4-2015

The promise and peril of intensive-site-based ecological research: insights from the Hubbard Brook ecosystem study

Timothy J. Fahey
Cornell University

Pamela H. Templer
Boston University

Bruce T. Anderson
Boston University

John J. Battles
University of California - Berkeley

John L. Campbell
USDA-Forest Service's North Research Station

See next page for additional authors

Recommended Citation

Timothy J. Fahey, Pamela H. Templer, Bruce T. Anderson, John J. Battles, John L. Campbell, Charles T. Driscoll, Jr., Anthony R. Fusco, Mark B. Green, Karim-Aly S. Kassam, Nicholas L. Rodenhouse, Lindsey Rustad, Paul G. Schaberg, and Matthew A. Vadeboncoeur 2015. The promise and peril of intensive-site-based ecological research: insights from the Hubbard Brook ecosystem study. Ecology 96:885–901. http://dx.doi.org/10.1890/14-1043.1

Authors
Timothy J. Fahey, Pamela H. Templer, Bruce T. Anderson, John J. Battles, John L. Campbell, Charles T. Driscoll, Anthony R. Fusco, Mark B. Green, Karim-Aly S. Karrim, Nicholas L. Rodenhouse, Lindsay E. Rustad, Paul G. Schaberg, and Matthew A. Vadeboncoeur

ESA CENTENNIAL PAPER

Ecology, 96(4), 2015, pp. 885–901

The promise and peril of intensive-site-based ecological research: insights from the Hubbard Brook ecosystem study

Timothy J. Fahey,[1,11] Pamela H. Templer,[2] Bruce T. Anderson,[3] John J. Battles,[4] John L. Campbell,[5] Charles T. Driscoll, Jr.,[6] Anthony R. Fusco,[3] Mark B. Green,[7] Karim-Aly S. Kassam,[1] Nicholas L. Rodenhouse,[8] Lindsey Rustad,[5] Paul G. Schaberg,[9] and Matthew A. Vadeboncoeur[10]

[1]*Department of Natural Resources, Cornell University, Fernow Hall, Ithaca, New York 14853 USA*
[2]*Department of Biology, Boston University, Boston, Massachusetts 02215 USA*
[3]*Department of Earth and Environment, Boston University, Boston, Massachusetts 02215 USA*
[4]*Department of Environmental Science, Policy and Management, University of California, Berkeley, California 94720 USA*
[5]*USDA Forest Service, Durham, New Hampshire 03827 USA*
[6]*Department of Civil and Environmental Engineering, Syracuse University, 151 Link Hall, Syracuse, New York 13244 USA*
[7]*Center for the Environment, Plymouth State University, MSC 63, 17 High Street, Plymouth, New Hampshire 03264 USA*
[8]*Department of Biological Sciences, Wellesley College, 106 Central Street, Wellesley, Massachusetts 02481 USA*
[9]*Northern Research Station, Forest Service, U.S. Department of Agriculture, University of Vermont Aiken Center, 81 Carrigan Drive, Room 208B, Burlington, Vermont 05405 USA*
[10]*Earth Systems Research Center, Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, 8 College Road, Durham, New Hampshire 03824 USA*

Abstract. Ecological research is increasingly concentrated at particular locations or sites. This trend reflects a variety of advantages of intensive, site-based research, but also raises important questions about the nature of such spatially delimited research: how well does site based research represent broader areas, and does it constrain scientific discovery? We provide an overview of these issues with a particular focus on one prominent intensive research site: the Hubbard Brook Experimental Forest (HBEF), New Hampshire, USA. Among the key features of intensive sites are: long-term, archived data sets that provide a context for new discoveries and the elucidation of ecological mechanisms; the capacity to constrain inputs and parameters, and to validate models of complex ecological processes; and the intellectual cross-fertilization among disciplines in ecological and environmental sciences. The feasibility of scaling up ecological observations from intensive sites depends upon both the phenomenon of interest and the characteristics of the site. An evaluation of deviation metrics for the HBEF illustrates that, in some respects, including sensitivity and recovery of streams and trees from acid deposition, this site is representative of the Northern Forest region, of which HBEF is a part. However, the mountainous terrain and lack of significant agricultural legacy make the HBEF among the least disturbed sites in the Northern Forest region. Its relatively cool, wet climate contributes to high stream flow compared to other sites. These similarities and differences between the HBEF and the region can profoundly influence ecological patterns and processes and potentially limit the generality of observations at this and other intensive sites. Indeed, the difficulty of scaling up may be greatest for ecological phenomena that are sensitive to historical disturbance and that exhibit the greatest spatiotemporal variation, such as denitrification in soils and the dynamics of bird communities. Our research shows that end member sites for some processes often provide important insights into the behavior of inherently heterogeneous ecological processes. In the current era of rapid environmental and biological change, key ecological responses at intensive sites will reflect both specific local drivers and regional trends.

Key words: *ecosystem; experimental manipulation; historic legacy; Hubbard Brook Experimental Forest, New Hampshire, USA; intensive sites; long-term studies; monitoring; scaling up; simulation models.*

Manuscript received 2 June 2014; revised 7 October 2014; accepted 7 October 2014; final version received 5 November 2014. Corresponding Editor: G. A. Fox.

Editors' Note: This paper was commissioned by the journal editors to commemorate the ESA Centennial celebration. A virtual Table of Contents with links to all the Centennial Papers will be available on the journals' web site (esajournals.org) by the fall of 2015.
[11] E-mail: tjf5@cornell.edu

Introduction

In recent decades there has been a trend to concentrate ecological research at particular locations. This trend began with the International Biological Program (IBP), which ran from 1964 to 1974 and continued with the U.S. National Science Foundation's Long-term Ecological Research Network (LTER). The LTER program was established in 1980 with six intensive sites, and has since grown to 26 sites with annual funding of over $25 million. In addition to core funding from the NSF, all LTER sites attract complementary studies funded by myriad scientific research agencies. This trend toward concentrating ecological research at specific sites continues with the initiation of the NSF National Ecological Observatory Network (NEON), that funds research infrastructure development and maintenance at twenty intensive ("core") sites distributed strategically around the United States to attract researchers to conduct competitively funded studies at these locations. Similar trends in research implementation are observed in other regions of the world. The concentration of ecological and environmental research represents a consensus view that multidisciplinary research at intensive sites facilitates and enhances discovery and application of scientific knowledge.

Among the earliest intensive research sites in North America, the Hubbard Brook Experimental Forest (HBEF) in New Hampshire was established by the U.S. Forest Service in 1955 as a location for forest hydrology research and was designated as a NSF LTER site in 1988. Our long experience at the HBEF affords some useful perspectives on the implications of the trend towards intensive-site-based research for scientific discovery in ecology. The overall objective of this paper is to evaluate whether and how an intensive research site can reliably represent a larger region to provide general understanding of ecological and environmental processes and patterns.

Defining Site and Region

A site is defined most simply as an area on the Earth's surface. The uniformity or variability of environmental and ecological characteristics differs across the Earth, and the site requirements for ecological research projects also vary markedly. Hence, the spatial scale of intensive sites cannot be defined uniquely. Moreover, the scale of a surrounding region for which an intensive site can be regarded as representative varies depending upon the process or application of interest. The HBEF encompasses a ~3000-ha landscape in which a suite of experimental small catchments of 10–30 ha were located to construct hydrologic and element budgets (Fig. 1). The soils, vegetation, and surface water chemistry of the HBEF exhibit variation that is closely related to the physiography of the mountainous terrain, and they respond to the elevational influence on climate over the range from 250–950 m above sea level that encompasses the transition from northern hardwood forest below to spruce–fir above. Thus, the HBEF is representative to varying degrees of the White Mountain region of New Hampshire (scale = 10^4 km^2); the Northern Forest region of northern New England and New York (scale = 10^5 km^2; Fig. 1); and the glaciated Appalachian Highlands of eastern North America (scale = 10^6 km^2).

The process whereby intensive research sites have been chosen is nearly as variable as the sites themselves. In many cases in the United States, land management agencies with a research mission (e.g., the U.S. Forest Service (USFS), National Park Service, Agricultural Research Service, Bureau of Land Management, U.S. Fish and Wildlife Service) chose intensive sites on the basis of available land, suitability for a particular project, or because of previous research activities. The establishment of baseline data and environmental monitoring at these sites then attracted scientists to conduct additional studies. Similarly, many universities have established field research stations and facilities on land donated by alumni. The HBEF, like many other USFS experimental forests (e.g., Coweeta Hydrologic Laboratory, Fernow Experimental Forest, H. J. Andrews Experimental Forest), was initially established to evaluate forest management effects on water yield using small watersheds. The site, which was selected from several candidate sites on available National Forest land, was chosen because it had many small headwater streams with watertight bedrock that could be paired for experimental studies. At the HBEF, the realization that the small watershed approach would allow the construction of accurate ecosystem element budgets (Bormann and Likens 1967) resulted in expansion of research activities into allied fields, such as biogeochemistry, ecology, and soil science, and their application to the problems of human-accelerated environmental change (e.g., atmospheric deposition, climate change). Thus, the HBEF was not chosen to be representative of ecological and biogeochemical conditions in the region, but because of its suitability for hydrologic studies and its availability within the National Forest system.

By comparison, some intensive research sites have been identified largely on the basis of how well they represent a particular biome. For example, establishment of the Konza Prairie Biological Station by researchers at Kansas State University followed a process of site identification and inventory for purposes of representing well-developed tallgrass prairie near the University (Reichman 1987), and similar approaches were applied for other LTER sites.

We conducted a survey of primary contacts (e.g., site directors) for LTER sites, Organization of Biological Field Stations sites, and "relocatable" sites within the NEON network to assess the primary and secondary reasons that resulted in the original decision to situate intensive research sites. We received a total of 118 responses out of 213 inquiries; among these, 32.5% represented sites with terrestrial research, 12.8% aquatic, 52.1% both terrestrial and aquatic, and 2.6% represented agricultural sites. The most common primary reason (Fig. 2) for originally situating intensive research sites was that sites were available or affordable (e.g., donated

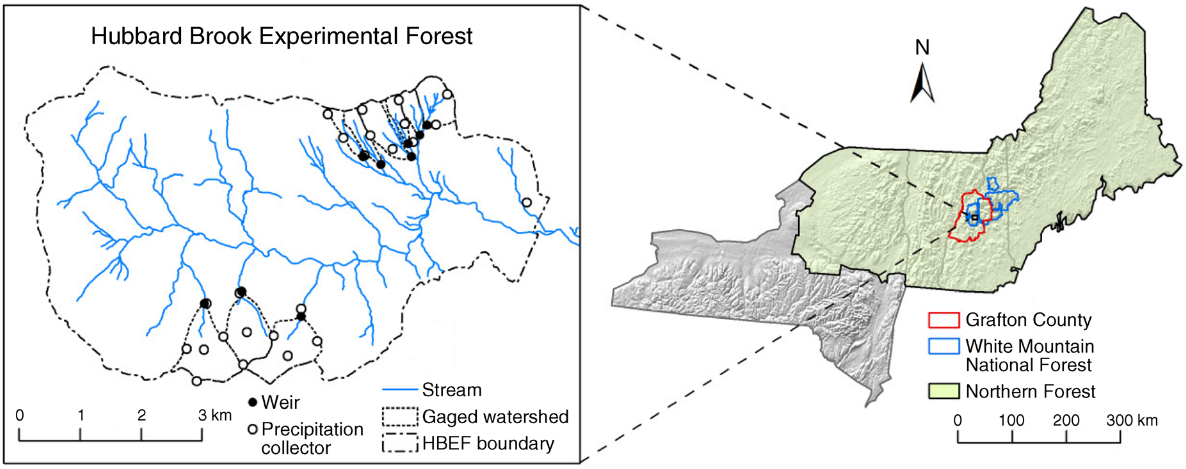

FIG. 1. Location of the Hubbard Brook Experimental Forest (HBEF) within the Northern Forest Region, the White Mountain National Forest, and Grafton County, New Hampshire, USA.

land). The most common secondary reason for situating an intensive research site was that it was well suited to address scientific research questions or hypotheses (Fig. 2). Less than one-quarter of all respondents (22.2% and 24.1% for primary and secondary reason, respectively) indicated that the original reason for situating an intensive research site was to be representative of a regional biome.

