Hydrologic Connectivity in the High-Elevation Tropics: Heterogeneous Responses to Land Change

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In the high-elevation humid tropics, human- and climate-driven land transitions can alter hydrologic connections between the atmosphere and surface waters, with local and downstream effects. We conducted a data synthesis to examine the influence of forest-to-grassland conversion, agroforest-to-nonforest conversion, tree plantation establishment on nonforest land, and recent glacier retreat on throughfall, evapotranspiration, runoff, and nitrate fluxes in montane Latin America (including the Caribbean) and Hawaii. Our synthesis reveals heterogeneous—sometimes unexpected—responses to land change. For example, in contrast with temperate highlands, forest-to-grassland conversion in the high-elevation tropics often results in little runoff increase and lower streamwater nitrate loss. Tree plantation establishment leads to diminished runoff; the magnitude of this effect is tenfold greater than with forest-to-grassland transitions. We highlight cases in which land use, land cover, and water relationships derived from temperate ecosystems do not apply to and, therefore, should not underpin watershed management programs in the high-elevation tropics.

Keywords: land change, hydrologic connectivity, biogeochemistry, tropical montane forest, payments for watershed services

Tropical mountains have captivated the imagination of Western scientists since the Age of Exploration. A key figure in the study of tropical montane landscapes was Alexander von Humboldt, whose work with Aimé Bonpland elucidated the important controls of latitude, altitude, climate, and soils on the spatial patterning of ecosystems. During an ascent of Chimborazo volcano, in Ecuador, for example, Humboldt and Bonpland (2009 [1817]) made meticulous observations of the biophysical environment along an elevational gradient spanning roughly 6000 meters (m), comparing and contrasting their measurements with records for temperate mountains and keenly noting the greater breadth of climatic and vegetation zones in the tropics (figure 1):

> In the temperate zones at 45 degrees, the limit of permanent snow, which is also the limit for all organized life, is only at 2533 meters above sea level. The result is that on mountains in temperate zones, nature can develop the variety of organized beings and meteorological phenomena on only half the surface offered by tropical regions, where vegetation ceases to exist at only 4793 meters. (von Humboldt and Bonpland 2009 [1817], p. 78)

Humboldt appreciated that these biophysical conditions influenced the diverse land-use practices that he observed in the high-elevation tropics, which, in some regions with long human histories, have given rise to landscapes resembling intricate patchwork mosaics (Young 2009).

Today, two centuries after Humboldt's expedition, human populations continue to modify land cover in tropical highlands through various activities, including deforestation, animal husbandry, tree plantation establishment, agriculture, urban development, mining, and wetland drainage. Approximately half of all tropical montane cloud forest has now been converted to these and other land uses (Mulligan 2011), although some upland regions are experiencing forest recovery after land abandonment (Aide et al. 2013). At the highest elevations (more than 4500 m above sea level), recent climate-driven glacier retreat is exposing new land for ecosystem succession (Schmidt et al. 2008) and for human use as well.

Whether direct or indirect, land-use and land-cover change (hereafter, *land change*) in the high-elevation tropics (defined as at least 1000 m above sea level and up to 23 degrees [°] 27 minutes [′] north [N] and 23°27′ south [S]) can have a disproportionate influence on water resources through effects on water input, nutrient transport, and

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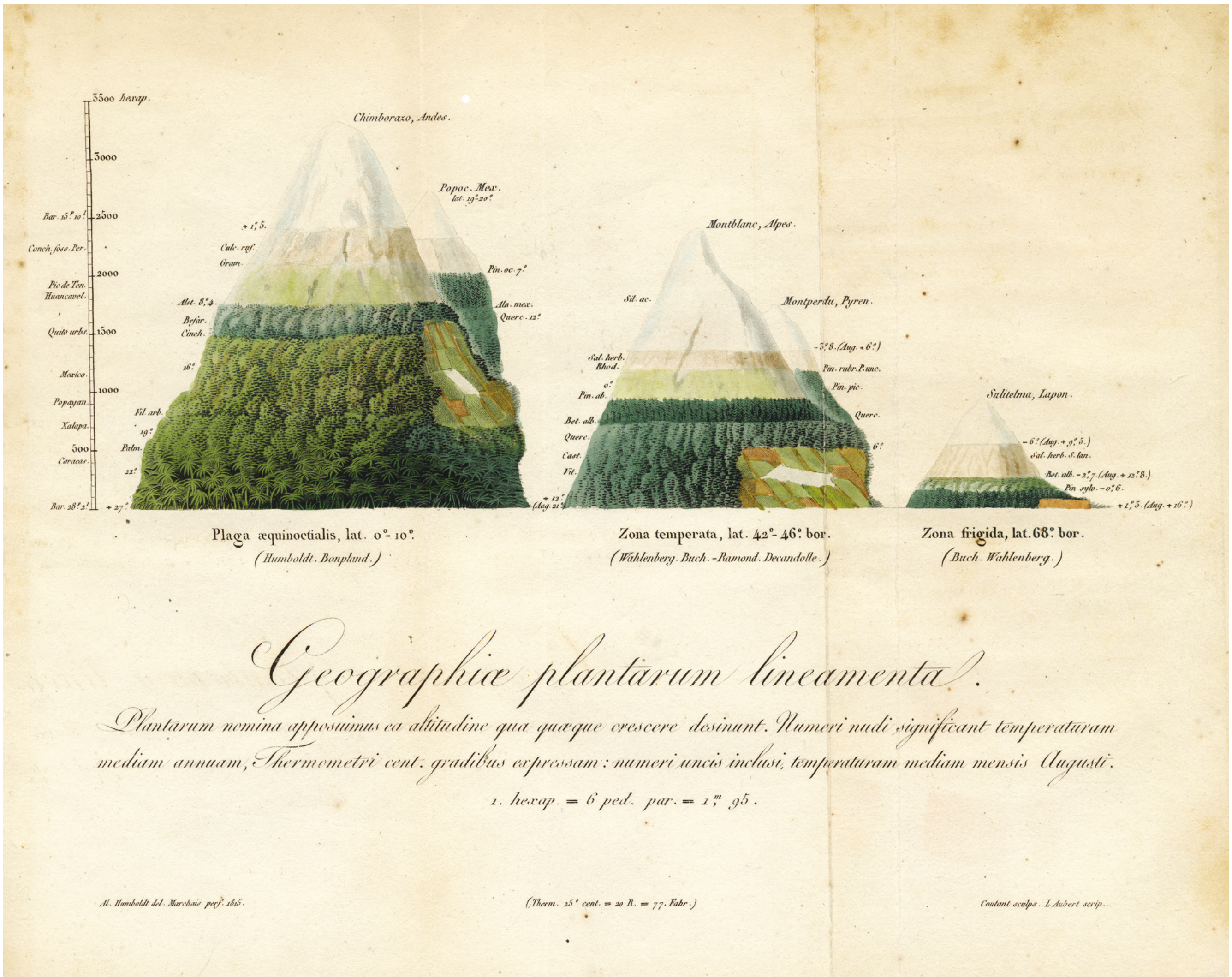


