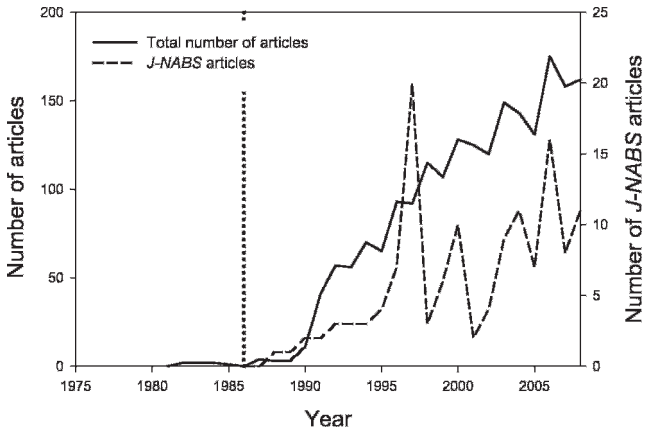


FIG. 2. Trends in published papers on disturbance in stream ecology and in *J-NABS*. The number of papers/y was determined by a database search of Web of Knowledge® on 29 July 2009 using ''disturbance* and stream* or disturbance* and river* as topic keywords. The search was restricted to a specified list of journals that publish original research in aquatic biology, conservation, ecology, and environmental management (Appendix). The vertical line marks the year 1986.

The number of articles that specifically invoked concepts of disturbance was limited in the 1980s, but a paradigm shift that laid the groundwork for the large amount of the work to come in the 1990s was under way in community ecology. Deterministic equilibrium models of community structure were giving way to nonequilibrium views, and disturbance was increasingly being recognized as a cause of spatial and temporal variability in several different environments (Sousa 1984), including streams (**Resh et al. 1988**). Early signs that the disturbance theme was emerging in stream research include publication of papers emphasizing ''environmental extremes'' or ''harshness'' as controlling the intensity of biotic interactions (particularly competition; Matthews and Hill 1980, Peckarsky 1983). A handful of papers in early 1980s were critical in calling specific attention to disturbance as a significant ecological phenomenon that could alter biotic interactions (Hemphill and Cooper 1983, McAuliffe 1984, Power et al. 1985; Fig. 1) and community composition in streams (Fisher et al. 1982, Grossman et al. 1982, Reice 1985; Fig. 1). These now-classic studies opened the door for the next generation of stream community ecology research that incorporated disturbance as a matter of course.

In the early 1980s, while community ecologists debated the forces structuring communities, researchers interested in ecosystem dynamics also began to explore disturbance ideas. The small watershed approach championed by Bormann and Likens (1979) had revolutionized ecosystem ecology and demonstrated the effects of disturbance on forested ecosystems. Streams played an unheralded but essential role in this research as neutral integrators of terrestrial processes. However, some investigators recognized that streams were not entirely neutral to these terrestrial perturbations and were able to document how watershed disturbance affected stream ecosystem dynamics (Webster and Patten 1979, Bilby 1981, Meyer and Tate 1983). Studies of aquatic disturbances also began to appear at this time. One of the first comprehensive investigations explicitly couched within the context of disturbance was provided by Fisher et al. (1982), who described patterns of ecosystem recovery following flash floods. A final critical piece of the foundation was provided by Webster et al. (1983; Fig. 1), who introduced the theory-derived concepts of resistance (the degree of change caused by a disturbance) and resilience (a measure of the rate of subsequent recovery) to the stream community and provided a demonstration of their utility as tools for studying disturbance.

J-NABS arrived during a time of transition in this history of the disturbance paradigm (i.e., recognition and study of disturbance as a fundamental determinant of ecological pattern and process) in stream ecology. Ecologists were increasingly aware that equilibrium models were often poor fits for stream communities and that disturbances could have profound effects on population, community, and ecosystem attributes. Thus, the stage was set for an explosion of research on all aspects of disturbance in streams.

1986 to 2008

The transition under way in community ecology was only one facet of a larger sea change in general ecological thinking in the 1980s. Publication of Pickett and White's book on disturbance in 1985 formalized the idea of patch dynamics (see **Winemiller et al. 2010**). Forman and Godron's (1986) text heralded the development of landscape ecology as a discrete subdiscipline and drew important attention to the concepts of scale and hierarchy (e.g., Urban et al. 1987, Wiens 1989, **Johnson and Host 2010**). These frameworks emphasized a dynamic and stochastic view of the world and incorporated disturbance as a fundamental determinant of pattern and process for communities, ecosystems, and landscapes. Disturbance was unfamiliar territory for many stream ecologists, so new terms and concepts needed to be developed and defined, and *J-NABS* played a central role in this process.

