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A synoptic survey of ecosystem services from headwater catchments in the United States

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ABSTRACT

Ecosystem production functions for water supply, climate regulation, and water purification were estimated for 568 headwater streams and their catchments. Results are reported for nine USA ecoregions. Headwater streams represented 74–80% of total catchment stream length. Water supply per unit catchment area was highest in the Northern Appalachian Mountains ecoregion and lowest in the Northern Plains. C, N, and P sequestered in trees were highest in Northern and Southern Appalachian and Western Mountain catchments, but C, N, and P sequestered in soils were highest in the Upper Midwest ecoregion. Catchment denitrification was highest in the Western Mountains. In-stream denitrification was highest in the Temperate Plains. Ecological production functions paired with published economic values for theses services revealed the importance of mountain catchments for water supply, climate regulation, and water purification per unit catchment area. The larger catchment sizes of the plains ecoregions resulted in their higher economic value compared to the other ecoregions. The combined potential economic value across headwater catchments was INT \$14,000 ha^{-1} yr^{-1}, or INT \$30 million yr^{-1} per catchment. The economic importance of headwater catchments is even greater considering that our study catchments statistically represent more than 2 million headwater catchments in the continental United States.

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1. Introduction

Headwater streams and their catchments have received much attention in recent years, with issues ranging from their contribution to, and connection with, larger downstream ecosystems (Nadeau and Rains, 2007), to the loss of headwater streams to burial and routing through underground pipes (Roy et al., 2009; Kaushal and Belt, 2012). An emerging concern is the underestimation of the extent of headwater stream channels, even when mapped at scales finer than 1:100,000 scale (Roy et al., 2009). Headwater streams are defined as the terminal branchings of a stream drainage network, the point where water flowing in a catchment first coalesces into defined stream channels (Gomi et al., 2002). Nadeau and Rains (2007) extend the definition of headwater streams to first- and second-order streams (Strahler, 1957) on 1:100,000 scale maps, even though researchers have demonstrated the underestimation of headwater streams at this larger (coarser) map scale (Meyer and Wallace, 2001; Roy et al., 2009). Because of stream network scaling properties (Dodds and Rothman, 2004), the proportion of total basin-wide headwater stream length is approximately 70% of total stream length on both 1:100,000 and 1:24,000 scale maps (Leopold et al., 1964; Nadeau and Rains, 2007; Lassaletta et al., 2010).

In addition to their dominance in terms of numbers and cumulative length, headwater streams also exert controls on stream runoff and downstream fluxes of dissolved and particulate matter organic matter and nutrients (Alexander et al., 2007; Dodds and Oakes, 2008; Lassaletta et al., 2010). Using spatial regression models, Alexander et al. (2007) estimated that headwater streams deliver 60% of the runoff and 45% of the nitrogen load in downstream reaches in northeastern US streams and rivers. They attribute this result to the high density of headwater streams and the frequency of their connections to higher-order stream channels. In a review of the influence of headwater streams on downstream reaches, MacDonald and Coe (2007) reported an even greater proportion of runoff and nutrient loading is directly attributable to headwater streams. Similarly, Dodds and Oakes (2008) reported that nutrient chemistry in fourth-order Kansas streams was best predicted by riparian land cover adjacent to

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upstream first-order streams. These results are similar to those reported for European streams (Lassaletta et al., 2010).

This downstream influence by headwater streams indicates a hydrologic connectivity that links headwater catchments, their soil, and groundwater resources, with larger-order streams (Gomi et al., 2002; Wipfli et al., 2007; Freeman et al., 2007). Headwater streams are not specifically protected by the Clean Water Act (CWA), but until recently they were included as necessary for the maintenance of healthy, productive, and navigable streams and rivers. Their protection under the CWA has recently been limited by the Supreme Court (Rapanos v. United States 547 US 715, 2006) to only those headwater streams that are directly connected to, or have demonstrated a significant influence on, navigable waters (Nadeau and Rains, 2007). Even with CWA protections, headwater streams have been lost from the landscape, primarily by human-driven changes in catchment land use including agriculture, urbanization, and mining (Meyer and Wallace, 2001; Roy et al., 2009; Kaushal and Belt, 2012). An analysis of 106 catchments from around the world revealed that nearly one-third of them experienced extensive conversions ($>$50% of the catchment) of forests to agriculture or urban development (Postel and Thompson, 2005).

Ecosystem services are the result of direct and indirect contributions of ecosystems to human well-being (Burkhard et al., 2012). The Millennium Ecosystem Assessment (2003) classified ecosystem services into four categories: provisioning services which provide goods for direct human use (food, freshwater, timber); regulating services to maintain biophysical properties for living beings (climate stability, water purification); cultural services including aesthetic and spiritual benefits; and supporting services which are necessary for the maintenance of functioning ecosystems (nutrient cycling, primary production, soil formation). Catchments represent a discrete unit for accounting for the delivery of ecosystem goods and services to society (Postel and Thompson, 2005). Catchment ecosystem services are many, including biodiversity, climate regulation, recreation, timber and crop production, and water supply and purification. Timber markets are globally well established, carbon exchange markets are developing (Intercontinental Exchange, 2012), and water supply is easily valued as a commodity (Krieger, 2001; Postel and Thompson, 2005; Nunez et al., 2006; de Groot et al., 2012; Townsend et al., 2012); but the value of water purification via nitrogen and phosphorus sequestration in biomass and soils, and through denitrification, are only beginning to receive economic consideration (Dodds et al., 2009; Turpie et al., 2010, Compton et al., 2011). Some of these catchment ecosystem services co-vary while others compete, and understanding the interplay and relationships among ecosystem services under varied management of these resources is critical to the sustainable delivery of catchment ecosystem goods and services (Bennett et al., 2009; de Groot et al., 2010; Deal et al., 2012; Townsend et al., 2012).

Our objectives in this paper are to highlight the importance of headwater catchments by focusing on the quantity and value of a few ecosystem services derived from them, and to extrapolate that importance from regional to national scales within the continental United States. We focus on headwaters because that is a particular category of streams that is of interest in the US regulatory community. As an under-protected resource, we wanted to highlight their particular value. We combine data collected from headwater streams as a part of the US Environmental Protection Agency's (USEPA) National Rivers and Streams Assessment (NRSA) with catchment attributes related to water supply, the sequestration of C, N, and P, and the removal of N via denitrification. We use these data to develop ecological production functions related to the delivery of ecosystem services from headwater catchments, and combine these services with published valuations to estimate potential cumulative benefits derived from headwater catchments in the United States.