Figure 1. Alexander von Humboldt's illustration of tropical (Chimborazo, Ecuador), temperate (Mont Blanc, Alps), and subarctic (Sultielma, Lapland) mountains. In this 1817 diagram, Humboldt depicted the influence of latitude and altitude on climate, vegetation, and land use along elevational gradients. Source: Reprinted from von Humboldt (1817).

sedimentation (McClain and Naiman 2008). Such effects are likely to be compounded at wet sites characterized by abundant rainfall or high-intensity storms (Ponette-González et al. 2010a). Because human populations in tropical regions often depend on water supplied by montane ecosystems during dry periods (Bradley et al. 2006) and, in some cases, throughout the year (Buytaert et al. 2006), montane land changes that affect water quantity and quality can have significant socioeconomic consequences for local and downstream communities. This is especially true in regions where mountains make up a large percentage of the land area (e.g., Central America), enhance precipitation recycling (e.g., Andes–Amazon), or abut arid to hyperarid lowlands (e.g., Central Andes).

With tropical land change on the rise (Lindquist et al. 2012), a better understanding of human impacts on water pathways, linkages, and associated fluxes of matter and energy across the full range of tropical landscapes, from montane to lowland, is crucial to improving water management. For example, payments for watershed services (PWS)—programs in which downstream water users financially compensate upstream residents to maintain or adopt land-use practices that enhance watershed protection (Stanton et al. 2010)—are being rapidly implemented in tropical highlands. In Latin America, the total number of PWS programs grew sevenfold (from 5 to 36) between 1999 and 2008 (Stanton et al. 2010). Seven such projects were implemented in the northern Andes during this time frame (Goldman-Benner et al. 2012). Despite the growth in PWS initiatives, there is little empirical science indicating how multiple land-change trajectories in the high-elevation tropics affect water resources (Quintero et al. 2009). Much of the existing data stem from research conducted in temperate systems. However, differences in environmental variability and land management between tropical and temperate highlands are expected to have contrasting outcomes for water quantity and quality. Given these differences, an evaluation of the state of knowledge about land change in tropical highlands and its effects on water resources is needed.

To this end, we synthesized data from the literature to assess the potential impacts of four major land transitions that frequently occur at wet sites (at least 1000 millimeters [mm] of precipitation per year) in montane tropical Latin America and the Caribbean (LAC) and in Hawaii—forest-to-grassland conversion, coffee agroforest-to-nonforest (i.e., cropland or grassland) conversion, tree plantation establishment on nonforest land, and recent glacier retreat (figure 2)—on water quantity (as throughfall, evapotranspiration [ET], and runoff) and quality (as throughfall, soil solution, and streamwater nitrate [NO_3^-] fluxes). We included Hawaii in our analysis because it has experienced a suite of land transitions similar to those in LAC since European colonization. In addition, the extensive body of research conducted at high elevations in Hawaii complements the existing literature for LAC. We aimed to discern patterns in the responses of water quantity and quality to land change in the high-altitude tropics and evaluate the degree to which these patterns differ from those expected on the basis of research in temperate ecosystems. Therefore, our results suggest when it may not be appropriate to extrapolate findings from temperate ecosystems to the tropics. We also identify gaps in our current understanding of land-change effects on water resources and highlight research needs in order to improve the management of tropical montane watersheds.

