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Control Points in Ecosystems: Moving Beyond the Hot Spot Hot Moment Concept

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Abstract

The phrase ''hot spots and hot moments'' first entered the lexicon in 2003, following the publication of the paper ''Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems'' by McClain and others (Ecosystems 6:301–312, 2003). This paper described the potential for rare places and rare events to exert a disproportionate influence on the movement of elements at the scale of landscapes and ecosystems. Here, we examine how the cleverly named hot spot and hot moment concept (hereafter HSHM) has influenced biogeochemistry and ecosystem science over the last 13 years. We specifically examined the extent to which the HSHM concept has: (1) motivated research aimed at understanding how and why biogeochemical behavior varies across spatiotemporal scales; (2) improved our ability to detect HSHM phenomena; and (3) influenced our approaches to restoration and ecosystem management practices. We found that the HSHM concept has provided a highly fertile framework for a substantial volume of research on the spatial and temporal dynamics of nutrient cycling, and in doing so, has improved our understanding of when and where biogeochemical rates are maximized. Despite the high usage of the term, we found limited examples of rigorous statistical or modeling approaches that would allow ecosystem scientists to not only identify, but scale the aggregate impact of HSHM on ecosystem processes. We propose that the phrase ''hot spots and hot moments'' includes two implicit assumptions that may actually be limiting progress in applying the concept. First, by differentiating ''hot spots'' from ''hot moments,'' the phrase separates the spatial and temporal components of biogeochemical behavior. Instead, we argue that the temporal dynamics of a putative hot spot are a fundamental trait that should be used in their description. Second, the adjective ''hot'' implicitly suggests that a place or a time must be dichotomously classified as ''hot or not.'' We suggest instead that each landscape of interest contains a wide range of biogeochemical process rates that respond to critical drivers, and the gradations of this biogeochemical topography are of greater interest than the maximum peaks. For these reasons, we recommend replacing the HSHM terminology

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with the more nuanced term *ecosystem control points*. ''Ecosystem control'' suggests that the rate must be of sufficient magnitude or ubiquity to affect dynamics of the ecosystem, while ''points'' allows for descriptions that simultaneously incorporate both spatial and temporal dynamics. We further suggest that there are at least four distinct types of ecosystem control points whose influence arises through distinct hydrologic and biogeochemical mechanisms. Our goal is to provide the tools with which researchers can develop testable hypotheses regarding the spatiotemporal dynamics of biogeochemistry that will stimulate advances in more accurately identifying, modeling and scaling biogeochemical heterogeneity to better understand ecosystem processes.

Key words: biogeochemistry; hot spots; control points; ecosystem.

INTRODUCTION

Scientific papers may become classics by describing entirely new ideas or methods, or through new synthesis of a body of thought and literature. In 2003, McClain and others published a paper entitled ''Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems'' in the journal Ecosystems that integrated perspectives from landscape ecology with a growing number of empirical studies reporting high heterogeneity in biogeochemical process rates within ecosystems. The paper galvanized researchers into focused study of these phenomena. By September 2015, when we initiated our analysis, McClain and others (2003) had been cited 666 times, making it one of the most highly cited papers ever published in Ecosystems. In this paper, we assess how the hot spot hot moment concept (hereafter referenced as the HSHM concept) introduced by McClain and others (2003) has influenced ecosystem science since its publication.

Recognizing the lack of equivalency between numerical abundance and ecological dominance is a recurrent theme in ecology, from Robert Paine's recognition of the role of rare *keystone predators* in structuring communities and food webs (Paine 1966, 1969) to our more recent fascination with the unique biogeochemical capacities of *rare biosphere* microorganisms (for example, Lynch and Neufeld 2015). The HSHM concept falls directly in line with this theme, recognizing that there can be rare areas or times possessing such exceptionally high rates of biogeochemical activity that ecosystem fluxes or mass balance could not be understood without taking them into account. The HSHM concept extends beyond a strictly biological concept of species interactions to a biogeochemical and ecohydrological one that utilizes classic landscape ecology approaches to explore how the location and connectivity of patches shapes their role within ecosystem processes. The HSHM concept is widely appealing because it converts a previously annoying problem, ecosystem processes vary and all sampling efforts are limited, into an important property of ecosystems that itself deserves concentrated study.

In the HSHM paper, McClain and others (2003) coined the term biogeochemical ''hot spots'' to describe ''a specific form of spatial heterogeneity represented by a patch of higher biogeochemical reaction rates.'' They suggested that for some biogeochemical processes, total ecosystem rates may be strongly controlled by the conditions, resources and biota occurring in a very small proportion of the total ecosystem volume. To recognize that biogeochemical processes also vary in time, they further suggested that high biogeochemical rates could be restricted to ephemeral or brief events, that is, ''hot moments'' which are events that ''change resources, substrate availability or the physical environment.''

The idea of ''hot spots'' and ''hot moments'' within ecosystems was not entirely new in 2003; instead what was exciting and novel about the HSHM paper was the synthesis of many studies that collectively reported peak biogeochemical activity at ecotones and confluences within landscapes. The term ''hot spots'' had previously appeared in the titles of papers describing variation in the distribution of soil organic matter and soil faunal activity (Bonkowski and others 2000) and preferential flow paths through soils (Fisher and others 1998; Hill and others 2000; Bundt and others 2001). A large literature was synthesized and drawn upon to contextualize the HSHM concept, but research on the special properties of riparian habitats was most influential. Previous work documenting the special role of riparian zones in controlling watershed nutrient exports (for example, Peterjohn and Correll 1984) and the high rates of denitrification along hyporheic flowpaths (for example, Holmes and others 1994; Hedin and others 1998) were especially important. Other research examining the redox variation within soil aggregates (for example, Parkin 1987) and the special biogeochemical properties of river confluences (for example, Gadel and others 2000) were used to extend the concept farther upslope and downstream from riparian zones. McClain and others (2003) employed the term ‘‘hot moments’’ to describe phenomena as diverse as the effects of very small amounts of rainfall on plant nutrient uptake or trace gas fluxes in arid ecosystems (for example, Gallardo and Schlesinger 1992; Davidson and others 1993; Gebauer and Ehleringer 2000; Hartley and Schlesinger 2000); and the large fluxes of DOC lost from watersheds during floods (for example, Lewis and Grant 1979; Boyer and others 2000).

Although biogeochemical evidence for HSHMs was mounting in the decades preceding McClain and others (2003), the field of landscape ecology was simultaneously developing theories and methods to understand spatial heterogeneity in complex landscapes. Recognition of the explicitly spatial dimension of many ecological processes led ecologists to develop quantitative descriptions of landscape patterning and to describe the fluxes of energy and materials among landscape patches (Forman and Godron 1981; Risser and others 1983). McClain and others (2003) attempted to combine these theoretical advances in landscape ecology with our increasing ability to measure high spatial variation in biogeochemical process rates by suggesting we describe the scale dependence (that is, grain and extent) and the nonrandom distribution of HSHMs within ecosystems.

The success and appeal of the HSHM concept is clearly illustrated in the volume of interdisciplinary research that has evolved from and with it over the past 15 years. Through comprehensive analysis of the papers citing McClain and others (2003), we examine the extent to which the HSHM concept has met the goals stated in the original paper. The authors of the HSHM concept intended that their effort would allow ecosystem scientists to: ‘‘(a) investigate the nature and occurrence of natural hot spots and hot moments in the cycles of a larger number of elements and at different scales; (b) hone our ability to predict the spatial distribution of hot spots and the temporal distribution of hot moments based on underlying hydrologic, geomorphic, or edaphic patterns in space and time; (c) use the methods of landscape ecology to evaluate the roles of hot spots and moments in landscape biogeochemistry; and (d) evaluate the utility of natural and created hot spots and hot moments as resource management tools.’’ We agree with the original authors that these are priority goals for ecosystem science and application.