2. Materials and methods

2.1. Study sites

Catchments included in this study were those drained by the 568 first- and second-order (Strahler, 1957) streams that were sampled during the NRSA (Fig. 1). The sampling design was spatially-balanced and employed an unequal probability survey with the unequal selection based on stream order. The design selected a single point along the center line of each stream as depicted by the National Hydrography Dataset (NHDPlus, Version 1; http://horizon-systems.com/nhdplus; based on 1:100,000 scale maps). All sample sites were selected using NHDPlus as the sample frame. Each site included in the survey represented a known stream or river length based on the population of streams included in the survey design, the probability of that site being selected for sampling, and the number of sites actually sampled. These stream and river lengths were summed to estimate the cumulative extent of streams sampled (Olsen and Peck, 2008).

The NRSA design allows the assessment of ecological conditions of streams at three hierarchical spatial scales: national, regional, and ecoregional (Olsen and Peck, 2008). Here we report results nationally and for nine ecoregions: Northern Appalachian Mountains, Southern Appalachian Mountains, Coastal Plains, Northern Plains, Southern Plains, Temperate Plains, Upper Midwest, Western Mountains, and Xeric ecoregions (Fig. 1).

2.2. Catchment attributes

Total catchment area (A, ha) for each site was calculated by summing the areas of all NHDPlus catchments intersected while navigating upstream from each sampling site. Cumulative catchment area (Cum A, ha) within an ecoregion was calculated as the product of mean A and the total number of catchments (n) in that ecoregion (Table 1; Fig. 2). Percent of the catchment in forests (% forest), grasslands (% grassland), row crops (% agriculture), and wetlands (% wetland) were extracted from the National Land Cover Database (NLCD, USGS, 2006; Fig. 2). The NLCD, derived from multi-temporal and terrain-corrected satellite imagery, provides consistent land cover estimates for the United States. Targeted assessments found accuracy of land cover estimates ranged from 78 to 89% (Xian et al., 2009).

Catchment stream lengths (L, km) were estimated using NHDPlus flow line and stream order data layers (Fig. 2). NHDPlus codes flow lines as connectors, canals and ditches, underground pipes, intermittent and perennial streams, artificial paths, and coastlines. We excluded underground pipes and coastlines from our analyses, and the remaining types of water conveyances are collectively treated as streams. Each stream segment of a given order was included in the estimate of L by stream order, and cumulative catchment stream length (Cum L, km) was calculated as the product of L and n.

Catchment-scale estimates of soil organic carbon (SOC) and % sand were derived from US Department of Agriculture soil survey data (SSURGO and STATSGO2; http://soildatamart.nrcs.usda.gov/; Fig. 2) and associated with each headwater catchment as the mean of the 30-m pixels included in each catchment. Soil drainage index (DI), previously called the natural soil wetness index, is a measure of the long-term wetness of a soil (Schaetzl et al., 2009). Catchment-scale estimates of DI were estimated from area-weighted STATSGO2 map units (http://www.drainageindex.msu.edu; Fig. 2) that intersected our study catchments.

Data on the wet deposition of atmospheric N were available from the National Atmospheric Deposition Program (NADP, http://nadp.sws.uiuc.edu). We used annual (2005–2009) precipitation-weighted mean TN concentrations in precipitation. Estimates of

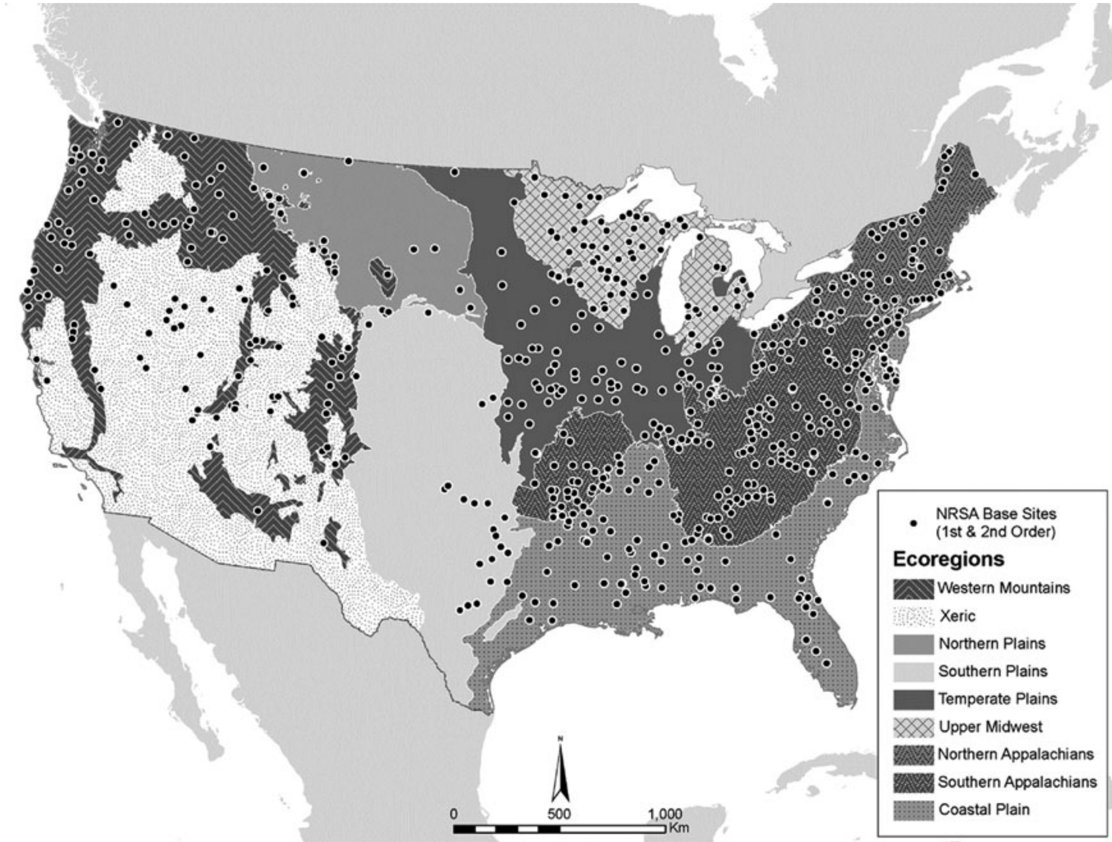

Fig. 1. Locations of headwater streams sampled during the National Rivers and Streams Assessment. The nine ecoregions for NRSA reporting are delineated.

wet TN deposition on each of our study catchments were based on NADP station data that were intersected with spatially-interpolated national grids (http://nadp.sws.uiuc.edu/isopleths). These interpolated data were averaged across the years of our study.