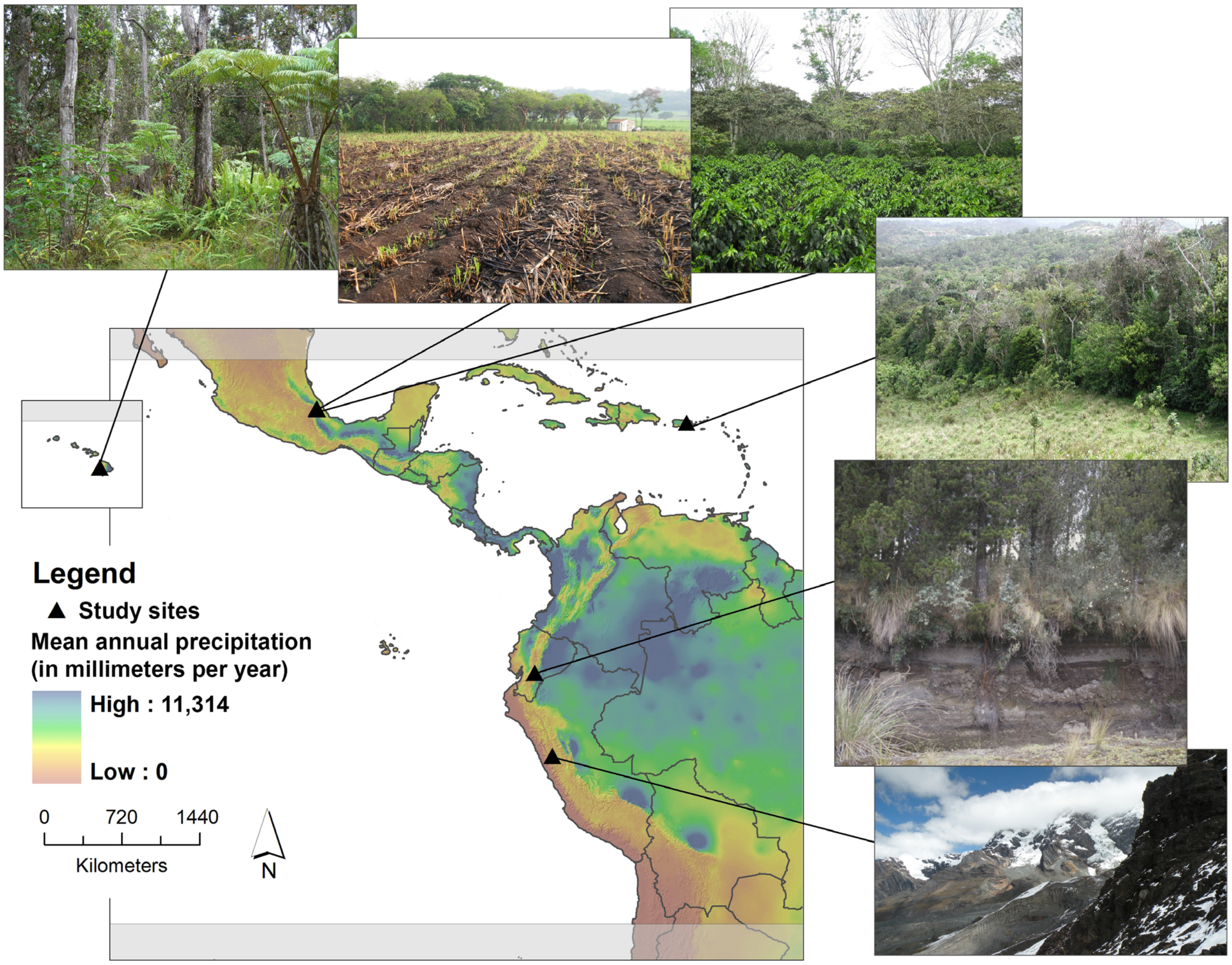
Toward an understanding of hydrologic connectivity in the high-elevation tropics

We use *hydrologic connectivity*—broadly defined as "water-mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle" (Pringle 2001, p. 981)—as an organizing framework because of its utility in tracing the movement of constituents across multiple ecosystem boundaries. Drawing from research in highland (primarily temperate) regions, we also use this framework to predict the influence of diverse land transitions on the direction of water and NO_3^- fluxes in the high-elevation tropics (figure 3). Below, we describe expected hydrologic and NO_3^- responses to land change; in the sections that follow, we compare these predictions with data from the growing literature for tropical highlands.

Predicted effects of land change on water fluxes. Land change affects the partitioning of water among various hydrologic pathways: interception, throughfall, stemflow, ET, infiltration, and runoff. In high-elevation wet tropical regions, annual rainfall inputs range from around 1000 to more than 6000 mm, storm intensity can be high, and there is a large precipitation gradient across space. At equatorial latitudes (10° N to 10° S), rainfall tends to decrease with elevation, whereas between 10° and 30° north and south, rainfall peaks at middle elevations and then declines, sometimes substantially, at the highest elevations (Rundel et al. 1994). Where ecosystems are immersed in fog seasonally or throughout the year, fog water deposition to plant canopies can be a significant additional source of water (from less than 5% to more than 75%; Bruijnzeel et al. 2011). Trees intercept more precipitation than nonwoody vegetation does, and in high-elevation tropical forests, the fraction of water that falls from the canopy to the soil as throughfall ranges from 54% to 179% (throughfall values greater than 100% are the result of fog drip; Bruijnzeel et al. 2011). A smaller proportion of incoming precipitation is funneled down plant stems as stemflow (less than 1%–31%; Bruijnzeel et al. 2011). Evaporation from soil or leaf surfaces and transpiration to the atmosphere (ET) is one pathway of water loss from ecosystems. Research in temperate ecosystems shows that woody vegetation, with its deeper roots, has more access to water and, therefore, has higher rates of ET than do grasses (Bosch and Hewlett 1982). Water that does not exit the ecosystem as ET exits as surface runoff on the landscape, infiltration into soil, and groundwater flow. Therefore, we expected conversion of any forested tropical high-elevation ecosystem to result in more surface runoff because of reduced canopy interception and ET in nonforest ecosystems and vice versa (figure 3a–3c). On ice-capped tropical mountains, glacier retreat results in greater meltwater inputs to watersheds and exposes once-buried substrates to primary succession, which is likely to lead to an increase in ET over the long term as plants occupy ice-free sites (Huss et al. 2008). However, in the short term, we anticipated that glacier retreat would increase surface runoff (figure 3d). When runoff was insensitive to changes in precipitation or ET, we inferred that a change in soil water storage had occurred.

