Chapter 18
Ecological Thresholds and Resilience in Streams

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Abstract Ecological thresholds and resilience are powerful heuristics for understanding how lotic ecosystems change. Ecosystems may exist in self-organized states based on their taxonomic composition or the range of ecosystem functions, which are influenced by environmental drivers such as thermal or hydrologic regimes, channel morphology, and availability of nutrients. Changes in these underlying drivers may exceed an ecosystem's ability to maintain its characteristic attributes and shift the system into alternative states of organization, which are often regarded as degraded or undesired. The boundaries where transitions occur are known as ecological thresholds and often show a rapid ecosystem response across a relatively small change in the environmental driver. Resilient ecosystems have the capacity to retain attributes in the face of disturbances. However, at some disturbance magnitude an ecosystem may become altered, and the magnitude necessary for a regime shift decreases as resilience declines. While ecological resilience remains largely metaphorical in lotic ecosystems, we describe some approaches for identification and assessment.

Keywords Ecological resilience · Ecological thresholds · Headwater streams · Land use · Disturbance

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18.1 Introduction

As discussed in previous chapters, complex, nonlinear processes may operate at multiple spatial and temporal scales to simultaneously control physical and chemical properties of running waters. Examining the biological attributes of riverine systems increases the complexity of the picture significantly because lotic organisms and the processes they affect are simultaneously influenced by the geomorphic, thermal, hydrologic, and chemical properties of the systems in which they reside. Even the shape of lotic ecosystems presents a challenge to organisms: the linear-dendritic structure and continuous downstream flow of river networks renders dispersal, a critical process for organisms, difficult. Streams also integrate many processes that occur in the terrestrial portion of their watersheds (Hynes 1975; Allan and Johnson 1997), and legacies of land use or other modifications can remain within streams for decades even when watersheds return to a system resembling a pre-disturbance state (Harding et al. 1998). In addition to being literally immersed in the products of upstream and upslope drivers, lotic organisms must cope with disturbance regimes perhaps without parallel in terrestrial and marine systems, from catastrophic floods that can completely reorder their physical habitat to droughts that may cause their environment to effectively disappear. Thus a high degree of environmental variability is the norm for most stream ecosystems.

Lotic organisms have evolved numerous strategies to persist and thrive in such highly dynamic ecosystems. As a prime example, floods may appear to be catastrophic events, but organisms possess diverse adaptations to cope, and many species rely on flooding to maintain habitats necessary to fulfill life history requirements (Lytle and Poff 2004). Some aquatic insects can recognize cloud cover to detect eminent high flow events and move to refuge habitat (Bogan and Lytle 2011), while others have evolved flattened or streamlined body shapes to minimize drag (Alba-Tercedor 2008). In the opposite extreme, drought and desiccation may seem intuitively disastrous, but many organisms have adapted to cope with this stressor as well. For instance, the embryonic life stage of some invertebrates may enter a state of diagenesis to allow persistence of populations through decades-long dry periods (Jenkins and Boulton 2007), while others use atmospheric or ionic signals of impending drought to cue migration towards perennial stream reaches (Lytle et al. 2008). Adaptive traits for surviving dynamic riverine environments are by no means limited to multicellular organisms. Seemingly sessile benthic diatoms disperse within lotic ecosystems by riding currents until a favorable patch is encountered (Stevenson and Peterson 1991).

Even well adapted organisms possess limited tolerance to extreme events, chronically elevated physicochemical stress, or simply changing environmental conditions that at some point no longer allow for persistence. Floods and droughts can be severe enough to eliminate all individuals in populations of fishes or invertebrates (Adams and Warren 2005; Roghair et al. 2002; Bogan and Lytle 2011). Chronically elevated temperatures or chemical stressors may also induce local extirpations. Among the most pervasive threats to lotic organisms are

landscape-scale stressors such as agricultural and urban development, both of which influence multiple physicochemical stressors in receiving waters and frequently cause widespread biodiversity loss (Allan 2004). Ecological changes are not limited to state variables: natural or anthropogenic change can fundamentally alter bio-geochemical processes such as nutrient retention and whole-system metabolism (Gibbins 2015, this issue). Periphyton growth may increase nonlinearly if concentrations of key chemical constituents of lotic ecosystems, such as inorganic nitrogen or phosphorous, exceed critical values (Dodds et al. 2002). When such restructuring events or responses exhibit large shifts across a narrow range of an environmental driver, they are known as ecological thresholds (Fig. 18.1). While many ecological responses are nonlinear, not all are necessarily thresholds. Rather it is the rapidity of change in an ecological attribute over a small change in the driver variable that constitutes a threshold.

