Climate change and lakes: Estimating sensitivities of water and carbon budgets

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[1] As humanity develops strategies to manage and adapt to climate change, potential changes to carbon cycles are of increasing interest. The potential sensitivity of carbon sources and sinks in lakes may be of global importance, yet the direction and magnitude of possible changes are poorly understood across entire lake-rich regions. We used a spatially explicit simulation model of water and carbon cycling to explore the potential behavior of 6739 lakes and watersheds to changes in climate. Our study site was the Northern Highland Lake District of northern Wisconsin and the Upper Peninsula of Michigan. We developed two perturbation scenarios built from observed extreme high and low precipitation and evaporation values. Despite a spatially uniform change in precipitation across the region, individual lakes responded differently. Hydrologic responses were mostly predictable at both individual and regional scales, but the routing of carbon in lakes was both more sensitive and varied. We estimate that in today's climate, 7.3E+10 g of carbon are vented annually from lake surfaces in the District to the atmosphere. Compared to today's climate, total regional flux of carbon from lake surfaces was 31% higher in the wet scenario and 45% lower in the dry scenario. Some measures of carbon fluxes (such as net ecosystem production) appear to change uniformly and gradually at the regional scale, though aggregate change was driven primarily by considerable changes in relatively few large lakes. The simulations demonstrate that simple, spatially homogeneous perturbations in these complex connected watersheds can have both predictable and surprising effects.

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1. Introduction

[2] Freshwater systems, particularly in lake-rich regions in the upper Midwestern U.S., eastern Canada and Scandinavia, are important in regional carbon balances [*Cole et al.*, 2007]. Lakes are a remarkably varied resource, with sizes ranging over many orders of magnitude [*Downing et al.*, 2006] and often strong links to the surrounding landscape [*Cole*, 1999]. As receptacles of organic material from uplands, wetlands, and other uphill lake systems, lakes process terrestrial carbon which leads to net heterotrophy in a large range of lake sizes [*Alin and Johnson*, 2007; *Biddanda and Cotner*, 2002]. Recent analyses indicate that the global surface area of lakes is greater than earlier thought [*Downing et al.*, 2006]. The small lakes that had been overlooked are among those that process the most carbon per unit area [*Cole et al.*, 2007].

[3] Understanding the relationships between the carbon cycles of lakes and their surrounding landscapes is a long-standing challenge. In a pioneering study of landscape-scale drivers of lake carbon content, *Rasmussen et al.* [1989] called for "a study of humic matter budgets of a series of lakes (inflows and outflows), aimed at empirical modeling of both loading and clearance rates." After decades of dedicated effort, it remains difficult to understand the dynamic nature of the water and carbon cycles in suites of lakes, in part due to the complexity of their surface and subsurface connections. Despite these challenges, recent studies of lakes across landscapes have revealed temporal and spatial patterns of properties in sets of interconnected lakes [*Quinlan et al.*, 2003; *Soranno et al.*, 1999; *Webster et al.*, 2008]. For example, lake chains with water residence times close to or greater than 1 year showed synchronized

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responses to perturbations [*Soranno et al.*, 1999]. Eighty lakes in Sweden were highly synchronous for Ca, SO_4, and ANC [*Folster et al.*, 2005]. In chains of Arctic lakes, downhill connections help produce spatial and temporal connections among many limnological variables [*Kling et al.*, 2000]. The strength and persistence of connections between lakes and processes can vary, however: lake groups can behave synchronously for some factors but not for others, and physical and chemical variables are much more clearly synchronized than are biological variables [*George et al.*, 2000]. In groundwater-dominated systems, these connections are mostly hidden from view and difficult to observe. Yet understanding these connections is likely important to a comprehensive view of lake districts: lateral fluxes of matter and energy can influence lake and watershed behavior under perturbations [*Jenerette and Lal*, 2005; *Turner and Cardille*, 2007].

[4] With anticipated changes in global climate, the hydrology and carbon dynamics of lake districts are also likely to change. Long-term climate in the region has varied within the instrument record [*Greenland and Kittel*, 2002; *Greenland et al.*, 2003], and ecological effects of phenomena such as ENSO have been detected for lakes of the Northern Highlands [*Greenland*, 1999]. In the NHLD, short-term climate fluctuations affect lakes in many ways [*Magnuson et al.*, 1997], linking temperature, calcium, and chlorophyll dynamics in study lakes [*Baines et al.*, 2000]. Lake water and carbon budgets are also related to each other in groups of lakes, and connection strength can change in droughts [*Webster et al.*, 1996]. Seasonal fluctuations have been correlated in time among lakes for DOC but not other variables, in a localized subset of NHLD lakes [*Pace and Cole*, 2002]. Because their hydrology and carbon cycles are closely linked to landscapes, lakes may be important nodes of sensitivity to climate change; however, it remains to be seen whether lakes will serve as either a buffer or an enhancer of changes in the upstream landscape elements that provide them with water and carbon.

[5] In earlier work, we demonstrated [*Cardille et al.*, 2004] and implemented [*Cardille et al.*, 2007] the LUWI (Lake, Uplands, Wetlands Integrator) model, a simple spatially explicit simulation model of both carbon and water balance for groundwater-dominated regions. Testing the model against hydrological and lake carbon data sources in an interconnected 72-lake set of lakes of the Northern Highland Lake District (NHLD) of Northern Wisconsin and the Upper Peninsula of Michigan, we found that the model predicted well the carbon and water processing characteristics of this relatively small subset of lakes in the NHLD in today's climate. LUWI revealed important links between the hydrologic and carbon cycles, yet that initial study covered only a very small subset of the thousands of lakes of the NHLD and was limited to today's climate. To address the uncertainty of the effects of future climate changes in this complex region, we developed two scenarios built from the extremes of the observed instrument record. Under scenarios of a wetter future and a drier future, we explored the potential sensitivity of the region to long-term changes in precipitation, asking the following questions: Question 1: How might key hydrologic measures change in climate scenarios of wetter and drier futures? Question 2: Do these changed climates affect carbon fluxes and concentrations at the regional or per lake scale?