Predicted effects of land change on NO_3^- fluxes. Because water pathways connect montane landscapes longitudinally to upstream and downstream environments, land changes that enhance or reduce water flow can have cascading effects on ecosystem nutrient dynamics (Likens et al. 1970, Pringle 2001, McClain and Naiman 2008). We focus here on NO_3^- because nitrogen may be a limiting (Vitousek and Farrington 1997) or excessive (Matson et al. 2002) nutrient in tropical montane ecosystems and because NO_3^- flux is particularly sensitive to land transitions. NO_3^- is considered the most mobile form of nitrogen, and its movement within and across ecosystems is tightly coupled to the hydrologic cycle (Likens et al. 1970, Vitousek et al. 1979). In addition, nitrogen deposition is increasing worldwide (Galloway et al. 2008), especially in tropical regions that are undergoing rapid land change (Matson et al. 1999).

Atmospheric nitrogen is deposited to ecosystems in precipitation (wet and fog deposition) or directly onto surfaces in particulate or gaseous form (dry deposition). In temperate regions, total (wet plus dry and fog) atmospheric NO_3^- inputs to forest canopies are greater than those to cropland



Land transition	Forest-to-grassland conversion	Agroforest-to-nonforest conversion	Tree plantation establishment	Glacier retreat
Type	Conversion of forest to grassland	Replacement of shaded coffee agroforest (trees intercropped with *Coffea* spp.) with unshaded cropland or grassland	Establishment of tree plantations on nonforest land	Exposure of bare rock following ice melt
Elevation	Up to snowline	Middle elevations but no higher than 1600 m	Up to snowline; prevalent above 3000 m	Above snowline
Canopy cover	Up to 100% decrease	20%–80% reduction	Up to 100% increase	No short-term change in canopy cover

Figure 2. Common land-use and land-cover types found at high elevations (at least 1000 meters [m] above sea level) in the Latin American and Caribbean tropics and Hawaii (clockwise from the top left): montane forest (photograph: Kate A. Brauman), cropland (photograph: Alexandra G. Ponette-González), coffee agroforest (photograph: Alexandra G. Ponette-González), pasture (photograph: Erika Marín-Spiotta), timber plantation (photograph: Kathleen A. Farley), and glacier ice (photograph: Kenneth R. Young). Characteristics of four prevalent land transitions, which are the focus of this synthesis: forest-to-grassland conversion, agroforest-to-nonforest conversion, tree plantation establishment on nonforest land, and recent glacier retreat.

or grassland because of enhanced fog and dry inputs to forest land cover (Fowler et al. 1999). As water passes from the atmosphere to the soil, plant canopies may retain NO_3^-, or, alternatively, NO_3^- may be leached from canopy surfaces and incorporated into throughfall along with dry-deposited materials (Weathers et al. 2006). The labile nitrogen that is

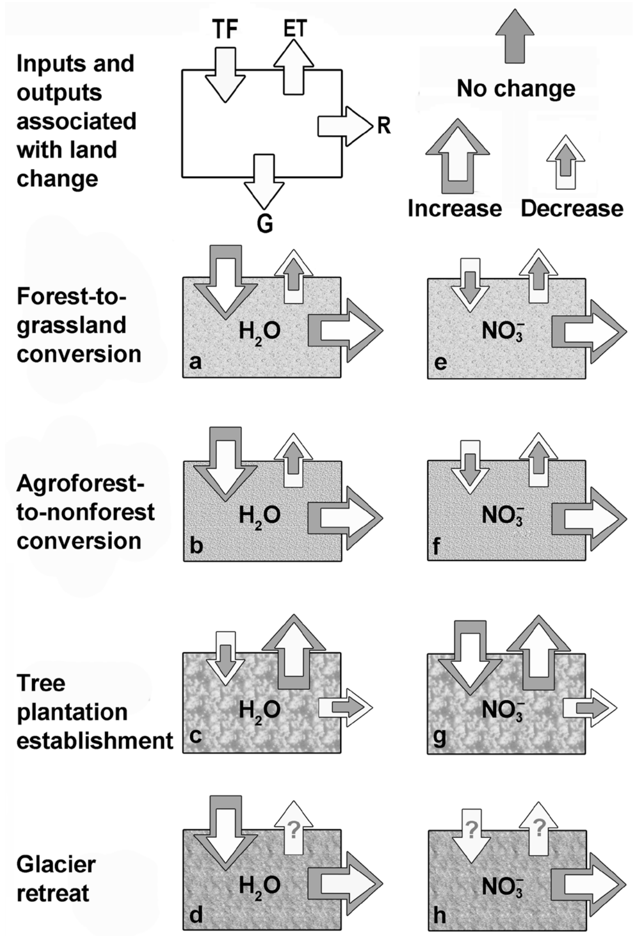


Figure 3. The predicted land transition effects on the direction of change in water (H_2O) and nitrate (NO_3^-) fluxes across ecosystem boundaries, including inputs in throughfall (TF) and outputs as evapotranspiration (ET), runoff (R), and groundwater flow (G). The white arrows represent fluxes in the initial land cover, and the gray arrows represent those in the replacement land cover; land change can increase (gray larger than white), decrease (white larger than gray), or have a neutral effect (gray and white the same size, as in panel [h]) on any of these fluxes. The predicted effects of forest-to-grassland conversion, agroforest-to-nonforest conversion, tree plantation establishment on nonforest land, and recent glacier retreat on water (a–d) and nitrate (e–h) inputs and outputs to ecosystems are largely based on research from highland temperate regions.

deposited to soil may then be taken up by plants and microbes and retained in biomass. Nitrogen in soil solution that moves below the rooting zone can be lost to groundwater or exit the system in surface or subsurface runoff. When NO_3^- inputs to an ecosystem are not equivalent to NO_3^- outputs, it can often be assumed that a change in nitrogen storage or cycling has occurred (Pace 2013). Similar to temperate highlands (Likens et al. 1970), we expected that, in nitrogen-limited tropical montane regions, forest and agroforest conversion would increase streamwater NO_3^- loss. We anticipated that reduced plant water and NO_3^- uptake and increased runoff losses from nonforest ecosystems would offset the effect of lower levels of dry and fog atmospheric NO_3^- deposition (figure 3e, 3f). In contrast, tree plantation establishment was expected to increase NO_3^- inputs to soil—but also water uptake—thus decreasing runoff and hydrologic NO_3^- losses (figure 3g). In areas undergoing deglaciation, we predicted that increased runoff from watersheds would promote more NO_3^- loss (figure 3h).