Defining terms and concept

The definition of disturbance.—In their landmark text, White and Pickett (1985, p. 6) defined disturbance as

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''any relatively discrete event in time that disrupts the ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment.'' This definition is widely used, but has been subject to debate and modification by many stream ecologists on 2 grounds: 1) its requirement for biotic consequence and 2) lack of specificity about the spatial or temporal extent of disturbance. Resh et al. (**1988**) used Pickett and White's definition as the starting point for their discussion, but they also highlighted the need to quantify disturbances in terms of characteristics of the event itself (e.g., the magnitude of a flood). However, this emphasis did not immediately curtail the tendency of ecologists to define disturbance in terms of realized biological consequences (e.g., see Townsend and Hildrew 1994). Resh et al. (**1988**) also expanded upon White and Pickett's definition, and stipulated that disturbances must be outside some predictable range of frequency or intensity. Thus, very predictable environmental fluctuations, such as spring spates in snow-fed mountain streams, would not qualify as disturbances. Their framework added the burden of developing criteria to distinguish between usual and unusual environmental fluctuations. In response, Poff (**1992**; Fig. 1) stated that this ''predictability clause'' was intractable for several reasons, including its inherent tautology in which biological response to disturbance and predictability of disturbance are expressed in terms of one another.

A 2nd point of discussion regarding some of the different definitions of disturbance focused on its discrete or punctuated nature. This stipulation fit well for floods, but was problematic for more protracted disturbances, such as drying (Stanley and Fisher 1992). Lake (**2000**) provided an important step forward by recognizing different categories of disturbances based on their duration and intensity over time. Lake (**2000**) built on the theoretical structure developed by Bender et al. (1984) to argue that disturbances could occur as pulses (rapid and discrete events, such as floods), presses (disturbances that rise sharply then are sustained at a relatively constant level, such as sediment inputs from a landslide), or as ramps (disturbance intensity increases over time, such as during prolonged drought). Recognition of different disturbance types is particularly useful for studying anthropogenic events that do not conform well to traditional definitions of disturbances as discrete events in space or time, and these terms are now well-established in the literature (e.g., Parkyn and Collier 2004, Harper and Peckarsky 2005).

The following points emerged from the process of defining disturbance. First, ecologists do not view an event as a disturbance unless it has some biological consequence. Indeed, hydrologists and geomorphologists have spent entire careers without using this term, whereas the same is unlikely to be true for stream ecologists. As Poff (**1992**) stated, disturbances are ''by definition, ecological events.'' That said, the biological consequence should be viewed simply as a filter that answers the yes/no question: 'Is it a disturbance?' Second, after passing through this filter, disturbances must be quantified by physical measures of the event itself (e.g., intensity, duration, frequency) rather than in terms of biotic responses to allow objective comparisons among events (**Resh et al. 1988**, **Poff 1992**, **Lake 2000**). Perhaps some of the confusion regarding how to define disturbance resulted from a misunderstanding over which of these steps was being emphasized: simple recognition of an event as a disturbance (inferred from measures of biotic responses) or examination of its consequences (relative to abiotic measures of disturbance). Third, debates regarding the definition of disturbance might, at times, seem strictly academic, but these discussions brought other issues into focus. Notably, attempts to resolve the question ''What is a disturbance?'' for streams and rivers contributed immensely to the recognition of the importance of scale and the need to specify the spatial and temporal extent of investigation (cf. Fisher 1987, Peckarsky 1987). Some chapters in the development of disturbance terminology have, at times, seemed maddening or dangerously esoteric. However, these kinds of discussions are a normal and essential part of the process of theory maturation (sensu Loehle 1987) during which concepts progress from vague and qualitative to precise, predictive, and informed by empirical evidence. *J-NABS* has provided a central venue for this dialog (Fig. 1) through publication of articles, such as Poff (**1992**) and Lake (**2000**), in its ''Perspectives'' section.

Quantifying disturbance.—Once the relevance of disturbance was recognized, researchers quickly rose to the challenge of deciphering its various influences on streams and used streams as laboratories to test general ecological principles about disturbance. Numerous case studies that spanned a wide range of spatial and temporal scales, levels of organization, and taxonomic groups appeared in the literature. Multiple methodological approaches were employed, but from our vantage point, publications that became particularly influential often used either experimental or comparative approaches. These approaches required quantitative measures of disturbances so that objective comparisons could be made among different events or experimental treatments (**Townsend et al. 1997a** [Fig. 1], **Lake 2000**). Efforts to quantify distur-

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bances generated a variety of metrics and, as a consequence, often provided fresh insights about disturbances in streams. In particular, these efforts helped facilitate a progression from focusing on single types of disturbance and single disturbance events to appreciating disturbance regimes. The event-specific approach is illustrated clearly by the foundation papers discussed in the prior section, which are dominated by case studies of individual disturbances. However, the pioneering work by Poff and Ward (1989 [Fig. 1], 1990) offered a rigorous quantitative framework that expanded the typical monthly to annual scope of study to interannual scales and the spatial extent from individual reaches to regional and continental scales. This work provided a novel way to characterize and visualize the disturbance regime of individual sites and a geographic context for evaluating the significance of hydrologic disturbance in different regions of the US. The value of this flow-regime perspective extends far beyond studies of disturbance, and it has become a new paradigm for the study and management of lotic ecosystems (Poff et al. 1997).