2. Site Description

[6] More than 6700 open water bodies fill the 8000 km^2 Northern Highland Lake District (Figure 1), covering about 20% of the surface area to form one of the most lake-rich regions of the world [*Magnuson et al.*, 2006]. Deciduous forests, coniferous forests, and wetlands surround the lakes of the NHLD [*WISCLAND*, 1992], contributing differing amounts of water through runoff and infiltration. Soils of the region are dominated by sandy loams [*STATSGO*, 1994], and groundwater flowing through them can influence both abiotic and biotic conditions in downstream lakes [*Krabbenhoft and Webster*, 1995]. This region of slight topographic variation sustains a wide array of lake sizes and shapes, with many groundwater lakes having water budgets with neither surface inlets nor outlets. In a typical lake of the NHLD, carbon input is provided through primary productivity, litterfall on the lake's surface, and several possible water-borne sources: precipitation, wetland flow, groundwater, and streams (Figure 2). Connections among the watershed units can have important downstream influences: as driven by exceedingly slight relief changes among nearby groundwater-dominated lakes, the position of a lake in the landscape can have dramatic effects on its hydrology and chemistry [*Kratz et al.*, 1997]. The lake order and connections among lakes influence a large set of morphometric and ecological variables [*Martin and Soranno*, 2006; *Riera et al.*, 2000]. Each of the thousands of lakes processes carbon from somewhere upstream, receiving inputs that change by season and as a factor of both recent weather and long-term climate, serving as hot spots for storage and respiration of organic carbon. Despite their potential importance to local and regional carbon balances, the sheer number of lakes means that only a small subset of them has been scientifically studied.

3. Methods

3.1. Model

[7] The model structure and a validation using a complex study area with 72 lakes was described elsewhere [*Cardille et al.*, 2007]. Here we present only a brief description (Figure 2). The model computes water and carbon pools for a spatial mosaic of 6739 watersheds and their lakes. The fundamental spatial unit is a watershed and its lake. A watershed represents a spatially explicit estimate of the immediate groundwater capture zone for a given lake. Each unit is potentially connected hydrologically to upstream and downstream units as well as to groundwater and the atmosphere. Algorithms for the estimate of watershed boundaries, the network of hydrological connections, water flow, and carbon flow were identical to *Cardille et al.* [2007]. For each scenario (see below) the model was run to steady state for 300 years. Comparisons of scenarios are based on steady state values.

3.2. Scenarios and Driving Data

[8] To explore the sensitivity of lake hydrology and carbon cycling in NHLD, we contrasted modeled results

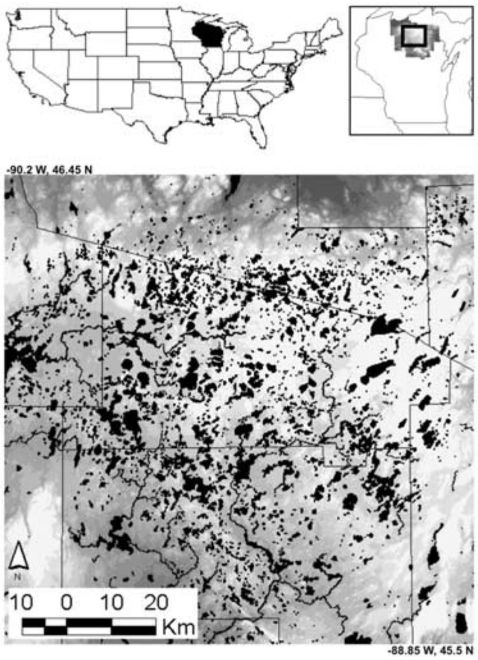

Figure 1. Location of Northern Highland Lake District in Wisconsin and Michigan, USA.

driven by today's climate [*Cardille et al.*, 2007] with two scenarios of precipitation and evaporation change. The scenarios perturbed the terrestrial/aquatic system with sustained, spatially uniform precipitation increase (the "wet" scenario) or decrease (the "dry" scenario) and were designed to isolate the first-order effects of long-term change of hydrologic drivers in connected NHLD lakes. The wet and dry scenarios were derived from observations from the second half of the twentieth century. For rainfall in the wet scenario, we averaged the monthly precipitation from the 5 years with the highest total precipitation between 1951 and 2000 (1951, 1968, 1978, 1985, 1991) as measured at the Minocqua Dam weather station (45.87°N, 89.71°W) near the center of the NHLD. For rainfall in the dry scenario, we averaged the monthly precipitation from the 5 driest years (1963, 1970, 1976, 1989, 1998) between 1951 and 2000 as measured at the same station [*Kratz*, 2000]. For evaporation from the lake surface, we used the estimated evaporation from the 2 wettest (1991, 1996) and 2 driest (1989, 1998) years in the 1989–1998 evaporation record [*Lenters et al.*, 2005] from Sparkling Lake (46.01°N, 89.70°W), a lake near the center of the region studied as part of the Northern Temperate Lakes Long Term Ecological Research program [*Magnuson et al.*, 2006]. Compared to today's climate, the wet scenario had 32% more annual precipitation and 1% more evaporation from lake surfaces. The dry scenario had 70% less annual precipitation and 14% more evaporation than today's climate average.

[9] To estimate the terrestrial water budget, each scenario was used as driving data for the IBIS terrestrial ecosystem model [*Foley et al.*, 1996; *Kucharik et al.*, 2000] according to methods outlined by *Vano et al.* [2006], and run to steady state. Uplands were simulated as Mixed Forest, the most representative land cover in the region; the soil was assumed to be Sandy Loam, the most representative soil type in the region [*Vano et al.*, 2008]. Evaporation from wetlands was simulated as if from open water, with carbon added to water flowing through them with concentrations estimated from field data [*Cardille et al.*, 2007]. These simplifications were made to better isolate the effects of the substantial hydrologic input changes, and were consistent with the