The process of choosing core sites in NEON was more objective and quantitative in that they were distributed among 20 "domains" (i.e., areas across the United States representing distinct landforms, vegetation, climate, and ecosystem dynamics), and a combination of multivariate analysis and ecological expertise was used to evaluate their representativeness of a domain. Nevertheless, in most cases the sites that were chosen for NEON had a long history of research and contained level terrain suitable for eddy flux tower measurements (Hargrove and Hoffman 2004, Keller et al. 2008). Thus, it is clear that the locations of intensive research sites usually have not been chosen primarily to be representative of a landscape or region.

REPRESENTATIVENESS OF INTENSIVE SITES

It is reasonable, then, to ask whether intensive research sites can provide a general understanding of

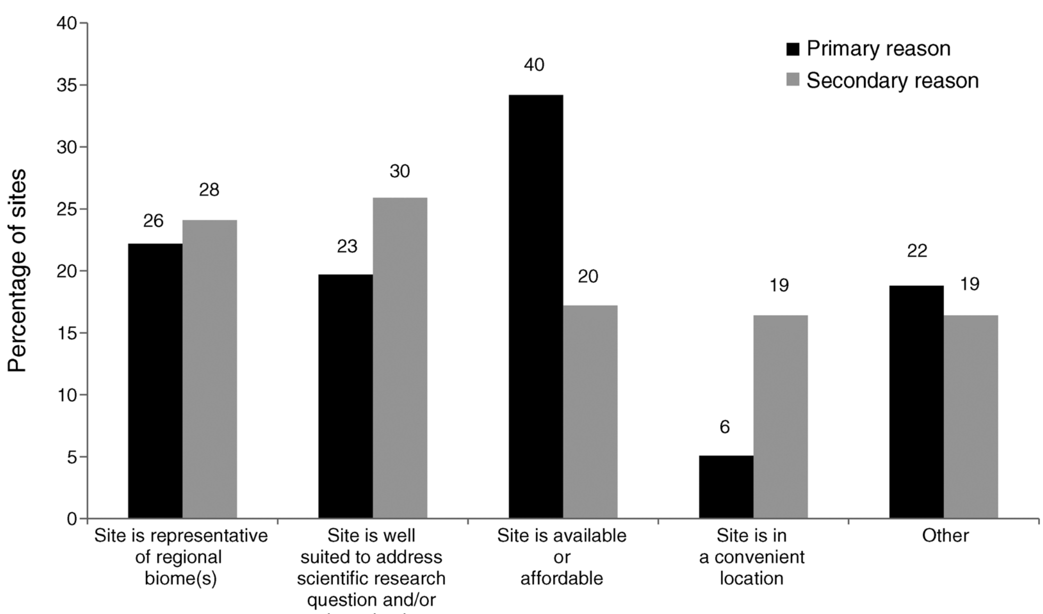

FIG. 2. Results of a survey of primary contacts (e.g., site directors) at a suite of 117 intensive field research sites in the United States. Respondents were asked to choose the primary and secondary reason for originally choosing the location of their site. Values above bars represent number of sites.

Box 1: Integrated site-based research in the Anthropocene

Intensive site-based ecological research is increasingly confronting sociocultural elements. The Anthropocene is characterized by complex, subtle, dynamic, and interconnected ecological and social impacts indicating that humanity is permanently embedded within ecological systems (Crutzen and Stoermer 2000, Ohl et al. 2007, Robertson et al. 2012). Human cultures do not exist outside of nature even though they may fail to perceive this linkage (Redman et al. 2004, Kassam 2009). As a result, intensive site research not only enhances human perceptibility of ecological phenomena but also interconnected sociocultural phenomena; and hence, increasing human understanding (Magnuson 1990). Often, biological and social scientists seek to understand systems by disturbing them or by studying perturbations generated through anthropogenic influences. Much like ecological processes, sociocultural flows are nonlinear and are not in equilibrium (Hobbie 2003). In fact, ecological and sociocultural processes have unique metabolic rhythms that are constrained by similar biophysical processes (Georgescu-Roegen 1971, Haberl et al. 2006). Land-use has both an ecological and sociocultural legacy that is not easily rendered into cause and effect chains because the consequences, in the long-run, become causes that drive other processes (Hobbie 2003). Moreover, human activities often alter environmental heterogeneity and the connectedness of ecosystems, reducing the likelihood that a single intensive site in a natural area will be representative of the surrounding region.

The rates of flows affecting temporal and spatial scales of impact in sociocultural and ecological systems exhibit obvious differences. Here lies the tension in integrating the sociocultural with the ecological: interdisciplinary or transdisciplinary research has the potential to change the system while under investigation (Greenwood and Levin 1998, Haberl et al. 2006). In contrast, traditional biophysical research involves controlled experiments characterized as 'objective', which may give the perception of detachment from social values. While ecological research is also driven by societal norms and objectives, community-based studies overtly try to improve human well-being in the system under investigation. The effects of human beings on their environment depend in part on their cultures. These effects are somewhat independent of the biophysical endowments within a particular context and may differ in research intensive sites depending on sociocultural mechanisms that govern human behavior. Arguably, basic ecology seeks to understand how the system works rather than trying to improve it. However, ecological research driven by conservation objectives is a normative process similar to sociocultural research on poverty alleviation or climate change adaptation.

Human community-based research is fundamentally participatory where individuals and groups affected are self-aware and reflective. There is a diversity of explanations and generalizations based on actions informed by a people's knowledge and beliefs. Therefore, a study of consequences can be a guide to behavior and the study of behavior can be a guide to consequences. In intensive-site research that includes a social component, we must consider the interpretations of self-reflecting humans; that is, both self-interpretation and the relation to the context studied may explain people's actions. Reflexivity, the ability of an entity to react back upon itself, is essential because it is capable of producing change. Therefore, the integration of sociocultural and ecological knowledge generated through intensive-site research may always be highly context-dependent.

broader-scale patterns and processes in ecology and environmental science. Of course, the representativeness of field sites is not always essential for gaining scientific insight. Moreover, key site characteristics encompass many dimensions, including social elements, so that no site can be comprehensively representative of the region within which it is located. Indeed, a strong case can be made that research to integrate sociocultural and ecological knowledge is inherently context dependent (see Box 1). Nevertheless, in many cases the extrapolation of local patterns to a broader scale is central to the application of the research insights, both for scientific discovery and to inform natural resource management. For example, in the NSF LTER program, regionalization efforts have been actively encouraged for the individual site-based projects (Hobbie et al. 2003).

One way to establish a standard of representativeness is to evaluate how much various characteristics or processes within a site deviate from the region within which it resides. One conceptual basis for choosing such criteria would be the state factor approach originated by Jenny (1961) for soils and ecosystems. We compared a suite of state factors and ecological processes of the Hubbard Brook ecosystem relative to the broader Northern Forest of northern New England and New York (Fig. 1): climate, physiography, biota (forest biomass and selected animal populations), and land-use history, as well as watershed hydrology and biogeochemistry. In particular, we evaluated for this suite of variables the rank (relative cumulative fraction) of its value and, when appropriate, its rate of change at the HBEF compared with the larger Northern Forest region.

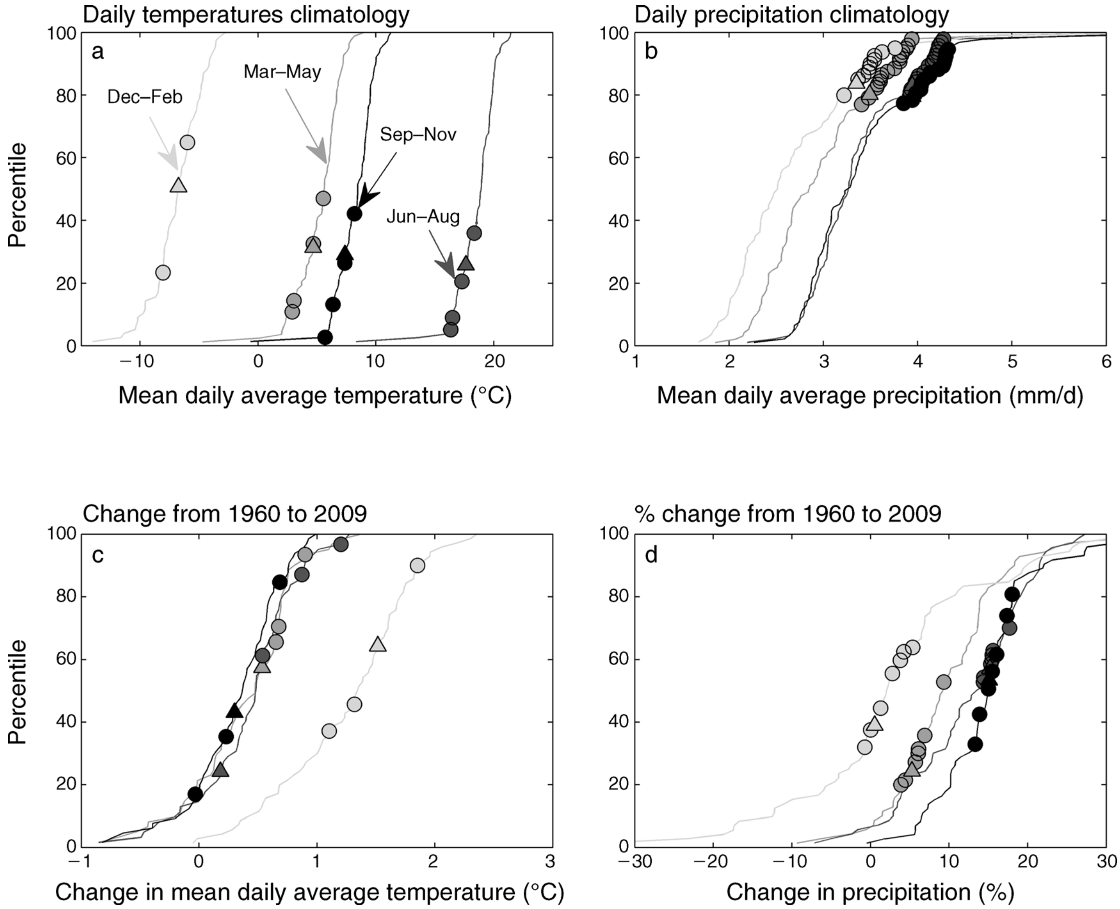

FIG. 3. (a) Relative cumulative fraction (percentile) of climatological seasonal mean daily average temperatures ($T_{avg} = [(T_{max} + T_{min})/2]$) for 91 stations across the Northeast (>42.75° N, <76.0° W) for the period 1960–2009. Only years in which <10% of the days (for a given season) are missing are included in the average; only stations with <10% of the yearly values missing are plotted. Hubbard Brook Experimental Forest (HBEF) stations are indicated by solid circles; the solid triangle is HBEF Station #1. (b) Same as (a) but for seasonal mean daily average precipitation amounts. (c) The change in the seasonal mean daily average temperatures between the period 1990–2009 and the period 1960–1979. Only stations with <10% missing years within both 20-year periods are plotted. (d) Same as (c) except for the percentile change in seasonal mean daily average precipitation, where percentile changes are calculated as the actual change divided by the climatological value (over the entire 50-year period).