Our primary objective in evaluating the usage and impact of the HSHM concept has been to refocus attention on how ecosystem scientists might more effectively identify, classify, quantify and scale the biogeochemical processes that control ecosystem mass balance and element fluxes. Extended discussions over the course of a year have led us to the conclusion that, with time the HSHM concept has been used widely but not rigorously. Although the HSHM concept has effectively raised awareness of the problem that rare (and thus easy to miss) habitat patches and events can have highly disproportionate effects on ecosystem processes, there has been far too little progress in incorporating this understanding into ecosystem mass balances and models. We explore possible reasons behind this lack of progress and chart a path forward that we hope will improve our ability to accurately incorporate spatiotemporal variation in biogeochemical rates into our conceptual and quantitative descriptions of ecosystem science.

METHODS

Primary Citations

We used ISI Web of Science to identify all publications that cited McClain and others (2003) as of August 17, 2015. We then collected basic demographic information about the citing papers. For each citing paper, we recorded the authors, title, year of publication, and publication journal. We then classified each citing paper by the type of article: primary research, literature review, conceptual paper, data synthesis/meta-analysis, or other (book chapter; Figure 1).

We used the complete data set of citing papers to conduct our first tier of analysis. Our goals were to demonstrate the cumulative impact of the HSHM concept on the ecosystem ecology literature, understand how it was being used to motivate new research, and determine whether this varied among subdisciplines. To assess how the HSHM concept was being used in the literature, we recorded the location of each individual citation of the HSHM paper within each citing paper (that is, introduction, methods, results, discussion, conclusion, or other) and we classified each citation into one of five usage categories: (1) definition—the HSHM paper was used to define hot spots or hot moments as phenomena that occur in ecosystems; (2) justification—the HSHM paper was used as motivating evidence in support of the research; (3) explanation—the HSHM paper was used, often post hoc, to clarify observed spatially or temporally

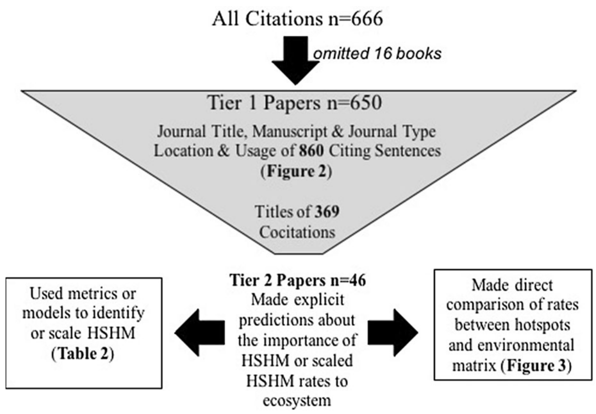


Figure 1. Schematic illustrating how we processed all initial (n = 666) citations of McClain and others (2003). We removed book chapters to refine the initial citations to a Tier 1 group of papers (n = 650). From the Tier 1 papers, we recorded demographic and citation usage data for all individual citing sentences. We created a list of Tier 2 papers (n = 46) refined from the Tier 1 papers which used McClain and others (2003) to predict or scale HSHM.

heterogeneous data; (4) prediction/scaling/testing—the HSHM paper was used to motivate some empirical scaling of observed rates or to develop a predictive framework for the occurrence of hot spots or hot moments; or (5) other—the HSHM paper was used in a way not captured by usage categories 1–4.

Co-citations

We next wanted to evaluate which articles were commonly cited in tandem with McClain and others (2003) as further evidence of the concept's ecological importance. To do this, we collected information on every citation that was listed with McClain and others (2003) in parenthetical sets of citations (co-citations). For example, if the citation was McClain and others (2003) and Vidon and others (2010), we recorded the authors, title, year of publication, and journal of Vidon and others (2010). In cases in which a citing sentence included multiple sets of citations, we included co-citations that were outside of the same parenthetical grouping only when the sentence clearly linked separate citation groupings into a single idea.

Tier 1 Analysis: HSHM Influence on the Literature

To examine which scientific communities or disciplines were using the HSHM concept, we examined the journals in which papers citing the HSHM paper commonly appeared. We identified those journals in which at least five published articles cited McClain and others (2003), and classified these journals into their major fields or disciplines (that is, biogeochemistry, ecology, environmental science hydrology, soil science, or general science). To determine the papers most frequently co-cited with McClain and others (2003), we summed the instances of each co-citation across all papers in our analysis. Finally, to assess the general themes of each manuscript citing McClain and others (2003), we examined frequency diagrams of the words in the pool of all manuscript titles. Using the ''tm'' (version 0.6-2) package in R version 3.2.2 (Feinerer and Hornik 2015), we removed stop words (for example, the, and, is) and punctuation from manuscript titles. We then compiled a frequency table of each word's occurrence. We conducted these analyses with and without self-citations to ensure that our findings represented the scientific field as a whole, and not simply a subset composed of the authors of the original paper.

Tier 2 Analysis: Extra Hot Papers

The Tier 1 analysis allowed us to broadly assess how the HSHM paper was being used in the scientific literature and to gauge its impact in various subdisciplines. However, we also wanted to look more closely at individual publications that used the HSHM paper to advance the predictive framework of the HSHM concept or to refine the conceptual framework for understanding spatially and temporally heterogeneous phenomena. To do this, we narrowed the initial set of citing papers to a second set that either made attempts to predict, scale, or test elements of the HSHM concept, or that explicitly compared the rates of a biogeochemical process between a putative hot spot or hot moment and the surrounding environmental matrix (often referred to as the ''cold matrix''). This resulted in a set of 46 Tier 2 papers—approximately 7% of the initial set of Tier 1 citations.

One important characteristic of many Tier 2 publications was the comparison of biogeochemicals pools or rates between the identified hot spot or hot moment and the surrounding environmental matrix. Whenever possible, we calculated a response ratio for HSHM activity by dividing the mean hot spot rate or pool size by the mean ''cold matrix'' rate or pool size (as per Kuzyakov and Blagodatskaya 2015). Finally, we examined the quantitative metrics by which hot spots or hot moments were identified in these Tier 2 papers. We identified 34 articles that used quantitative methods to identify or define hot spots or hot moments within a study, and compiled and categorized the types of quantitative approaches that were used.

RESULTS

We initiated our review by downloading a bibliography of all articles citing McClain and others (2003) as of August 17, 2015. As of August 17, 2015, McClain and others (2003) had been cited 666 times. We restricted our analysis to the 650 citations within journal articles (excluding citations that occurred in book chapters), with these citing papers appearing in a total of 181 different journals (Electronic supplementary material). McClain and others (2003) was most commonly cited in literature from the disciplines of Biogeochemistry, General Ecology or Hydrology (Figure 2A), and was most frequently cited in biogeochemistry journals, particularly JGR Biogeosciences and Biogeochemistry. McClain and others (2003) was cited 24 times in the journal Ecosystems, in which the original article appeared, and more than 20 times in three different hydrology journals: Water Resources Research, Hydrological Processes and the Journal of Hydrology as well as in the journal Ecosystems in which the original article appeared (Figure 2A).

Most citing papers cited McClain and others (2003) only within their introduction (346 papers, or 52% of Tier 1 papers), whereas another 267 (40% of Tier 1 papers) cited it in the discussion (Figure 2B). Half of the citing papers (n = 336) used the citation as a justification or motivation for their study, whereas 35% (n = 234) used it to explain their findings, often as a post hoc explanation for highly variable data (Figure 2C). A set of 47 papers used the citation only to define the term ''hot spots or hot moments'' (7% of tier 1 papers).