Several analytical methods and metrics for quantifying disturbances and disturbance regimes have been proposed (e.g., Richter et al. 1996, Puckridge et al. 1998, Fritz and Dodds 2005, Sabo and Post 2008). Many of these methods involve detailed analysis of hydrographs or quantifying high flow events and associated mobilization of substrata (Death and Winterbourn 1995, **Townsend et al. 1997a**, Downes et al. 1998). The variety of metrics is no surprise given the diversity of disturbance types and scales of study. That any one framework will serve all of our needs is unlikely, given the range of disturbance types now experienced by streams and rivers. Nonetheless, the occurrence of multiple disturbances provides a new challenge to develop metrics that can reasonably quantify disparate types of disturbance (discussed further below).

Quantifying ecological responses.—In addition to quantifying disturbances, a common terminology was needed to describe or measure the consequences of disturbance. The resistance–resilience framework presented by Webster (Webster 1975, Webster et al. 1983) has been embraced widely in stream research. These terms derive from mathematical definitions of stability, are ecologically intuitive, easily quantified (but see Ives 1995), and versatile in that they can be applied to population, community, or ecosystem variables. Grimm and Fisher (**1989**; Fig. 1) provided one of the earliest stream applications of resistance and resilience measures for community and ecosystem responses to flash floods in desert streams. They were able to demonstrate differential stability to flooding across assemblage types and season and in response to nutrient availability. Stream ecosystems generally are considered to have low resistance but high resilience because of the short generation times of many stream taxa (Yount and Niemi 1990b, Fisher and Grimm 1991). However, responses to disturbance are influenced by a range of factors that can be categorized as attributes of the disturbance and attributes of the environment. Examples of studies using resistance and resilience to examine effects of different disturbances or environmental attributes are provided in Table 1 and illustrate the utility and popularity of this approach for understanding how disturbances influence stream and river dynamics.

The disturbance renaissance

By the 1990s, the disturbance paradigm had arrived for stream ecology. Resh et al. (**1988**) and a special feature in the journal *Environmental Management* crystallized this new awareness and supported the subsequent explosion in research activity (Figs 1, 2). Although studies of flood and scour remained prevalent, the diversity of disturbance types considered also began to expand. Stream ecologists were quick to use this new, rapidly growing empirical knowledge to modify or develop conceptual models of stream dynamics that explicitly incorporated disturbance.

Community dynamics.—Community-level questions dominated disturbance research in streams both before and after the arrival of *J-NABS*. Resh et al. (**1988**) firmly endorsed the idea that most stream communities were structured by disturbance, and if their arguments had not been sufficient to persuade stream ecologists, the widely cited *J-NABS* article by Townsend (**1989**; Fig. 1) put most lingering skepticism to rest. Townsend (**1989**) adapted the patch dynamics concept (White and Pickett 1985) to lotic ecosystems and presented a view of the processes shaping stream communities that was based on ''the profound influence of disturbance'' in these environments. Both Resh et al. (**1988**) and Townsend (**1989**) reviewed prevailing community models of the day and considered which was the best fit for streams (and were not in agreement on this point).

Testing general community models has received substantial and persistent attention from lotic ecologists. Connell's (1978) intermediate disturbance hypothesis (e.g., Townsend et al. 1997b, Fayolle et al. 1998, Bertrand et al. 2004) and patch dynamics (see **Winemiller et al. 2010**) have perhaps garnered the most attention. In recent years, model evaluation has been supplemented by themes, such as evolutionary adaptations to disturbance using trait-based approaches to understand how disturbance regimes

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TABLE 1. Examples of studies of resistance or resilience of different ecological response variables in relation to characteristics of the disturbance or the environment.

Attribute	Disturbance type	Response variable(s)	Reference
Disturbance attributes			
History	Floods, drying	Invertebrate density	**Miller and Golladay 1996**
	Scour	Invertebrate density, richness	Death 1996
Timing	Flood	Algal density, community structure	Peterson and Stevenson 1992
	Flood	Macrophyte cover, richness	Barrat-Segretain and Amoros 1995
	Flood	Ecosystem metabolism	**Uehlinger and Naegeli 1998**
Type	Flood vs drought	Invertebrate community structure	Boulton et al. 1992
Type, intensity	Flood, drying	Invertebrate community structure	Fritz and Dodds 2004
Intensity	Drying	Microbial activity	Larned et al. 2007
Intensity, timing	Floods	Algal biomass, invertebrate density	**Grimm and Fisher 1989**
		Invertebrate community structure	Bradt et al. 1999
Frequency	Floods	Invertebrate richness and density	Matthaei et al. 1996
Interactions	Drying and fire	Algal density, community structure	Cowell et al. 2006
	Flood and fire	Insect density, community structure	Vieira et al. 2004
Environmental attributes			
Refugia			
Hyporheic zone	Floods	Invertebrate density	Palmer et al. 1992
Multiple types	Drying	Invertebrate abundance	Boulton 1989
Microform bed clusters	Floods	Algal biomass	Francoeur et al. 1998
Substrate crevices	Scour	Algal biomass	Bergey 2004
Hydraulic refugia	Flood	Invertebrate abundance	Negishi and Richardson 2006
Abundance	Flood	Invertebrate abundance	**Gjerlov et al. 2003**
Hyporheic linkage	Floods	Algal biomass	Valett et al. 1994
Grazing pressure, nutrients	Light elimination	Algal biomass	Steinman et al. 1991
	Chlorine	Algal biomass	Steinman et al. 1992
Geomorphic setting	Flood	Ecosystem metabolism	Uehlinger 2000
Canopy structure	Flood	Algal and invertebrate density	Fuller et al. 2008
		Ecosystem metabolism	**Acuña et al. 2007**
Habitat type	Water diversion	Invertebrate density	Hax and Golladay 1998
Substrate size	Floods	Invertebrate density	Imbert et al. 2005
Light and nutrients	Floods	Algal biomass	Biggs et al. 1999
Nutrients	Floods	Algal biomass, assemblage structure, production	**Peterson and Grimm 1992**