IS HUBBARD BROOK REPRESENTATIVE OF THE NORTHERN FOREST REGION?

Physiography

The HBEF is situated within the Appalachian Uplands physiographic province, a region of exceptionally complex geologic history and moderately high topographic relief. In such mountainous terrain, one of the most important physiographic variables driving differences in ecosystem processes is slope angle; landscapes of more gentle relief generally have deeper, more fertile soils; more extensive poorly drained areas; and less microclimatic variation. We conducted a terrain analysis of the entire Northern Forest region using a 30-m digital elevation model, and classified each pixel in the model by average slope angle (omitting lakes and ponds). The Hubbard Brook Experimental Forest is steeper, on average, than about 90% of the Northern Forest landscape, and the biogeochemical reference watershed (WS6) is even steeper (Fig. 1). However, the HBEF is quite similar in relief to both the White Mountain National Forest and the surrounding Grafton County. Thus, we would conclude that, in terms of physiography, the HBEF is representative of a limited proportion of the surrounding landscape but not of the wider Northern Forest region, and that extrapolation of patterns and processes that are sensitive to physiography must be made with due caution.

Changes in climate and hydrology

Long-term and spatially extensive records of climate provide a particularly informative example of how well particular sites represent regions. The climate of the HBEF nicely illustrates both conformity and deviation from regional patterns (Fig. 3). We compared air temperature and precipitation data from five temperature gauges and 17 precipitation gauges at the HBEF, with data collected at 91 U.S. Historical Climatology

PLATE 1. V-notch weir for measuring stream discharge from a small watershed at the Hubbard Brook Experimental Forest, New Hampshire, USA. Photo credit: Northern Research Station, USDA Forest Service.

Network sites across the Northern Forest region. Given the relatively high average elevation of the HBEF, most seasons (with the exception of winter) tend to be cooler than most monitored locations across the forested Northeast (Fig. 3a). More strikingly, however, the HBEF receives much greater amounts of precipitation throughout the year (Fig. 3b), lying in the top 90th percentile during all seasons, possibly due to its higher elevation (also in the top 90th percentile for the climate sites) and local orographic effects.

As with most regional stations, temperatures at the HBEF have increased over the last 50 years, particularly during the winter season (Fig. 3c). In addition, temperature changes during winter and spring at the HBEF tend to be greater than other monitored locations across the Northeast. More interestingly, however, the relative warming across the HBEF-specific sites during summer and fall spans the range of warming experienced across the broader Northern Forest region, suggesting that intra-site microclimatic temperature changes at the HBEF during these seasons can be used advantageously as a proxy for inter-site regional climatic changes.

With regard to seasonal precipitation changes, stations across the HBEF have experienced enhanced precipitation during summer and fall, but little to no change during winter and spring (Fig. 3d). In addition, the increased precipitation at the HBEF during summer (in particular) and fall tends to be greater than at other monitored locations across the forested Northeast, whereas the increased spring precipitation tends to be less than at other stations. The absence of precipitation changes at the HBEF during winter is fairly representative of the median changes experienced across the region. When combined with changes in temperature, though, seasonal climatic changes across the HBEF fall well within the distribution experienced across the forested Northeast with the possible exception of spring, which tends to have become warmer but drier relative to other locations.

These changes in climate have influenced stream discharge across the region. The U.S. Geological Survey (USGS) measures streamflow throughout the country as part of its National Water Information System. Currently, 62 gaging stations in this network have been in operation for at least 50 years in the Northern Forest region. These stations are located on rivers draining larger watersheds (31 to 17 347 km^2) relative to the HBEF watersheds (<1 km^2). However, when these streamflow data are normalized by watersheds area (i.e., expressed as mm of streamflow per year), they provide a standardized frame of reference (Pilgrim 1983). We compared 50 years of data (1960–2009) from these USGS gaging stations with data from four watersheds at the HBEF with records of the same length (Watersheds 1–4; Figs. 1 and 4a; Plate 1). Streamflow at the HBEF watersheds is above the 94th percentile, reflecting high

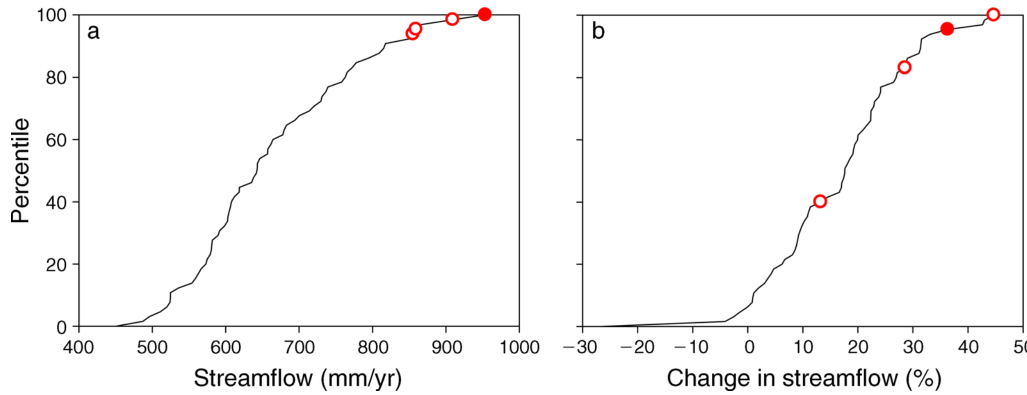

FIG. 4. Relative cumulative fraction (percentile) developed from 62 USGS gaging stations in the Northern Forest showing (a) mean annual streamflow (mm) and (b) the change in streamflow (%) from 1960 to 2009. Symbols represent the watersheds at the HBEF with data from the same time period, including three watersheds that have been experimentally manipulated (Watersheds 1, 2, and 4; open circles) and a relatively undisturbed reference watershed (Watershed 3; solid circle).

runoff in this mountainous terrain. Relatively high precipitation and cool temperatures, resulting in low potential evapotranspiration, probably contribute to this higher runoff, compared to other watersheds in the region.

Across the Northern Forest, streamflow has increased over the last 50 years in response to increases in precipitation (Fig. 3d). Only five of the 62 stations show negative trends in streamflow, with the rest showing increases of up to 45%. The change in streamflow for the relatively undisturbed reference watershed at the HBEF (Watershed 3) is at the 95th percentile, and is exceeded slightly by a watershed that was amended with Ca (W1; Green et al. 2013). Forest harvesting experiments caused high flows early in the record, which affected the streamflow trends at these sites, resulting in less dramatic increases (13% and 29% change). Some of the USGS gauges are on rivers that have been affected by human influences (e.g., impoundment, water withdrawals, land-use change), which could impact this analysis. However, limiting consideration to USGS sites that are minimally affected by human influences (i.e., stations in the USGS Hydro-Climatic Data Network) reduced the number of gauges substantially ($n = 17$), but had minimal impact on the results.

Acid deposition effects

Research at the HBEF has long informed science and policy on acid deposition and its effects on soils and surface water (Likens et al. 1996, Likens and Buso 2012). Virtually all surface waters in the Northern Forest are experiencing decreasing concentrations of sulfate and increases in acid neutralizing capacity in response to decreases in atmospheric emissions of sulfur dioxide and sulfate deposition (Kahl et al. 2004, Warby et al. 2005). So, how well does HBEF represent surface water chemistry in the northeastern region and its response to decreases in acidic deposition?

To illustrate, we position the concentrations and rates of change of sulfate and acid-neutralizing capacity (ANC) of the stream draining the biogeochemical reference watershed (W6) at the HBEF in relation to a relative cumulative fraction diagram of surface waters for the Northern Forest region. The latter is based upon regional lake–watershed surveys carried out by the U.S. Environmental Protection Agency Direct/Delayed Response Project (DDRP; Adirondack, Central New England, and Northern New England subregions; Warby et al. 2005). We show data for two stream reaches in W6: at the headwaters of the drainage (732 m) and at the gaging station (541 m, elevation, 13.2-ha catchment area; Fig. 1). Concentrations of sulfate at W6 are at the 72nd percentile for surface waters across the Northern Forest region (Fig. 5a). Long-term monitoring shows that at the high-elevation headwater reach in W6, rates of decrease in stream sulfate (-2.5 $\mu eq \cdot L^{-1} \cdot yr^{-1}$) are greater than values at the gaging station (-1.5 $\mu eq \cdot L^{-1} \cdot yr^{-1}$) (Warby et al. 2005; C. B. Fuss and C. T. Driscoll, *unpublished manuscript*; Fig. 5b). These values are at the 27th and 71th percentiles of the range of rate of surface water sulfate change for the Northern Forest region. These data show that 44% of the variation in rate of change in surface water sulfate observed across the Northern Forest is evident within a small (13.2-ha) watershed at Hubbard Brook.

Acid neutralizing capacity is a widely used metric for the acid–base status of surface waters and sensitivity to acidic deposition. ANC at the gauge of W6 is near the lowest value observed in DDRP surface waters of the Northern Forest (2 μeq/L; Fig. 5c). Indeed, the ANC value of the headwater reach of W6 (−40 μeq/L) is considerably lower than that of any of the DDRP watersheds. This considerable sensitivity is probably due to the relatively small area of W6 (13.2 ha) compared to the DDRP watersheds, that range up to ~3000 ha. Stream water at W6 shows a temporal trend of increasing ANC (headwater reach 1.3 $\mu eq \cdot L^{-1} \cdot yr^{-1}$

58th percentile; gaging station 0.4 $\mu eq \cdot L^{-1} \cdot yr^{-1}$, 38th percentile), a pattern that is evident for most of the DDRP watersheds (Warby et al. 2005; Fig. 5d).

