

Expanding the scale of aquatic sciences: the role of the National Ecological Observatory Network (NEON)

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Abstract: The current and future direction of aquatic ecological research leans toward addressing questions that cover multiple scales and levels of complexity. Historically, the ability to do comparative aquatic research across large spatial and temporal scales has been impeded by a lack of comparable measurements, standard methods, and a well organized data management and retrieval system. The National Ecological Observatory Network (NEON) is the first continental-scale ecological observation system designed to collect and provide freely available data on the drivers and responses of ecological change. In this paper, we describe past and present attempts to work across multiple scales in aquatic ecology, and the potential use of NEON aquatic data and infrastructure by researchers to integrate and expand ecological research programs and address novel ecological questions.

Key words: aquatic ecology, NEON, large scale, networks, microbial ecology, large river ecology

The greatest challenge faced by ecological researchers is the ability to detect drivers and responses to environmental change across large spatial and temporal scales. Aquatic systems are intimately linked to the surrounding terrestrial environment (Hynes 1975), so they are excellent indicators of changes occurring within and across atmospheric, terrestrial, and aquatic boundaries (Williamson et al. 2009). However, integration of landscape processes requires that ecologists can understand, detect, and predict how large-scale changes will affect aquatic processes and alter ecosystem structure, function, and services (e.g., drinking water, sport fisheries).

The International Biological Program (IBP; 1964–1974; Table 1) was the first large-scale, long-term ecological research program after the International Geophysical Year effort (1957–1958). The IBP supported collection and distribution of scientific data globally, united scientists, and promoted ‘Big Science,’ and encouraged work across na-

tions and disciplines to address ecological questions spanning greater spatial and temporal scales than previously considered. The IBP ended in 1974 after failing to create an organized data-management system and comprehensive biological models (Aranova et al. 2010). However, the program highlighted the need to evaluate long-term ecological change. The US National Science Foundation (NSF) later initiated the Long-Term Ecological Research (LTER) program (Table 1), designed to capture long-term changes across multiple spatial scales (Hobbie et al. 2003). In 1963, Hubbard Brook researchers used a small watershed approach to study nutrient retention, fluxes, and cycling (Bormann and Likens 1969, Likens et al. 1977) and presented streams as indicators of whole-ecosystem function. In 1968, the Experimental Lakes Area (ELA), a long-term monitoring and ecosystem-scale lake experiment was established (Johnson and Vallentyne 1971) to evaluate whole-system function.

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Table 1. Examples of large-scale aquatic ecological programs. Chl = chlorophyll *a*, EMAP = Ecological Monitoring and Assessment Program, EPA = US Environmental Protection Agency, GLEON = Global Lake Ecological Observatory Network, IBP = International Biological Program, LTER = Long-Term Ecological Research, NARS = National Aquatic Resource Surveys, NAWQA = National Water-Quality Assessment, NSF = National Science Foundation, OECD = Organization for Economic Co-Operation and Development, PI = principal investigator, USGS = US Geological Survey, WISE = Water Information System for Europe.

Program	Location	Impact	Duration	Key data
IBP	North America, Europe, Australia	5 biome studies, tracers for nutrient and energy-flow experiments	1964–1974	Grassland Biome Project, Eastern Deciduous Forest Biome Project
OECD eutrophication modeling	18 countries (US, Canada, Australia, Japan, and 14 western European countries); lakes and reservoirs, mostly temperate zone, some alpine, arctic, and subtropical	International effort to establish a basis to control eutrophication of inland waters and to develop guidelines for fixing nutrient loading criteria compatible with water-use objectives; P-loading reduction; eutrophication management strategies	1970s	Relationships between nutrient loading and water-quality metrics (chl, Secchi depth, O ₂ depletion); predictive eutrophication relationship models
LTER network	Continental US, Alaska, Caribbean and Pacific Islands, Antarctica	Wide variety of projects from nutrient addition to ecosystem function	1980–present	NSF-funded, PI-driven research projects and publications
GLEON	Lakes worldwide (6 continents)	Grassroots network of ecologists and limnologists, network of instrument platforms and sensors around the world, connected by cyberinfrastructure	2005–present	International sensor-derived data sets, web portal
EMAP	Continental US, Alaska, Hawaii, Puerto Rico, Pacific Islands	Assess status and trends of US streams, ecological risk assessment	1990–2006 (rolled into NARS in 2006)	Rapid Bioassessment Protocols
EPA NARS	Continental US, Alaska, Hawaii, Puerto Rico, Pacific Islands	First large-scale study using statistically valid survey techniques; standardized field and laboratory methods to yield unbiased estimates of the condition of rivers and streams, lakes, wetlands, and coastal waters	2006–present	Includes National Rivers and Streams Assessment and National Lakes Assessment
USGS NAWQA	Continental US	Provide information on the condition and sustainability of our nation's water supply	1991–present	Comparable information on water resources in 60 river basins and aquifers
WISE	Europe	Web portal to bring together water-research data	2007–present	Interactive public access to data