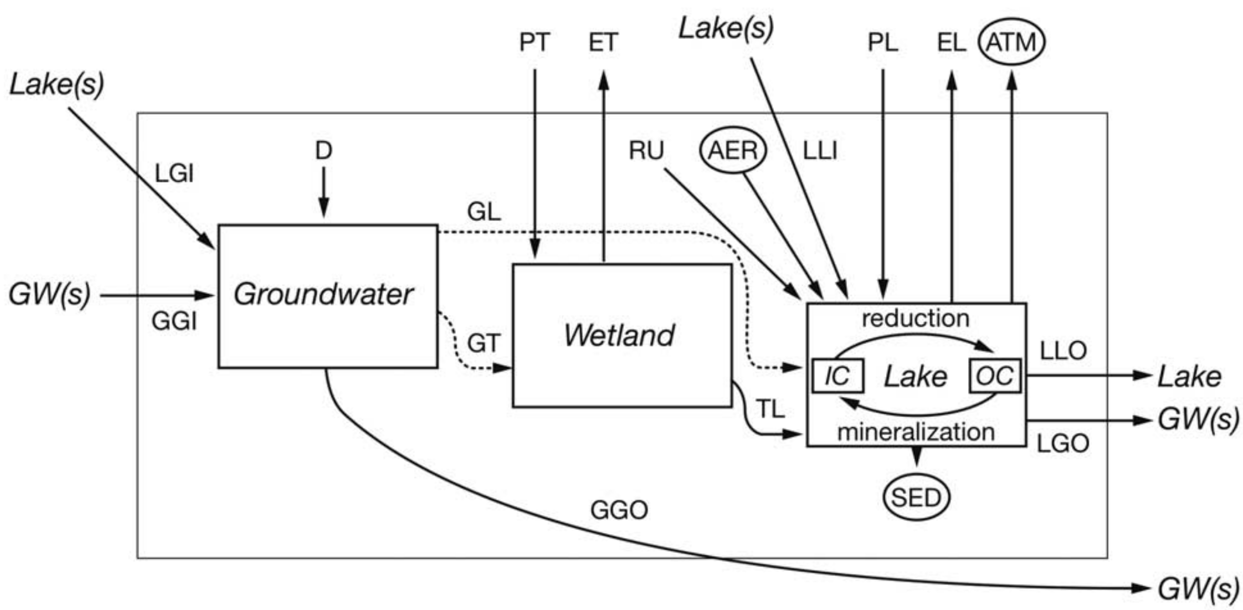

Figure 2. Conceptual graph of hydrologic and carbon fluxes and stocks in the LUWI (Lake, Uplands, Wetlands Inte model. Described in full detail by *Cardille et al.* [2007].

result of other analyses of first-order effects on lake hydrology [*Breuer et al.*, 2006].

3.3. Data Analysis

[10] To address our motivating questions, we analyzed hydrologic and carbon-cycle indicators for each lake under each scenario. Hydrologic measures were (1) lake water residence time; (2) watershed water residence time and (3) groundwater input, as a proportion of the hydrologic input budget. Four carbon-cycle measures were analyzed for each lake: (4) annual atmospheric flux of carbon; (5) net ecosystem production (NEP); (6) inorganic carbon (IC) amount and concentration; and (7) organic carbon (OC) amount and concentration.

3.4. Lake Subsets

[11] We assessed potential changes in the 6739 lakes to climate changes using three analysis sets. These were: (1) the aggregate value across all lakes; (2) values traced in a randomly selected 1% subset (n = 67). This set was used to view the responses of individual lakes; and (3) values traced in lakes along a size gradient. For this, we used the lakes of the 10th, 25th, 50th, 75th, and 90th size percentiles of lake surface area.

4. Results

4.1. Effects on the Water Cycle

4.1.1. Water Residence Times

[12] Lake water residence time and watershed water residence time responded predictably to the scenarios at both the regional scale (Figures 3a and 3b, left) and the lake scale (Figures 3a and 3b, middle). Neither lake water residence time nor watershed residence time in today's climate, nor the effect of the changes in precipitation, appear to be related consistently to lake area (Figure 3a, right and Figure 3b, right). At the regional scale, increasing amounts of water in the system had consistent inverse effects on these two comprehensive measures of water residence times. In wetter scenarios the water flux through the lake and watershed changed more than the water volume of the lake or watershed, thus lowering the water residence times relative to drier scenarios. The consistency of changes in water residence times suggests that the hydrologic changes of the scenarios provided a mostly predictable amount of total water to each lake and watershed. The partitioning of water delivery between ground and surface sources, however, varied substantially from lake to lake, as will be seen in the next section.

4.1.2. Groundwater Proportion of Lake Water Budget

[13] Groundwater input to lakes changed in frequently nonintuitive ways that depended on spatial scale. The aggregated regional response is easily described: across the entire region (Figure 3c, boxplots on left), the proportion of the lake water input budget supplied by groundwater decreased as rainfall increased. However, this consistent regional-scale behavior masked a large amount of variability at the lake scale. In each of a selection of lakes of different sizes (Figure 3c, right), the groundwater proportion increased slightly with increasing precipitation. In a larger random set, the reaction of individual lakes (Figure 3c, middle) sometimes differed considerably among scenarios, particularly in the difference between today's scenario and the dry scenario. For some lakes in which groundwater provides about 50% of today's input budget, groundwater became much more important in the dry scenario, due to the decreased precipitation on the lake surface and drying of some streams that are active today. This behavior was not uniform, however: the dry scenario did not affect some of the lakes relying equally on groundwater in today's climate (Figure 3c, middle).

4.1.3. Water Budget Changes

[14] Lakes may receive water from three sources: precipitation on the lake surface, as runoff or groundwater that fell on land in the lake's immediate groundwater watershed), and from upstream watersheds. In the 67 randomly selected lakes, the proportions of these three sources of water were relatively stable and did not change greatly for most lakes in the scenarios (Figures 4 and 7). Changes to the proportions comprising the budgets of water sources to individual lakes were mostly smaller than a 10% increase in one component at the expense of the other two. In particular, those lakes with little upstream hydrologic connectivity today (Figure 4, left edge) were largely insensitive to change in the proportional sources of their water budgets. More generally, the reactions of lakes connected to upstream in today's climate (in the middle of Figure 4) were more complex and varied, and thus less readily predictable than those with little upstream hydrologic connectivity (Figure 4, left edge). With increasing precipitation, some lakes became more dominated by upstream inputs while many others reacted like smaller lakes, becoming increasingly reliant in wetter climates on in-watershed hydrologic sources. This response may have been related to the type of upstream input, with those receiving upstream groundwater inputs reacting differently than those receiving upstream surface inputs.