Land change and hydrologic connectivity in high-elevation humid tropical landscapes. LAC and the island of Hawaii provide an excellent geographic template for examining the hypotheses outlined above regarding potential land-change impacts on hydrologic connectivity in the high-elevation tropics (figure 3). LAC contains more than 50% of the global tropical mountain area, as well as the world's largest watershed (the Andes–Amazon) and its associated river systems (Latrubesse et al. 2005). Although LAC is half the size of the Asia–Pacific region in terms of mountain area and population, the urban population living higher than 1000 m above sea level in LAC is double that of the Asia–Pacific region (Huddleston et al. 2003). Moreover, a staggering 40% of the people residing at more than 1000 m above sea level in LAC live above 2500 m above sea level (Huddleston et al. 2003). In addition, LAC boasts the largest number of PWS programs worldwide (Stanton et al. 2010). PWS is also an important policy tool for watershed management on the island of Hawaii, where, in contrast to LAC, human populations are concentrated in low-lying areas. However, vast areas of highland forest in Hawaii have been cleared and converted for cattle grazing and agricultural production. Therefore, land-change effects on water quantity and quality in high-elevation LAC and Hawaii have the potential to result in extensive local impacts for mountain communities and cities and for downstream users.

Evaluating land-change impacts on water quantity and quality: Data synthesis

To assess these impacts, we synthesized a database of empirical studies published in peer-reviewed journals and the gray literature. Using the Web of Science and Google Scholar, we used the search terms *land use*, *land cover*, *throughfall*, *evapotranspiration*, *runoff*, *nitrate*, *mountains*, *tropics*, *Latin America*, *Caribbean*, and *Hawai'i* in multiple combinations in English, Spanish, and Portuguese to locate papers listed between 1999 and 2013 for water quantity and between 1995 and 2013 for water quality. We chose these time frames because the vast majority of research on land change and water resources in the high-elevation tropics has been published in the last two decades (see the supplemental material). Data were included from studies in which two or more land-use or land-cover types were compared at one site, except in one case, in which the data for only one land use or land cover were reported but in which

Table 1. The number of study sites and the number of observations (n) of water quantity and quality in the high-elevation tropics of Latin America (including the Caribbean) and Hawaii, grouped by land-transition and flux type.

	Water						Nitrate					
	Throughfall		Evapotranspiration		Runoff		Throughfall		Soil solution		Streamwater	
Land transition	**Study sites**	***n***	**Study sites**	***n***	**Study sites**	***n***	**Study sites**	***n***	**Study sites**	***n***	**Study sites**	***n***
Forest to grassland	27	34	4	4	6	6	20	25	–	–	7	7
Agroforest to nonforest	9	15	4	5	5	8	7	9	2	2	–	–
Tree plantation establishment	6	8	2	2	4	5	–	–	–	–	–	–
Glacier retreat	–	–	–	–	2	3	–	–	–	–	–	–

measurements for the alternate land use or land cover in the same region were located (see supplemental table S1). Separate studies conducted at the same site were included in the data set as independent observations if the measurements were for different fluxes or different land uses or if the sampling occurred during different time periods (Farley et al. 2005). Across studies, the measurement periods ranged from 6 months to several years. When multiple years of continuous data were reported in one study, the average was taken over the study period and included in the data set as a single data point. There were few published studies for some land transitions (e.g., tree plantation establishment) and processes (e.g., soil NO_3^- loss; table 1). For this reason, we included a few studies conducted on low mountains with sites less than 1000 m above sea level but greater than 600 m above sea level (see table S1). We found a total of 53 studies conducted in Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Jamaica, Mexico, Peru, Puerto Rico, Venezuela, and Hawaii (see table S1 for a list of references included in the synthesis and site locations).

For water quantity, we included a total of 37 studies and 90 observations (91% of the observations were from higher than 1000 m above sea level) of throughfall, ET, or surface runoff fluxes (in mm per year) measured in forest, coffee agroforest, tree plantation, and glaciated sites (tables 1 and S1). We could not find sufficient data on stemflow, infiltration, and groundwater recharge, and these processes were therefore not included in the analysis. Given the large amount of variability in precipitation across the sites (from about 1000 to about 5000 mm per year), we examined the relative effect of land change on water fluxes. For each observation, we calculated water flux as a percentage of the total measured precipitation in the initial and replacement land use and land cover and then estimated the relative hydrologic response to land change as the difference between the two. Medians and ranges were used to assess the average and variation in response within each land-transition type.

For water quality, we assembled data from a total of 16 studies and 43 observations (93% of the observations were from at least 1000 m above sea level) of throughfall, soil solution, or streamwater NO_3^- fluxes (in kilograms per hectare per year; tables 1 and S1). We found no data on NO_3^- flux following tree plantation establishment or glacier retreat in the high-elevation tropics; therefore, our analysis is constrained to forest and agroforest conversion effects on NO_3^- fluxes. For these data, the change in NO_3^- flux was calculated as the flux in the replacement minus the flux in the initial land cover divided by the flux in the initial land cover and expressed as a percentage.