Ecosystem variability makes it necessary to incorporate heterogeneity in hydrologic (Beven et al. 1988, McDonnell et al. 2007), habitat (Palmer and Poff 1997), or landscape patterns (Scarsbrook and Townsend 1993, Huryn et al. 2005) in aquatic ecosystem studies to transition from small, patch-scale studies to large, watershed analyses (Allan and Johnson 1997, Fisher et al. 1998). Integrating variability and heterogeneity into predictive modeling (McClain et al. 2003) is essential in addressing the “Grand Challenges in Environmental Sciences” and predicting responses to change across multiple scales (NRC 2001).

Temporal and spatial variability of ecosystems have long been pivotal foci in ecology (Hobbie et al. 2003). Spa-

tial variability at the landscape scale has been addressed by using geomorphologic and environmental gradients to predict community structure and function (Hynes 1975, Vannote et al. 1980), habitat templates based on physical characteristics of watersheds (e.g., slope, canopy cover; Frissell et al. 1986), and gradients of environmental severity (Southwood 1988). Within ecosystems, the effects of top-down and bottom-up control on stream or lake ecosystem structure (Carpenter et al. 1987, 2001, Pace et al. 1999) and function (Paine 1980, Power et al. 1988, Rosemond et al. 2001) are well documented. However, studies done at larger spatial and temporal scales, such as the US Geological Survey (USGS) National Water-Quality

Assessment (NAWQA; Hirsch et al. 1988), US Environmental Protection Agency (EPA) Environmental Monitoring and Assessment (EMAP; Messer et al. 1991), and National Aquatic Resource Surveys (NARS) programs (Table 1), tend to concentrate on stream health and monitoring rather than on questions of ecosystem structure or function.

International-scale programs and portals, such as the Organization for Economic Co-Operation and Development (OECD; Vollenweider and Kerekes 1982), Global Lakes Observatory Network (GLEON; Weathers et al. 2013), and Water Information System for Europe (WISE), merge global data, but lack consistency in sampling design, data collection, and quality control (Table 1). NSF-funded collaborative research projects have also worked at large scales (e.g., Lotic Intersite Nitrogen eXperiment [LINX]; Peterson et al. 2001, Mulholland et al. 2008) and have spearheaded standardized, network experimentation studies (e.g., STream Experimental Observatory Network [STREON]; Utz et al. 2013). Researchers in many of these programs evaluate aquatic ecosystems across time or space, but their ability to expand data to multiple scales is limited because many programs are site-specific (LTER, ELA), lack temporal coverage (NARS, LINX), or lack consistent methods (LTER, GLEON).

The current direction of ecological research is to address questions covering multiple scales and levels of complexity. This approach requires sampling strategies designed for comparability and extrapolation across disparate ecosystems and regions coupled with the ability to identify processes affecting regime shifts within sites (Heffernan et al. 2014, Rüegg et al. 2014). Missing elements from previous work needed to answer large-scale ecological questions include well organized data management and retrieval systems capable of sharing real-time data (Aronova et al. 2010), comparable measurements and standard methods over various scales (Johnson et al. 2010), and the ability to scale to regional, continental, and global scales.

The National Ecological Observatory Network (NEON) is the first continental-scale ecological observation system designed to collect data focused on drivers of (i.e., climate change, land use, invasive species) and responses to (i.e., biodiversity, biogeochemistry, ecohydrology, infectious disease) change needed to address the “Grand Challenges in Environmental Sciences” (NRC 2001). NEON’s goal is to enable understanding and forecasting of the effects of large-scale changes on natural resources over long time periods by combining site-based data (terrestrial, atmospheric, and aquatic instrumentation and field sampling) with remotely sensed data (airborne observations) to provide a range of scaled data products. Data will be collected at 106 sites across 20 ecoclimatic domains, 19 of which contain aquatic sites, delineated to maximize the representation of continental-scale environmental variability (Keller et al. 2008). Thirty-six of these sites are aquatic

(29 streams/large rivers and 7 ponds/lakes), and 10 of 36 include downstream STREON sites (Fig. 1; Utz et al. 2013). NEON sites include ‘core’ sites, at which data will be gathered over a period of 30 y, and ‘relocatable’ sites, which will change every 5 to 7 y to capture changing ecological phenomena across gradients. Data collected at NEON aquatic sites encompass physical, hydrogeological, chemical, and biological variables. Data collection combines continuously monitoring instrumentation with field observations (Utz et al. 2013). All NEON data are open access and available via a web portal immediately after analysis and rigorous quality assurance/quality control validation (Taylor and Loescher 2013).