shape communities (e.g., Lytle 2002, Lytle and Poff 2004, **Poff et al. 2006**, Bonada et al. 2007), the role of refugia in modulating disturbance effects on biota (e.g., Sedell et al. 1990, **Lancaster and Hildrew 1993**, Davey and Kelly 2007), consequences of nonhydrological disturbances on communities (e.g., Harper and Peckarsky 2005, Hartman et al. 2005), and effects of disturbance on predator–prey interactions (e.g., Lancaster 1996, Thomson et al. 2002).

Foodweb dynamics lie at the interface of communities and ecosystems, and Power et al. (1985; Fig. 1) set the stage for understanding how disturbances could affect trophic relationships in streams. These investigators clearly demonstrated that the presence of bass (*Micropterus* spp.) caused a trophic cascade in pool habitats of an Oklahoma stream, then went on to show how floods reshuffled bass distribution and, thus, the occurrence of these top-down effects on minnow and algal populations. The trophic cascade theme was continued in studies focusing on trade-offs between vulnerability to disturbance and vulnerability to predation (Wootton et al. 1996, Nyström and McIntosh 2003). Other investigations revealed substantial simplification of foodweb structure (Closs and Lake 1994, Townsend et al. 1998, **Mantel et al. 2004**), changes in food chain length or strength of trophic cascades (Parker and Huryn 2006, Power et al. 2008; but see Walters and Post 2008), and shifts in the major pathways of energy flow (Mihuc and Minshall 1995) by different kinds of disturbances. Recent interest in foodweb subsidies has led to examination of how natural and anthropogenic disturbances alter the timing, amount, or locations of energy subsidies to and from streams (Laeser et al. 2005, Mitchell and Lamberti 2005, Greenwood and McIntosh 2008).

Ecosystem processes.—Ecosystem-level studies of stream responses to disturbances developed more slowly than community studies in the 1990s, and many of the first publications in this era documented changes in structural variables (e.g., algal biomass or

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detrital standing crops) or focused on organic matter decomposition. These trends in variable selection undoubtedly reflected the labor-intensive requirements of measuring functional processes, such as primary production or nutrient retention. However, new methods and technologies (e.g., data-logging dissolved O_2 sensors) have reduced some of the logistical challenges and allowed detailed investigations of changes in ecosystem processes in response to disturbance. Temporally intensive measurements of dissolved O_2 dynamics have revealed low resistance of metabolism to floods, a greater effect of floods on primary production than on respiration (**Uehlinger and Naegeli 1998**, Roberts et al. 2007a), and an often strong influence of upland disturbances on stream metabolism (**Houser et al. 2005**, **McTammany et al. 2007**, **Atkinson et al. 2008**).

Methodological advances also have fostered a greater understanding of the effects of disturbance on nutrient cycling in streams. Several studies have considered the consequences of upland disturbance (e.g., logging, fire, rapid landuse change) on stream biogeochemistry, perhaps because of the large influence of early small watershed studies such as the Hubbard Brook experiment (Bormann and Likens 1979), or perhaps simply because of the substantial effect of land use on streams (Allan 2004). For example, rapid loss of forest cover often is associated with increased nutrient inputs to streams. However, these sorts of disturbances also can lead to higher rates of nutrient retention because greater insolation stimulates instream biological activity (**Sabater et al. 2000**, Bernhardt et al. 2003). Consistent nutrient responses to other watershed disturbance have not yet emerged (Groffman et al. 2004, **Roberts et al. 2007b**), perhaps because instream changes might be disturbance specific.

Just as streams have been excellent laboratories for testing general theories of community composition, they also have proven useful for examining models of ecosystem dynamics in response to disturbance. Repeated disturbances and short generation times of organisms in streams were first exploited by Fisher et al. (1982) to test (and largely reject) Odum's (1969) model of ecosystem development. Streams also have provided an interesting venue for testing Vitousek and Reiners' (1975) nutrient retention hypothesis. This hypothesis, developed for forested ecosystems, suggests that nutrient retention is initially extremely low following forest disturbance, increases during early succession in association with plant establishment and growth, then declines in the later stages of succession as biomass accretion slows. In one of the first stream studies of disturbance and nutrient cycling, Grimm (1987) found that patterns of algal regrowth and N retention after flash floods in desert streams were well described by the Vitousek and Reiners (1975) model. Valett et al. (2002) provided a slightly different perspective in their test of the model by contrasting P retention in streams draining old-growth and second-growth forests. P retention was significantly lower in the second-growth streams compared to those in the old-growth forest, suggesting that streams become progressively more retentive over the decades and even centuries of forest recovery.