Ecological thresholds have parallels to abiotic components of rivers in that they can appear at multiple spatial or temporal scales (Church 2002). Two examples of geomorphic thresholds in flowing water systems include exceeding the shear stress that induces sediment transport, which represents a threshold at a fine temporal resolution, and the transition from a braided to a single-channel system when sediment supply diminishes—an example of a long-term regime shift. Ecological thresholds exhibit similar heterogeneity. A localized flood may temporarily extirpate a population of organisms until migration from nearby reaches recolonizes the disturbed habitat. At the opposite end of the spectrum, assemblages of fishes and macroinvertebrates may entirely turn over when stream networks fed by glaciers transition from turbid to clear water subsequent to glacial retreat.

Not all ecosystem-environment relationships within riverine systems behave in threshold fashion. In fact, most interactions probably do not result in rapid non-linear changes. While the documented number of threshold relationships is

Fig. 18.1 Examples of ecological thresholds as an ecosystem attribute responds across the range of an environmental driver. The direction of the response can also be upwards
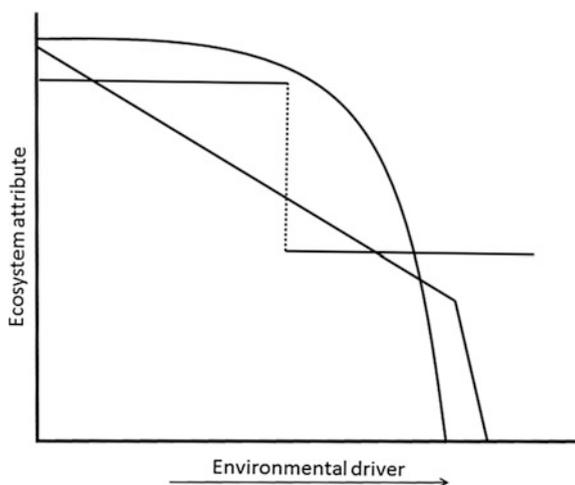
increasing, their continued relative rarity in riverine systems calls their importance into question (Groffman et al. 2006). However, where thresholds exist, they are rarely known until crossed, and many such relationships may yet be discovered.

18.2 Thresholds and the Challenge of Scale

Where threshold responses exist, few exhibit consistency among species or locations because the response scale to a gradient of change is often highly idiosyncratic. Detrimental conditions for one species may be tolerable or even beneficial to another. For example, aquatic insects requiring clean, stable substrates may be extirpated by fine (≤2 mm) sediment deposition, while populations of burrowing taxa may grow under such conditions. Even for drivers that trigger a threshold response, the inflection point will likely be site-, region-, or taxon-specific. Thus, a single, all-encompassing threshold value is rarely applicable to multiple biological attributes excepting catastrophic events such as a toxic chemical spill or volcanic eruption. Such inconsistencies among thresholds largely result from the highly variable conditions under which stream biota have evolved and the substantial heterogeneity in physical and chemical templates among basins.

As with most environment-ecological interactions, biotic responses to environmental change can unfold at different spatial and temporal scales (Box 18.1). The effects can be immediate, as happens when physiological thresholds are exceeded and organisms die, whereas other threshold responses may transpire over one or more generations when changing conditions trigger sublethal effects such as depressed reproductive output. In the latter case, rapid nonlinear reproductive declines may occur, but one or more generations are required for the result to be expressed at the population level.

> **Box 18.1 A closer look at examples of ecological thresholds** Streams in alumino-silicate dominated watersheds with low acid neutralizing capacities may have water quality suitable for resident biota almost year round. However, large precipitation events, particularly snowmelt, may overwhelm a stream's buffering capacity resulting in a large, rapid drop in surface water pH (Jeffries et al. 1979). Consequently, elevated acidity may leach lethal concentrations of aluminum from the substrate and into streams for only a few hours. Acute exposure to aluminum may cause extensive mortality to fish and many of the aquatic invertebrates in a very short time (Baker et al. 1996, Van Sickle et al. 1996; Lepori et al. 2003) with the water quality later returning back to habitable, baseline conditions and remaining suitable for long periods afterwards until the next major event. As second example, water temperatures directly affect the biota by governing the rate of enzymatic processes and physiological performance because almost all stream-dwelling biota maintain temperatures equal to that of the surrounding water. Temperatures directly