In this *BRIDGES* cluster, we explore cases in which NEON aquatic data and infrastructure can be used to expand ecological research programs and questions across multiple scales, from small to large watershed studies (see below, Sobczak and Raymond 2015). McDowell (2015) discusses the challenges and opportunities of such a research platform. We focus on 2 Grand Challenges: biodiversity (aquatic microbial ecology) and ecohydrology (large river ecology) to illustrate the breadth of potential uses and how researchers can build on the NEON platform at multiple scales.

STREAM MICROBIAL ECOLOGY

The microbiota of stream ecosystems drive nutrient-cycling dynamics with a disproportionately strong influence at the landscape scale (Hynes 1975, Fisher et al. 1998). Streams are conduits of water, organic C, and nutrients across the landscape and are prominent locations of microbially mediated C and nutrient processing, uptake, and transport (Vannote et al. 1980, Peterson et al. 2001, Mulholland et al. 2008). The importance of heterotrophic microbial C cycling in streams is well established. Microbiota can contribute 22 to 27% of total leaf mass loss directly (Hieber and Gessner 2002). Indirectly, microbiota feed invertebrates that cause physical loss of coarse organic material (Hall and Meyer 1998). When considering all ecosystem components, microbial transformations of C are a main contributor to whole-stream respiration and C flow to higher trophic levels (Lindeman 1942, Meyer 1994, Tank et al. 2010), and whole-stream respiration strongly affects nutrient uptake and export (Fellows et al. 2006, Valett et al. 2008).

Stream ecologists have a history of interest in microbial processes and of presenting and testing concepts that link biodiversity and ecosystem processes at organismal, reach, and landscape scales. However, little research has been done on the microbial biodiversity of stream habitats, despite widespread use of molecular methods to evaluate microbial structure and function in ecosystems (Findlay 2010). Current advances in molecular methods will enable researchers to quickly fill gaps in baseline descriptive data and to move toward testing hypotheses relating microbial biodiversity to stream ecosystem processes.