Nutrient spiraling is a dominant paradigm in stream ecology today (**Mulholland and Webster 2010**). However, applications of spiraling methods and models in the context of disturbance are still relatively scarce (Maltchik et al. 1994, **Martí et al. 1997**, **Orr et al. 2006**), particularly compared to the wealth of measurements made during baseflow conditions (Ensign and Doyle 2006). These process-based studies emphasized the role of disturbance in altering the contribution of transient storage and biotic uptake to reach-scale nutrient retention, but disturbance also can affect nutrient dynamics via other mechanisms. For example, disturbances can alter oxidation–reduction conditions, thereby favoring different nutrient transformations (Baldwin et al. 2005), or can amplify the importance of sorption dynamics in cases in which sediment inputs are part of the disturbance (Stanley and Doyle 2002). Understanding changes in nutrient uptake parameters in response to different types of disturbance is currently an active area of research, and we expect substantial empirical and theoretical progress over the next 5 to 10 y.

New models of lotic ecosystems

Explicit incorporation of disturbance into many conceptual models of stream ecology over the past 20 y is a clear demonstration that the disturbance paradigm now permeates our understanding of streams and rivers. Despite its substantial value, many researchers recognized that the river continuum concept (RCC; Vannote et al. 1980) did not capture the dynamic nature of streams or fully represent their physical structure. Consequently, a 2nd generation of conceptual papers, many of which explicitly included disturbance as a fundamental controller, began to appear in the mid-1980s. Some of these articles were informative rebuttals or amendments to the RCC. For example, the serial discontinuity concept (Ward and Stanford 1983) highlighted the effect of disruptions by dams (interruptions that **Lake 2000** would later define as press disturbances) on the river continuum. Montgomery (1999; Fig. 1) and Benda et al. (2004; Fig. 1) emphasized the importance of drainage basin form and geomorphic processes in creating or modify-

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ing disturbance regimes in streams in the process domain concept and network dynamics hypothesis, respectively (discussed further by **Poole 2010**). Other conceptual frameworks incorporating disturbance that were not obviously related to the RCC also emerged, most notable of which was Townsend's (**1989**) paper on the patch dynamic concept for stream communities. At the ecosystem scale, the telescoping ecosystem model (Fisher et al. 1998; Fig. 1) focused on nutrient retention as a functional metric for measuring response to disturbance. Fisher et al. (1998) hypothesized that resistance and resilience of nutrient retention varied among channel subsystems, and that whole-ecosystem resistance and resilience were a function of the strength of the linkages between these subsystems. More recently, Burcher et al. (2007) presented the land cover cascade, a framework for quantifying the effects of land cover disturbances on stream biota, and more generally, a consideration of disturbance propagation from terrestrial to lotic ecosystems. These examples illustrate the rapid movement from the deterministic perspective of the RCC to alternative views in which disturbance regimes are key drivers of ecological phenomena and creators of spatial and temporal heterogeneity in lotic ecosystems.

Operationalizing disturbance

Despite an inordinate fondness for floods, in the last 20 y, stream ecologists have become increasingly cognizant of disturbances caused by human activities. Anthropogenic disturbances often are distinct from events, such as floods, so terms and concepts derived from studies of natural disturbances can be a poor fit for anthropogenic phenomena. The most conspicuous example is the term *disturbance* itself. Streams that are modified, degraded, or otherwise changed by human activity are now routinely described as disturbed without necessarily identifying a disturbance responsible for the condition. This altered use of the term is formally incorporated into bioassessment techniques in which degradation is determined by comparison of test sites to undisturbed reference sites without identification of the cause of the degradation (**Dolédec and Statzner 2010, Hawkins et al. 2010**). This new, modified use of disturbance includes changes caused by disturbances in the conventional sense and changes attributable to phenomena typically labeled as stressors, with either or both producing a disturbed condition. Put another way, many of us now use disturbance to refer to virtually any human activity that has a measurable effect on some facet of a stream.

One consequence of the growing recognition of increasing human modification of rivers is the application of our understanding of disturbance to management of lotic ecosystems. As with the science of disturbance, these activities developed quickly in the past decade and include restoration of disturbed streams and use of disturbance as a management tool. We highlighted the special issue of the journal *Restoration Ecology* that focused on the Kissimmee River restoration project (Cummins and Dahm 1995) in the disturbance timeline (Fig. 1) to emphasize a new phase of disturbance ecology in which ecosystem management and restoration are increasingly important motives for research. The Kissimmee project is remarkable because it represents one of the earliest and largest river restoration projects in the US and because ecological concepts have guided restoration activities and evaluation of project success.

Disturbance is increasingly being used as a tool to manage degraded systems. One of the first and most famous examples of this strategy was the managed flooding of the Grand Canyon in 1996 (Collier et al. 1997; Fig. 1). This very public event occurred because researchers successfully argued that floods were critical drivers of the Grand Canyon ecosystem and should be reintroduced, even if only on a limited basis. Managed floods have been used subsequently in several other river and floodplain systems (Molles et al. 1998, Uehlinger et al. 2003, Henson et al. 2007) and have provided unprecedented opportunities for research. Flow manipulations represent a new wave of management strategies based on establishment of a more natural flow regime (Poff et al. 1997) that includes reintroduction of both high- and low-flow events (Boulton et al. 2000).