4.2. Effects on the Carbon Cycle

4.2.1. Carbon Fluxes

[15] Under current climate, the simulations indicate 0.073Tg of carbon vented to the atmosphere annually from the 1650 km^2 of lake surface of the NHLD (Table 1). This was equivalent to 44 g C m^{-2} a^{-1} if evenly spread across lake surfaces. Flux to the atmosphere differed substantially in small and large lakes, however: most lakes were small and vented more carbon to the atmosphere per unit area than the large lakes that dominate area estimates. As a result, in today's scenario the median per-lake carbon flux value was 116 g C m^{-2} a^{-1}. Annual atmospheric flux increased with increased precipitation, both for the regional total (Table 1) as well as in most individual lakes (Figure 5a, middle). Atmospheric flux was related to lake size, with the smallest lakes having the highest atmospheric flux per unit lake area in all scenarios (Figure 5a, right). Compared to today's climate, total regional flux of C from the lake surfaces was 31% higher in the wet scenario and 45% lower in the dry scenario (Table 1). In many lakes, this change in carbon processing was due to changes in the amount of carbon transported to them from nearby wetlands. Because of the more extreme sensitivity in higher-flux lakes, there was considerably higher variation in atmospheric flux in progressively wetter scenarios (Figure 5a, left).

[16] Nearly all lakes had negative NEP [*Lovett et al.*, 2006] in all scenarios (Figure 5b, left). The amount of NEP

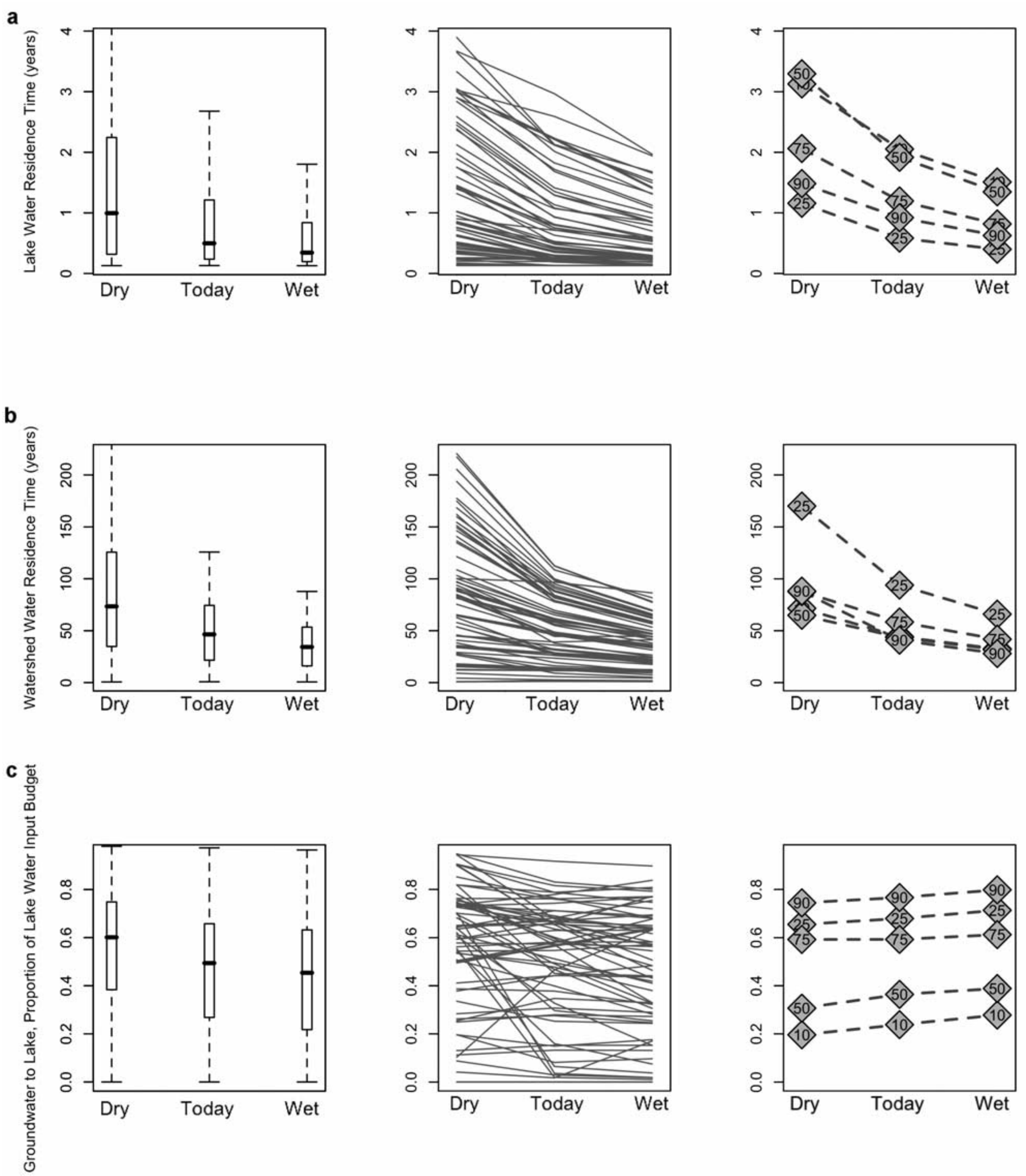

Figure 3. Sensitivity of key hydrologic measures to climate scenarios in modeled NHLD lakes. In each plot, the *y* axis represents the value in each of the three scenarios described in the text. (left) Box plots show the distribution of each hydrologic measure in all lakes (n = 6739) for each scenario. (middle) Elbow diagrams show the values from dry to wet conditions for a randomly selected 1% subset (n = 67) of modeled lakes. Lines connect the values in each sample lake. Lines that cross indicate sets of lakes whose reactions to a perturbation differ substantially from each other. (right) Five dashed lines explore the variation of these variables along a gradient of lake surface area. The lakes of the nth percentile (10, 25, 50, 75, 90) are identified in each diamond. (a) Lake water residence time (years), (b) watershed water residence time (years), and (c) groundwater to lake, proportion of lake water input budget.