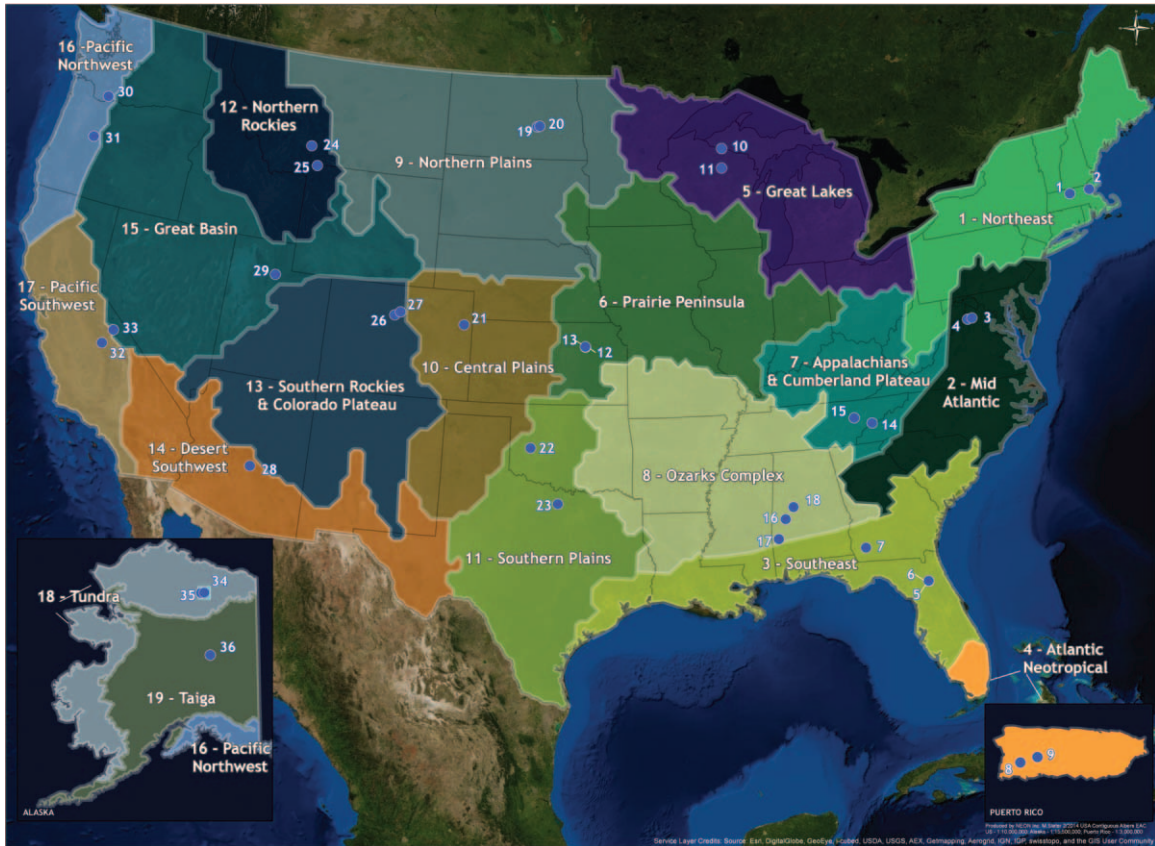


Figure 1. Map of National Ecological Observatory Network (NEON) North American domains and associated candidate aquatic sites. Site numbers correspond to site names, as follows: 1. West Branch Bigelow Brook, Massachusetts, 2. Sawmill Brook, Massachusetts, 3. Mill Run, Virginia*, 4. Posey Creek, Virginia, 5. Suggs Lake, Florida, 6. Barco Lake, Florida, 7. Ichawynochaway Creek, Georgia, 8. Rio Cupeyes, Puerto Rico*, 9. Rio Guilarte, Puerto Rico, 10. Crampton Lake, Wisconsin, 11. Pickerel Creek, Wisconsin, 12. Kings Creek, Kansas*, 13. McDowell Creek, Kansas, 14. LeConte Creek, Tennessee, 15. Walker Branch, Tennessee*, 16. Black Warrior River, Alabama, 17. Lower Tombigbee River, Alabama, 18. Mayfield Creek, Alabama*, 19. Prairie Pothole, North Dakota, 20. Prairie Lake, North Dakota, 21. Arikaree River, Colorado, 22. South Pond, Oklahoma, 23. Pringle Creek, Texas, 24. Bozeman Creek, Montana, 25. Blacktail Deer Creek, Wyoming, 26. West Saint Louis Creek, Colorado, 27. Como Creek, Colorado, 28. Sycamore Creek, Arizona*, 29. Red Butte Creek, Utah, 30. East Branch Planting Creek, Oregon, 31. McRae Creek, Oregon*, 32. Providence Creek, California, 33. Convict Creek, California*, 34. Toolik Lake, Alaska, 35. Oksrukuyik Creek, Alaska*, 36. Caribou Creek, Alaska*. * indicates collocated NEON Aquatic and STREAM Experimental Observatory Network (STREON) sites.

Microbial diversity is relatively understudied in stream habitats, but numerous individual surveys or experiments have addressed microbial diversity in stream ecosystems. A full review of these studies is beyond the scope of our paper, but we take this opportunity to mention several studies that are of general interest. The stream water column carries a dynamic assemblage of terrestrially derived and aquatic bacterial taxa that may track seasonal and event-driven water chemistry (Bell et al. 1982, Crump et al. 2012). Epilithic biofilm diversity also varies temporally, by season (Hullar et al. 2006), and via successional dynamics (Besemer et al. 2007). Successional patterns also occur on leaf biofilms as decomposition progresses (Suberkropp et al. 1983, Gessner et al. 1993, Wymore et al. 2013). Biofilm assemblages differ among leaf, rock, sediment, and water-column habitats, even within the

same stream reach (Hullar et al. 2006, Beier et al. 2008, Larouche et al. 2012). Microbial diversity is correlated with ecosystem functions, e.g., bacterial productivity or nutrient uptake (Judd et al. 2006, Adams et al. 2010). Experimental studies are less common than descriptive studies, but they indicate increasing epilithic bacterial diversity and faster biofilm C uptake in response to increasingly heterogeneous bed flow dynamics (Singer et al. 2010). When aquatic ecosystems are altered, microbial diversity and activity may respond dramatically; e.g., the sediment bacterial community can differ downstream of a wastewater treatment plant (Wakelin et al. 2008), drought can have lasting impacts on stream sediment bacterial diversity (Rees et al. 2006), and fungal communities can be homogenized following exposure to heavy metal contamination (Sridhar et al. 2008). Microbes are diverse and

dynamic. Therefore, they are responsive to factors that threaten streams at reach and landscape scales; e.g., channel engineering, altered flow regime, temperature, pH, and water chemistry (Malmqvist and Rundle 2002).