Emerging Ideas and Opportunities

In the 22 y since the publication of Resh et al. (**1988**), disturbance as a concept has progressed from being a bold new frontier to being a broadly recognized driver of lotic ecosystems. The accumulation of empirical studies along with review, synthesis, and concept papers underscores this rapid growth. However, we are far from done with the task of understanding all the ways that disturbances influence streams and rivers. In this section, we highlight some emerging research frontiers.

Spatial dimensions of disturbance and recovery

During our review process, we recognized 2 strategies with respect to the spatial and temporal scales of research. In one strategy, researchers examine site-specific patterns or conduct small-scale experiments and emphasize the temporal axis. Alternatively, a comparative approach is often used to describe or

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identify differences among sites with distinct disturbance regimes or with similar disturbance regimes but divergent physical structure. These studies are often temporally limited but their spatial extent can vary from a few sites to extensive regional surveys. Thus, an opportunity for new insights about disturbance in streams resides at the interface of temporally intensive and spatially extensive perspectives. In particular, we draw attention to the growing interest in how spatial patterns, including basin shape and drainage network structure, affect the spatial distribution and character of disturbances and their ecological responses.

The idea that spatial structure of drainages can modulate disturbance and response can be traced back to Fisher (**1997**) and Montgomery (1999). Fisher proposed the idea of functional morphology in which the physical form of the stream influences ecological function. He also emphasized the branched structure of river systems and made the case for relating the shape of these branching systems to functional measures, such as nutrient retention. Montgomery's contribution was to draw attention to the nonrandom distribution of geomorphic processes, and thus, disturbance regimes within drainage basins. Similarly, geomorphic structure can also dictate the spatial distribution of disturbances at multiple spatial scales (Stanley et al. 1997). The network dynamics hypothesis (Benda et al. 2004) integrates these lines of thinking and links the distribution of geomorphic processes that create disturbances with river network structure to understand spatial and temporal patterns of habitat heterogeneity and community composition. In effect, Benda et al. (2004) formalized the idea that basin structure affects both the occurrence of disturbances and their ecological consequences. Conceptual models that emphasize the relationship between basin shape, disturbance, and specific categories of ecological response variables (Stanley et al. 2004, Lowe et al. 2006), new quantitative tools (Ganio et al. 2005, Peterson et al. 2007, Cote et al. 2009), and general ecological theory (Grant et al. 2007) specific to network analysis are now available. Studies that integrate a network framework into understanding disturbance effects are beginning to emerge (e.g., Davey and Kelly 2007, Svendsen et al. 2009), although empirical tests of these relatively new models of basin shape and disturbance have, to the best of our knowledge, yet to appear.

Anthropogenic disturbances and interactions among disturbances

The anthropogenic footprint on ecosystems—particularly streams and rivers—is pervasive, often large, and in many places in the world, rapidly increasing (**Benke 1990**, Sala et al. 2000, Nilsson et al. 2005). These facts are neither new nor particularly controversial. Nevertheless, during our examination of the literature, we found that natural and anthropogenic perturbations consistently were treated as distinct categories of disturbance (e.g., **Resh et al. 1988**, Balcombe et al. 2006). We argue that this dichotomy is false, or at best, trivial. Anthropogenic activities are pervasively and inextricably superimposed on the natural template, thus, separating natural and human contributions to the disturbance regime of streams and rivers is often not possible.

Resh et al. (**1988**) pointed out that most streams and watersheds experience several different kinds of disturbance, and that the collection of disturbance types and their relative influences on streams vary as a function of geography, climate, and human activity. However, their discussion did not progress beyond drawing attention to this multidisturbance reality. Meanwhile, consideration of how disturbances or their responses overlap in time or space or interact with each other has been limited, and an integrated understanding of how drivers interact to regulate processes in streams is yet to develop (Groffman et al. 2006).

Ecologists studying other ecosystems have recognized that disturbances can interact to yield unpredictable ecological consequences (Collins 1987, Veblen et al. 1994). In streams, consideration of disturbance interactions has been most common in systems that experience both flooding and drying (e.g., Boulton and Lake 1992, Boulton and Stanley 1995, Fritz and Dodds 2004) and in places where natural disturbances are imposed on landuse change. Many of these investigations have demonstrated disturbance intensification in these situations. For example, storms transport significantly more sediment to streams in deforested (Keim and Schoenholtz 1999, Swank et al. 2001) or burned (Vieira et al. 2004) watersheds than in undisturbed watersheds, and invertebrate populations can be less resilient to repeated flooding in streams draining agricultural watersheds than in forested streams because of loss of refugia (Collier and Quinn 2003, Parkyn and Collier 2004). Most disturbance interaction studies have focused on structural biotic consequences, but such interactions also should affect functional responses, such as nutrient retention (Lottig et al. 2007).