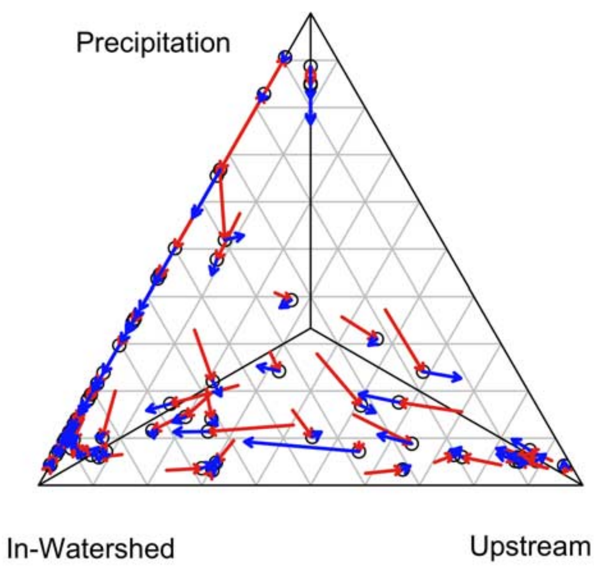

Figure 4. Effects of wet and dry scenarios on major components of the hydrologic cycle in the 67 randomly chosen lakes of the Northern Highland Lake District. For each lake in a given scenario, the proportional balance among possible sources of water is shown. To read the graphic: (1) open circles between arrows represent the balance among hydrologic input sources for each lake in today's climate, as in the work of *Cardille et al.* [2007]; (2) lakes are positioned according to the relative balance among their input hydrologic budget's three major components: precipitation (on the lake surface), in-watershed (water falling on land in the lake's immediate groundwater watershed), and upstream; (3) gray lines represent 10% intervals along the three axes, which bisect each side of the triangle; (4) thus a lake at the middle of Figure 4 would represent an input budget composed of about one-third precipitation, one-third from water first falling on land within the immediate watershed; and one-third from upstream watersheds; (5) arrows indicate changes in these sources under each scenario and point in the direction of the effect of increased water in the system: red arrows begin at the dry scenario and point toward today's nominal scenario (the open circles), and blue solid arrows begin with today's scenario and point toward the input balance in the wet scenario. Note that the changes in the lake budgets were relative, not absolute, since each scenario provided different amounts of water to the systems. Although flux volumes changed in each of the scenarios, water budget input proportions were mostly insensitive. Further assessment of Figure 4 is given in the text.

per unit lake area was related to lake area itself, with larger lakes being more nearly in balance and smaller lakes having more negative NEP per m^2 (Figure 5b, right), consistent with field observations in many temperate lakes [*Cole et al.*, 2000; *Duarte and Prairie*, 2005]. In today's climate, the simulation indicated an annual regional NEP of -0.029Tg (Table 1). Long-term carbon accumulation in the lakes through sedimentation (0.0074Tg/a) was an order of magnitude smaller than what is vented to the atmosphere in today's climate (Table 1). The precipitation changes affected sedimentation less dramatically than atmospheric flux, particularly in the wet scenario.

4.2.2. Carbon Stocks

[17] Dissolved inorganic carbon concentration increased with precipitation in most lakes (Figure 5c, middle), in part because of increased delivery of IC-rich groundwater both from within the immediate watershed and from upstream watersheds. At the regional scale, the amount of organic carbon dissolved in NHLD lake water increased along the precipitation gradient (Table 1). Although the total stock increased with precipitation, the median organic carbon concentration declined, in part due to the increased volume of individual lakes along the gradient of increasing precipitation (Figure 5d, left). Yet the median concentration declined not because individual lakes declined consistently (Figure 5d, middle), but because the concentration in a small proportion of lakes declined dramatically from dry to wet conditions. Most of the downward trend in median OC concentration along the precipitation gradient appears to have been driven by lakes with high OC in today's climate (i.e., above 10mg/l) (Figure 5d, middle).

[18] In today's climate, we estimate that lakes of the Northern Highland Lake District hold nearly twice as much dissolved inorganic carbon as dissolved organic carbon (Table 1). Yet the median inorganic carbon concentration (3.35 mg/l) is only about one-fifth of the median organic carbon concentration (15.71 mg/l). This is due to the uneven distribution of IC and OC across lakes: the typical lake in the region is small and dark, with OC much higher than IC; in the region, the largest part of the stock of IC is in a few large low-lying lakes [*Hanson et al.*, 2007]. These lakes dominate the total volume of lake water and form a large part of the regional IC stock without strongly influencing the median IC concentration value. Along the gradient of increasing precipitation, many lakes became more like today's large, low-lying lakes as IC stock grew more quickly than lake area. Organic carbon stock, meanwhile, grew more slowly along the increasing precipitation gradient (Table 1), while roughly keeping pace with lake area in most lakes (Figure 5d).

4.2.3. Carbon Budget Changes

[19] Climate scenarios altered carbon budgets (Figure 6) more than water budgets (Figure 4). For a randomly selected subset of lakes, we observed substantial changes in the balance among the three potential fates of carbon in a lake: flux to the atmosphere, storage in sedimentation, and routing to one or more downstream lakes (Figures 6 and 7).

[20] For many of the lakes, increased precipitation resulted in a lower proportion of sedimentation in lake output budgets, despite the overall increase in sedimentation amount (Table 1). As more water was added to the system, lakes with little downstream flow of carbon became more tightly connected to downstream watersheds. In particular, highly sedimenting lakes with little flux to the atmosphere and no downstream connections (Figure 6, bottom left) increased both the lake carbon budget proportion sent downstream and the proportion vented to the atmosphere. This increase was at the expense of sedimentation propor-

Table 1. Regional Fluxes and Stocks Across Scenarios in All Lakes of the Northern Highland Lake District[a]

Scale	Dry	Today	Wet	Units	Description	Notes
			Carbon Fluxes			
All lakes in region	4.0E + 10	7.3E + 10	9.6E + 10	g/a	atmospheric flux	1
	−2.3E + 10	−2.9E + 10	−3.2E + 10	g/a	NEP	1
	5.7E + 09	7.4E + 09	9.4E + 09	g/a	sediment	1
Individual lake	99.16	116.45	142.37	$g/m^2/a$	flux to atmosphere per m^2 lake	2
	−82.17	−78.85	−74.25	$g/m^2/a$	NEP per m^2 lake	2
	18.20	12.18	11.09	$g/m^2/a$	sedimentation per m^2 lake	2
			Carbon Stocks			
All lakes in region	2.4E + 10	4.7E + 10	7.6E + 10	g	inorganic carbon	3
	1.7E + 10	2.4E + 10	3.3E + 10	g	organic carbon	3
Individual lake	2.84	3.35	3.94	g/m^3	IC concentration	4
	17.66	15.71	14.71	g/m^3	OC concentration	4

[a]Notes: n = 6739. 1, Annual total among all lakes in landscape; 2, median among annual values among lakes; 3, average total monthly stock in all lakes; 4, median monthly concentration among all lakes.

tion, which decreased in nearly all lakes under increasing precipitation.