Ollinger et al. (1993) examined spatial patterns of atmospheric deposition across the Northeast, finding that although the HBEF experiences local elevated deposition due to orographic effects, overall its deposition is intermediate along a regional gradient of deposition decreasing from the Adirondacks to Maine. The concentrations of stream sulfate at the HBEF in comparison to regional surface waters are consistent with this pattern of intermediate regional deposition relative to generally higher concentrations to the west and lower concentrations to the east (Driscoll et al. 1998). Moreover, the rates of decreases in stream sulfate (the major determinant of changes in surface water acidification from acid deposition) are comparable and indicative of the response of watersheds and surface waters in the Northern Forest to decreases in atmospheric sulfate deposition. In contrast, stream water draining W6 is characterized by low ANC, showing that this small, high-elevation watershed with shallow surficial deposits and flashy hydrology is highly sensitive to acidic deposition, particularly when compared to other watersheds studied in the Northern Forest that are generally larger in area (ranging to 3000 ha) and lower in elevation. It is noteworthy that the rates of increase in ANC at the HBEF are comparable and indicative of the widespread recovery of the Northern Forest in response to decreases in acid deposition (Kahl et al. 2004, Warby et al. 2005). This relatively uniform rate of recovery seems consistent with the observation that the magnitude of historical acidification (i.e., estimated loss of ANC from 1850 to present) in streamwater at the HBEF (Gbondo-Tugbawa and Driscoll 2003) is comparable to values projected across the Northern Forest (Chen and Driscoll 2005*a*, Zhai et al. 2008). Because of its inherent sensitivity, Hubbard Brook experiences among the most acidic conditions documented for watersheds in the Northeast. Although Hubbard Brook is not representative of the range of acid-impacted watersheds across the Northern Forest, this sensitivity positions it as a valuable site at which to conduct experiments on effects of acidification and its mitigation (Hall et al. 1980, Hedin et al. 1990, Battles et al. 2014) and to test and apply models of ecosystem acidification (Gbondo-Tugbawa et al. 2001, Gbondo-Tugbawa and Driscoll 2003).

Land use history and forest biomass

The ecological and land-use history of intensive research sites can exert an important influence over the patterns and processes occurring presently in these landscapes. The legacy of particular disturbance events on the structure and function of ecosystems has been pointed out (Foster et al. 1998, Cuddington 2011, Bain et al. 2012), and the natural disturbance regime or prevailing human influences may not be well represented at a particular intensive site. In the Northern Forest region, agricultural land use can have particularly pervasive and persistent effects on soil processes such as nitrogen (N) mineralization (Compton and Boone 2000), potentially affecting the trajectory of change in ecosystem properties onto which experimental treatments are imposed and subsequently affecting the interpretation of responses. Agricultural development in the Northern Forest region moved up the major river valleys in the late 18th and early 19th centuries, and agricultural activity peaked around the time of the Civil War (Harper 1918, Foster et al. 1998). Lowlands of the major river valleys were intensively settled and cleared at this time, predominantly for grazing. Upland areas of rugged terrain saw minimal agricultural clearing, but these areas were commercially harvested for timber beginning in the late 19th century. Although timber harvest has more transient effects on ecosystem processes than agricultural clearing, the legacy of forest cutting can strongly affect forest composition and biomass for at least a century.

To examine how well the land-use history in the HBEF represents the larger region, we summarized the percentage of area in each of the 52 counties comprising the Northern Forest region and reported as "agriculturally improved" in the 1860 Census of Agriculture (Fig. 6). We then compared these values to those of the county surrounding the HBEF (Grafton County, New Hampshire). To take account of the smaller scale of the HBEF, we also evaluated land-use history for Grafton County based on a 1860 land-use map (Walling map) at a grid resolution comparable to the scale of the HBEF (32 km^2). Compared at both scales (i.e., Northern Forest and Grafton County), the HBEF lies at the low end of the distribution, representing lands that were unsuitable for even the small-scale subsistence agriculture that was practiced elsewhere in the Pemigewasset Valley of Grafton County during the 19th century. Thus, the HBEF landscape represents the land-use history of only the most rugged portions of the Northern Forest landscape. At Hubbard Brook and within the permanently forested landscape of most of the Northern Forest, industrial timber harvest occurred in the 19th century and the early 20th century. In this respect, Hubbard Brook is typical, having first been selectively logged for high-grade spruce and subsequently heavily logged for all merchantable trees throughout most of its extent. Thus, the age and size structure and species composition of the Hubbard Brook forest is comparable to the entire White Mountain National Forest. In contrast, some extensive areas of the Adirondack Preserve and remote areas of northern Maine were not logged. However, the structure and composition of the second-growth Hubbard Brook forest is similar to that of a nearby, unlogged reference site (The Bowl Research Natural Area; Schwarz et al. 2001), illustrating the limited, long-term influence of logging.

Land-use history influences a suite of ecological patterns and processes, and understanding these influ-

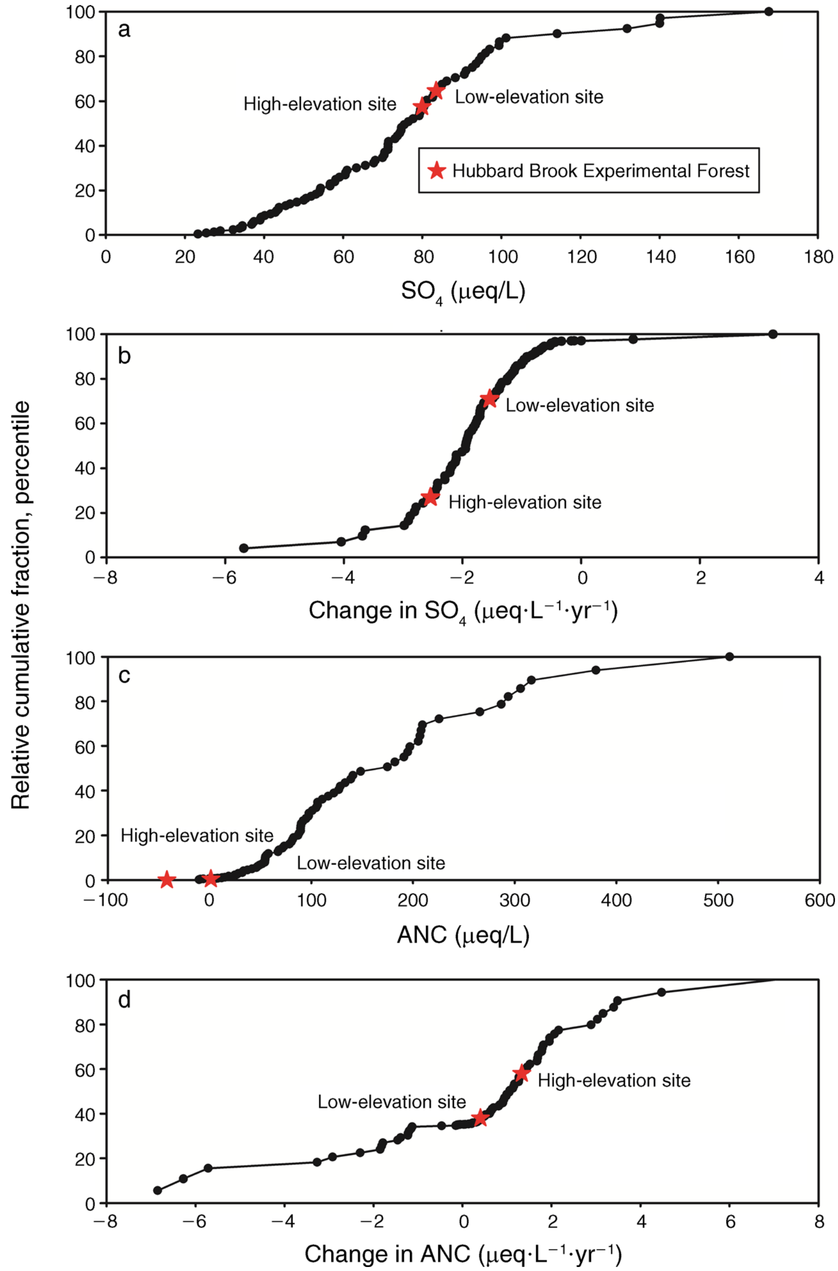

FIG. 5. Relative cumulative fraction (percentile) of concentrations and rate of change of concentrations of (a, b) sulfate and (c, d) acid neutralizing capacity (ANC) for lake watersheds from the Adirondacks and Central and Northern New England subregions of the U.S. Environmental Protection Agency Direct/Delayed Response Program (modified from Warby et al. 2005). Shown for comparison are values from a headwater (high elevation; 731 m) site and the gaging station (low elevation; 541 m) of Watershed 6, the biogeochemical reference watershed at the Hubbard Brook Experimental Forest. The reference year for the chemical concentration data is 2001.

ences is crucial for extrapolating from local, intensive-site observations to broader regions, for projecting future trends, and for designing management strategies. For example, the important role of biomass accumulation in temperate forests as a sink for atmospheric C has been demonstrated by large-scale surveys (Woodbury et al. 2007) and model inversion approaches (Fan et al. 1998), but the future of this sink remains uncertain, even while approaches for maintaining the sink are being devised (Fahey et al. 2010). We compared the current C stocks and rates of C accumulation in the northern hardwood forest at the HBEF with those reported for this forest type in the Northern Forest region by the USDA Forest Service Forest Inventory Assessment program. Because of its particular historic and recent land use, forest biomass at the HBEF lies at

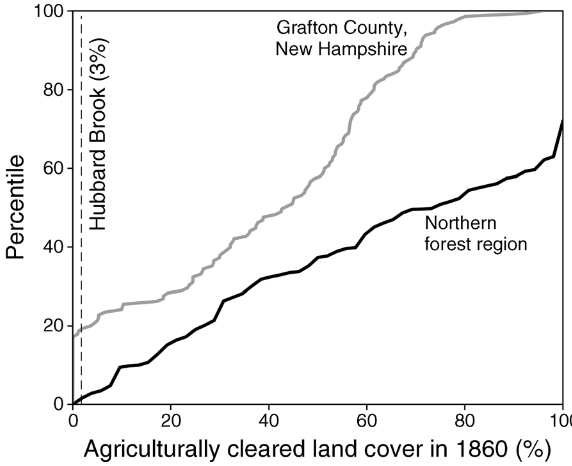

FIG. 6. Relative cumulative fraction (percentile) of area in each of the 52 counties in the Northern Forest region reported as agriculturally "improved" (i.e., plowed, mowed, or grazed) in the 1860 Census of Agriculture (black line). The gray line is derived from subdividing an 1860 land-use map of Grafton County, New Hampshire (matching the 1860 census schedules to the 1860 Walling Map) at a grid resolution of 5.6 km (3160 ha per pixel).

the upper end of a cumulative fraction distribution for C storage across the entire Northern Forest region (Fig. 7), where more varied land uses have reduced the current extent of forest and C stocks of forested lands. In contrast, current changes in forest C storage at the HBEF are near the median value for the region. The low rate of forest biomass accumulation at the HBEF is explained in part by depletion of soil nutrients, especially base cations, by acid deposition; the inherently low natural base status of Hubbard Brook soils appears to have predisposed the forest to decline, especially the foundational species: sugar maple and red spruce (Battles et al. 2014). Projecting broadscale future trends in biomass accumulation and C sequestration for the purpose of regional forest management must overcome limited current understanding of C accumulation in older forests subjected to human-accelerated environmental change.