Nonlinear responses and regime shifts

Traditional views of ecological succession and stability (i.e., resistance and resilience) presume a return to a predisturbance state after a period of

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recovery, and recovery is typically assessed with linear or log-linear models. But other trajectories are possible. For example, Lake (**2000**) suggested that not only disturbances but also the resultant ecological response trajectories can be described as press, pulse, or ramp changes. Pulse responses are consistent with the conventional wisdom of high resilience to disturbance, but press and ramp responses are not. Similarly, nonlinear models can sometimes imitate interesting ecosystem behaviors (Dent et al. 2002) and do not assume full, rapid, or linear recovery trajectories.

Models describing nonlinear behaviors, such as hysteresis, threshold responses to disturbance, and alternate states are receiving substantial interest in the general ecological literature (e.g., Scheffer et al. 2001, Beisner et al. 2003, Mayer and Rietkerk 2004, Groffman et al. 2006), but are only just beginning to gain a foothold in stream ecology. Regardless of their cause, ecosystem changes that are rapid, pronounced, and persistent represent regime shifts (Carpenter 2003). In some cases, regime shifts can be driven by small short-lived disturbances. In these situations, processes within the ecosystem (i.e., internal feedbacks or endogenous controls) play a key role in maintaining the new configuration.

In streams and rivers, regime shifts driven by external drivers in the form of wholesale changes in the physical template by human hands (e.g., building a dam or constraining an urban stream to a concrete channel) are widespread. The pervasive approach to examining such shifts is to describe or contrast systems with different physical templates (e.g., compare regulated and unregulated stream reaches). Consequently, little information is available on the transition from one regime to another. However, ecosystem management activities provide new opportunities for studying rates and patterns of ecological change following the reconfiguration of the physical template. For example, Molles et al. (1998) hypothesized that restructuring the flow regime (in their case, reintroducing a flood pulse) would first produce a 'reorganization phase' characterized by high variance in state variables and processes, followed by a less variable steady-state phase characteristic of the new physical template. Such temporal changes in variance were demonstrated by Robinson and Uehlinger (2008) following the introduction of experimental floods in a regulated river. These investigators also noted that ecological changes can unfold more slowly than expected following a major physical reconfiguration of the system.

Regime shifts that involve alternate states, i.e., cases in which discrete ecosystem states might exist under similar external environmental conditions (Schröder et al. 2005), are less well understood in stream ecology. In these cases, internal processes are required to maintain ecosystem configuration despite external drivers that would otherwise change community and ecosystem structure. Conventional wisdom among both stream ecologists and theoretical ecologists has been that streams are controlled by external drivers and lack the internal feedbacks needed to maintain alternative states (Lake et al. 2007; Fig. 1). Such positive feedback mechanisms do, in fact, exist in streams, but the best known examples to date involve geomorphic or hydrologic phenomena (Dent et al. 2002). Establishment of riparian and instream vegetation can also play a critical role in creating and maintaining distinct alternate 'vegetated' states within stream channels (Corenblit et al. 2007, Heffernan 2008), which is characterized by markedly different ecological communities and processes compared to the unvegetated condition (Heffernan et al. 2008). Regardless of the cause of regime shifts, examples in which streams and rivers are pushed into a new configuration or state by disturbances or changes in the disturbance regime are plentiful. The potentially prevalent, but understudied, existence of nonlinear responses to disturbances and alternate states in streams make this area ripe for future research, and we return to this point in the following section.

Continued application of disturbance concepts and understanding

Widespread and increasing degradation of streams and rivers underscores the need for improved and increased protection, management, and restoration of these ecosystems. This need already has elicited a response. For example, stream restoration has become a multimillion dollar industry in the US (Bernhardt et al. 2005). However, the practice of restoring streams and rivers has preceded the science despite some early efforts, e.g., the Kissimmee River project, to integrate ecological principles into project design and assessment. There is now a clear opportunity and need to infuse ecological understanding into restoration and management activities. We call attention to the recent paper by Lake et al. (2007) because it provides an overview of the relevant ecological theory for stream restoration and makes a compelling case for improved implementation of this theory for the benefit of researchers and practitioners alike. Indeed, restoration projects can be excellent whole-ecosystem experiments in which a disturbance (the restoration action) occurs at a known time (Stanley and Doyle 2002).

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The convergence of ideas about restoration and disturbance is logical, and attempts at integration began as early as the 1980s (see Cairns 1990). Unfortunately, for lotic systems, this integration has not progressed far in the last 20 y (Lake et al. 2007). We return to the notion that human activities often result in rapid, nonlinear changes. Thus, management and restoration of degraded or disturbed ecosystems are appropriately considered within a regime-shift framework. Restoration activities can be viewed as a disturbance intended to move an ecosystem into a different, preferred state. Adopting a regime-shift framework provides a reminder that nonlinear and hysteretic trajectories following restoration might be common, and that the effort to restore a stream to a prior alternate state might require more time and energy than expected (Mayer and Rietkerk 2004), and in the end, might not be possible (Stanley and Doyle 2003, Doyle et al. 2005). Nonlinear models also highlight the fact that human activities can produce limited changes in ecosystem structure and function for several years, but then might precipitate a sudden and catastrophic shift. Alternate state theory should help researchers anticipate incipient regime shifts (Carpenter and Brock 2006, Scheffer et al. 2009), and new statistical tools are emerging to identify disturbance thresholds (Brenden et al. 2008, Randhir and Ekness 2009). Both of these developments could potentially allow managers to intervene in advance of ecosystem changes that would otherwise be difficult or prohibitively costly to reverse a posteriori.