To reveal gaps in the literature, we examined the number of sites and observations for each land-transition and flux type (table 1). The processes with the largest number of observations were throughfall water and NO_3^- flux. These data were normally distributed and complied with the assumption of homogeneity of variances. Therefore, we conducted paired *t*-tests to examine the mean differences between paired land-use and land-cover types. Given the limited sample sizes for all other processes (table 1), no additional statistical analyses were conducted. In the following sections, we report the patterns that emerged from our synthesis of the literature and include references that serve as examples of the patterns found (see table S1 for a complete list of references included in the synthesis).

Land-change influences on water quantity

Unlike in temperate systems, in which conversion of forest to grassland typically generates a substantial increase in runoff (Bosch and Hewlett 1982), our synthesis of recent studies from the high-elevation tropics of LAC and Hawaii (e.g., Crespo et al. 2011) indicates that forest-to-grassland transitions often produce little increase in runoff. In addition, tree plantation establishment has been shown to have a greater relative effect on ET and runoff than forest conversion to grassland does (e.g., Buytaert et al. 2007).

Conversion of forest and agroforest to nonforest land. In montane tropical LAC and Hawaii, we found throughfall to be highly sensitive to changes in land use and land cover. For example, in our data set, water input was at most 53% higher in grassland than in forest and at most 58% higher in cropland and grassland than in coffee agroforest (figure 4a, 4b; e.g., Fleischbein et al. 2005, Cannavo et al. 2011). Where fog water inputs to vegetation canopies were high enough to result in fog drip to soil, these land transitions actually reduced the total throughfall flux by as much as 22% (e.g., Brauman et al. 2010, Ponette-González et al. 2010a). In total, the

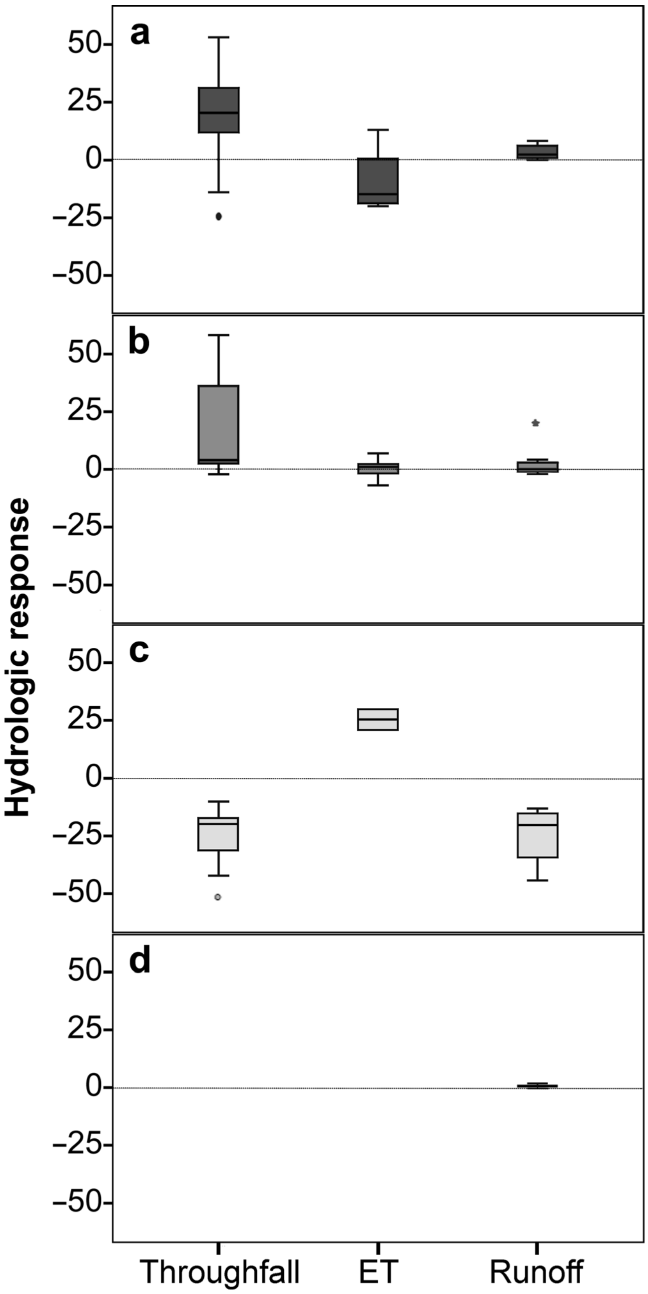


Figure 4. The range and distribution of hydrologic responses to land change at high elevations (at least 1000 meters above sea level) in the Latin American and Caribbean (LAC) tropics and Hawaii. Hydrologic responses are expressed as the percentage change in throughfall, evapotranspiration (ET), and runoff following (a) forest-to-grassland conversion, (b) agroforest-to-nonforest conversion, (c) tree plantation establishment on nonforest land, and (d) recent glacier retreat. The whiskers show the highest and lowest values (excluding outliers, which are shown as dots, and an extreme outlier, which is shown as an asterisk). Ninety-one percent of the observations are from highland LAC. See supplemental table S1 for a list of references included in the analysis.

replacement of forest or agroforest with nonforest resulted in a 20% and 4% mean increase in throughfall, respectively (forest conversion, $t(33) = -6.52$, $p < .000001$; agroforest conversion, $t(14) = -2.99$, $p < .01$).