Topics and Themes in Usage of the HSHM Concept

To assess the general themes of articles citing McClain and others (2003), we analyzed the word composition of: the titles of citing articles (n = 650), the sentences where the citation occurred (n = 860), and the titles of articles co-cited with McClain and others (2003) (n = 369). Overall, our text analysis revealed higher usage of ''hot spots'' as compared to ''hot moments'' (33 vs. 15 uses in titles of citing articles; 465 vs. 132 in citing sentences; and 107 vs. 77 in titles of co-cited articles).

Our text analysis revealed that papers that cite and are co-cited with McClain and others (2003) tend to focus on nitrogen as compared to other elements. Across all the titles of all citing articles, ''nitrogen'' was the most frequent word, occurring 90 times. A diverse set of terms relating to nitrogen biogeochemistry (for example, ammonium, ammonia, annamox, denitrification, denitrifying, dinitrogen, nitrate, nitrogen, nitrous, N_2O, ^{15}N) collectively occurred a total of 249 times in citing article titles and 302 times in the titles of co-cited articles. Terms related to carbon mineralization (for example, carbon, carbonate, CO_2, diox-

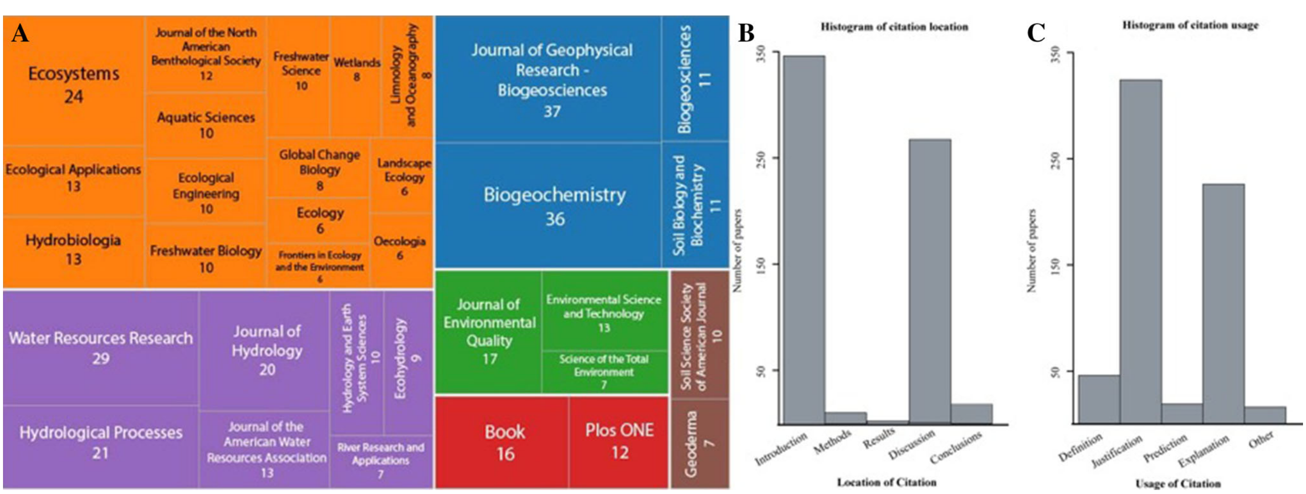


Figure 2. **A** Number of journals (n = 34) citing McClain and others (2003) more than five times encompasses 436 of Tier 1 papers. The size of each journal box corresponds to the number of Tier 1 papers published therein, and the number in parentheses of each journal box refers to the number of Tier 1 papers published in that journal. Journals are *color-coded* by the discipline of the journal (*orange* Ecology, *purple* Hydrology, *blue* Biogeochemistry, *green* Environmental Science, *red* General Science, *brown* oil science. *Numbers* in *parentheses* alongside each discipline in the key are the number of citations in each discipline. *Histograms* of the **B** location and **C** usage type of citing sentences in all 650 citing articles.

Table 1. Most Frequent Articles Co-cited with McClain and others (2003)

# Co-citations	Citations	Type of paper	Focal constituent(s)	Focal process(es)	Scale/zone of interest
34	Groffman and others (2009)	Conceptual	Nitrogen	Denitrification	All of interest to denitrification
23	Vidon and others (2010)	Review	N, C, P, Hg, S, OM and pesticides	N transformations; P mobilization/immobilization; OM mineralization; pesticide/degradation/desorption; Hg mobilization/methylation	Stream, riparian zone, upland continuum
11	Hedin and others (1998)	Primary research	Key electron acceptors and donors (NO_3, N_2O, NH_4, SO_4, CH_4, DOC)	Denitrification; methanogenesis	Subsurface water in riparian wetlands
11	Harms and Grimm (2008)	Primary research	Nitrogen; carbon	Rates of microbial activity; N transformations (nitrification, denitrification)	Soils within riparian zones
10	Peterjohn and Correll (1984)	Primary research	Nitrogen; carbon; phosphorus	N, P, and C retention	Riparian forest
10	Hill and others (2000)	Primary research	Nitrogen	Denitrification	Riparian forest

For each article, we list the number of time it was co-cited (out of 629 total co-citations), the type of paper (see ''Methods'' section), which biogeochemical processes and chemicals were examined, and the spatial scale of the study.

ide, DOC, DOM, methane) occurred 76 times in the titles of citing articles. ''Phosphorus'' appeared in only 11 titles (''phosphate'' was not used). Terms relating to other elemental cycles appeared far less frequently in the titles of citing articles (mercury: 6, calcium: 3; iron: 2; magnesium: 1). The themes and focus of citing articles were consistent over time. Despite a nearly eightfold increase in the number of citing articles published between 2003–2005 and 2013–2015, we found little evidence for major thematic shifts between the time periods. Consistent with our overall analysis of the themes of citing articles, ''nitrogen,'' ''carbon,'' ''denitrification,'' and ''stream(s)'' were some of the most frequently occurring title words of citing articles in both time periods. ''Soil'' moved from being the fifth most frequent title word immediately following the publication of McClain and others (2003) to the most common title word of more recent articles.

Changes in the Application of the HSHM Concept Over Time

To assess whether usage of the HSHM concept has shifted over time, we compared the text of citing article titles in the 5 years following publication of McClain and others (2003) (that is, 2003–2008) to those published in 2010–2015. With eight of the top 10 most frequently used title words being identical in both time periods (nitrogen, riparian, river, water, denitrification, carbon, soil, stream), we found little evidence that the HSHM concept has shifted in research focus over time.

Six papers were co-cited with McClain and others (2003) in at least ten different articles (Table 1). Three of the most frequently co-cited articles predated McClain and others (2003) (Peterjohn and Correll 1984; Hedin and others 1998; and Hill and others 2000). Each of these papers was cited by McClain and others (2003) and each reported empirical data on biogeochemical transformation of nitrogen within riparian zones. Although these papers brought to attention the importance of missing reactants for unusually high rates of biogeochemical activity, they did not yet incorporate landscape ecology into their understanding of HSHM. Two of the more recently published highly co-cited papers shared authors with McClain and others (2003), Harms and Grimm (2008) and Groffman and others (2009) while the third paper's author list was independent (Vidon and others 2010). Harms and Grimm 2008 (co-cited 11 times)