2.3. Carbon, nitrogen and phosphorus sequestration

Carbon sequestered in woody vegetation was estimated by multiplying catchment area by the proportion of the catchment covered by forests, and then by mean above and below ground C standing stocks for living tree biomass in the Eastern Highlands (Northern and Southern Appalachian Mountains ecoregions; 18,400 Mg km^{-2}), Plains and Lowlands (Coastal, Northern, Southern and Temperate Plains, Upper Midwest, and Xeric ecoregions: 20, 700 Mg km^{-2}), or Western Mountains (18,900 Mg km^{-2}; US Department of Agriculture, 2008; Heath et al., 2011; US Environmental Protection Agency (USEPA), 2011; Fig. 2). Nitrogen and phosphorus sequestered in tree biomass were estimated from global measures of tree C, N, and P stoichiometry (Schade et al., 2005). These C, N, and P standing stock estimates were divided by median forest stand age (Smith et al., 2009) to estimate annual C, N, and P sequestration by trees in US headwater catchments. It was assumed that non-woody catchment vegetation contributed negligibly to overall catchment C, N, and P sequestration. Sequestration of C, N, and P in agricultural crops was estimated by multiplying catchment area by the proportion of the catchment covered by row crop agriculture, and then by mean C, N, and P standing stocks (Vitousek et al., 2009).

Soil C content was estimated from US Department of Agriculture soil survey data (SSURGO and STATSGO2; http://soildatamart.nrcs.usda.gov/; Fig. 2) applied at the catchment scale (Bliss, 2003). Soil N and P content were based on average soil C, N, and P stoichiometry (Cleveland and Liptzin, 2007). Annual increments of soil C, N, and P sequestration were based on a 500 yr average age for soil organic matter, and assuming a linear increase in C, N, and P sequestration through time (Trumbore, 2000; Six and Jastrow, 2007).

2.4. Catchment and in-stream denitrification

Catchment-scale denitrification (Catch DN) was estimated from a regression model employing average % sand and DI for the 30-m pixels of each catchment (Groffman et al., 1992; Table 1; Fig. 2). Cumulative catchment DN was estimated as the product of Catch DN and Cum *A*. Mulholland et al. (2008) developed a model for predicting in-stream denitrification based on stream NO_3^- concentrations (Table 1; Fig. 2). We applied their DN model to measured NO_3^- concentrations from the NRSA streams to predict in-stream DN (Stream DN). Catchment-wide Stream DN was estimated as the product of Stream DN and Cum *L*.

2.5. Hydrology and water supply

Mean annual precipitation (PPT, mm yr^{-1}) was acquired as an NHDPlus data layer for each of our study catchments. NHDPlus uses a spatial interpolation model based on 30 yr of precipitation data (1981–2010) from the National Weather Service precipitation gauge network (http://water.weather.gov/ahps/). Mean annual discharge (*Q*, m^3 s^{-1}) from each catchment was also available as an NHDPlus data layer. NHDPlus uses a spatial interpolation model of unit runoff based on 30 yr of US Geological Survey stream gage data (http://waterdata.usgs.gov/nwis). Streamflow data were converted from volumetric rates (m^3 s^{-1}) to the more commonly

Table 1
Definitions of the physical and chemical dimensions of the study catchments and ecosystem services metrics.

Label	Name, units	Derivation	Reference/source
n	Number of study catchments		
A	Catchment area (ha)		[a]NHDPlus
Cum A	Cumulative A (ha)	$A \times n$	
L	Catchment stream length (km)		[a]NHDPlus
Cum L	Cumulative L (km)	$L \times n$	
% HW	% of total streams that are headwaters		[a]NHDPlus
% Forest	% of A in forests		[b]NLCD
% Grassland	% of A in grasslands		[b]NLCD
% Wetland	% of A in wetlands		[b]NLCD
% Agriculture	% of A in row crops		[b]NLCD
PPT	Precipitation (mm yr^{-1})		[a]NHDPlus
RO	Runoff, (mm yr^{-1})	Converted from discharge, $m^3 s^{-1}$	[a]NHDPlus
ET	Evapotranspiration, (mm yr^{-1})	PPT-RO	
ET index	Evaporative index	ET/PPT	Jones et al. (2012)
RO ratio	Runoff ratio	RO/PPT	Jones et al. (2012)
% Sand	% of soil column as sand		[c]SSURGO/STATSGO
DI	Drainage index		Schaetzl et al. (2009)
N deposition	Total N deposition (kg N ha^{-1} y^{-1})		[d]NADP
Tree C	C stocks in trees (Mg ha^{-1})		
	Northern and Southern		
	Appalachian Mountains:	18,400 × % Forest	[e]FIA
	Western Mountains:	18,900 × % Forest	[e]FIA
	Other ecoregions:	20,700 × % Forest	[e]FIA
Tree N	N stocks in trees, Mg ha^{-1}	3000:45:1C:N:P stoichiometry	Schade et al. (2005)
Tree P	P stocks in trees, Mg ha^{-1}	3000:45:1C:N:P stoichiometry	Schade et al. (2005)
Crop C	C stocks in crops, Mg ha^{-1}	200 × % Ag	Vitousek et al. (2009)
Crop N	N stocks in crops, Mg ha^{-1}	14.5 × % Ag	Vitousek et al. (2009)
Crop P	P stocks in crops, Mg ha^{-1}	2.3 × % Ag	Vitousek et al. (2009)
Soil C	C stocks in soil, Mg ha^{-1}	Soil OC, total profile	[c]SSURGO/STATSGO
Soil N	N stocks in soil, Mg ha^{-1}	186:13:1C:N:P stoichiometry	Cleveland and Liptzin (2007)
Soil P	P stocks in soil, Mg ha^{-1}	186:13:1C:N:P stoichiometry	Cleveland and Liptzin (2007)
Catch DN	Catchment denitrification, Mg ha^{-1}	0.34 (DI) − 0.40 (% sand) + 11.8	Groffman et al. (1992)
Stream DN	In-stream denitrification, Mg km^{-1}	$(-0.493 \times ln\ NO_3) - 2.975) \times NO_3$	Mulholland et al. (2008)