Relative changes in ET following forest and agroforest conversion were smaller and less variable than changes in water input were (figure 4a, 4b). This may be because of the lower vapor pressure deficit characteristic of the humid tropics (Brauman et al. 2012). ET declined 12%–20% after forest-to-grassland conversion and, in one case, increased by 13% (figure 4a; Ataroff and Rada 2000). A comparison of coffee agroforest and nonforest ecosystems similarly indicated the potential for enhanced (increases of 1%–7%) or reduced (reductions between 2% and 7%) ET with shade-tree removal (figure 4b; e.g., Harmand et al. 2007). On average, ET decreased by 15% with forest-to-grassland and increased by 1% with agroforest-to-nonforest land change.

Given the clear impact of vegetation change on water fluxes, we were surprised to find that, with the exception of one case, in which runoff from a bare field was 19% greater than from a coffee agroforest (Bellanger et al. 2004), surface runoff was little affected by transitions from forest and coffee agroforest to nonforest ecosystems at high elevations in tropical LAC and Hawaii (figure 4a, 4b; e.g., Bellanger et al. 2004, Salemi et al. 2013). On average, runoff increased by 2% with forest-to-grassland and by 0% with agroforest conversion, despite higher levels of throughfall and often less ET, which suggests that recharge was the process most influenced by land change.

Tree plantation establishment on nonforest land. Changes in water cycling following tree plantation establishment on nonforest land in tropical montane LAC and Hawaii have been examined in relatively few studies. The data that we could find showed that throughfall water fluxes were 10%–54% lower on plantations than on nonforest sites (figure 4c; e.g., León Peláez et al. 2010) and 20% lower on average ($t(7) = 4.67$, $p < .002$). In the two cases in which ET has been measured (Buytaert et al. 2007, de Almeida 2012), increases in ET of similar magnitude were reported: 21%–30%. Consistent with the decrease in water input and the increase in canopy water loss, we found that surface runoff decreased by between 13% and 44% following the establishment of tree plantations on nonforest land (figure 4c; e.g., Crespo et al. 2011, Salemi et al. 2013). Although these results support our initial hypothesis of lowered throughfall and increased ET from woody vegetation (figure 3c), we did not expect this land-transition type to impart a greater relative change in ET and runoff than forest conversion did. Of particular significance is that the median change in runoff following tree plantation establishment was tenfold greater (a decrease of 20%) than with conversion of forest to grassland (figure 4).

Glacier retreat. Glacier cover represents an important but understudied hydrologic control on water dynamics in tropical landscapes, with important consequences for water security (Bradley et al. 2006). For this synthesis, we were unable to find direct comparisons of ET rates in glaciated and deglaciated watersheds. However, as we had anticipated, runoff generation increased with glacier retreat, by as much as 2% annually (figure 4d; e.g., Mark and McKenzie 2007).

Heterogeneous hydrologic responses to land change in the high-elevation tropics. We detected heterogeneous and sometimes unexpected hydrologic responses to land change in the high-elevation tropics of LAC and Hawaii. Forest and agroforest conversion to nonforest resulted in more throughfall and often less ET but generated a minimal increase in runoff, contrary to the findings for temperate regions, in which a reduction in forest cover is known to significantly increase water yield (Bosch and Hewlett 1982, Brown et al. 2005). These results underline the important influence of soil physical properties and geologic substrate on surface runoff. Moreover, they suggest that, when soil disturbance and compaction are kept to a minimum, tree canopy removal will have negligible effects on runoff flux in tropical montane regions (Bruijnzeel 2004, Molina et al. 2007).

In contrast, tree plantation establishment on nonforest land led to a significant decrease in surface runoff, and the effect of this land transition on ET and runoff was greater in magnitude than that observed with forest loss. Previous studies have suggested that the hydrologic effects of tree plantations are strongly mediated by tree species (Farley et al. 2005, van Dijk and Keenan 2007). For example, in high-elevation Hawaii, Kagawa and colleagues (2009) attributed higher rates of ET in nonnative timber plantations than in native forest to species-specific differences in water use. Likewise, streamflow reductions following the establishment of tree plantations on grassland have been shown to vary according to the original land-cover type and plantation species, with the greatest declines occurring in catchments planted with water-demanding species (e.g., *Eucalyptus* spp.) and in areas formerly covered by tropical alpine grassland (Farley et al. 2005).

As we expected (figure 3d), glacier retreat on tropical mountains enhanced surface runoff. Over longer time scales, such losses have been shown to be more dramatic. In the Cordillera Blanca mountain range of north-central Peru, for example, glacier recession increased runoff by 23% between 1998–1999 and 2001–2004 (Mark et al. 2005). More recently, historical and inferred hydrographs constructed by Baraer and colleagues (2012) for this region indicate that many watersheds have transitioned to a declining dry season discharge regime, with the pulse of water released by negative glacial balance already having moved through the system. Therefore, any increases in runoff caused by deglaciation may be ephemeral (Bury et al. 2013). Moreover, as tropical glacier retreat proceeds and the hydrologic regime is increasingly dominated by rainfall, seasonal streamflow variability will also be amplified (Mark et al. 2005).

Land-change effects on water quality

In tropical montane LAC and Hawaii, forest and agroforest systems are being converted to more intensive land uses, and these land transitions may have contrasting effects on water quality. Our synthesis of recent research for the high-elevation tropics (e.g., Bücker et al. 2011) suggests that streamwater NO_3^- losses frequently decline with forest-to-grassland change. However, conversion of shaded to unshaded coffee agriculture leads to elevated levels of soil NO_3^- loss and probably to streamwater export (e.g., Harmand et al. 2007, Vázquez et al. 2011), similar to what has been observed following deforestation in temperate mountains (Likens et al. 1970).