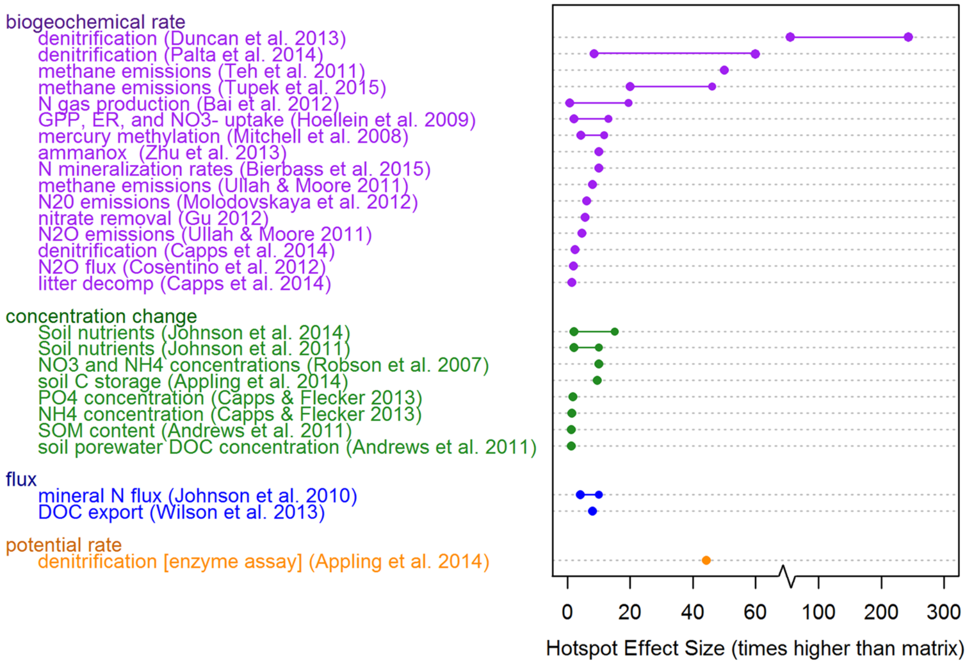


Figure 3. Magnitude of control points relative to the surrounding matrix. *Points* show the reported mean magnitude of the control point relative to background conditions; if ranges of values were reported, we use lines to indicate the range of relative magnitudes.

applied the HSHM concept to C and N cycling in desert riparian zones whereas Groffman and others (2009) (co-cited 34 times) is a conceptual paper that explores the challenges of incorporating HSHM behavior into denitrification models. The Vidon and others (2010) paper (co-cited 23 times) reviews the state of knowledge on riparian zone HSHM in the hopes of providing information that can improve the management of riparian zones.

Hot or Not? Identifying, Predicting, and Defining HSHM

Of the 46 Tier 2 papers that used McClain and others (2003) to predict, explain or scale hot spot behavior, we identified only 22 papers (3.3% of total) that explicitly compared biogeochemical rates or element concentrations between hot spots and the ''cold matrix'' (Figure 3). The majority of the papers in this subset studied fluxes or transformation of nitrogen (17 of 22), and, most papers (21 of 22) measured changes in the export or concentrations of the compound of interest as opposed to directly measuring process rates. Hot spots of pool size or concentration ranged from 1.25 to 15 times greater than those of the surrounding matrix. In contrast, fluxes from purported biogeochemical hot spots were 0.61–270 times greater than fluxes from the surrounding matrix (Figure 3).

We identified 34 papers from the Tier 2 publications that described quantitative methods to delineate which spots or moments could be considered ''hot''. We categorized these delineation methods into five ''Hotness Indices'' (Table 2). In general, reaction rates or fluxes were classified as hot if they: (1) differed statistically from the average/matrix/antecedent rate or flux; (2) represented some ''substantial'' percentage of the total flux; (3) differed statistically among or between a priori defined categories, such as landscape elements (for example, upland vs. riparian); (4) were identified as statistical outliers in the data distribution; or (5) contributed above a predefined proportion (as defined by authors) to the total flux/rate than would be expected from their areal (or temporal) extent. Determination of statistically significant differences among categories (Hotness Index 3) and identification of outliers (Hotness Index 4) were the most common ways in which hot spots were identified, followed by computation of percentage to total (Hotness Index 2) and comparison with a reference time or place (Hotness Index 1; Table 2). Only three papers developed an index that compared the contribution of the habitat or the moment of interest to total ecosystem fluxes (Hoellein and others 2009; Gu and others 2012; Weyer and others 2014).

DISCUSSION AND NEW SYNTHESIS

McClain and others' (2003) high citation count suggests that the conceptual framework described by the phrase ''hot spots and hot moments'' has had broad appeal to and impact on ecosystem scientists, biogeochemists and hydrologists. It is clear

Table 2. Hotness Indices Used to Define or Demonstrate Hot Spots and Hot Moments in Tier 2 Publications

Type of index	Times used	Citations
Simple comparison to average, antecedent, or matrix	5	Archer and others (2015), Jenerette and others (2008), Richardson and others (2007), Robson and others (2007) and Wilson and others (2013)
Substantial percentage of total flux	7	Arrigoni and others (2008); Bai and others (2012); Christenson and others (2010), Tall and others (2011), Teh and others (2011), Troxler and Childers (2010) and Ullah and Moore (2011)
Statistically significant difference between or among landscape elements or time periods categorized a priori	10	Andrews and others (2011), Appling and others (2014), Bierbass and others (2015), Capps and Flecker (2013); Capps and others (2014), Duncan and others (2013), Iribar and others (2008), Morse and others (2014), Tupek and others (2015) and Zhu and others (2013)
Outlier in distribution of data	9	Harms and Grimm (2008), Johnson and others (2010, 2011, 2014), Mitchell and others (2008), Molodovskaya and others (2012), Palta and others (2014), van den Heuvel and others (2009) and Woodward and others (2013)
Contribution to flux/ contribution to total area or time	3	Gu and others (2012), Hoellein and others (2009), Weyer and others (2014)
Total	34	

that the HSHM concept helped codify a growing understanding that certain landscape patches have disproportionate effects on ecosystem biogeochemistry. Though widely cited and discussed, we found that very few citations of McClain and others (2003) were associated with developing or testing specific hypotheses about HSHM dynamics within individual studies. We also uncovered very few instances (but see, van den Heuvel and others 2009; Gu and others 2012; Duncan and others 2013) in which researchers attempted to scale the impact of ''hot spots or hot moments'' to whole ecosystem or landscape-level processes. Indeed, only 7% of all citing papers specifically articulated hypotheses or predictions, whereas the predominant usage of the HSHM concept was as an a priori motivation for studying a specific habitat patch or as a post hoc way to explain outliers. As a consequence, the HSHM concept itself has experienced limited empirical and theoretical advance despite wide usage.

Papers using the term ''hot spot'' often point to the unusual characteristics of a patch relative to the surrounding matrix. The focal patches are not always described biogeochemically. As a fairly typical example, Ademollo and others (2011) describe the spatial patterns of sediment deposition in response to repeated river flood events, and characterize high deposition areas as ''hot spots'' simply because they differ from the surrounding areas in their amount of sediment. Although we agree that flooding patterns generate spatial heterogeneity of sediment deposits, their characterization as biogeochemical hot spots requires two distinct types of information. First, researchers must demonstrate that biogeochemical activity within the depositional areas is distinct (for example, higher rates, different dominant processes or different process ratios) from the surrounding matrix. Second, to have ''disproportionate effects on ecosystem processes'' a study must provide an estimate of the impact of these putative ''hot spots'' at the scale of their predefined ecosystem boundaries.

This general lack of rigor or overuse of the HSHM terminology dilutes the intended impact of the concept. A limited but powerful body of research demonstrates the important contribution of rare ecological phenomena to local, regional and even global biogeochemical cycles. For example ''hot moments'' of microbial respiration following a single dry–wet cycle can represent up to 10% of annual net ecosystem productivity (Lee and others 2004) whereas rhizosphere ''hot spots'' can account for up to 33% of C and N mineralization in terrestrial forested ecosystems despite occupying only 8–26% of the soil volume (Finzi and others 2015). We spent many months trying to understand the conceptual, technical and methodological issues that may be constraining the rigorous application of the HSHM concept to predictive ecosystem science and management. Below we explore the progress in each of the four goals set by McClain and others (2003) and develop a new conceptual model of ''hot spot'' behavior that we believe will further advance our understanding of ecosystem biogeochemistry.