influence the rates of processes as diverse as nutrient uptake (Rasmussen et al. 2011) and enzymatic activity (Ward and Stanford 1982). Aquatic biota have upper thermal limits that behave as thresholds above which a species rarely survives (Quinn et al. 1994; Beitinger et al. 2000). Many coldwater species, such as salmonids, have difficulty surviving temperatures exceeding 25 °C, while many warm water stream fishes have thermal thresholds around 30 °C (Allan 1995). Geomorphic changes to streams such as channel widening will allow greater solar-conductive water heating and consequently may change thermal regimes to exceed thresholds. Thermal regime shifts can produce acute responses from rapid heating or chronic, longer-term responses if elevated temperatures are not lethal but rather increase physiological stress. As a final example, the effects of fine sediment dynamics in streams may influence biological processes over multiple time scales. As seen in earlier chapters, sediment size heterogeneity is both present and necessary for channel equilibrium and maintenance. A lack of fine particles can result in channel armoring, particularly downstream of dams where the channel may be sediment-starved. However, excessive fine sediment in the channel has been regarded as one of the most pervasive biological stressors in stream ecosystems (Waters 1995). Fine sediments exceeding around 20 % areal coverage of the streambed produces threshold responses in some benthic macroinvertebrate communities (Burdon et al. 2013). For salmonid embryos incubating in the hyporheic zone, fine sediments may be particularly lethal: volumetric percentages of fine particles exceeding 10 % typically cause high mortality (reviewed in Jensen et al. (2009)), which may result in a multi-year time lag in population declines. Fine sediment deposition may also reduce hydraulic conductivity between the stream and its hyporheos, which may account for substantial portions of the total whole stream system metabolism (Fellows et al. 2001). We expect declines in stream metabolism to become rapid and nonlinear as some yet to be defined porosity threshold is exceeded, and the steepness of the decline proportional to hyporheic depth.

The question of whether thresholds are detected can be contingent on the response scale of the observations. For example, threshold responses of tolerance to landscape-scale changes associated with urbanization in the form of pavement and rooftops (collectively referred to as impervious surface area, hereafter ISA) are evident for many benthic insects (Utz et al. 2009; King and Baker 2010). In many cases, populations of sensitive organisms may disappear at very low levels of ISA within a watershed. The most sensitive taxa are lost at about 3 % watershed ISA while nearly half of all resident taxa may be extirpated by 15–20 % ISA, although site-specific values may vary among geoclimatic settings (Utz et al. 2009) and the degree of ISA connectivity to stream channels (Collier and Clements 2011). However, aggregating individual taxa responses by considering total taxonomic richness rather than individual taxa produces a linear decline across the same ISA

gradient (Fig. 7 in Utz et al. 2009). Although taxa richness is a common community-level metric, other metrics exhibit threshold responses to ISA (Hilderbrand et al. 2009; King et al. 2011). Thus, the choice of both taxonomic resolution and how it is measured can substantially influence whether or not a threshold is detected.

18.3 Thresholds and the Challenge of Covariates

Ecological thresholds have tremendous allure both as heuristic devices to understand how streams behave and as potentially powerful tools for environmental management. Unfortunately, thresholds are often assumed to be static such that maintaining an environmental driver below a critical value can preserve stream ecosystem structure and function. In theory, thresholds can be used to optimize the degree to which a system may be altered and still maintain ecological function. In practice, however, numerous interacting factors often distort or shift threshold boundaries. Failure to recognize such limitations through adherence to static values can result in considerable damage to ecosystems. For example, early research on the effects of urbanization on streams noted negative changes in ecosystem structure and function as watershed ISA levels exceeded around 10–15 % (Klein 1979; Schueler 1995). The 10 % value grew in notoriety and became recommended for land use planning activities (US EPA 2004). Multiple subsequent studies, however, have detected significant changes in species richness and community structure at watershed ISA levels well below 10 %.