Diversity and abundance of animals

Whether spatial patterns or temporal trends within a particular site can be extrapolated reliably to a larger region depends on the ecological phenomenon of

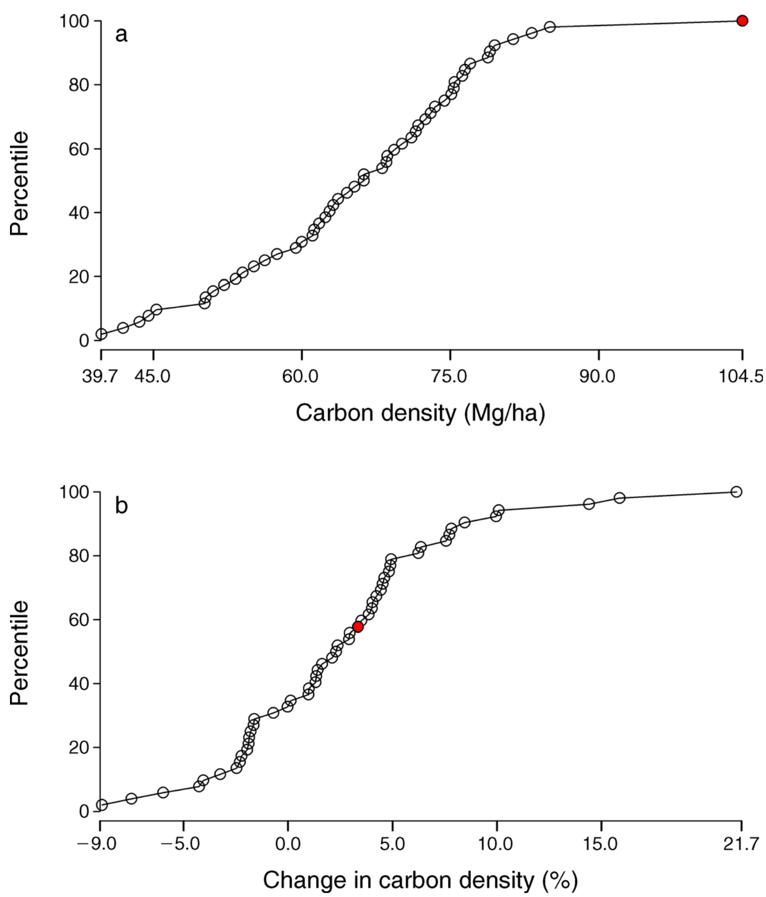

FIG. 7. Relative cumulative fraction (percentile) of (a) the carbon density of aboveground live trees in the 52 counties of the Northern Forest region for forests classified as northern hardwood and (b) percentage change in the carbon density between 2007 and 2012. The values for Hubbard Brook Experimental Forest are identified by solid red circles.

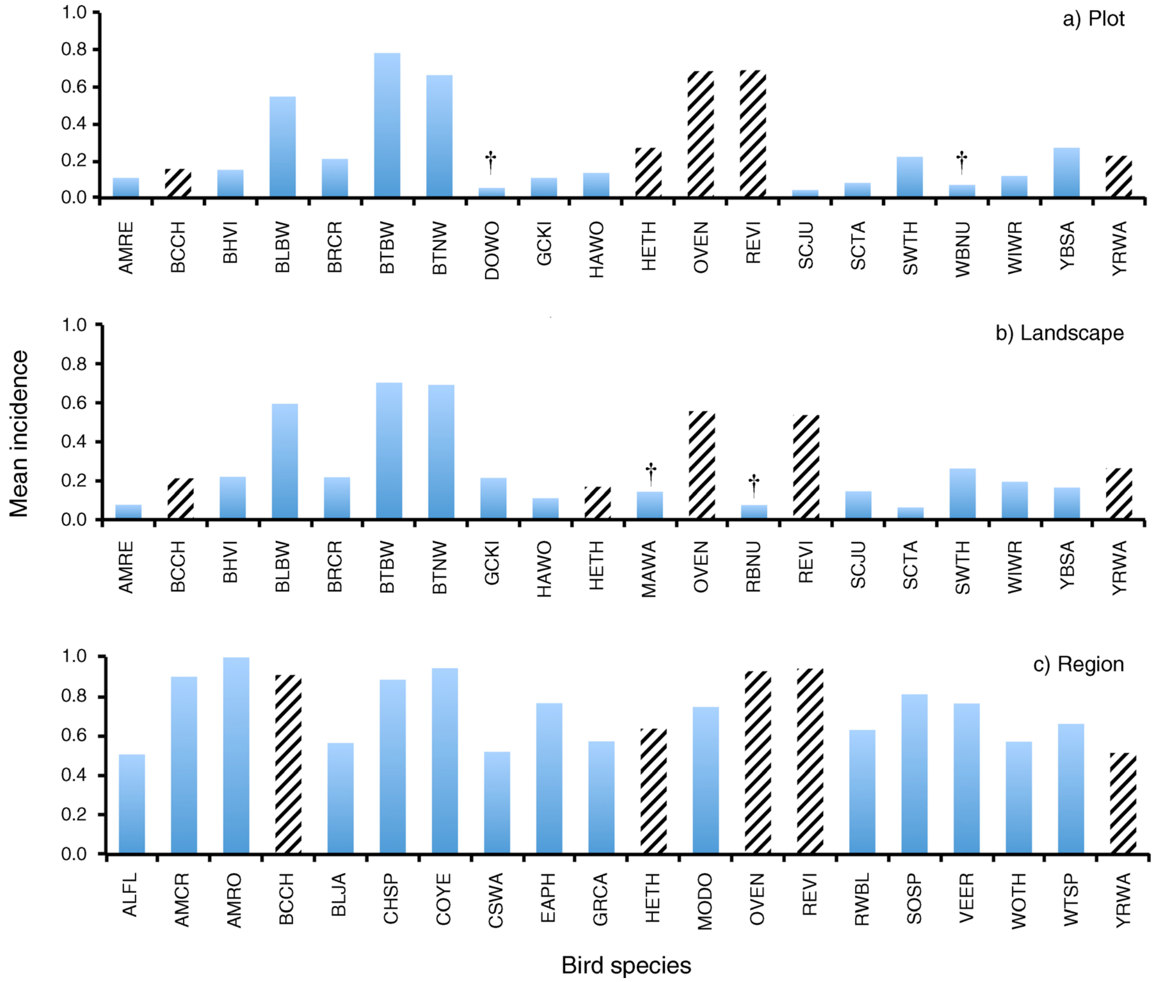

FIG. 8. Incidence of common breeding birds across three spatial scales in and around the intensive site at the HBEF: (a) a 50-ha plot that is the basis for long-term trend analyses; (b) the larger HBEF Valley landscape; and (c) the entire Northern Forest region, the latter being based on Breeding Bird Survey routes in Bird Conservation Regions #14 and #28 (Sauer et al. 2014). Daggers denote species whose incidence differs between the plot and landscape scale within the Hubbard Brook forest. Abbreviations for birds exhibiting variation across scales include: AMCR, American Crow; AMRO, American Robin; BLJA, Blue Jay; COYE, Common Yellowthroat; DOWO, Downy Woodpecker; MAWA, Magnolia Warbler; MODO, Mourning Dove; RBNU, Red-breasted Nuthatch; SOSP, Song Sparrow; WBNU, White-breasted Nuthatch.

interest as well as the environmental template of the comparisons. Moreover, sampling methods that can influence the interpretation of such comparisons may necessarily differ between studies at local vs. large scales. The spatial scale of measurement is known to influence the composition and diversity of various animal taxa (Parmesan et al. 2005, Field et al. 2009, Mattsson et al. 2013). We illustrate these points by comparing the abundance of common breeding birds across three spatial scales in and around the HBEF (Fig. 8): we used point counts from a 50-ha area that encompasses the plot used for long-term trend analyses (Holmes and Sherry 2001) as the plot-level scale; the larger HBEF Valley (347 point count locations spread in a stratified manner throughout northern hardwoods forest in the 32-km^2 Hubbard Brook Valley); and the entire Northern Forest region. Data for the latter come from Breeding Bird Survey (BBS) routes in Bird Conservation Regions #14 and #28 (Sauer et al. 2014). Within the HBEF, the incidence of forest bird species differs between the plot and larger landscape scale only for species with very low incidence: Downy Woodpeckers (DOWO) and White-breasted Nuthatches (WBNU) being among the 20 most common species only at the plot scale and Magnolia Warblers (MAWA) and Red-breasted Nuthatches (RBNU) occurring among the most common species only at the landscape scale. These subtle differences reflect forest composition: the local plot is centered on northern hardwood forest, whereas the larger landscape includes areas of coniferous habitat that support the MAWA and RBNU.

In contrast, the bird community composition differs greatly between the HBEF landscape and the larger regional scales. Among the 20 species with greatest incidence, only five species appear at all three spatial scales (Fig. 8). This observation is explained primarily by differences in the variety of habitats encountered at the regional scale, but also by the sampling methods employed. Many of the species that appear at the regional scale are associated with edge habitats (e.g., Common Yellowthroat, Song Sparrow) or anthropogenic habitats (e.g., American Robin, Blue Jay). In addition, because BBS sampling targets individuals located within 0.4 km of a roadside stop, large species and those easily detected from a long distance (e.g., American Crow, Mourning Dove) achieve high incidence at the regional scale. However, long-term trends in abundance of breeding birds on the intensively studied plot at the HBEF appear to be mirrored across the region, because six common species (American Redstart, Least Flycatcher, Tree Swallow, Veery, Wood Thrush, White-throated Sparrow) have declined in average incidence at both the local (Holmes and Sherry 2001) and regional scales (Sauer and Link 2011).

Limitations to Generalizing from Intensive Sites

For some ecological phenomena, it may be very difficult to generalize from an intensive site, and it would be useful to elaborate some principles that help to identify such phenomena. Some phenomena exhibit exceptionally high spatiotemporal variation that may not be adequately characterized at any single site. At the HBEF there have been no significant irruptions of defoliating insects in the past 40 years (Holmes 2011), whereas such irruptions, including native Lepidoptera, have been common regionally (Hunter 2002, Lovett et al. 2002). Moreover, ecological phenomena that are particularly sensitive to the influence of unique historical events (e.g., natural or human disturbance) might seldom be well represented at a particular site. This category would include soil N retention, distribution of organisms with limited dispersal ability, and population cycles involving predator–prey interactions. Notably, extreme weather events that profoundly influence ecosystem structure and dynamics have occasionally visited the region, introducing high spatial variability. For example, the 1938 hurricane and the 1998 ice storm both damaged extensive areas of forest at the HBEF (Foster and Boose 1992, Irland 1998, Rhoads et al. 2002), leaving a patchy legacy of severe forest disturbance. Most recently, an intense downburst in June 2013 severely damaged extensive sections of the HBEF.