Breadth and Impact of Current HSHM Research

The first HSHM research priority identified by McClain and others (2003) was to ''investigate the nature and occurrence of natural hot spots and hot moments in the cycles of a larger number of elements and at different scales.'' The allied disciplines of biogeochemistry, ecosystem science, and hydrology have made some headway in expanding the application of the HSHM concept to a larger number of element cycles, though studies of denitrification within riparian zones (the primary focus of the McClain and others 2003 paper) remain the most prevalent usage among citing papers. Indeed, both ''nitrogen'' and ''denitrification'' are among the ten most frequently used words in titles of papers citing McClain and others (2003). Terms that describe environmental locations that typically support high denitrification rates (for example, ''riparian'') are also extremely common in paper titles. Moreover, the prevalence of these terms has not changed over time, suggesting that research on denitrification ''hot spots'' at aquatic and terrestrial interfaces remains highly productive, and that the conceptual understanding of other types of biogeochemical ''hot spots'' lags behind.

There are examples of the HSHM concept being applied to research on CH_4 emissions (for example, Teh and others 2011), DOC lability (Olefeldt and Roulet 2012) and, to a lesser extent, the cycling of base cations (Ca, Mg, K) in soil (Johnson and others 2008; Lezama-Pacheco and others 2015). Research on ''hot spots'' has also expanded to include rhizosphere biogeochemistry (recently reviewed by Kuzyakov and Blagodatskaya 2015); the distribution and biogeochemical impact of large animal feces (Christenson and others 2010); and variation in N cycling rates as a function of plant trait distribution (McGill and others 2010). Despite this expansion in scope, our citation analysis uncovered little evidence of progress in our ability to identify or predict biogeochemical ''hot spots'' or ''hot moments'' (but see Richardson and others 2007). Without this, it is not surprising that we have made only limited progress in incorporating HSHM behaviors and phenomena into quantitative ecosystem models or into prescriptive ecosystem management (for example, Chaves and others 2008; Burt and others 2010).

Challenges in Applying the HSHM Concept

The lack of coherent quantitative definitions and methods to identify HSHM makes the concept difficult to apply. Our ability to detect HSHM behaviors should be improving as a result of increasingly sophisticated and widespread environmental sensor networks (for example, Kirchner and others 2004; Rode and others 2016). Yet we can only detect phenomena that we have rigorously and quantitatively defined. The first step toward quantification is recognizing the divergent mechanisms by which HSHMs may affect ecosystem dynamics. The second is developing clear statistical conventions for distinguishing patches and periods of time with biogeochemical rates (that is, Table 2) that are elevated above the background signal. Finally, the resulting models of HSHM behavior should be used to generate and test a priori predictions about the role of HSHM in total ecosystem rates.

From HSHM to Control Points: Integration of Process and Transport Phenomena

The heterogeneous distribution of biogeochemically important elements is a central and well-accepted premise of the HSHM concept. As highlighted by McClain and others (2003), biogeochemical processing of elements varies across landscapes as a function of reactant supply and environmental conditions (often oxygen, temperature, or moisture). The potential for any given patch to perform biogeochemical work is also constrained by transport phenomena: the residence time within and the hydrologic connectivity between patches. Thus space, time and connectivity are essential controls on the biogeochemical rates in any landscape patch. Despite this, we find that very often researchers are only considering the spatial (hot spot) or the temporal (hot moment) component of biogeochemical variation within individual studies. This unfortunate splitting of HSHM is a constraint to progress, as all HSHM phenomena must necessarily incorporate both temporal and spatial components. We propose refinements to the original HSHM concept that begin with replacing the problematically dichotomous ''hot spot and hot moment'' terminology with the simpler term ''ecosystem control points'' (Figure 4). Ecosystem control points are areas of the landscape that exert disproportionate influence on the biogeochemical behavior of the ecosystem under study. Control points always have a spatial component since biogeochemical processes cannot occur in a vacuum. They also always have a temporal component, with great variation in the frequency, duration and periodicity with which patches support disproportionately high biogeochemical rates. We suggest that careful distinction between the mode of action (transport vs. process) and the timescale of activity (ephemeral to permanent) results in at least four very different mechanisms by which a landscape patch might have a disproportionate effect on landscape or ecosystem scale budgets.

1. PERMANENT CONTROL POINTS are landscape patches where continuous delivery of reactants and nearly constant appropriate environmental conditions allow for sustained high rates of biogeochemical activity relative to the surrounding landscape. The hydrologically connected flowpaths running through riparian zones and hyporheic zones are well-established examples of *permanent control points* within landscapes (Peterjohn and Correll 1984; Hedin and others 1998; Triska and others 1993).
2. ACTIVATED CONTROL POINTS are landscape patches that support high transformation rates only when the delivery rate of one or more limiting reactants increases and when abiotic conditions required for a particular biogeochemical process are optimized. For example, organic matter oxidation is constrained in many areas of the landscape (for example, low-lying topographic positions) by oxygen supply; denitrification in these same areas may be constrained by low delivery of nitrate. Events that provide one or more limiting resources or conditions can initiate high activity rates in these locations (Jenerette and others 2008; Harms and Grimm 2012).
3. EXPORT CONTROL POINTS are landscape patches in which reactants accumulate until a hydraulic gradient or diffusion threshold is overcome, allowing for export. It is important to note that these areas could have very low in situ rates of transformation accompanied by efficient retention, or they may be *permanent* or *activated control points* in which the products of high biogeochemical reaction rates accumulate over time until conditions allow for their export. For example, the consequences of an export control point were infamously observed at Lake Nyos when accumulating deep water CO_2 reached sufficiently high concentrations to explosively degas, leading to mass suffocation (Kling and others 1987). Less dramatic but far more commonly encountered examples are the high rates of DOC export during storms as DOC that has accumulated in upslope portions of the landscape is transported to receiving streams (for example, Boyer and others 1997, 2000).
4. TRANSPORT CONTROL POINTS are landscape patches that have exceptionally high transport capacity for water and gases and thereby contribute disproportionately to the movement and losses of biogeochemically important elements without themselves possessing high activity rates. *Transport control points* can also potentially mask nearby *permanent control points* by quickly and efficiently removing product from the site of processing, leading to low concentrations or pools of the product in situ. Macropore flow paths are a classic example of a transport control point within many soils (Bundt and others 2001). In the Anthropocene, stormwater pipes and tile drains are designed examples of *transport control points* found throughout urban and agricultural landscapes.

Progress in applying the HSHM concept has been constrained by a failure to distinguish between these divergent underlying mechanisms. Our refined ecosystem control point concept recognizes that biogeochemical behaviors vary widely in both space and time and there are particular characteristics of the landscape that can be used to predict the likely heterogeneity in rates, chemical concentrations, and concentration ratios that occur. Perhaps more importantly, describing these distinct mechanisms by which a landscape patch can act as an *ecosystem control point* also forces researchers to recognize that high biogeochemical rates are not necessarily well correlated with high element concentrations. Large pool sizes or high fluxes can result simply from being a place of very low (*export control points*) or very high (*transport control points*) hydrologic connectivity. Similarly, *activated* or *permanent control points* may be hidden from view using these proxy measures due to their short retention times. Many papers referencing the HSHM concept have relied on differences in element concentrations to identify ''hot spots,'' while our new classification of mechanism would require further analysis to distinguish whether such large pool sizes resulted from high in situ rates, long residence times or high connectivity. Without identifying the mechanisms that create ecosystem control points, we will have very limited ability to model, scale and estimate their impact.