The NEON platform will enable evaluation of multi-scale stream ecosystem dynamics in space and time. For example, microbial diversity data collected during the STREON whole-stream nutrient addition will be useful in identifying when and where microbial diversity is most sensitive to nutrient addition. Experiments have been done to test effects of elevated nutrient concentration on microbial diversity, but their results differ. A clear shift in bacterial assemblage composition toward dominance of certain taxa caused a decrease in biofilm diversity after dissolved nutrient concentrations were doubled (Van Horn et al. 2011). Added nutrients can also influence fungal diversity (Gulis and Suberkropp 2003). However, increased organic C may have a stronger effect than increased inorganic nutrients on microbial communities (Olapade and Leff 2006), and inorganic nutrient effects may be secondary to seasonal heterogeneity (Olapade and Leff 2005) or even undetectable (Findlay and Sinsabaugh 2003). In sum, effects of nutrient addition on stream microbial communities can be site or time specific. However, context-specific effects are difficult to tease apart because studies are typically site specific and not comparable because of inconsistent methods across diverse sites and times. Microbial diversity data collected during the STREON whole-stream nutrient-addition experiments will allow scientists to move beyond site-specific interpretation.

Overall, the NEON project and STREON experiment will provide data on microbial abundance and diversity from dominant substrates in streams across the USA—a valuable resource. Collection and analysis of these data with standardized methods at multiple sites and numerous time points at each site will enable researchers to address questions about microbial biogeography and temporal variability. Furthermore, concurrent data on stream physiochemical factors, abundance, diversity of higher trophic levels, and whole-stream ecosystem processing rates (e.g., dissolved organic matter flux; Sobczak and Raymond 2015), will enable researchers to link microbial diversity and microbial processes within a whole-stream ecosystem context (Findlay 2010).

Studying and interpreting the role of microbial life at stream reach and landscape scales are challenging, but the opportunities presented by this type of research are exciting. Microbial life is a key component of the organic-matter and nutrient-cycling processes, food webs, and biodiversity of aquatic ecosystems, and microbial diversity data collected as part of the NEON aquatics program are an example of the potential to inform mechanistic hypotheses of aquatic ecosystem function at multiple spatial and temporal scales (McDowell 2015).

LARGE RIVER ECOLOGY

The NEON aquatics program is focused primarily on wadeable streams, but the design also includes 3 non-wadeable sites, 2 of which are on large rivers in Alabama, USA. These sites are nested within the Mobile River drainage basin along a hydrogeomorphic gradient in river size from a wadeable stream site (Site 18; Fig. 1) to the Black Warrior–Tombigbee River system (Sites 16 and 17; Fig. 1). Allocation of NEON resources to these systems is in recognition of the need to document the influence of climate change, landuse alteration, and aquatic invasive species along an ecohydrologic gradient. The reasons for studying large rivers have become so diverse and of interest for such a wide range of applications that use of the NEON infrastructure to support long-term data collection on large rivers is particularly timely.

Advances in data collection using continuously monitoring sensors deployed on buoys or other stationary structures for water monitoring will allow researchers to circumvent some of the previous limitations of sampling large rivers and increase the temporal resolution of measurements (Cohen et al. 2013). NEON is collaborating with the US Army Corps of Engineers in placing sensors at the Alabama River sites near USGS gauging stations for real-time discharge monitoring. NEON instrumentation will provide long-term measurements of surface-water variables (water temperature, dissolved O₂, turbidity, pH, conductivity, chlorophyll *a*, NO₃⁻, and fluorescent dissolved organic matter) that have never been measured continuously, in full, for multiple years in a large US river. In addition, surface-water and sediment chemistry, river bathymetry, and biotic community dynamics (fish, macroinvertebrates, algae, and prokaryotes) will be measured at various time scales.