Ecological phenomena that are highly sensitive to subtle geologic and physiographic influences also might not be well represented at a local, intensive site, especially in regions of complex and heterogeneous geology. This could include organisms with narrow soil habitat requirements and processes that critically depend upon thresholds in the soil environment (e.g., O_2, frost). At the HBEF, a good example is groundwater seeps that occur sporadically across the landscape (Zimmer et al. 2013) and influence denitrification, soil freezing, and habitat for animals such as amphibians. Similar reasoning would apply to phenomena that are particularly sensitive to microclimatic variation. Notably, the NEON sites have been chosen to accommodate eddy flux measurements (e.g., CO_2 flux) that now can only be made accurately on relatively level topography.

Advantages of Site-based Research

Despite the limited ability of intensive sites to accurately represent the more complex and varied surrounding landscape, concentrating research efforts at single locations can greatly aid scientific discovery. Perhaps the most practical advantage is the cost savings associated with routine measurements and monitoring needed to support a wide variety of research studies: climate, hydrology, environmental chemistry, and selected biological populations (e.g., dominant vegetation or animals). Another notable value of the LTER network is the maintenance of these monitoring activities over long periods, the provision of these data sets in publically accessible formats, and the standardization of some protocols for data acquisition and management across the entire network (e.g., ClimDB/HydroDB, *available online*).[12] At the HBEF, the availability of long-term precipitation and streamflow measurements has attracted complementary investigations of geohydrology (Winter et al. 1999), stream invertebrates (Hall et al. 2001), and microbial biogeochemistry of aquatic ecosystems (Bernhardt and Likens 2002). The HBEF also maintains an indexed sample archive (*available online*)[13] used by researchers to develop new approaches for addressing biogeochemical questions (e.g., isotopic methods; Alewell et al. 1999). The wider adoption and provision of funding for sample archives could greatly benefit future generations of environmental scientists.

Long-term records from an intensive site often reveal nonintuitive patterns of change or variation that seed interest in experimental manipulations, mechanistic studies, and broader comparative surveys. For example, annual variation in nitrate flux from the Hubbard Brook watersheds was tentatively tied to unusual winter weather, a pattern that became further evident across a range of regional sites (Mitchell et al. 1996). These observations stimulated experimental manipulations of winter snowpack at the HBEF (Groffman et al. 2001), which demonstrated the key role played by fine-root damage in driving this pattern (Tierney et al. 2001, Cleavitt et al. 2008, Campbell et al. 2014). Further studies have recently tied sublethal damage of fine roots to altered physiology, nutrition, and growth of trees (Comerford et al. 2013), and likely implications for

[12] http://www.fsl.orst.edu/climhy/

[13] http://www.hubbardbrook.org/samples/

regional forest health in a changing climate (Groffman et al. 2012).

In the field of community ecology and ecosystem biology, perhaps the greatest advantage of intensive-site-based research is integrating a process or taxon of interest into the larger web of interactions. A typical rationale for researchers choosing to address a research question or hypothesis at particular intensive sites is because of the availability of complementary site information for data interpretation, or to build on prior experiments and knowledge gained at the site. Additional benefit derives from cross-fertilization of ideas among disciplines that is afforded by the wide range of researchers attracted to intensive sites. At the HBEF, a Committee of Scientists that includes all participating researchers meets quarterly to discuss, assess, and plan the research program at the site. New investigators are encouraged to participate by explaining their ideas and plans for discussion of how they would integrate their work into the context of the larger program of ecosystem study. In addition to cross-fertilizing among evolutionary and population biologists, ecosystem biologists, atmospheric scientists, geohydrologists, and other scientific disciplines, these activities increasingly include social scientists and humanists. The inclusion of social scientists in the research dialogue is particularly prominent in the LTER network for selected sites that receive matching funding from the NSF ESB Directorate (Coweeta, North Temperate Lakes) and for the urban sites (Baltimore Ecosystem Study, Central Arizona-Phoenix).

Ecosystem and environmental science increasingly use complex simulation models to provide new insights on the behavior and dynamics of ecological systems. These models typically require extensive inputs and parameterization of physical and biological attributes, and calibration of outputs that can be provided by data collected at intensive research sites. Validation of the predictive capabilities of these models can be achieved by comparison of output against long-term records or the results of ecosystem manipulations. At the HBEF, modelers have taken advantage of such detailed information by developing or applying simulation models of surface water chemistry (PnET-BGC; Aber and Driscoll 1997), forest growth (JABOWA; Botkin et al. 1972), soil organic matter (DAYCENT and ROTHC; Dib et al. 2014), multiple-element limitation (MEL; Rastetter et al. 2013), and hydrology (BROOK; Federer and Lash 1978). Similarly, testing and validation of new or automated measurement approaches can be facilitated at intensive sites where exceptionally detailed data sets are available. For example, detailed studies of forest bird habitat and abundance at the HBEF have allowed novel tests of the efficacy of Lidar remote sensing for predicting bird habitat quality (Goetz et al. 2010). Similarly, global models often rely on intensive sites for evaluating model predictions and performance (e.g., Running et al. 2004).

Finally, by distributing research effort across a broad network of intensive sites, the problem of scaling up can be addressed. This is the principal reason that NEON sites were distributed among domains. Other research networks have similarly been designed to achieve broad spatial coverage, usually for the purpose of monitoring, as for example the U.S. EPA National Acid Deposition Program sampling network (Lynch et al. 2000) and the U.S. DOE Ameriflux network (Hargrove et al. 2003).

Experiments at Intensive Sites

Regardless of whether a particular site represents a larger region, the patterns and trends revealed by monitoring and surveys at intensive sites often stimulate design of experiments to test specific hypotheses. Probably the single greatest advantage to experiments afforded by intensive sites is existence of long-term, pretreatment data that aid in statistical model formulations. Natural ecosystems are notoriously noisy and variable, and sample size limitations for expensive field experiments constrain the detection of responses. Moreover, because the duration of funding for experimental research is usually confined to a single granting agency funding cycle or the brief program of a graduate student, the adequacy of pretreatment data is a recurrent problem for one-off studies and sites. A common approach in the NSF LTER program has been augmentation of funding through additional competitive grants to individual or multiple investigators to establish an experiment, with continued monitoring of the experimental responses beyond the duration of the grant using base funds from the LTER programs. For example, at the HBEF several expensive whole-watershed treatments have been conducted with funding from the NSF Ecosystem Science program, and long-term monitoring of responses has been maintained with LTER funding: deforestation of Watershed 2 (W2; Reiners et al. 2012), whole-tree harvest of Watershed 5 (W5; Dib et al. 2014), and restoration of soil Ca on Watershed 1 (W1; Battles et al. 2014). Experiments at intensive sites can be carried out at relatively large spatial scales, which may be more representative of landscape and regional patterns compared to smaller-scale experiments. One notable difficulty that is created by this approach is significant commitment of base funding to maintaining experiments.

Scientific discovery from unplanned, or "natural," experiments is commonly facilitated by the baseline long-term monitoring data sets at intensive sites (Diamond 1983). The effects of natural disturbance events, invasive species, and other phenomena sometimes provide basic new insights into ecosystem structure and function. For example, at the HBEF, detailed study of watershed and forest response to the aforementioned 1998 ice storm demonstrated the dominant role of plant uptake over microbial activity in regulating the cycling of N (Houlton et al. 2003). The increase in

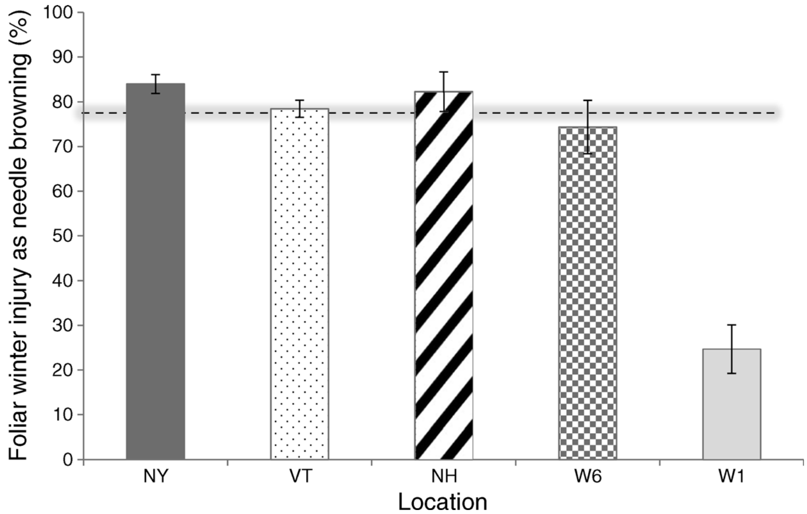

FIG. 9. Foliar winter injury (percentage of needle browning, mean ± SE) of dominant and co-dominant red spruce (*Picea rubens*) trees across New York, Vermont, and New Hampshire relative to the biogeochemical reference watershed (W6) at HBEF in 2003 (a high-injury year throughout the region; Lazarus et al. 2004). The dashed line depicts mean winter injury (with SE shown by the gray boundary around the line) across the three-state region. Injury means among states are not significantly different ($P = 0.30$) from each other or the mean for W6, based on ANOVA. There was a significant reduction ($P \leq 0.01$; Hawley et al. 2006) in winter injury for a HBEF watershed that was supplemented with calcium (W1) compared with the non-fertilized reference (W6).

rates of N losses was due to disruption of plant uptake of N, rather than changes in microbial transformation of N.

The ways in which field experiments at intensive sites can profitably interface with wider observations, natural experiments, and mechanistic process studies to inform environmental policies is well illustrated by studies of forest decline in the Northern Forest region. There have been numerous declines of tree species (e.g., red spruce, sugar maple, paper birch) across the region, and acid deposition-induced depletion of available soil Ca has been implicated as a contributing factor to these declines (Bailey et al. 2004, Halman et al. 2011). Measurements at reference sites at the HBEF confirmed that pollution-induced alterations in Ca nutrition are pertinent to the HBEF (e.g., Likens et al. 1996). Furthermore, experimental applications at the HBEF have led to a more explicit understanding of how perturbations of Ca nutrition predispose tree species to decline (e.g., Hawley et al. 2006, Juice et al. 2006). The influence of acid-induced depletion of available Ca in soil on red spruce foliar winter injury (freeze-induced mortality) provides an important case study. Laboratory-based research had implicated acid-induced available Ca loss in predisposing red spruce to increased foliar freezing injury (e.g., DeHayes et al. 1999). However, it was not until the severe 2003 region-wide winter injury event that field measurements verified the connection between available Ca depletion and foliar injury. During this event, over 90% of the red spruce assessed in New York, Vermont, and New Hampshire were injured, with the average injury of current year foliage for dominant and co-dominant trees being over 75% (Fig. 9). Injury of trees at the biogeochemical reference watershed at the HBEF (W6) was indistinguishable from regional levels, highlighting a synchrony in response. However, winter injury for red spruce at HBEF watershed 1 (W1, where Ca was added in 1999 to bring soil concentrations back up to calculated pre-pollution levels) was only about one-third of levels for W6 (Fig. 9), indicating that improved Ca nutrition helped to prevent injury. As an intensive, long-term monitoring site that also includes treatment manipulations of unusual scale, the HBEF provided information that not only exemplifies, but also clarifies, tree health and productivity issues important to scientists, managers, and policy makers.