Because each stream represents a unique combination of physical, chemical, climatic, and historical legacies, analyses of ecological thresholds have many co-varying attributes that interact to affect biota. Thus even where threshold responses are evident, factors that may not be directly related to the stressor of interest can distort threshold responses. For example, stream biota face particular challenges with osmoregulation because of a need to retain a higher salt balance than the surrounding freshwater. Most aquatic organisms have evolved to retain salts in water with low ionic concentrations, but elevated concentrations overwhelm their physiological tolerance and may become lethal. High concentrations of anionic salts (Cl^-, SO_4^{2-}) in particular can result in large-scale biodiversity loss over a relatively small gradient such as downstream of coal mining activities (Garcia-Criado et al. 1999; Pond et al. 2008). However, toxicity at a given anionic salt concentration decreases substantially as water hardness increases (Mount et al. 1997; Soucek and Kennedy 2005), making the use of a single threshold for all streams dubious. Similar blurring of threshold boundaries occur when atypical geologic settings result in a cool, stable water temperature regime, which allows typically sensitive species such as brook trout (*Salvelinus fontinalis*) to persist in streams with watershed ISA above levels that cause brook trout extirpation elsewhere (Stranko et al. 2008). Thus, planning for system change using rigid, static approaches may

inadvertently shift the system into an undesired state if the threshold is not completely understood.

Because of the multidimensional and contingent nature of many thresholds, the exact mechanism affecting a stream ecosystem is often unknown or not measured. Thus cause and effect relationships with univariate drivers are rare in many ecosystems. When a particular environmental driver causes many disparate physicochemical changes, surrogates representing the combined effects are often used. An example involves the use of watershed urbanization or agricultural land uses as a surrogate for the numerous physicochemical stressors associated with landscape-scale anthropogenic change. The combined effects of urbanization is akin to death by a thousand cuts; urbanization is associated with increases in fine sediment, bed armoring, elevated specific conductance, higher and more variable water temperatures, increased flood frequency and magnitude, greater concentrations of toxic metals, and numerous other stressors (Paul and Meyer 2001). In an urban stream, biological structure or processes may be responding to any or all of the above-mentioned stressors, but rarely do sufficient data exist to identify the specific mechanism for ecological changes while controlling for all of the other potential drivers. A given biological attribute of interest could be responding directly to elevated salt concentrations or indirectly to an altered hydrologic regime and consequential changes in channel geomorphology.

Although we have cautioned about the uncertainties and potential misapplication of using ecological thresholds for management, they have value beyond heuristics. The fact that not every stream responds exactly the same way or to the same value of a driver known to elicit a response does not negate the threshold. Rather, the concept provides a range within which change is likely to occur (Schueler et al. 2009), and effective management will recognize the need to mitigate or plan for uncertainties within such ranges. Ecological thresholds also provide the opportunity to develop futures scenarios and forecast ecological changes (e.g., Van Sickle et al. 2004; Hilderbrand et al. 2010). While futures scenarios can be conducted for non-threshold responses as well, the results are often instructive when large ecosystem changes are forecasted to result from relatively small changes to input drivers. Such exercises may also be used to better understand the concept of ecological resilience, which can be lost when thresholds are crossed.

18.4 Ecological Resilience and Alternate States

In a resilient stream ecosystem, key ecological attributes such as species composition or the range of ecosystem functions will remain consistent over long time scales or return to pre-disturbance states following perturbations. Resilience can have many meanings such as the related concept of engineering resilience (Pimm 1984), which refers to the amount of time required for an ecosystem attribute to return to conditions prior to a disturbance. While ecosystem recovery time is an important attribute of ecological resilience, it is incomplete. Ecological resilience as

we use it in this chapter is the degree to which an ecosystem can absorb or withstand environmental stress or disturbance and still maintain self-organization (i.e., characteristic structure and function; (Holling 1973; Gunderson and Holling 2001). Our treatment hereafter will be with respect to lotic ecosystems and may not follow all of the classical definitions, as streams and rivers possess different attributes and behavior relative to the systems where the foundational concepts of ecological resilience were developed (shallow lakes, terrestrial, and socioeconomic ecosystems). Thus, we may raise as many questions as answers, and we encourage the reader to identify similarities and differences and to challenge our perceptions because ecological resilience can be highly abstract. Several excellent, more comprehensive treatments place ecological resilience in a broader context (Holling 1973; Carpenter et al. 2001; Gunderson and Holling 2001).