[a] National Hydrography Datasets (http://www.horizon-systems.com/NHDPlus/NHDPlusV2_data.php).
[b] National Land Cover Database (http://www.mrlc.gov/nlcd06_data.php).
[c] National and State Soil Survey Geographic Databases (http://soildatamart.nrcs.usda.gov/).
[d] National Atmospheric Deposition Program (http://nadp.sws.uiuc.edu/isopleths).
[e] Forest Inventory and Analysis (http://www.fia.fs.fed.us/tools-data/default.asp).

reported runoff (RO, mm yr^{-1}) to facilitate the calculation of actual evapotranspiration (ET=PPT-RO; mm yr^{-1}), evaporative index (ET Index=ET/PPT), and runoff ratio (RO Ratio=RO/PPT; Jones et al., 2012; Table 1; Fig. 2).

2.6. Economic value of ecosystem services

As a relative comparison among ecosystem services and between ecoregions, we estimated the potential economic value of ecosystem services provided by headwater catchments as the product of units of production (production function) and published economic values for those units of production. Economic values are reported in International $, where 1INT $=1 US $ (de Groot et al., 2012). We restrict our comparisons to considerations three ecosystem services, (1) water supply; (2) climate regulation (C sequestration), and (3) water purification (N and P sequestration and denitrification). The economic value of water supply was estimated as INT $0.35 m^{-3} (INT $40 acre - ft^{-1}; Sedell et al., 2000; Krieger, 2001; Nunez et al., 2006; Brauman et al., 2007). The value of the C sequestered in catchment biomass and soil was INT $0.12 Mg^{-1} (Mg=1000 t; Intercontinental Exchange, 2012). The value of N sequestered in catchment biomass and soil, and removal via DN was INT $160 Mg^{-1} (US Environmental Protection Agency (USEPA), 2007; Dodds et al., 2009; Compton et al., 2011). P sequestered in catchment biomass and soils were conservatively valued at INT $1600 Mg^{-1} (Sano et al., 2005; US Environmental Protection Agency (USEPA), 2007; Stanton et al., 2010).

2.7. Statistical analyses

We calculated mean values for catchment attributes; annual precipitation and runoff; C, N, and P sequestration; and N removal; and their economic values. Catchment means among ecoregions were compared using a non-parametric one-way analysis of variance on ranked scores (Wilcoxon) with the Kruskal–Wallis test. All analyses were done using SAS for Windows, release 9.2 (SAS Institute, Inc., Cary, NC, USA).

3. Results

3.1. Catchment attributes and ecosystem services production functions

The average size of the headwater catchments in our study ranged from <2000 ha for catchments in the Eastern US (Northern and Southern Appalachian Mountains and Coastal Plains) to >8000 ha in the Northern and Southern Plains ecoregions (Table 2). Headwater stream length was shorter in the Eastern US and longer in the Northern and Southern Plains and Xeric ecoregions. Overall, headwater streams represented 74–80% of total catchment stream length (Table 2). Percent of the catchment in forest land cover was greatest in the Northern and Southern Appalachian and Western Mountains; grasslands were greatest in the Northern and Southern Plains; wetlands were more prevalent in the Coastal Plains and in the Upper Midwest; and the Temperate

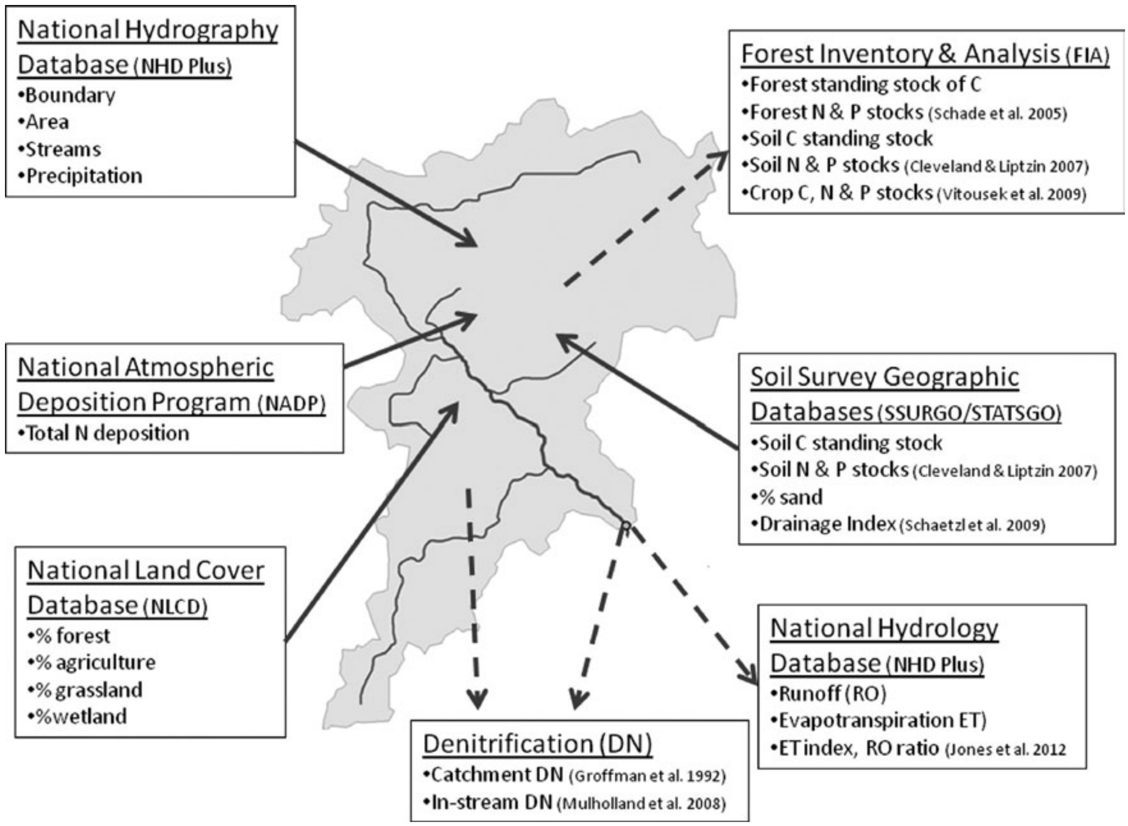

Fig. 2. Conceptual model of a headwater stream catchment (gray-shaded area) annotated with sources for data inputs (solid arrows) and ecosystem service outputs (dashed arrows). Details of data uses and ecosystem services calculations are presented in Table 1. Conceptual catchment model.