5. Discussion

[21] In the Northern Highland Lake District, lakes have a complex relationship to climate and connectivity. At the regional scale, climate scenarios had predictable, consistent effects on both water and carbon stocks and fluxes (Figures 3 and 5 and Table 1). For example, the distribution of water residence times (Figure 3b, left) tightened with increasing precipitation. Although the water residence times of lakes and watersheds decreased consistently with increasing precipitation, the balance of hydrologic inputs to lakes remained quite stable. This stability was seen in all parts of the continuum of lake inputs (Figures 4 and 7). In contrast to the modest sensitivity of the hydrologic cycle, the strength of this lake district as a C source is extremely sensitive to long-term precipitation changes. In the direction of more precipitation, the additional inorganic and organic carbon delivered to the lakes through wetlands was largely vented to the atmosphere. In wetter scenarios, sedimentation in lakes increased more modestly and was of an order of magnitude smaller than the flux of C to the atmosphere from the lake surface. As a result, lakes would be even more of a source of C to the atmosphere under wetter conditions than they are today [*Hanson et al.*, 2003, 2004].

[22] For many key variables, however, regional change across all lakes may not be mirrored in similar changes in individual lakes. For example, the median proportion of groundwater in lake hydrologic budgets (Figure 3c, left) decreased by about 10% with increasing precipitation. However, the decrease was not due to a uniform decrease in individual lakes (Figure 3c, middle), nor was there a predictable decline in groundwater proportion in lakes of different sizes (Figure 3c, right). Rather, the regional trend was driven by a small number of lakes whose reliance on groundwater declined substantially in wetter scenarios. This complex sensitivity was also seen in estimates of NEP (Figure 5b) and organic carbon concentration (Figure 5d). Despite monotonic effects of the scenarios at the regional scale, "scaling up" from individual lake studies to regional estimates may not be simple.

[23] Lake responses reveal that they are not independent elements reacting to the same perturbation. Because the balance between aboveground and belowground flux is determined dynamically during a given simulation, the scenarios show the responses of sometimes-coupled and sometimes-uncoupled lakes, with many of the elements that influence carbon and water budgets having several highly nonlinear characteristics. Because of these nonlinear lake-landscape connections, scenarios sometimes produced non-intuitive changes in lake water and carbon budgets as the balance among lake-landscape connections changed. For example, for nearly all lakes in the 1% subset (Figure 4), the importance of lake surface precipitation declined as precipitation itself increased. Yet any of several factors could drive this change: for some lakes, it was driven by increasingly important surface connections with upstream watersheds; for the majority, it was due to an increased reliance on groundwater derived from precipitation falling within the lake's immediate watershed. More generally, the variety of behavior among different lakes appeared to be related to a wide array of factors, including lake and watershed size and shape, upstream and downstream connections and the composition of land cover in the lake's watershed. These results suggest that the susceptibility of interconnected lakes to climate change effects is not uniform, and is more evidence that lake districts should be studied as a whole.

[24] The annual modeled lake-atmosphere C exchange in this study (median lake evasion 116 g C m^{-2} a^{-1}, mean for all lake area 44 g C m^{-2} a^{-1}) is of comparable magnitude to exchange between atmosphere and upland forests of the region. The average net uptake of CO_2 in forests of the North Central U.S. has been estimated at 130–140 g C m^{-2} a^{-1} [*Turner et al.*, 1995]. Individual eddy-covariance CO_2 flux measurements in upland forests in the NHLD region have given annual NEE values ranging from about 100 g C m^{-2} a^{-1} (old growth hardwood forest) to about 500 g C m^{-2} a^{-1} (mature hardwood forest) of flux from the atmosphere into the forest [*Desai et al.*, 2005, 2008]. Because the uptake of carbon into forests is in the opposite direction from the carbon leaving lakes toward the atmosphere, these results suggest that venting from many of the small lakes of the region offsets a substantial amount of the carbon taken up in nearby forests of similar surface area. This