Exceeding the limits of resilience and crossing an ecological threshold may shift a system from one ecosystem state into an alternate state (Fig. 18.2). State shifts often entail transitioning from a desired to an undesired state. Figure 18.2 depicts an urbanizing stream with the ball-in-cup model illustrating resilience and alternative
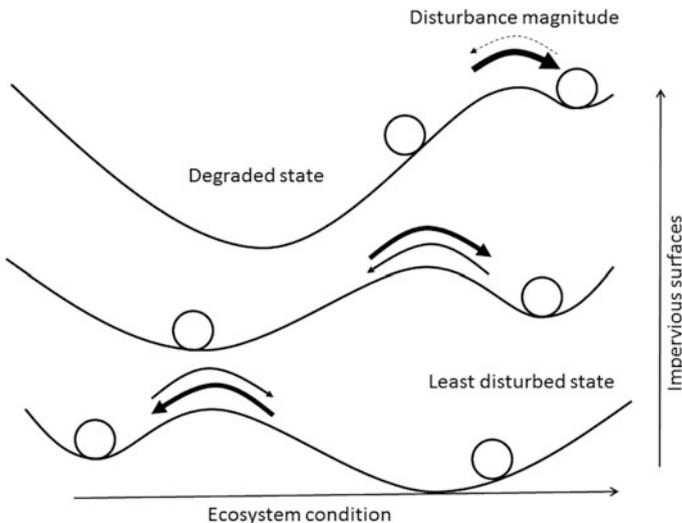
Fig. 18.2 Lotic ecosystems may exist as multiple alternate states, or domains, (*troughs*) separated by thresholds (*ridges*) dividing the states. An ecosystem at a specific point (*open circles*) may have variation in its attributes, but still belong within a state having substantially different attributes, such as taxonomic composition or nutrient processing rates, from other states. Ecological resilience is represented by the width of the domain, while engineering resilience is the depth or steepness of the sides. As the underlying drivers change, as can happen due to increases in impervious surfaces in the watershed, some domains will begin to lose resilience, while others may increase. As the resilience decreases, progressively smaller disturbances (*arrows*) can shift the stream from one alternate state into another. These regime shifts may be semi-permanent on human time scales if the drivers have been substantially altered or there are no dispersal paths for organisms to recolonize after extirpations

stable states as developed by Holling et al. (1995) and used later by Beisner et al. (2003); Scheffer and Carpenter (2003). This heuristic device can represent both biological community and ecosystem frameworks. With respect to biological communities, ecosystem drivers are relatively constant, and the community composition changes mostly from internal, biologically controlled drivers such as competition or predation. In the ecosystem perspective, the system responds to changes in the underlying environmental drivers (Scheffer et al. 2001). Both community and ecosystem frameworks are possible within lotic ecosystems because the relative importance of external (abiotic) factors versus internal (biotic interactions) factors forms a continuum along which communities may be structured (Zalewski and Naiman 1985). Streams dominated by changing environmental conditions are more externally controlled by abiotic variables, while streams in more stable environments tend to be structured more internally by biotic interactions.

Changes in ecosystem state, also known as regime shifts, occur when the resilience of an ecosystem has been exceeded. Resilience, state changes, and thresholds are closely intertwined because thresholds represent boundaries between ecosystem states. While not couched explicitly as alternative states, the lotic literature is rich with examples because the concept is foundational to biomonitoring and assessment. As the physical, chemical, or thermal conditions of a stream change beyond levels observed due to natural variation, detectable changes in taxonomic composition ensue (e.g., Brenden et al. 2008) or ecological functions no longer exhibit expected behavior (Dodds 2006; Earl et al. 2006). Thus with a changing environment, the same section of a stream or river can fundamentally change ecosystem attributes.

Many examples of transitions between alternative states involve rapid, catastrophic shifts (e.g., Carpenter et al. 1999; Scheffer et al. 2001), but loss of resilience may also prove gradual as the drivers change slowly or taxa are sequentially lost. In such cases, the alternate states may behave similarly to how taxonomists define closely related species—differences may be clear at the extremes, but the exact point where the change occurs is uncertain. As detailed below, we believe that more gradual changes are the more common mode of state change in streams because lotic ecosystems are highly influenced by many environmental variables and disturbance regimes (Resh et al. 1988).