In all, the NEON large-river sampling design provides researchers with an opportunity to broaden the spatial scale at which stream theory is tested by making ecological measurements concurrently along a hydrologic gradient. The sites along this gradient experience similar geochemical and climatological conditions, but may respond differently to disturbance events (e.g., invasive species, floods, landuse change) or seasonality because of differences in geomorphic structure associated with the widening and deepening of larger river channels. This approach has been particularly successful in free-flowing rivers, where it has been used to test conceptual models, such as the River Continuum Concept (RCC; Vannote et al. 1980), the Flood Pulse Concept (FPC; Junk et al. 1989), and stoichiometric theory (Elser et al. 1996). Researchers have challenged these current paradigms in river ecology, finding either little support for patterns predicted by the RCC for the downstream portions of a river network (Huryn et al. 2002) or suggesting modifications of FPC to increase global applicability (Puckridge et al. 1998). Also in contrast to predicted patterns (Alexan-

der et al. 2000), Tank et al. (2008) found an unexpectedly large influence of biota on N retention in downstream reaches in nutrient uptake kinetics along a gradient from low- to high-order rivers in a single watershed.

Variation in ecological processes along a large river is a response to a hierarchically structured set of variables that are directly or indirectly controlled by variation in geomorphic structure, including water depth and velocity, sediment particle size, and abundance of planktonic algal cells or suspended sediment. These variables can constrain microbial community structure at broad spatial scales (Tatariw et al. 2013), and control the supply of labile organic matter in river C pools (Mortillaro et al. 2012). Spatial variation along large rivers is coupled with facets of flow regime that can be complex and system specific. These factors make it difficult to link life-history traits with alterations in hydrologic variables without high-frequency measurements (Puckridge et al. 1998). Cohen et al. (2013) required very high temporal resolution of river data (on the scale of minutes) to distinguish between biotic and abiotic mechanisms of nutrient retention in a Florida river, suggesting that NEON's continuous monitoring on the Black Warrior–Tombigbee River system is a strong approach for documenting the influence of multiple variables on ecosystem processes.

Our challenge as a scientific community is to test and expand basic theory to generate new ideas regarding the ecology of large, heavily modified rivers (Stanley et al. 2010). Measurements of C cycling and foodweb structure in impounded rivers have highlighted regional-scale control of floodplain and planktonic subsidies created by anthropogenic alterations in geomorphic form (Thomas et al. 2005, Hoeinghaus et al. 2007, Ochs et al. 2010, 2013, Castello et al. 2013). NEON's river monitoring program will document variability in material loadings and faunal population structure, allowing researchers to contrast patterns in free-flowing streams with those of managed systems. These data will be available for validation of river modeling efforts, such as that of Global NEWS 2 (Mayorga et al. 2010), which link biological processes in river networks to coastal estuaries. This linkage is critical for addressing concerns related to eutrophication and declining commercial fisheries, and governmental monitoring agencies are making a strong plea for increased collaborative efforts to address applied research questions with a cohesive, broad-scale sampling design (McCain 2013). Data collected at the NEON river locations will be similar to those used in other ecosystems for flood-hazard assessment, estimating foodweb structure, and identifying sources of suspended solids to assess abatement strategies. Thus, NEON data will contribute to watershed management decisions (Ghizzoni et al. 2012, Turner and Edwards 2012, Westhorpe and Mitrovic 2012, Zhang et al. 2012, Saintilan et al. 2013).

The NEON sampling effort in large rivers can be considered a scaffold upon which researchers can build their own program for answering a variety of research questions. Current interest in large-river ecology includes partitioning sediment-associated and water-column metabolic activity, determining the fate of primary production in the water column, linking river geomorphic structure to nutrient cycling, and considering the role of hydrologic retention in influencing pelagic microorganisms. In addition to these current questions, NEON's large-river sampling design could be used to inform yet-unconsidered, future research efforts.

Conclusion

NEON is a comprehensive platform that provides new opportunities for implementing research that spans spatial and temporal scales. Information collected at NEON aquatic sites can be linked with atmospheric, terrestrial, and airborne observations, documenting ecological change in a more comprehensive manner than is often possible within individual research programs. Access to NEON sites, instrumentation, and data will provide a mechanism for linking stream ecosystem structure and function with landscape and climatic drivers (Sobczak and Raymond 2015). The addition of the NEON platform as an open-source tool will provide researchers with unprecedented access to high-quality data generated using standardized collection methods across various scales. These data will enable researchers to answer novel ecological questions and integrate their own research into the NEON platform.

ACKNOWLEDGEMENTS

NEON is a project sponsored by the NSF and managed under cooperative agreement by NEON, Inc. This material is based upon work supported by the NSF under the following grants: EF-1029808, EF-1138160, EF-1150319, and DBI-0752017. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the NSF.

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