Table 2
Mean catchment area (*A*, ha) and stream length (*L*, km); proportion of total catchment *L* that is headwaters (% HW); proportion of the catchment cover by forests, grasslands, wetlands, or row crop agriculture (%); annual precipitation (PPT, mm yr^{-1}), evapotranspiration (ET, mm yr^{-1}), runoff (RO, mm yr^{-1}), evaporative index (ET index = ET/PPT), runoff ratio (RO ratio = RO/PPT), proportion of the soil column that is sand (% sand), drainage index (DI) and atmospheric N deposition (kg N ha^{-1} yr^{-1}) for headwater catchments in the nine NRSA ecoregions. Results of comparisons among ecoregions were based on Wilcoxon Rank sum scores and the Kruskal–Wallis test (χ^2 and P < χ^2).

Variable (*n*)	NAP[a] (71)	SAP[b] (1 3 5)	CPL[c] (1 0 0)	NPL[d] (12)	SPL[e] (26)	TPL[f] (77)	UMW[g] (61)	WMT[h] (83)	XER[i] (35)	χ^2	P < χ^2
A	1263	1427	1615	11,437	8260	3054	2093	2598	2466	91.2	< 0.0001
L	5	6	6	14	18	9	7	10	11	48.7	< 0.0001
% HW	78	77	78	74	78	77	75	80	80	5.32	0.7229
% Forest	67	63	42	19	16	18	40	69	42	202	< 0.0001
% Grassland	1	4	3	39	46	7	2	8	5	128	< 0.0001
% Wetland	4	< 1	13	2	1	1	18	1	< 1	271	< 0.0001
% Agriculture	15	21	23	22	17	65	29	< 1	< 1	255	< 0.0001
PPT	1101	1227	1322	471	712	933	804	1142	526	350	< 0.0001
ET	454	634	748	363	618	677	465	474	341	170	< 0.0001
RO	1124	833	742	109	117	384	450	999	250	234	< 0.0001
ET index	0.41	0.52	0.57	0.77	0.87	0.74	0.58	0.52	0.65	158	< 0.0001
RO ratio	0.99	0.68	0.56	0.23	0.17	0.38	0.56	0.73	0.47	157	< 0.0001
% sand	47	34	44	34	37	21	51	46	39	116	< 0.0001
DI	49	43	56	30	34	57	50	37	26	223	< 0.0001
N deposition	13.5	12.3	10.9	4.80	8.60	14.2	11.6	3.33	3.10	405	< 0.0001

[a] Northern Appalachian Mountains.
[b] Southern Appalachian Mountains.
[c] Coastal Plains.
[d] Northern Plains.
[e] Southern Plains.
[f] Temperate Plains.
[g] Upper Midwest.
[h] Western Mountains.
[i] Xeric ecoregions.

Plains were dominated by row crop agriculture (Table 2). Precipitation (PPT) was higher in the East (Northern and Southern Appalachian Mountains, and Coastal Plains) and lower in the Northern Plains and Xeric ecoregions; evapotranspiration (ET) was greater in the Coastal, Southern and Temperate Plains ecoregions, and lower in the Northern Plains and Xeric ecoregions

(Table 2).The combination of high PPT and low ET resulted in higher runoff (RO) from the Appalachian and Western Mountain catchments, while low PPT and high ET resulted in lower RO from Northern and Southern Plains catchments. The resulting runoff coefficients, the proportion of PPT that leaves the catchment via runoff, ranged from 0.99 in the Northern Appalachian Mountains to 0.17 in the Southern Plains (Table 2). Annual runoff (or water supply, $m^3\ ha^{-1}\ yr^{-1}$) was 2–5 times higher in the Northern and Southern Appalachian Mountains, the Coastal Plains, and the Western Mountains than in the other ecoregions (Table 4). The sand content of catchment soil profiles ranged from 21% (Temperate Plains) to 51% (Upper Midwest), and the soil drainage index, a measure of relative soil moisture retention, ranged from 26 in the Xeric region to >50 in the Coastal and Temperate Plains and the Upper Midwest ecoregions. Neither of these soil properties exhibited statistical ecoregional differences (Table 2).

Carbon stocks sequestered in trees were highest in the Northern and Southern Appalachian and Western Mountains ecoregions and lowest in the Northern, Southern, and Temperate Plains (Table 3). This pattern was repeated for tree N and P stocks, because of the stoichiometric assumptions (Schade et al., 2005; Table 3). C stock sequestered in catchment soils was highest in the Upper Midwest ecoregion, but few other discernible patterns were noted. This relationship among ecoregions was also applicable to soil N and P, due to our stoichiometric assumptions (Cleveland and Liptzin, 2007; Table 3). C, N, and P sequestered in harvested agricultural crops were highest in the Temperate Plains and lowest in the Western Mountains and Xeric ecoregions (Table 3).

C, N, and P stocks sequestered in trees were annualized by dividing the cumulative catchment values by median stand age (Smith et al., 2009) to yield an annual sequestration increment ($Mg\ yr^{-1}$). Similarly, soil C, N, and P stocks were annualized on a

Table 3
Mean amounts of C, N, and P stocks ($kg\ ha^{-1}$) in forest and crop biomass and soil and removed through catchment and in-stream denitrification (DN, $kg\ N\ ha^{-1}\ yr^{-1}$) for headwater catchments in the nine NRSA ecoregions. Results of comparisons among ecoregions were based on Wilcoxon Rank sum scores and the Kruskal–Wallis test (χ^2 and $P<\chi^2$).