Refining the HSHM Concept: Predicting the Impact of Ecosystem Control Points

The third goal of the HSHM paper was (*c*) *to use the methods of landscape ecology to evaluate the roles of hot*

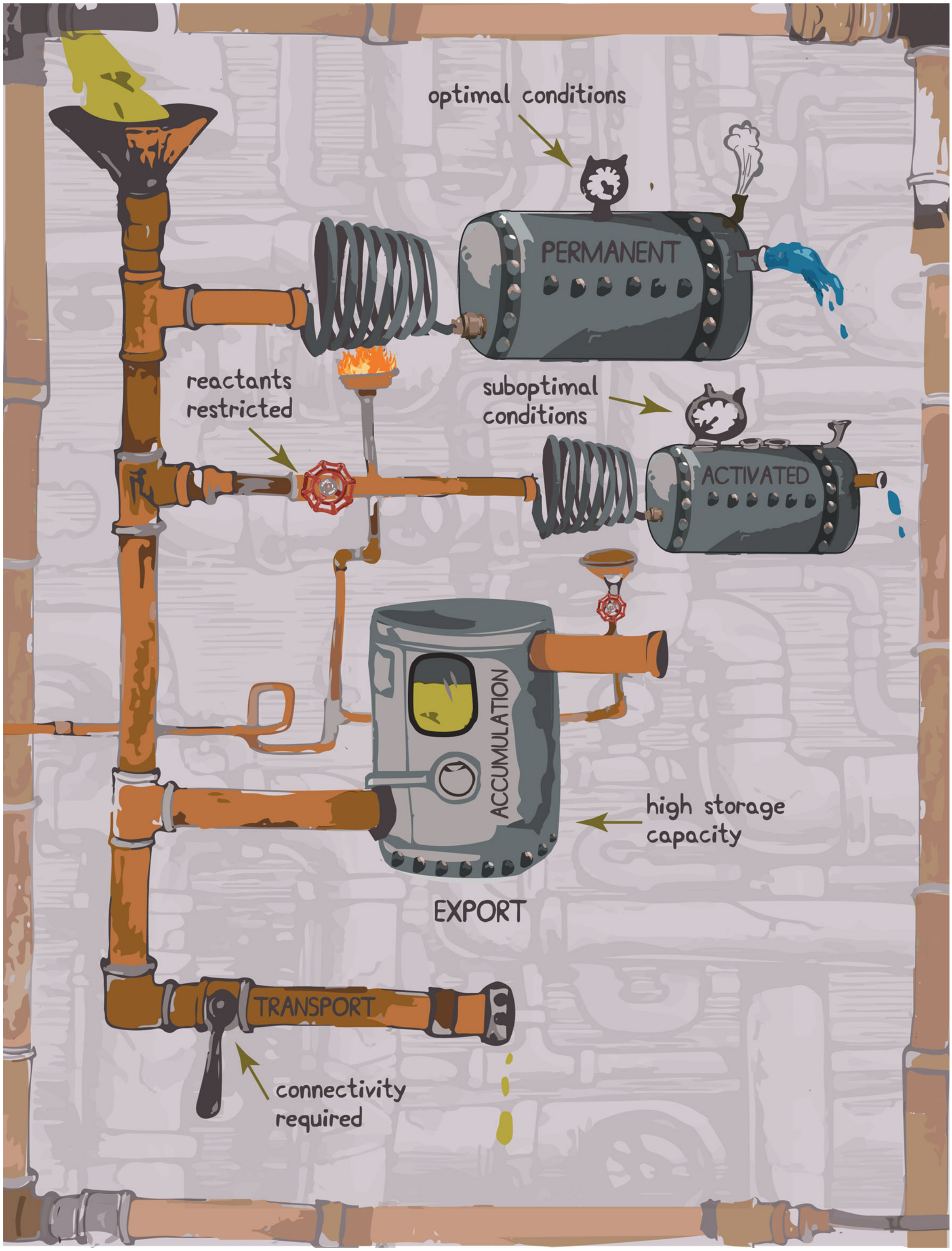


Figure 4. A machine metaphor for the four mechanisms by which an area of the landscape may act as a biogeochemical control point. Each mechanism is defined in the text. Figure designed by Terra Communications.

spots and moments in landscape biogeochemistry. Although efforts have been made to scale ''hot spot'' behavior to ecosystems in a limited number of cases (for example, Duncan and others 2013), on the whole, we seem to have made little progress along this trajectory. That is unfortunate, as the goal of understanding these high rates and fluxes is, ultimately, to be able to better understand ecosystems. After delineating the different mechanisms through which landscape patches may be classified as *ecosystem control points* (Figure 4), it should be much easier to generate sophisticated a priori predictions about how different types and different extents of ecosystem control points may affect ecosystem-level behavior.

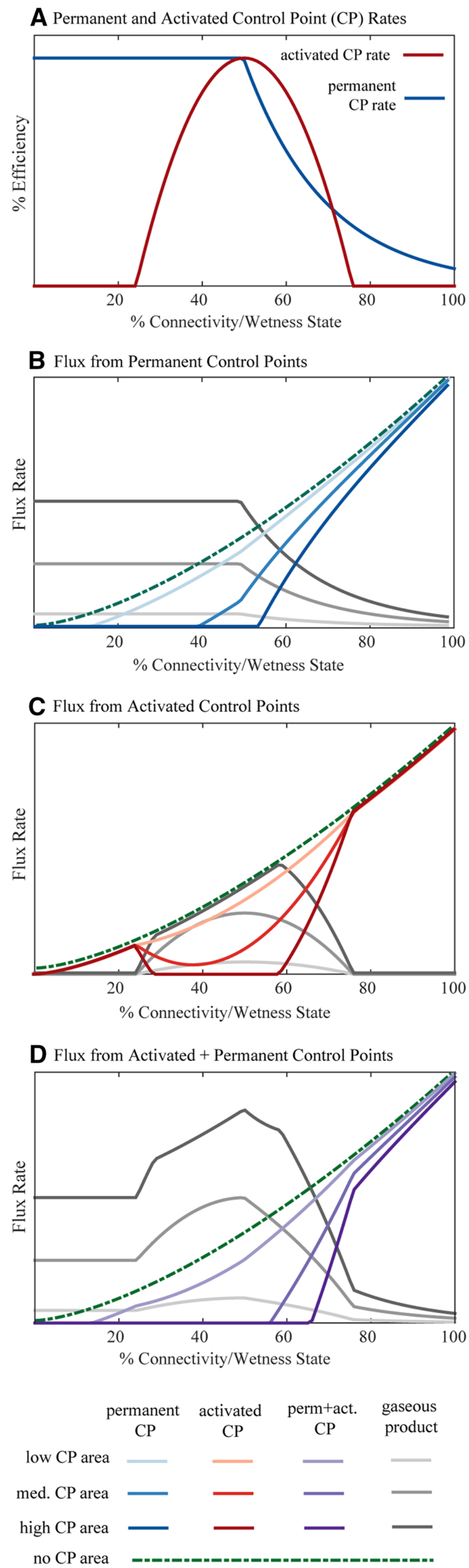
To explore how the ecosystem-level effects of permanent versus activated ecosystem control points may differ we created a conceptual, non-spatially explicit model of a catchment including inactive matrix mixed with both *permanent* and *activated control points*. We ran a watershed nitrogen mass balance model and varied both the absolute and relative extent of both types of processing ecosystem control points. Our goal with this simple model was to demonstrate: (1) how different the impacts of *activated* versus *permanent control points* are likely to be in affecting the magnitude and timing of ecosystem fluxes; and (2) the importance of knowing the spatial and temporal extent of control points in order to estimate their ecosystem impact.