Although nonlinear models are likely to be more appropriate than traditional linear approaches for management and restoration of streams, their application will be challenging and might not be appropriate or necessary in all situations. Nonlinear models require more data (more variables and a longer temporal record) and more quantitative sophistication than do linear models. Moreover, the whole-ecosystem approach and appropriate measurement and monitoring strategies needed to predict an impending state change are only now beginning to emerge (Groffman et al. 2006). However, a critical first step is simply recognizing the existence of nonlinear behaviors.

Conclusion

This look at the history of the disturbance paradigm revealed a remarkable breadth of research activity and accumulation of new understanding about disturbances and stream dynamics in general. *J-NABS* has played a significant role in this relatively rapid development by providing a forum for sorting out terms and concepts during the 1990s. The journal has also been an outlet for empirical studies of disturbance (Fig. 2, Table 1) and early papers that considered a wide variety of disturbance types (e.g., **Wallace et al. 1986**, **Golladay et al. 1987**). However, in most cases, conceptual articles have been the journal's highest impact publications. The Perspectives section of the journal has been particularly valuable in the development of disturbance science. In fact, the very first paper in the Perspectives series dealt with disturbance (**Cushing and Gaines 1989**). Whether this tradition will continue is not known, but fewer disturbance-related articles have appeared in Perspectives over the past 5 to 8 y than in the 1990s. Instead, much of the interest in disturbance has shifted to practical issues of identifying and managing disturbed streams. Evidence for this shift includes a growing number of papers on bioassessment in *J-NABS*. However, a handful of recent articles in *J-NABS* are grounded in basic concepts and terminology of disturbance and present new ideas and approaches to understanding and restoring lotic ecosystems in the face of pervasive, large-scale change (**Walsh et al. 2005**, **Angeler 2007**; Fig. 1). During the 25 y of the journal's existence, disturbance has gone from being rarely acknowledged to being the focus of intense research and recognized as a fundamental agent capable of shaping pattern and process in streams. In this sense, one might predict that interest in disturbance as a topic might slow in the next 25 y. However, a decline in interest is *not* our prediction.

We live in an era of unprecedented global change (Millennium Ecosystem Assessment 2005). Rivers and streams are described routinely as regulated, unstable, stressed, impacted, polluted, fragmented, drained, dammed, diked, channelized, and, in the ambiguous language described earlier, *disturbed*. In this context, evolution of the term, disturbance, to reflect the realities of anthropogenic activities was inevitable. Great opportunity comes with these challenges to the state of streams and to our conventional approaches to thinking about and studying disturbance. Technological, methodological, and quantitative advances will continue to enhance our ability to understand stream and river processes. Successes in our efforts to reinvent disturbance—including applying it within complex and humanized systems, examining it at a broader spatial extent, understanding it as a component of regime shifts, and applying it as a management tool—will contribute to an improved basis for the stewardship and restoration of streams and rivers.

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APPENDIX. Journals included in the topic search for number of articles published/y using ''disturbance* and stream*'' or ''disturbance* and river*'' as topic keywords on Institute for Scientific Information (ISI) Web of Knowledge®. Journals that have undergone a name change are listed under both names.

African Journal of Ecology	Conservation Biology	Journal of the American Water Resources Association
Ambio	Copeia	Journal of Animal Ecology
American Midland Naturalist	Ecological Applications	Journal of Applied Ecology
American Naturalist	Ecological Monographs	Journal of Ecology
Annales de Limnologie–International Journal of Limnology	Ecological Research	Journal of Environmental Management
Annual Review of Ecology and Systematics	Ecology	Journal of Environmental Quality
Aquatic Botany	Ecology and Society	Journal of Fish Biology
Aquatic Conservation: Marine and Freshwater Ecosystems	Ecology Letters	Journal of Freshwater Ecology
Aquatic Ecology	Ecology of Freshwater Fish	Journal of Phycology
Aquatic Sciences	Environmental Management	Journal of the North American Benthological Society
Archiv für Hydrobiologie	Ecoscience	Limnology and Oceanography
Australian Journal of Ecology	Ecosystems	Marine and Freshwater Research
Australian Journal of Marine and Freshwater Research	Environmental Biology of Fishes	New Zealand Journal of Marine and Freshwater Research
Biodiversity and Conservation	Environmental Conservation	Oecologia
Biogeochemistry	Freshwater Biology	Oikos
Biological Conservation	Frontiers in Ecology and the Environment	Regulated Rivers: Research and Management
BioScience	Fundamental and Applied Limnology	River Research and Applications
Biotropica	Global Change Biology	Science of the Total Environment
Canadian Journal of Fisheries and Aquatic Sciences	Hydrobiologia	Water Research
Canadian Journal of Zoology	International Review of Hydrobiology	

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