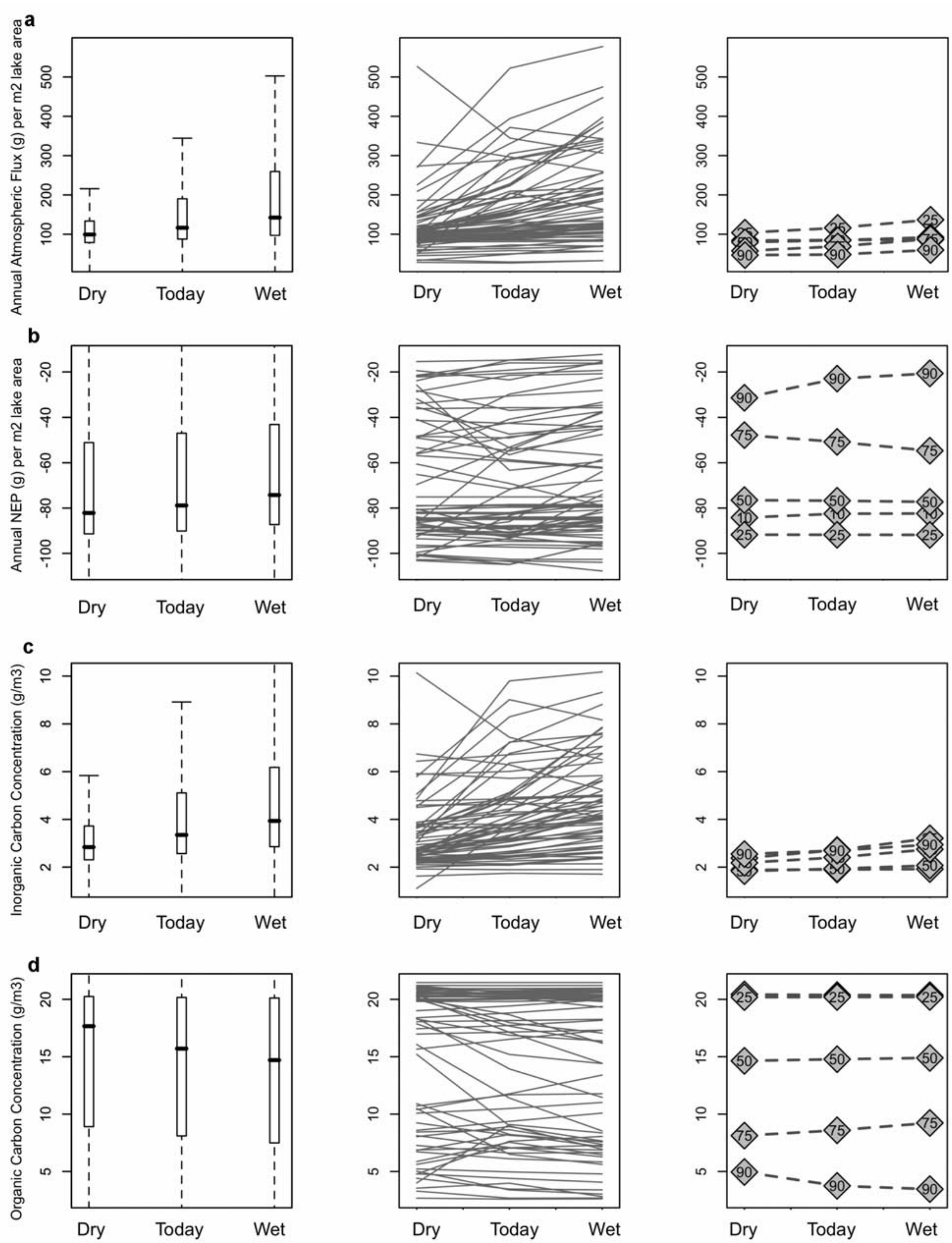

Figure 5. Sensitivity of key carbon stocks and fluxes to climate scenarios. (a) Annual atmospheric flux (g) per m^2 lake area. (left) Systematic changes in the regional response sometimes masked (middle and right) less predictable changes in individual lakes: this was most true for (b) net ecosystem production and (c, d) inorganic and organic carbon concentration.

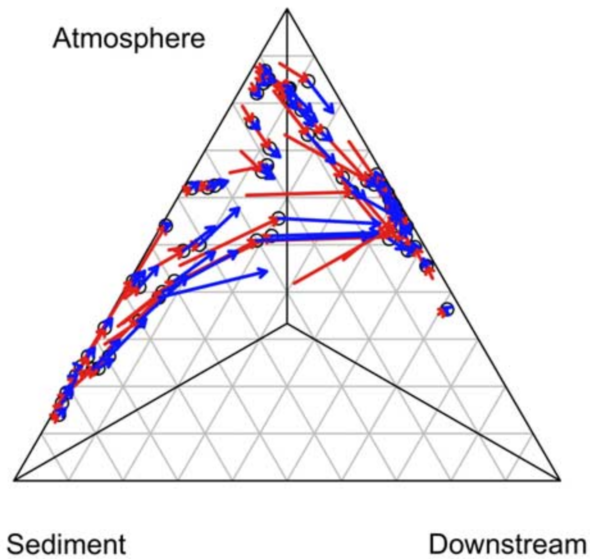

Figure 6. Effects of wet and dry scenarios on measures of the carbon cycle in the 67 randomly chosen lakes of the Northern Highland Lake District. The three potential destinations of lake carbon are shown; a dot at the center of the triangle would indicate a lake with a carbon output budget evenly divided among atmospheric flux, sedimentation, and downstream transport.

underscores the potential importance of lakes to the carbon budgets of lake-rich regions.

[25] Because our primary goal was an estimation of water and carbon budgets across a large region, these simulations have a number of simplifying assumptions. These assumptions must be considered in interpreting these results, prioritizing future work, and influencing field campaigns. First, hydrologic and carbon flow paths have been systematically studied in the Northern Highland Lake District in detail in only a handful of lakes. As a result, our models of groundwater flow and chemistry among the thousands of lakes and watersheds were greatly simplified. Second, surface flow of carbon was substantially simpler than reality, by assuming that inorganic and organic carbon flowing from wetlands to lakes scaled linearly with runoff. As a result, these estimates of lake-specific and regional behavior are highly sensitive to the balance between surface runoff and infiltration, which may be affected in future climates as precipitation amount and timing change. Third, to keep the interpretation of results as simple as practicable, important potential feedbacks between climate and vegetation were not modeled.

[26] Feedbacks and simplification may have played a role in at least one important case in which the model departed from field observations. The model estimated that at the regional scale, the median organic carbon concentration would increase slightly in the dry scenario (Figure 5, left). More precisely, there were a variety of responses to the dry scenario in the 67 randomly selected lakes (Figure 5, middle and right). In that scenario, the OC concentration decreased or increased slightly from today's values in many lakes, while in a few lakes it increased greatly. Yet in a study of 20 NHLD lakes of a range of sizes, *Pace and Cole* [2002] found that in a single drought year, organic carbon concentration dropped in most lakes. Though it is possible that Pace and Cole observed transient effects that would diminish in a sustained drought, we believe the discrepancy is primarily due instead to limitations of the model. In particular, because there were no modeled feedbacks between climate and vegetation, the amount of carbon deposited from land for a given length of lake perimeter was unchanged in the scenarios. In lakes that shrank in the dry scenario, perimeter shrank more slowly than area, which in turn shrank more slowly than volume [*Cardille et al.*, 2004]. As a result, the amount of carbon contributed to lakes by that component decreased more slowly than volume, inching the concentration upward in many lakes. Although the timescales of the observation and model differ (a single year versus steady state), this discrepancy between model results and the observations suggests that it may be fruitful to refine this part of the model in future studies. The simplifying assumptions and long modeling timescales underline the model's intended purpose: as a way to sharpen questions about the interacting parts of this complex system, rather than as a predictive tool.