Multiple pathways can cause ecosystem state shifts by altering the underlying drivers (Beisner et al. 2003). Changes to any number of drivers such as sediment supply, altered thermal regime, or channel confinement and their interactions can fundamentally change the environmental conditions and result in loss of ecosystem structure or function. Excellent examples involve rivers where a dam regulates discharge, and the resulting altered discharge regime alters hydro-geomorphic attributes such as sediment delivery, resulting in ecological regime shifts (Poff et al. 1997). The dynamic, disturbance-prone nature of lotic systems that exerts strong external controls on community structure in streams may also promote the formation of alternative states (Didham and Watts 2005). Seasonal and annual variation in temperature, discharge, and sediment dynamics probably discourage the

development of tightly coupled biotic interactions in many, but not all, riverine systems. Rather, biota must respond to a constantly changing and challenging physical fluid environment, and species sort along their preferred environmental conditions. As long as the collective suite of abiotic drivers remains within certain bounds, an ecosystem will likely remain loosely organized based on the existing physical habitat template (sensu Southwood 1977; Poff and Ward 1990) and distinguishable from states associated with degraded conditions. However, easily identified, discrete states seem less common than assortments of species driven by a few common taxa.

Disturbances that directly affect the actual organisms or processes may also produce shifts to alternate states. Examples include population losses resulting from a chemical spill, harvest, disease, extreme drought, or other event that causes excessive mortality without the ability to recover or recolonize (e.g., Franssen et al. 2006; Bogan and Lytle 2011). State shifts may also arise from internal controls due to biotic interactions, particularly when a top predator or keystone species is affected (e.g. Power et al. 1985; Bechara et al. 1992; Carpenter et al. 2011). In the case of Power et al. (1985), the exclusion of largemouth bass (*Micropterus salmoides*), a piscivorous predator, shifted a stream ecosystem state from one with substantial periphyton production to one with clean substrates. The regime shift occurred because largemouth bass preyed on small herbivorous grazing fish (central stoneroller, *Capostoma anomallum*), and the exclusion of largemouth bass released these herbivores to feed in areas they would normally avoid in the presence of their predators. Reintroducing largemouth bass reverted the system back to one with heavy periphyton production. In another case study, the catadromous, top predator American Eel (*Anguilla rostrada*) seems to exert significant influence on the lower trophic levels (Stranko et al. 2014). Large dams preclude eel migrations and result in changes in the densities of the benthic fish and macroinvertebrates.

18.5 Assessing Resilience

Assessing ecological resilience has proven challenging, and the science is still in an early state. Advances in resilience theory have greatly outpaced applications (Thrush et al. 2009). The disparity may exist because measuring ecological resilience requires us to identify a specific ecosystem component and the stressor against which resilience is assessed as well as the necessary time scale of natural recovery to the stressor (Carpenter et al. 2001). Not all ecosystem components respond similarly to a given driver nor are we always able to extract the effect of a single driver from contingent interactions. Thus most advances in assessing resilience have been theoretical (e.g., Petchey and Gaston 2009) or based on simulation models (e.g., Carpenter and Brock 2006). Rarely has resilience been assessed on empirical data (but see Carpenter et al. 2011). Emerging evidence suggests that systems approaching a threshold and regime shift will exhibit higher variance in response (Carpenter and Brock 2006) or a critical slowing down of recovery time

after disturbance (Scheffer et al. 2009; Drake and Griffen 2010; Lindegren et al. 2012; Veraart et al. 2012). However, non-catastrophic state shifts may also exhibit similar behaviors (Kéfi et al. 2013). Nonetheless, such information can be quite useful for predicting when a system is undergoing change regardless of its speed. Ideally, several years or decades of data will exist on multiple ecosystem attributes and drivers, but such data are extremely rare. Thus, resilience is often assessed through retrospective analysis and inferred from large datasets not explicitly collected specifically for resilience assessments and often using space-for-time substitutions (Box 18.2). Multiple ecological thresholds may need to be crossed in order to measure resilience. With sufficient time and data however, advances in identifying ecological thresholds, alternate states, and resilience are likely to emerge.