Some constraints of intensive sites for experimental research are notable. At the HBEF and other USFS research sites, the small number of paired experimental watersheds significantly limits the availability of locations for whole-watershed experiments, and difficult decisions are necessary when assigning a watershed unit for experimental manipulation. Similar issues of land availability are common throughout the LTER network (Knapp et al. 2012). Also, because intensive sites are unlikely to span a very wide range of environmental and biological conditions, the generality and regional representativeness of observed responses to experimental manipulations can be questioned on the basis of pseudoreplication. For some field experiments, this limitation can best be addressed by replication outside the intensive site; for example, at the HBEF the effects of soil Ca supply have been examined at both the whole watershed and small plot scale. The latter approach provided replication that supported conclusions about mechanistic responses (e.g., Halman et al. 2013).

Future Prospects

The continuing trend toward increasing concentration of field ecology research at intensive sites in the United States seems unlikely to reverse, particularly given the large investment of the NSF in NEON and LTER. How can the scientific value of intensive-site research be maximized? Certainly, every site faces challenges of evaluating and demonstrating its representativeness and the limits to generalization based on results generated there. Our experience from the HBEF suggests that even though, in many respects, the setting is not typical for the larger Northern Forest region, the site captures highly informative patterns and processes. For example, the decline of sugar maple resulting from depletion of available Ca by acid deposition was most severe on thin soils at upper slope positions (Battles et al. 2014). This general finding can be applied to inform policy, in this case, by revealing the spatial patterning of critical loads for pollutants (Schulze et al. 1989). However, unless the mechanisms underlying patterns and trends are well understood, the broader application of observations from a particular site may be problematic. A better mechanistic understanding of biogeochemical and ecological phenomena therefore requires expanding the scope of observations outside the intensive site. In the case of acid deposition and soils, it has proven valuable to include comparative research on more base-poor or base-rich sites than those available within the HBEF (Cone Pond and Sleepers River, respectively; Hornbeck et al. 1997, Park et al. 2008). Similarly, complementary studies on nearby post-agricultural landscapes have demonstrated contrasting patterns of forest succession and soil C dynamics from those within the HBEF (Hamburg 1984, Vadeboncoeur et al. 2012).

These observations illustrate the importance of capturing the behavior of "end member" sites as well as representative sites in ecological research networks. Often, understanding of ecological phenomena may be best advanced through study of exceptional systems that prove valuable for testing models or characterizing the behavior of heterogeneous systems. Analogous challenges confront most intensive-research sites that seek to extrapolate ecological and environmental observations to larger domains. In NEON, the program design has addressed this challenge in the form of "relocatable" sites situated in different land-use settings from the core ("wildland") site, facilitating research to inform questions requiring such coverage. Finding an ideal balance of research funding for intensive sites and complementary studies will be an important challenge and deserves explicit consideration by researchers and their funding agencies. Finally, recognizing the potential for loss of the broadest possible involvement of individual scientists and their creative ideas that will inevitably accompany the concentration of research at a limited number of intensive sites, it is also important to maximize the opportunity of the most gifted researchers to conduct work at these sites.

Acknowledgments

The authors thank the following: R. Holmes, P. Doran, and numerous field assistants for the valley-wide surveys of birds in the HBEF and the many volunteers that conduct the Breeding Bird Survey; the W. M. Keck Foundation and R. Warby and C. Johnson for regional surface water surveys; L. Schneider and S. Hamburg for 1860 land-use map; A. Kosiba and P. Murakami for regional spruce decline analysis; Tom Luther for physiographic analysis; and all the field site managers who participated in the sites survey. This manuscript is a contribution of the Hubbard Brook Ecosystem Study. Hubbard Brook is part of the LTER network, which is supported by the National Science Foundation. The Hubbard Brook Experimental Forest is operated and maintained by the USDA Forest Service, Northern Research Station, Newtown Square, Pennsylvania, USA.

Literature Cited

Aber, J. D., and C. T. Driscoll. 1997. Effects of land use, climate variation and N deposition on N cycling and C storage in northern hardwood forests. Global Biogeochemical Cycles 11:639–648.

Alewell, C., M. J. Mitchell, G. E. Likens, and H. R. Krouse. 1999. Sources of stream sulfate at the Hubbard Brook Experimental Forest: long-term analyses using stable isotopes. Biogeochemistry 44(3):281–299.

Bailey, S. W., S. B. Horsley, R. P. Long, and R. A. Hallett. 2004. Influence of edaphic factors in sugar maple nutrition and health on the Allegheny Plateau. Soil Science Society of America Journal 68:243–252.

Bain, D. J., et al. 2012. Legacy effects in material flux: structural catchment changes predate long-term studies. BioScience 62(6):575–584.

Battles, J., T. J. Fahey, C. T. Driscoll, J. D. Blum, and C. E. Johnson. 2014. Restoring soil calcium reverses forest decline. Environmental Science and Technology Letters 1:15–19.

Bernhardt, E. S., and G. E. Likens. 2002. Dissolved organic carbon enrichment alters nitrogen dynamics in a forest stream. Ecology 83:1689–1700.

Bormann, F. H., and G. E. Likens. 1967. Nutrient cycling. Science 155(3761):424–429.

Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. Journal of Ecology 60:849–872.

Campbell, J. L., A. M. Socci, and P. H. Templer. 2014. Increased nitrogen leaching following soil freezing is due to decreased root uptake in a northern hardwood forest. Global Change Biology 20:2663–2673.

Chen, L., and C. T. Driscoll. 2005. Regional application of an integrated biogeochemical model to northern New England and Maine. Ecological Applications 15:1783–1797.

Cleavitt, N. L., T. J. Fahey, P. M. Groffman, J. P. Hardy, K. S. Henry, and C. T. Driscoll. 2008. Effects of soil freezing on fine roots in a northern hardwood forest. Canadian Journal of Forest Research 38:82–91.

Comerford, D. P., P. G. Schaberg, P. H. Templer, A. M. Socci, J. L. Campbell, and K. F. Wallin. 2013. Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. Oecologia 171:261–269.

Compton, J. E., and R. D. Boone. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology 81:2314–2330.

Crutzen, P. J., and E. F. Stoermer. 2000. The "Anthropocene." Global Change Newsletter 41:17–18.

Cuddington, K. 2011. Legacy effects: the persistent impact of ecological interactions. Biological Theory 6(3):203–210.

DeHayes, D. H., P. G. Schaberg, G. J. Hawley, and G. R. Strimbeck. 1999. Acid rain impacts calcium nutrition and forest health. BioScience 49:789–800.

Diamond, J. M. 1983. Ecology: Laboratory, field and natural experiments. Nature 304:586–587.

Dib, A. E., C. E. Johnson, C. T. Driscoll, T. J. Fahey, and K. Hayhoe. 2014. Simulating effects of changing climate and CO_2 emissions on soil carbon pools at the Hubbard Brook Experimental Forest. Global Change Biology 20:1643–1656.

Driscoll, C. T., G. E. Likens, and M. R. Church. 1998. Recovery of surface waters in the northeastern U.S. from decreases in atmospheric deposition of sulfur. Water, Air, and Soil Pollution 105:319–329.

Fahey, T. J., P. B. Woodbury, J. J. Battles, C. L. Goodale, Steven Hamburg, S. Ollinger, and C. W. Woodall. 2010. Forest carbon storage: ecology, management and policy. Frontiers in Ecology and the Environment 8:245–252.

Fan, S., M. Gloor, J. Mahlman, S. Pacala, J. Sarmiento, T. Takahashi, and P. Tans. 1998. A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. Science 282:442–446.

Federer, C. A., and D. Lash. 1978. Simulated streamflow response to possible differences in transpiration among species of hardwood trees. Water Resources Research 14:1089–1097.

Field, R., et al. 2009. Spatial species-richness gradients across scales: a meta-analysis. Journal of Biogeography 36:132–147.

Foster, D. R., and E. R. Boose. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. Journal of Ecology 80:79–99.

Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. Ecosystems 1(1):96–119.

Gbondo-Tugbawa, S. S., and C. T. Driscoll. 2003. Factors controlling long-term changes in soil pools of exchangeable basic cations and stream acid neutralizing capacity in a northern hardwood forest ecosystem. Biogeochemistry 63:161–185.

Gbondo-Tugbawa, S. S., C. T. Driscoll, J. D. Aber, and G. E. Likens. 2001. Evaluation of an integrated biogeochemical model (PnET-BGC) at a northern hardwood forest ecosystem. Water Resources Research 37:1057–1070.

Georgescu-Roegen, N. 1971. The entropy law and the economic process. Harvard University Press, Cambridge, Massachusetts, USA.

Goetz, S. J., D. Steinberg, M. G. Betts, R. T. Holmes, P. J. Doran, R. Dubayah, and M. Hofton. 2010. Lidar remote sensing variables predict breeding habitat of a Neotropical migrant bird. Ecology 91:1569–1576.

Green, M. B., et al. 2013. Decreased water flowing from a forest amended with calcium silicate. Proceedings of the National Academy of Sciences USA 110(15):5999–6003.

Greenwood, D. J., and M. Levin. 1998. Introduction to action research: social research for social change. Sage, London, UK.

Groffman, P. M., C. T. Driscoll, T. J. Fahey, J. P. Hardy, R. D. Fitzhugh, and G. L. Tierney. 2001. Colder soils in a warmer world: A snow manipulation study in a northern hardwood forest ecosystem. Biogeochemistry 56:135–150.

Groffman, P. M., et al. 2012. Long-term integrated studies show complex and surprising effects of climate change in the northern hardwood forest. BioScience 62:1056–1066.

Haberl, H., V. Winiwarter, and K. Andersson. 2006. From LTER to LTSER: Conceptualizing the socioeconomic dimension of long-term socioecological research. Ecology and Society 11:1–34.

Hall, R. J., G. E. Likens, S. B. Fiance, and G. R. Hendrey. 1980. Experimental acidification of a stream in the Hubbard Brook Experimental Forest, New Hampshire. Ecology 61:976–989.

Hall, R. O., Jr., G. E. Likens, and H. M. Malcom. 2001. Trophic basis of invertebrate production in two streams at the Hubbard Brook Experimental Forest. Journal of the North American Benthological Society 2093:432–447.