We initiated our model with several key simplifying assumptions. First, we assume that both *permanent control points* and *activated control points* have a potential maximum denitrification rate that can be reached given the right balance of N supply and O_2 availability. *Permanent control points* operate at their maximum denitrification rates at all times, whereas *activated control points* achieve maximum rates only under conditions when N supply is high and O_2 availability is low. In our model these conditions are met when rainfall both delivers high N fluxes and saturates soils, and we indicate this soil saturation status in our model output as catchment wetness (Box 1). We assumed nitrogen loading into these control points varied as a function of catchment wetness, with any remaining N that is not removed by a patch being exported from the catchment as a dissolved flux (Box 1). Both types of control points ultimately reach a threshold level of N loading where N supply overwhelms the capacity of biota to take up and process N, resulting in a decrease in the efficiency of N removal as N loading increases (that is, efficiency decreases at high levels of catchment wetness because more N is loaded to the system (Box 1A). Second, the control points in this watershed are not distributed in a spatially explicit manner, we represent their prevalence as a percentage of total catchment area. We used this model to compare various ecosystem control point scenarios to the reference scenario for a watershed with no ecosystem control points (inputs = outputs) (Box 1B–D, green dashed line).

From a model of such simple assumptions a variety of interesting emergent phenomena can be observed. Obviously, an increased extent of either type of control point within a landscape will be associated with greater relative transformation rates for nitrogen (Box 1B, C). Under all scenarios the efficiency of N transformations declines with increasing catchment wetness and N loading, but this capacity is quickly saturated in scenarios in which control points occupy only 1% of catchment area (Box 1B–D). This simple model quite effectively demonstrates a key determinant of whether a patch should qualify as a control point. Very rare patch types may have exceptionally high rates of activity, but if they occupy only a minute fraction of catchment area they will not exert control on ecosystem processes. Such patches are likely to be biogeochemically or microbially fascinating, but will contribute little to ecosystem scale understanding.

As the aggregated extent of control points increases to 5 or 10% of the catchment area, our model predicts dramatic reductions in dissolved NO_3^- (reactant) and increases in gaseous N (product) fluxes under most wetness conditions (Box 1B–D). In this scenario the effects of both *activated* and *permanent control points* are additive (Box 1D), with gaseous N export maximized and dissolved NO_3^- losses are near zero under conditions that foster optimal activity in both *activated* and *permanent control points* (Box 1D). Both *activated* and *permanent control points* create NO_3^- export patterns that lag NO_3^- inputs, with steep slopes in the NO_3^- export once control points are saturated (Box 1B–D). The onset of dissolved solute fluxes represents the point at which substrate loading finally overwhelms the capacity of ecosystem control points within the system to take up and process solutes. We hypothesize that this strong thresholding behavior in the precipitation–solute flux relationship might be characteristic of catchments with a high density of *permanent* or *activated control points*. The threshold conditions at which *permanent control points* are saturated and at which *activated control points* activate are critical determinants of the timing and the pattern of ecosystem fluxes.

In this simple model, we have ignored *export* and *transport control points* where processing does not occur. If one adds these into our simulated catchment, their roles would also be quite distinct. *Export control points* will increase watershed retention but would not result in enhanced gaseous N losses,



◀**Box 1.** We created a simple model to assess how control points of biogeochemical activity may influence temporal patterns of solute export when scaled to the catchment level. Using theoretical rate laws (**A**) and theoretical relationships between connectivity and nitrogen loading, we can begin to make predictions about how time series of solute flux may vary among watersheds with different areal coverage of *permanent* and *activated control points*. These modeled outputs describe emergent behavior at the ecosystem level as a result of control point behavior at smaller spatial scales. **A** Describes to reduce NO_3 fluxes in *permanent* and *activated ecosystem control points*. *Permanent ecosystem control points* (shown in *blue*) operate at their maximum rate until a threshold of watershed connectivity is reached, after which their rates diminish due to overwhelming transport dominance. In contrast, *activated ecosystem control points* (shown in *red*) experience maximum biogeochemical processing at an intermediate wetness state when the supply of N and O_2 availability are both optimized, **B** depicts gaseous flux (or product accumulated and stored in situ) and solute flux from a watershed with low, medium, and high areal coverage of *permanent control points* (1, 5, and 10% of watershed area, respectively). The *green dotted line* represents the reference scenario where no control points are present (or active) and in which solute loading equals watershed export (no net removal). As the percent of the watershed composed of *permanent control points* increases, the total amount of solute removed by control points and converted to gaseous flux increases (*gray gradient*), and export from the watershed outlet decreases (*blue gradient*), **C** demonstrates the effects of biogeochemical processing in *activated control points* on gaseous and solute fluxes in a watershed with low, medium, and high (1, 5, and 10% of watershed area) activated control point areal coverage. At low and high levels of connectivity, solute fluxes are equal to the reference scenario (*green line*, described in **B**). When the optimal conditions stipulated in **A** are achieved the *activated control points* "turn on" and convert dissolved solutes to gaseous products, leading to reduced solute fluxes from the watershed outlet. In this modeled scenario, a watershed with 10% of its area composed of *activated control points* was able to retain almost all solutes during periods of intermediate catchment wetness and effectively reduce solute flux to zero (*dark red line*), **D** combines the effects of both permanent (**B**) and activated (**C**) control points to assess the net effect of control points on solute fluxes from the watershed outlet. As the total fraction of the watershed composed of activated and *permanent control points* increases (*purple gradient*), fluxes of gaseous product from biogeochemical processing increase (*gray gradient*) and the solute flux trajectory deviates significantly from the steady-state reference flux (*green line*). In particular, increased control point area substantially delays the onset of dissolved solute fluxes until a point where transport overwhelms the capacity of the system to retain or process solutes.

while *transport control points* would enhance the coherence between precipitation and solute fluxes.

Managing and Protecting Ecosystem Control Points

The final stated goal of the McClain and others (2003) paper was (*d*) *to evaluate the utility of natural and created hot spots and hot moments as resource management tools.* We found few citing papers that suggested new or effective ways of incorporating the HSHM concept into resource management strategies (but see Vidon and others 2010 and literature cited therein). Certainly, efforts to restore and protect riparian zones and enhance hyporheic exchange are widespread (Fennessy and Cronk 1997; Jorgensen and others 2000; Boulton 2007; D'Arcy and others 2007; Kaushal and others 2008), but for the most part, these efforts do not appear to be referencing the mechanistic underpinnings of the HSHM concept (but see Peter and others 2011).

One of the challenges to applying the HSHM concept to ecosystem management, is that most of the previous empirical work on biogeochemical ''hot spots'' occurred at the scale of soil cores (<15 cm), small field plots (<1 m), or on hillslopes (10 s of meters), while most management is occurring at the scale of watersheds and cities (10 s of square kilometers) or river basins and political states (100–1000 s of square kilometers). Effective protection and restoration of ecosystem control points requires that we recognize how biogeochemical optima are organized at different scales. We suggest that the location of biogeochemical optima can be predicted, but will be under different priority controls at increasing scales of inquiry (Figure 5). Taking the well-studied process of denitrification, it is well established that denitrification rates are higher within soil aggregates than in bulk soil; and in riparian areas rather than ridges (Figure 5). At each of these scales, we can develop a response surface that predicts rates of denitrification as a function of nitrate (NO_3^-) supply and oxygen at the plot scale, and as a function of NO_3^- supply and soil moisture at the hillslope scale (Figure 5). When we move to larger landscapes, NO_3^- availability itself may vary as a function of vegetation (Lovett and Rueth 1999; Lovett and others 2004), geology (Morford and others 2011) or deposition. Finally, at very large scales infrastructure designed to accumulate and process wastes (for example, wastewater treatment plants, consolidated animal feeding operations, sewage lagoons, landfills) become the optima at that scale, so that organic N loading becomes a dominant driver. Although predicting the optimal conditions for peak denitrification at each scale is not difficult, our ability to link across scales and understand the aggregate impact of small scale control points remains poorly developed.