Box 18.2 Measuring ecological resilience Ecological resilience is an abstract concept. We therefore provide a more detailed example of an attempt at its quantification. Our research group (Hilderbrand and Raesly 2009) has studied ecological thresholds, alternate states, and resilience by retrospectively analyzing a large, long-term dataset on headwater streams collected by the Maryland Biological Stream Survey (Klauda et al. 1998). We focus specifically on the benthic macroinvertebrate community because it is an important measure of stream ecosystem health known to be sensitive to changes in channel structure, water quality, and general degradation (Resh and Jackson 1993). Streams in the least disturbed watersheds clustered into two identifiable and slightly overlapping alternate states (Fig. 18.3). The ellipsoids define sites in similarity space that are not statistically different from the least disturbed reference sites in terms of benthic macroinvertebrate community composition. Sites outside of either ellipsoid are statistically different from either reference state and may reside in a separate alternate state (not shown due to complexity). The boundary of each ellipsoid represents the edge of the domain occupied by each alternate state and may be construed as a threshold between alternate states. Environmental stressors at sites residing within a reference state can now be quantified and compared against stressor levels for sites outside of the ellipsoid. The community is resilient to a specific stressor when stressor levels do not differ among alternate states. In contrast differences in stressor levels among alternate states indicate sensitivity to the stressor, and the point where the community changes can be calculated. Using this approach, many potential stressors can be assessed against an ecosystem attribute. Using the approach described above is imperfect because statistical criteria are applied to demarcate a boundary, but the approach incorporates many of the important attributes of alternate states, thresholds, and resilience. The use of multiple least-disturbed sites to define the ellipsoid implicitly allows for the wide variation in community structure observed in nature and quantifies the presence of one or more alternate states. The approach also provides boundaries for use in
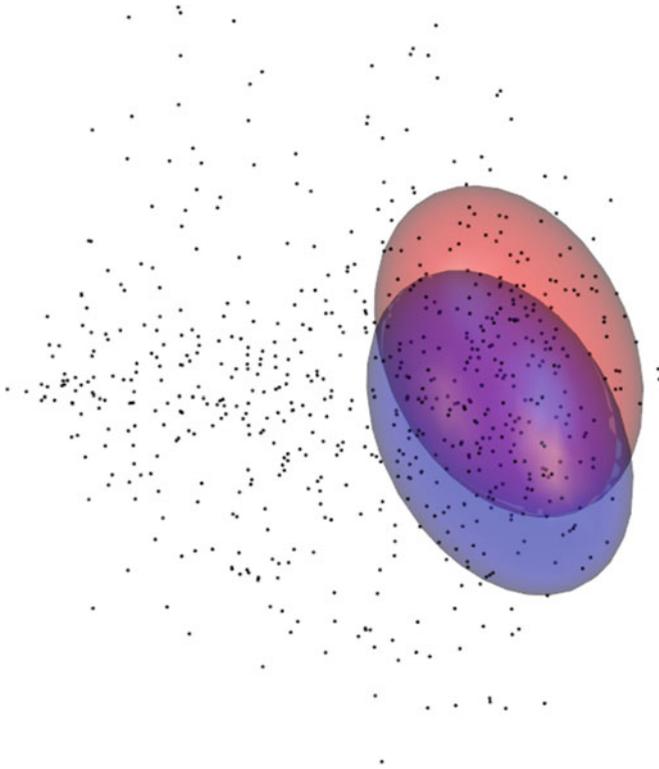
Fig. 18.3 Alternate states derived from nonmetric nondimensional scaling of benthic macroinvertebrate communities occurring in least disturbed watersheds. Ellipsoids define the boundaries of alternate ecological states identified in the least disturbed watersheds. Sites falling outside of an ellipsoid have benthic macroinvertebrate communities that are statistically different from the alternate state representing least disturbed conditions. In this example, there are two general community states for least disturbed systems. The edges of the ellipsoids represent boundaries of the alternate states. Axes have been removed for better visual clarity

determining if a state has been exited. Measuring the range of a given stressor across all sites falling within a reference ellipsoid is akin to measuring the width of the domain within which the alternate state resides with respect to that stressor and operationalizes the theory into something measureable. Thus we believe that many insights can be derived from retrospective analysis of the monitoring data that many agencies are charged with.

The choice of ecological response used to quantify resilience may exert a large influence due to the high degree of variability among rates of ecological processes. System aspects governed by microbial activity (e.g., nutrient uptake, stream

metabolism) may respond very rapidly because microbes reproduce rapidly and consequently an event or driver that alters the microbial community may respond or recover over short time scales. In contrast, longer-lived organisms, such as fish and freshwater mussels, may take much longer to respond or recover from a distur-bance. A long recovery time may be mistaken for a loss of resilience when it simply reflects the time required for reproduction or dispersal. Until sufficient time has passed however, we may be unable to separate a regime shift and loss of resilience from a slow recovery trajectory.