[27] This study suggests several avenues of future research. For lakes with sensitive carbon budgets, changes in carbon concentrations could affect limnological characteristics and how lakes respond to perturbations, such as climate change [*Williamson et al.*, 1999]. Lakes identified as particularly sensitive might be prioritized for field studies of color, UV penetration [*Morris et al.*, 1995] or temperature changes [*Snucins and Gunn*, 2000] during especially wet or dry years. Changes in the physical-chemical environment resulting from changing carbon loads may have important implications for, e.g., lake primary productivity and respiration [*Staehr and Sand-Jensen*, 2007], zooplankton community composition [*Leech and Williamson*, 2000] and processing of contaminants, such as mercury [*Watras et al.*, 1998]. These findings also highlight the importance for further research on the terrestrial-hydrologic connections governing C flux. This is especially important in the NHLD, where the region's carbon budget is heavily influenced by difficult-to-observe hydrologic connections among lakes, wetlands, and uplands [*Cardille et al.*, 2007]. Above ground, these simulations could be improved by better understanding the potential effects of changed precipitation on terrestrial C sequestration, which drives part of the available carbon pool that can be exported to lakes.

[28] Taken as a whole, the complex relationship among carbon and water budgets in the NHLD implies that lakes respond heterogeneously to climate change. Moreover, responses depend on landscape connections as well as individual characteristics of a particular lake. Water and carbon budgets show different sensitivities to climate change. The varied directions and magnitudes of budget changes (Figures 4 and 6) and the variability at the per lake scale (Figures 3 and 5) suggest that it may be useful to classify lakes not only according to the water and carbon cycles in today's climate, but also by incorporating additional characteristics that address potential responses to climate change. Furthermore, the susceptibility of a given

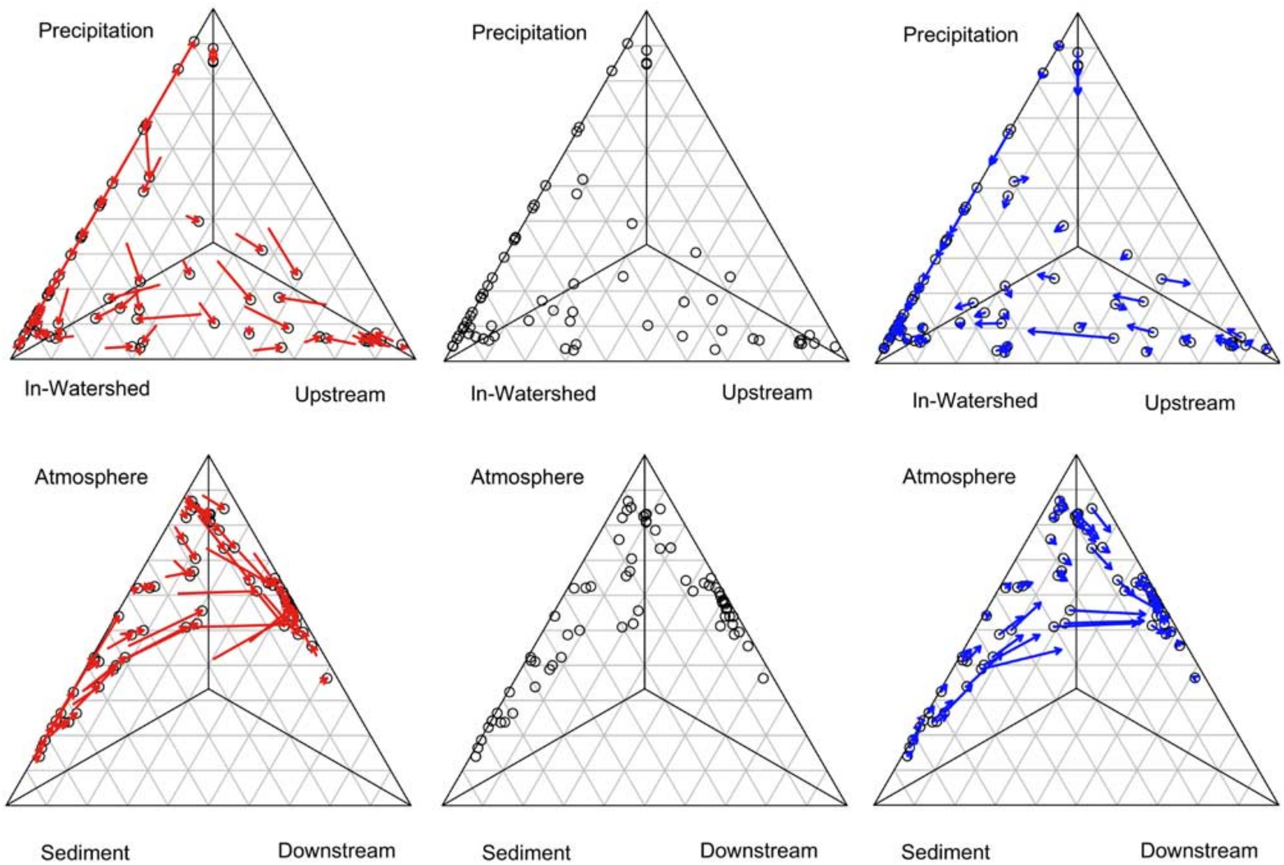

Figure 7. Scenario-by-scenario effects on major components of the hydrologic and carbon cycles in the 67 randomly chosen lakes of the NHLD. Red arrows begin at the dry scenario and point toward today's nominal scenario (the open circles). Blue solid arrows begin with today's scenario and point toward the balance in the wet scenario. (top) Effects of scenarios on the hydrologic cycle. Superposing these three plots on each other yields the image in Figure 4. (bottom) Effects of the scenarios on the carbon cycle. Superposing these three plots on each other yields the image in Figure 6.

lake to change is almost certainly related to that of its upstream neighbors, and is difficult to understand in isolation. Simple perturbations can have complex consequences in these highly interconnected systems.

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