Variable	NAP[a]	SAP[b]	CPL[c]	NPL[d]	SPL[e]	TPL[f]	UMW[g]	WMT[h]	XER[i]	χ^2	$P<\chi^2$
Forest C	123,485	115,617	86,565	39,061	33,751	37,390	82,503	129,897	80,199	172	<0.0001
Forest N	1,851	1,733	1,298	586	506	561	1,237	1,947	1,202	172	<0.0001
Forest P	41.2	38.5	28.9	13.0	11.2	12.5	27.5	43.3	26.7	172	<0.0001
Soil C	123,534	50,720	117,163	75,334	87,988	138,348	231,249	85,721	64,718	227	<0.0001
Soil N	8,639	3,547	8,193	5,268	6,153	9,675	16,171	5,994	4,526	227	<0.0001
Soil P	664	273	630	405	473	744	1,243	461	348	227	<0.0001
Crop C	308	419	465	439	347	1297	586	4.24	6.93	255	<0.0001
Crop N	22.4	30.4	33.7	31.8	25.2	94.0	42.5	0.31	0.50	255	<0.0001
Crop P	3.54	4.82	5.34	5.05	3.99	14.9	6.74	0.05	0.08	255	<0.0001
Catch DN	11.8	13.1	14.9	10.7	13.3	22.7	12.4	90.7	6.30	137	<0.0001
Stream DN	2.01	6.77	4.10	3.62	8.53	9.08	3.40	2.40	2.15	144	<0.0001

[a] Northern Appalachian Mountains.
[b] Southern Appalachian Mountains.
[c] Coastal Plains.
[d] Northern Plains.
[e] Southern Plains.
[f] Temperate Plains.
[g] Upper Midwest.
[h] Western Mountains.
[i] Xeric ecoregions.

Table 4
Stand age (yr) and mean annual ecosystems goods and services (water supply, $m^3\ ha^{-1}\ yr^{-1}$; climate regulation, C-sequestered in trees [a] and soil [b], $kg\ ha^{-1}\ yr^{-1}$; and water purification, N and P sequestered in trees [a] and soil [b], $kg\ ha^{-1}\ yr^{-1}$; N removal by catchment and in-stream denitrification, $kg\ ha^{-1}\ yr^{-1}$) derived from headwater catchments of the nine ecoregions. C, N, and P sequestration trees, crops, and soil was estimated as the product of sequestration ($kg\ ha^{-1}$) and catchment area, divided by stand or soil OM age. Stream denitrification was calculated as the product of denitrification and cumulative stream length.

Variable	NAP[c]	SAP[d]	CPL[e]	NPL[f]	SPL[g]	TPL[h]	UMW[i]	WMT[j]	XER[k]
Stand age	70	30	30	50	30	50	50	90	70
Water supply	11,244	8331	7424	1088	1171	3840	4502	9991	2502
Climate regulation									
C sequestration	2011	3955	3120	932	1301	1025	1641	1615	1275
Water purification									
N sequestration	43.7	64.9	59.6	22.2	29.2	30.6	50.0	33.6	26.2
P sequestration	1.92	1.83	2.22	1.07	1.32	1.74	2.88	1.40	1.08
Denitrification	13.7	20.2	19.7	14.2	24.4	31.8	16.3	11.8	8.08

[a] Median stand age ranges from 30 to 90 yr (Smith et al., 2009).
[b] Median soil organic matter age=500 yr (Trumbore, 2000; Six and Jastrow, 2007).
[c] Northern Appalachian Mountains.
[d] Southern Appalachian Mountains.
[e] Coastal Plains.
[f] Northern Plains.
[g] Southern Plains.
[h] Temperate Plains.
[i] Upper Midwest.
[j] Western Mountains.
[k] Xeric ecoregions.

presumed 500 yr median soil organic matter age (Trumbore, 2000; Six and Jastrow, 2007). The combined tree and soil C, N, and P sequestration at the catchment scale indicated that the highest sequestration increments (Mg yr^{-1}) were in the Southern Plains and Southern Appalachian Mountains, with all the remaining ecoregions being lower (Table 4).

There was a marked longitudinal trend in N deposition with highest deposition in the industrial Eastern (Northern and Southern Appalachian Mountains and Coastal Plains) and Midwestern (Temperate Plains and Upper Midwest) ecoregions and lower in the Western Mountains and Xeric ecoregions (Table 2). Lower % sand and a higher DI of catchment soils contribute to higher Catch DN, and these conditions led to Catch DN values in the Western Mountains ecoregion significantly higher than in any other ecoregion (Table 3). In-stream DN was highest in the Temperate Plains ecoregion and lowest in the Northern Appalachian Mountains ecoregion (Table 3), but when extrapolated to Cum *L*, Stream DN was highest in the Southern Appalachian and Western Mountains ecoregions, and lowest in the Xeric ecoregion. The combined annual Catch DN and Stream DN were highest in the Temperate Plains ecoregion and lowest in the Xeric ecoregion (Table 4).

3.2. Economic value of ecosystem services

We used published economic value estimates based on commodity price (water supply), market value (climate regulation), or damage cost avoidance (water purification) to assess the potential economic value of ecosystem services provided by headwater catchments. The economic value of water supply per unit catchment area (INT \$ ha^{-1} yr^{-1}) was higher in the Northern Appalachian and Western Mountains, and lower in the Northern and Southern Plains, than in the other ecoregions. The weighted average water supply value for headwater catchments in the United States was INT \$ 245 ha^{-1} yr^{-1} (Table 5). Extrapolation of these values to the entire catchment (INT \$ yr^{-1}) resulted in more similar water supply value among the ecoregions, with the exception of the Western Mountains ecoregions which was twice as high as the other ecoregions. The weighted average for headwater catchments was INT \$ 470,000 yr^{-1} (Table 5).

The economic value of climate regulation per unit catchment area was higher in the Southern Appalachian Mountains and Coastal Plains ecoregions than in the remaining ecoregions. The average economic value of climate regulation for headwater catchments was INT \$ 278 ha^{-1} yr^{-1} (Table 5). The Northern and Southern Plains ecoregions, with their larger catchment areas, sequester more than twice as much C as do the other ecoregions. Average climate regulation value for headwater catchments in the United States was INT \$ 553,000 yr^{-1} (Table 5).