18.6 Maintenance, Recovery, and Restoration of Resilience

Resilient ecosystems have the ability to recover from disturbances of differing magnitudes. Small disturbances may temporarily alter relative abundances of organisms or alter processing rates. As the magnitude of a disturbance increases to the point where taxa are locally extirpated, connections within the hydrologic network may be required for recolonization and a return to a recognizable, pre-disturbance state. Thus, maintaining resilient ecosystems in the face of larger perturbations requires the integration of increasingly larger spatial and temporal scales.

Across scales, resilience tends to decline with a loss of natural variation in environmental drivers and is often the result of human interventions in trying to manage or control the environment, such as with channel and floodplain alterations to limit flooding (Holling and Meffe 1996). As resilience decreases, smaller dis-turbances may cause regime shifts (Fig. 18.2). In contrast, maintaining variation in the external drivers tends to promote a larger range of ecosystem functions and greater biodiversity, thus increasing systemic capacity to adapt to, and recover from, changes without fundamentally altering the underlying structure. Such adaptive capacity is thought to be critical in maintaining resilient systems (Gunderson 2000). Unfortunately, designing resilient stream ecosystems for alter-nate states found in non-degraded watersheds can be very difficult. Invariably, 'managing' a system for resilience by focusing on an incomplete suite of drivers will neglect important and unknown drivers, likely reducing overall resilience. Thus, the best way to maintain resilience is to promote its retention by allowing physical and chemical attributes of the system to experience as much of the range of natural conditions as is possible.

Sometimes however, resilience is not a desired quality and may inhibit what we consider the proper functioning of lotic ecosystems. Some watersheds are so highly altered that only the most tolerant lotic biota are capable of surviving. These ecosystems tend to contain a small subset of the regional biodiversity and have highly altered ecosystem functions. However, they can be highly resilient systems because the magnitude of change in the drivers required to shift to a more biodi-verse or ecologically functional state is nearly insurmountable (Bernhardt and

Palmer 2011). These systems often exhibit hysteresis—the lack of reversion even after some suitable conditions are restored to a pre-disturbance state.

The visual and heuristic power of thresholds as tipping points and the resilience that prevents regime shifts naturally leads to a desire to integrate the concepts in restoration projects (Irvine 2012). If riverine ecosystems can shift into a different state due to changes in the underlying drivers, then the process should be reversible with directed management actions. However, because most ecological relationships are highly multidimensional the perceived ability to restore a system back to its predisturbance state is usually naïve (Hilderbrand et al. 2005). The hysteresis exhibited by many degraded streams makes reversion back to the original, or a less degraded, ecosystem state difficult or improbable because of fundamentally altered drivers or the inability of the biota to recolonize and persist even after repeated reintroductions. Despite thousands of restoration projects and billions of dollars spent on stream restoration (Hassett et al. 2005), we have little evidence of successfully restoring stream ecosystems back to an undisturbed state (Bernhardt and Palmer 2011; Stranko et al. 2012); post-restoration monitoring has largely been insufficient to determine if ecosystem attributes have moved into a more desirable condition (Palmer 2008). Nonetheless, many activities that highly degrade lotic ecosystems continue to assume that all aspects of a stream can be restored or even re-created in newly constructed channels (Palmer et al. 2010).

18.7 Conclusion

Thresholds and resilience have the potential to serve as powerful heuristics for understanding stream ecosystems and how they respond as the world around them changes. The utility of identifying ecological thresholds and quantifying ecological resilience for managing and maintaining the quality of our streams in an increasingly human modified world is tremendous. However, the allure can also result in problems because we cannot anticipate every interaction. We also cannot know how the hydrologic cycle and the resulting thermal and geomorphic adjustments in each river system will change as the climate and precipitation patterns change. Thus, these concepts should be primarily viewed more as guiding principles rather than as static decision points for management. The potential to over-manage watersheds (Holling and Meffe 1996) could easily end in a Sisyphus Complex (Hilderbrand et al. 2005) where a seeming endless suite of actions are initiated in response to topical symptoms rather than identifying and addressing the underlying changes. A difficult, but more long-term view will allow for change in such a way as to not dramatically alter the underlying processes and constraints under which each stream and its watershed evolved. Thus, we too must be resilient in our ongoing efforts to understand and ensure the ecological resilience and adaptive capacity of streams.

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