Halman, J. M., P. G. Schaberg, G. J. Hawley, and C. F. Hansen. 2011. Potential role of soil calcium in recovery of paper birch (*Betula papyrifera*) following ice storm injury in Vermont, USA. Forest Ecology and Management 261:1539–1545.

Halman, J. M., P. G. Schaberg, G. J. Hawley, L. H. Pardo, and T. J. Fahey. 2013. Calcium and aluminum impacts on sugar maple physiology in a northern hardwood forest. Tree Physiology 33:1242–1251.

Hamburg, S. P. 1984. Organic matter and nitrogen accumulation during 70 years of old-field succession in central New Hampshire. Dissertation. Yale University, New Haven, Connecticut, USA.

Hargrove, W. W., and F. M. Hoffman. 2004. The potential of multivariate quantitative methods for delineation and visualization of ecoregions. Environmental Management 34(5):S39–S60.

Hargrove, W. W., F. M. Hoffman, and B. E. Law. 2003. New analysis reveals representativeness of the AmeriFlux network. EOS, Transactions, American Geophysical Union 84:529–535.

Harper, R. M. 1918. Changes in the forest area of New England in three centuries. Journal of Forestry 16:442–452.

Hawley, G. J., P. G. Schaberg, C. Eagar, and C. H. Borer. 2006. Calcium addition at the Hubbard Brook Experimental Forest reduced winter injury to red spruce in a high-injury year. Canadian Journal of Forest Research 36(10):2544–2549.

Hedin, L. O., G. E. Likens, K. M. Postek, and C. T. Driscoll. 1990. A field experiment to test whether organic acids buffer acid deposition. Nature 345:798–800.

Hobbie, J. E. 2003. Scientific accomplishments of the Long Term Ecological Research Program: an introduction. BioScience 53:17–20.

Hobbie, J. E., S. R. Carpenter, N. B. Grimm, J. R. Gosz, and T. R. Seastedt. 2003. The US Long Term Ecological Research program. BioScience 53(1):21–32.

Holmes, R. T. 2011. Avian population and community processes in forest ecosystems: long-term research in the Hubbard Brook Experimental Forest. Forest Ecology and Management 262:20–32.

Holmes, R. T., and T. W. Sherry. 2001. Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. Auk 118:589–609.

Hornbeck, J. W., S. W. Bailey, D. C. Buso, and J. B. Shanley. 1997. Streamwater chemistry and nutrient budgets for forested watersheds in New England: variability and management implications. Forest Ecology and Management 93:73–89.

Houlton, B. Z., C. T. Driscoll, T. J. Fahey, G. E. Likens, P. M. Groffman, E. S. Bernhardt, and D. C. Buso. 2003. Nitrogen dynamics in ice storm-damaged forest ecosystems: Implications for nitrogen limitation theory. Ecosystems 6(5):431–443.

Hunter, M. D. 2002. Landscape structure, habitat fragmentation, and the ecology of insects. Agricultural and Forest Entomology 4:159–166.

Irland, L. C. 1998. Ice storm 1998 and the forests of the Northeast. Journal of Forestry 96:32–40.

Jenny, H. 1961. Derivation of state factor equations of soils and ecosystems. Soil Science Society of America Journal 25:385–388.

Juice, S. M., T. J. Fahey, T. G. Siccama, C. T. Driscoll, E. G. Denny, C. Eagar, N. L. Cleavitt, R. Minocha, and A. D. Richardson. 2006. Response of sugar maple to calcium addition to northern hardwood forest. Ecology 87(5):1267–1280.

Kahl, J. S., et al. 2004. Have U.S. surface waters responded to the 1990 Clean Air Act Amendments? Environmental Science and Technology 38:484A–490A.

Kassam, K.-A. 2009. Biocultural diversity and indigenous ways of knowing: human ecology in the Arctic. University of Calgary Press, Calgary, Alberta, Canada.

Keller, M., D. S. Schimel, W. W. Hargrove, and F. M. Hoffman. 2008. A continental strategy for the National Ecological Observatory Network. Frontiers in Ecology and the Environment 6:282–284.

Knapp, A. K., et al. 2012. Past, present and future roles of long-term experiments in the LTER network. BioScience 62:377–389.

Lazarus, B. E., P. G. Schaberg, D. H. DeHayes, and G. J. Hawley. 2004. Severe red spruce winter injury in 2003 creates unusual ecological event in the northeastern United States. Canadian Journal of Forest Research 34:1784–1788.

Likens, G. E., and D. C. Buso. 2012. Dilution and the elusive baseline. Environmental Science and Technology 46(8):4382–4387.

Likens, G. E., C. T. Driscoll, and D. C. Buso. 1996. Long-term effects of acid rain: response and recovery of a forest ecosystem. Science 272:244–246.

Lovett, G. M., L. M. Christenson, P. M. Groffman, C. G. Jones, J. E. Hart, and M. J. Mitchell. 2002. Insect defoliation and nitrogen cycling in forests. BioScience 52:335–341.

Lynch, J. A., V. C. Bowersox, and J. W. Grimm. 2000. Acid rain reduced in eastern United States. Environmental Science and Technology 34(6):940–949.

Magnuson, J. J. 1990. Long-term ecological research and the invisible present. BioScience 40:495–501.

Mattsson, B. J., E. F. Zipkin, B. Gardner, P. J. Blank, J. R. Sauer, and J. A. Royle. 2013. Explaining local-scale species distributions: relative contributions of spatial autocorrelation and landscape heterogeneity for an avian assemblage. PLoS ONE 8(2):e55097.

Mitchell, M. J., C. T. Driscoll, J. S. Kahl, G. E. Likens, P. S. Murdoch, and L. H. Pardo. 1996. Climatic control of nitrate loss from forested watersheds in the Northeast United States. Environmental Science and Technology 30(8):2609–2612.

Ohl, C., K. Krauze, and C. Grünbühel. 2007. Towards an understanding of long-term ecosystem dynamics by merging social-economic and environmental research criteria for long-term socio-ecological research sites selection. Ecological Economics 63:383–391.

Ollinger, S. V., J. D. Aber, G. M. Lovett, S. E. Millham, R. G. Lathrop, and J. M. Ellis. 1993. A spatial model of atmospheric deposition for the northeastern U.S. Ecological Applications 3:459–472.

Park, B. B., R. D. Yanai, T. J. Fahey, S. W. Bailey, T. G. Siccama, J. B. Shanley, and N. L. Cleavitt. 2008. Fine root dynamics and forest production across a calcium gradient in northern hardwood and conifer ecosystems. Ecosystems 11(2):325–341.

Parmesan, C., S. Gaines, L. Gonzalez, D. M. Kaufman, J. Kingsolver, A. T. Peterson, and R. Sagarin. 2005. Empirical perspectives on species borders: from traditional biogeography to global change. Oikos 108:58–75.

Pilgrim, D. H. 1983. Some problems in transferring hydrological relationships between small and large drainage basins and between regions. Journal of Hydrology 65:49–72.

Rastetter, E. B., R. D. Yanai, R. Q. Thomas, M. A. Vadeboncoeur, T. J. Fahey, M. C. Fisk, B. L. Kwiatkowski, and S. P. Hamburg. 2013. Recovery from disturbance requires resynchronization of ecosystem nutrient cycles. Ecological Applications 23:621–642.

Redman, C. L., J. M. Grove, and L. H. Kuby. 2004. Integrating social science into the Long-Term Ecological Research (LTER) network: Social dimension of ecological change and ecological dimensions of social change. Ecosystems 7:161–171.

Reichman, O. J. 1987. Konza Prairie: A tallgrass natural history. University Press of Kansas, Lawrence, Kansas, USA.

Reiners, W. A., K. L. Driese, T. J. Fahey, and K. G. Gerow. 2012. Effects of three years of regrowth inhibition on the resilience of a clear-cut northern hardwood forest. Ecosystems 15:1351–1362.

Rhoads, A. G., S. P. Hamburg, T. J. Fahey, T. G. Siccama, E. N. Hane, J. Battles, C. Cogbill, J. Randall, and G. Wilson. 2002. Effects of a large ice storm on the structure of a northern hardwood forest. Canadian Journal of Forest Research 32:1763–1775.

Robertson, G. P., et al. 2012. Long-term ecological research in a human-dominated world. BioScience 62:342–353.

Running, S. W., R. R. Nemani, F. A. Heinsch, M. Zhao, M. Reeves, and H. Hashimoto. 2004. A continuous satellite-derived measure of global terrestrial primary production. BioScience 54(6):547–560.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2014. The North American Breeding Bird Survey, results and analysis 1966–2012. Version 02.19.2014. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Sauer, J. R., and W. A. Link. 2011. Analysis of the North American Breeding Bird Survey using hierarchical models. Auk 128:87–98.

Schulze, E.-D., W. De Vries, M. Hauhs, K. Rosen, L. Rasmussen, C.-O. Tamm, and J. Nilsson. 1989. Critical loads for nitrogen deposition on forest ecosystems. Water, Air, and Soil Pollution 48(3–4):451–456.

Schwarz, P. A., T. J. Fahey, C. W. Martin, T. G. Siccama, and A. Bailey. 2001. Structure and composition of three northern hardwood–conifer forests with differing disturbance histories. Forest Ecology and Management 144(1):201–212.

Tierney, G. L., T. J. Fahey, P. M. Groffman, J. P. Hardy, R. D. Fitzhugh, and C. T. Driscoll. 2001. Soil freezing alters fine root dynamics in a northern hardwood forest. Biogeochemistry 56:175–190.

Vadeboncoeur, M. A., S. P. Hamburg, C. V. Cogbill, and W. Y. Sugimura. 2012. A comparison of presettlement and modern forest composition along an elevation gradient in central New Hampshire. Canadian Journal of Forest Research 42(1):190–202.

Warby, R. A. F., C. E. Johnson, and C. T. Driscoll. 2005. Chemical recovery of surface waters across the northeastern United States from reduced inputs of acidic deposition: 1984–2001. Environmental Science and Technology 39(17):6548–6554.

Winter, T. C., D. C. Buso, R. S. Parkhurst, D. O. Rosenberry, and M. L. Martinez. 1999. Hydrographs of lake stage, stream discharge, and hydraulic head in ground water for the Mirror Lake area, New Hampshire, 1979–1995. U.S. Geological Survey Open-File Report 99-239.

Woodbury, P. B., J. E. Smith, and L. S. Heath. 2007. Carbon sequestration in the U.S. forest sector from 1990 to 2010. Forest Ecology and Management 241:14–27.

Zhai, J., C. T. Driscoll, T. J. Sullivan, and B. J. Cosby. 2008. Regional application of the PnET-BGC model to assess historical acidification of Adirondack lakes. Water Resources Research 44:W01421.

Zimmer, M. A., S. W. Bailey, K. J. McGuire, and T. D. Bullen. 2013. Fine scale variations of surface water chemistry in an ephemeral to perennial drainage network. Hydrologic Processes 27:3438–3451.