We considered three metrics related to the economic value of water purification, N and P sequestration in catchment trees, crops, and soil, and catchment and in-stream denitrification. The value of N sequestration per unit catchment area was greatest in the Southern Appalachian Mountains ecoregion, followed by the Coastal Plains and Upper Midwest ecoregions. All other ecoregions had similarly lower economic value. The average value of N sequestration was INT \$ 7456 ha^{-1} yr^{-1}. The greatest sequestration of P per unit catchment area was in the Upper Midwest ecoregion, with lowest sequestration occurring in the Northern Plains and Xeric ecoregions. The weighted average economic value of P sequestration by headwater catchments was INT \$ 2977 ha^{-1} yr^{-1}. Denitrification per unit catchment area was highest in the Temperate Plains ecoregion and lowest in the Xeric ecoregion. The average economic value of denitrification by headwater catchments was INT \$ 2981 ha^{-1} yr^{-1} (Table 5). As was the case with climate regulation, the larger sizes on the Northern and Southern Plains catchments increased their potential economic value as sinks for N and P, or pathways for N removal via denitrification (Table 5).

Table 5
Mean annual catchment economic value of ecosystem services per unit catchment area (INT \$ ha^{-1} yr^{-1}) and cumulative catchment value (\$1000 yr) for water supply[a]; climate regulation [b], and water purification [c] provided by headwater catchments of the nine ecoregions. Values (\$ ha^{-1} yr^{-1}) are derived as the product of marginal unit value and annual ecosystem goods and services from Table 4; those values were multiplied by catchment area to derive the cumulative catchment values (\$ yr^{-1}). Bundled services are the sum of all the measured service catchments for a given ecoregion. Weighted average is the average value, adjusted for unequal sample sizes, of a given service across the ecoregions, i.e. a national average.

	Unit Value		NAP[d]	SAP[e]	CPL[f]	NPL[g]	SPL[h]	TPL[i]	UMW[j]	WMT[k]	XER[l]	*Weighted Average*
Water supply	\$0.035 m^3	\$ ha^{-1} yr	394	292	260	38	41	134	158	350	88	245
		\$1000 yr	497	416	420	435	339	410	330	908	216	470
Climate regulation												
C sequestration	\$0.12 Mg^{-1}	\$ ha^{-1} yr^{-1}	241	475	374	112	156	123	197	194	153	278
		\$1000 yr	305	677	605	1,297	1,290	376	412	503	377	553
Water purification												
N sequestration	\$160 Mg^{-1}	\$ ha^{-1} yr	6992	10,384	9,536	3,552	4,672	4,896	8,000	5,376	4,192	7,456
		\$1000 yr	8831	14,818	15,401	40,624	38,591	14,952	16,744	13,967	10,337	15,587
P sequestration	\$1600 Mg^{-1}	\$ ha^{-1} yr^{-1}	3072	2,928	3,552	1,712	2,112	2,784	4,608	2,240	1,728	2,977
		\$1000 yr	3880	4,178	5,736	19,580	17,445	8,502	9,645	5,820	4,261	6,628
Denitrification	\$160 Mg^{-1}	\$ ha^{-1} yr^{-1}	2192	3,232	3,152	2,272	3,904	5,088	2,608	1,888	1,293	2,981
		\$1000 yr	2768	4,612	5,090	25,985	32,247	15,539	5,459	4,905	3,188	7,544
Total bundled services by ecoregion		\$ ha^{-1} yr^{-1}	12891	17,311	16,874	7,686	10,885	13,025	15,571	10,048	7,454	13,938
		\$1000 yr	16281	24,701	27,252	87,921	89,912	39,779	32,590	26,103	18,379	30,782

[a] Krieger (2001), Nunez et al. (2006), Watanabe and Ortega (2011).
[b] Intercontinental Exchange (2012).
[c] Keplinger et al. (2003), Sano et al. (2005), US Environmental Protection Agency (USEPA), 2007, Dodds et al. (2009), Turpie et al. (2010), Compton et al. (2011), Watanabe and Ortega (2011).
[d] Northern Appalachian Mountains.
[e] Southern Appalachian Mountains.
[f] Coastal Plains.
[g] Northern Plains.
[h] Southern Plains.
[i] Temperate Plains.
[j] Upper Midwest.
[k] Western Mountains.
[l] Xeric ecoregions.

The total potential economic value of these bundled ecosystem services ranged from INT \$7454 $ha^{-1} yr^{-1}$ in the Xeric ecoregion to INT \$ 17,311 $ha^{-1} yr^{-1}$ in the Southern Appalachian Mountains ecoregion. The weighted average economic value of these bundled ecosystem services was INT \$ 13,938 $ha^{-1} yr^{-1}$ (Table 5). Potential economic value extrapolated to the whole catchment ranged from INT \$ 16 million yr^{-1} for catchments in the Northern Appalachian Mountain ecoregion to INT \$ 90 million yr^{-1} for catchments in the Southern Plains ecoregion. The weighted average economic value for headwater catchments in the United States was INT \$ 31 million yr^{-1} per catchment (Table 5).

4. Discussion

Studies of catchment ecosystem services have focused more often on those services that have established markets, such as water supply, forest products, and climate regulation (Creedy and Wurzbacher, 2001; Postel and Thompson, 2005; Nunez et al., 2006; Brauman et al., 2007; Woodbury et al., 2007; Watanabe and Ortega, 2011). Fewer studies have considered the interactions and trade-offs related to multiple ecosystem services (Stenger et al., 2009; Deal et al., 2012; Watanabe and Ortega, 2011; Kline and Mazzotta, 2012; Townsend et al., 2012). Our focus is on the importance of headwater catchments and the ecosystem services they provide. As such, we limited our considerations to catchment-scale services that do not limit the future provision of these ecosystem goods and services. Within this construct, land cover is a major driver of the kinds and potential amounts of ecosystem services that can be acquired from headwater catchments, and this construct allows us to compare these services across a national scale, without the constraint of identified local markets and users of the services (Wainger and Mazzotta, 2011).

While not the largest or most valuable ecosystem services, water supply and climate regulation benefit from having established markets for their sale and trading. As such, these services are among the best studied (Creedy and Wurzbacher, 2001; Watanabe and Ortega, 2011; de Groot et al., 2012; Townsend et al., 2012). Our estimates of the economic value of water supply are similar to climate protection regulation services. However, we believe our water supply values underestimate the true value of catchment water dynamics by ignoring the amount of water necessary to support the maintenance and growth of catchment biomass, and by not accounting for the climatological effects of ET (Jansson et al., 1999; Jackson et al., 2005).