Better recognition of the full complement of possible *ecosystem control point* mechanisms may be helpful in this regard. One critical step forward is to recognize that not all control points provide ecosystem services. In fact, a large number of environmental problems can be linked to the creation of infrastructure that moves water rapidly off landscapes and concentrates reactive materials. We build extensive networks of stormwater pipes, gutters, tile drains, roads, and drainage ditches that can vastly increase the density of *transport control points* within ecosystems (Skaggs and others 1994; Bernhardt and others 2008). We accumulate large quantities of reactive materials in landfills, waste lagoons, and stormwater ponds that occasionally become disastrous *export control points* (that is, coal ash pond or hog lagoon failures). We have developed technical solutions for wastewater management that serve as extremely high-functioning *permanent control points*. We have been far less effective in identifying and protecting those natural control points that are able to retain and transform nutrients and contaminants. Indeed, much of our infrastructure development works to bypass the riparian zones and wetlands that are known to provide these important ecosystem services (Groffman and others 2003; Walsh 2004; Hale and others 2014).

A final limitation in the application of the HSHM concept to ecosystem management is the nearly exclusive focus of the HSHM literature on nitrogen and carbon. Managers are faced with understanding the spatial distributions and fluxes of multiple constituents, rather than an individual nutrient or process, particularly in relation to water quality. For example, wetlands and wet riparian zones can be excellent at both denitrification (a critical ecosystem service) and mercury methylation (making a toxic metal highly bioavailable). Vidon and others (2010) reviewed research on HSHM for nitrate, phosphorus, organic matter, pesticides, and mercury processing and highlighted the fact that riparian zones can be ''hot spots'' for the removal of some constituents but sources of others. More research that follows this approach of studying linked element cycles within putative ecosystem control points is sorely needed to avoid the unintended consequences of single element management (for example, Ardon and others 2010; Finlay and others 2013).

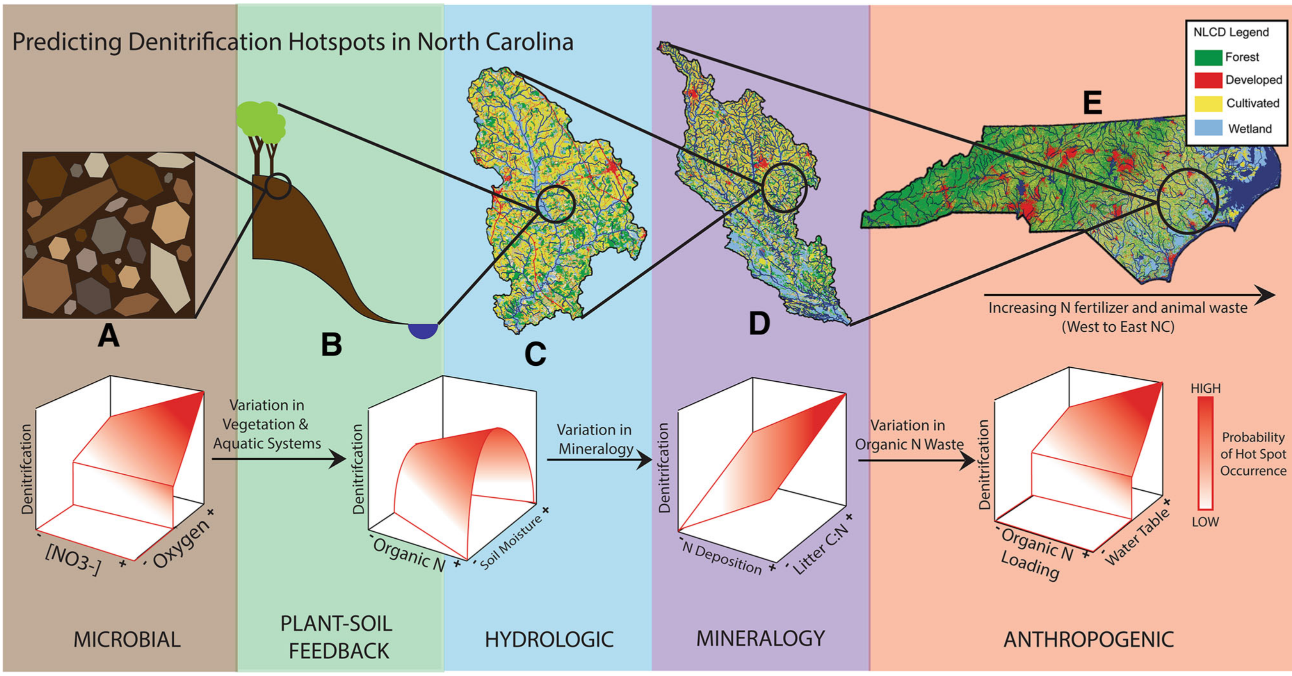


Figure 5. Conceptual predictions for the priority controls and locations of maximum denitrification activity at multiple scales of inquiry. *A* Beginning at the scale of a soil core, we assume that the dominant controls on denitrification rates are microbial responses to both nitrate and oxygen concentrations, with denitrification low except under high NO_3^- supply and limiting O_2. *B*, C At both the hillslope and small watershed scales, we predict that plant demand and topography will together affect the distribution of organic nitrogen and soil water, with denitrification optimized in locations and times when both are high. *D* As you increase to larger catchments, we expect mineralogy to influence vegetation type and litter quality and patterns of N deposition to vary with topography. At this scale, we suggest that litter C:N and N deposition may be the dominant determinants of denitrification optima. *E* At larger regional scales, we predict that areas where high anthropogenic N loading intersects with shallow water tables will be the locations of maximum denitrification.

CONCLUDING REMARKS

Understanding the factors that drive the movement of water, energy, and nutrients within and through ecosystems is a unifying goal of the fields of biogeochemistry, ecosystem science and hydrology. As such, the HSHM concept as synthesized by McClain and others (2003) has been important for providing a framework with which to appreciate the importance of spatiotemporal heterogeneity in biogeochemical processing rates. Given the volume of literature demonstrating high cycling rates under localized spatial or temporal conditions, the existence and potential importance of rare habitats and events in controlling ecosystem budgets are undeniable. To motivate a consolidated empirical effort toward improving the predictive power of HSHM research, we propose the new terminology ''ecosystem control points.'' The term *control* explicitly requires that the landscape patch exerts strong influence on element flux at the scale of interest, while the term *points* incorporates both spatial and temporal dynamics simultaneously. We further suggest that there are at least four unique mechanisms by which a landscape patch can qualify as an ecosystem control point that vary in their rates of substrate supply, substrate supply ratios and environmental conditions. We have demonstrated how exploratory models of control point behavior can be used to develop testable landscape-level predictions of nutrient export and retention. Finally, we have outlined how biogeochemical rates within control points can display different response surfaces under varying resource availability and environmental conditions. Efforts to identify biogeochemical optima within ecosystems will continue, but we suggest that the term ''ecosystem control points'' ought to be used both more rigorously and more sparingly than the HSHM concept from which it is derived. Designation of a patch as an ecosystem control point should be reserved for those places within an ecosystem that have a disproportionate effect on overall ecosystem processes. Going forward, we recommend developing a priori statistical conventions for classifying landscape patches based on whether they are common enough or have process rates large enough to fundamentally alter the timing or magnitude of ecosystem rates or fluxes. True control points have such exceptionally high rates of biogeochemical activity or such exceptional hydrologic connectivity that aggregate ecosystem behaviors cannot be understood without taking them into account. Go find them!

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