Private and public forests in the United States sequester 162 Tg C yr^{-1}, of which trees and soils were the two largest pools (Woodbury et al., 2007). Catchment C sequestration is related to forest cover (Creedy and Wurzbacher, 2001; Jackson et al., 2005; Boix-Fayos et al., 2009). Our estimates of forest C sequestration, both per unit catchment area and extrapolate to the whole catchment, are similar to those reported by previous researchers (Creedy and Wurzbacher, 2001; Jackson et al., 2005; Woodbury et al., 2007). And, given that headwater catchments represent the majority of forest lands in the United States, our estimates provide a unique view of the importance of headwater forest for climate protection.

Forest C sequestration, largely as trees, has been increasing over the past several decades (McKinley et al., 2011). Stoichiometric theory suggests that increases in C sequestration by trees and soil must be accompanied by increased N and P sequestration (Sterner and Elser, 2002; Hesson et al., 2004). Sequestration of elements other than C is infrequently represented in the published literature (McGroddy et al., 2004; Schade et al., 2005; Cleveland and Liptzin, 2007). Our research uses established C:N:P stoichiometries to extend the discussion of sequestration to N and P, and the importance of headwater catchments for sequestering N and P with subsequent economic savings from reduced costs for nutrient removal from surface waters (Keplinger et al., 2003; Sano et al., 2005; Dodds et al., 2009; Turpie et al., 2010; Compton et al., 2011; Watanabe and Ortega, 2011). Our results suggest that headwater forests are significant N and P sinks. From a standing stock perspective, C sequestered in soils is similar to that stored in trees, but because of their different stoichiometric ratios, soils sequester significantly more N and P than do trees. However, on an annual basis trees, because of their younger median age, sequester C, N, and P at rates that are several times greater than those for soil. A significant amount of C, N, and P sequestration is also attributed to agricultural crops (Vitousek et al., 2009; Post et al., 2012).

Denitrification is a special case of N removal not accounted for in our sequestration estimates. Seitzinger et al. (2006) reported that terrestrial catchments accounted for 22% of the global N removal via denitrification, second only to marine continental shelf ecosystems. Hofstra and Bouwman (2005), using the same denitrification model, suggested that agricultural soils may account more than half of all terrestrial denitrification. By comparison, streams and rivers accounted for 6% of global denitrification. Our estimates for headwater streams suggest even greater differences between streams and their catchments. From an N-budget perspective, the sum of Catch DN and Stream DN in our study catchments exceeds that of N input via wet deposition of atmospheric N. We report wet deposition because these are regularly collected as a part of the NADP network, while dry deposition of N is difficult to measure and is often modeled to estimate its contribution to the N budget. Because of these uncertainties, we rely on the empirical NADP wet deposition data, recognizing that it is likely only half of total (wet+dry) N deposition (US Environmental Protection Agency (USEPA), 2001; Anderson and Downing, 2006). Our N accounting also ignores significant sources of N that could support denitrification, including fertilizer N applied to row crop agriculture and commercial timber production, and biological N fixation. Together, these N inputs to catchments average about 40 kg N $ha^{-1} yr^{-1}$ across the conterminous United States (Sobota et al., 2013).

It is widely recognized that ecosystems provide multiple ecosystem services and there are several studies that demonstrate the integration of these multiple services (Bennett et al., 2009; de Groot et al., 2010, 2012; Deal et al., 2012; Kline and Mazzotta, 2012). One of the commonly observed trade-offs related to water supply is the inverse relationship between catchment water yield and forest land cover. Forests tend to increase water retention on the catchment due to a slowing of runoff and increased water lost through ET (Stednick, 1996; Creedy and Wurzbacher, 2001; Swank et al., 2001; Brown et al., 2005). Reducing the proportion of the catchment covered by forests is a one management strategy to increase runoff for downstream users (Stednick, 1996; Brown et al., 2005). This increase in water supply is often accompanied by increased export of base cations, anions, and sediment (Creedy and Wurzbacher, 2001; Swank et al., 2001). The opposite is true for afforestation of grasslands and agricultural lands, and the reforestation of harvested timber lands (Jackson et al., 2005; Townsend et al., 2012). This increased forest development comes with an additional demand for water and nutrients. Jackson et al. (2005) referred to this as “trading water for carbon.” Similarly, N and P sequestered in trees and soils will lead to better water quality of catchment runoff (Creedy and Wurzbacher, 2001; Swank et al., 2001; Postel and Thompson, 2005; Deal et al., 2012; Townsend et al., 2012). Our results demonstrate the complementary and contradictory relationships among a limited suite of ecosystem services. These results suggest that management of multiple ecosystem services may not yield win–win scenarios where more than one ecosystem service is maximized. More likely, management of multiple ecosystem services will result in an effective balance to optimize ecosystem services (Bennett et al., 2009; Deal et al., 2012).

We restricted our considerations of ecosystem services to a limited list of services provided by functioning headwater ecosystems. We would be remiss if we failed to at least mention some of the other commonly reported ecosystem services. For example, we considered only the climate regulation and water purification value of trees, but must also acknowledge the economic value of trees and forest products, which is reported to be in excess of INT \$250 billion yr^{-1} for all harvested catchments in the United States (US Energy Information Administration, 2001). Similarly, we have not reported on cultural ecosystem services and their economic value. Krieger (2001) reported that forested ecosystems provide recreational opportunities that are supported by services and suppliers for hunting (INT \$2 billion yr^{-1}), fishing (INT \$3 billion yr^{-1}), and other recreation (INT \$6 billion yr^{-1}). He places the aesthetics and spiritual value of forests in the United States at INT \$1.5 billion yr^{-1}. By comparison, the average economic value of the bundled ecosystem services we're reporting for our 568 headwater catchments, based on benefit transfer to estimate price and marginal changes in goods and services produced (water supply and climate regulation) or damages avoided (water purification), is about INT \$ 31 million yr^{-1} per catchment (INT \$ 14,000 ha^{-1} yr^{-1}). Extending these average values to our 568 study catchments yields a cumulative potential economic value of INT \$ 17.5 billion yr^{-1}. The national importance of headwater catchments, in terms of ecosystem services and their potential economic value, is even greater when one considers that our study catchments are a statistical representation of more than 2 million headwater catchments in the continental United States.

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