Forest-to-grassland transitions. Forest-to-grassland transitions in tropical montane LAC (we found no comparable studies for Hawaii) strongly influence the amount of NO_3^- delivered from the atmosphere to the soil surface (figure 5a). In 15 of 25 cases (table 1; e.g., Pérez-Suárez et al. 2008), the rainwater NO_3^- fluxes measured in grassland were larger, by 14%–273% (the median was 27%), than inputs measured in forest throughfall ($t(24) = 1.14$, $p < .262$). The single study that we found in which NO_3^- losses from forest soils were compared with those from a nearby forest gap documented a decrease in soil solution NO_3^- with canopy removal (Wilcke et al. 2009). Streamwater NO_3^- exports increased by up to 38% and decreased by as much as 100% with forest-to-grassland transitions, with a 34% median decline in streamwater NO_3^- export (figure 5a; e.g., Bücker et al. 2011). Therefore, it appears that conversion of highland tropical forest to grassland often results in lower levels of streamwater NO_3^- loss.

Conversion of coffee agroforest to nonforest. As with forest-to-grassland transitions, conversion of coffee agroforest to nonforest ecosystems caused a net increase of 51% in NO_3^- delivery to soil (figure 5b; $t(8) = -2.97$, $p < .018$). Comparisons of coffee agroforests and unshaded coffee monocultures under similar levels of fertilization have also shown higher rates of NO_3^- leaching from unshaded coffee systems (e.g., Harmand et al. 2007). In fact, agroforest conversion to monoculture coffee was found to double soil NO_3^- loss (figure 5b; e.g., Babbar-Amighetti and Zak 1995). We do not know of any studies in which streamwater NO_3^- export from shaded and crop-or grass-dominated watersheds have been measured simultaneously (figure 5b). However, in highland Mexico, NO_3^- concentrations were tenfold larger in streams draining shaded coffee than in those draining pasture, which highlights the influence of fertilizer application on streamwater chemistry (Vázquez et al. 2011).

Unexpected changes in water quality with forest-to-nonforest transitions in tropical highlands. There are still few contemporaneous measures of land-change effects on water quality in the high-elevation tropics of LAC and Hawaii (tables 1 and S1). Nonetheless, the data that do exist suggest that tropical forest-to-grassland transitions in these regions often result in less, rather than more, watershed NO_3^- loss (figure 5a). Various mechanisms have been put forth to explain this pattern, which has also been observed in lowland tropical LAC

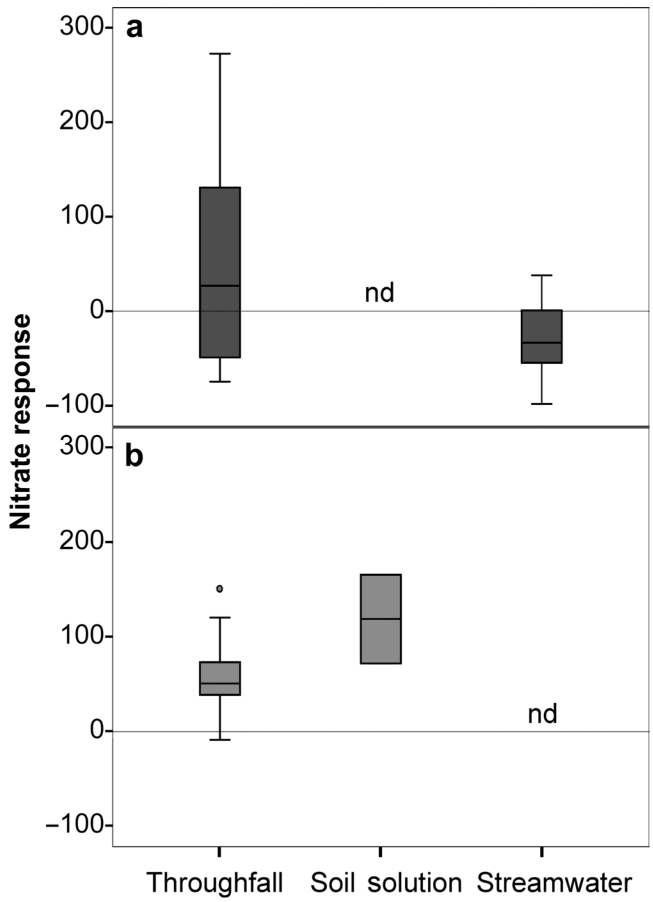


Figure 5. Nitrate responses to land change at high elevations (at least 1000 meters above sea level) in the Latin American and Caribbean tropics. (a) The percentage change in throughfall and streamwater nitrate flux following forest-to-grassland conversion. (b) The percentage change in throughfall and soil solution nitrate flux following agroforest-to-nonforest conversion. No data (nd) were found on soil solution flux following forest-to-grassland conversion or streamwater nitrate export following coffee agroforest conversion. The whiskers show the highest and lowest values (excluding outliers, which are shown as dots). See supplemental table S1 for a list of references included in the analysis.

(Neill et al. 2006, Chaves et al. 2009). Valiela and colleagues (2013) suggest that lower rates of atmospheric NO_3^- inputs to pasture than in forest could explain lower hydrologic NO_3^- export observed in pasture. Our synthesis for tropical highlands does not support this idea. NO_3^- inputs to grassland are frequently greater than those to forest because of preferential retention of NO_3^- by forest canopies (Clark et al. 1998, Ponette-González et al. 2010b). Because forest conversion decreases ET (figure 4a) and biotic demand for nitrogen, decreases in watershed NO_3^- export could be attributed to differences in terrestrial nitrogen cycling and storage between forest and pasture (Neill et al. 2006). Alternatively, NO_3^- may be retained in deep soil layers (Matson et al. 1999, Lohse and Matson 2005). The low levels of surface runoff from established grasslands (figure 4a) suggest that the maintenance of vertical hydrologic flow paths may play an important role in modulating soil NO_3^- loss (Lohse and Matson 2005, Boy et al. 2008).

In two studies (Wilcke et al. 2009, Vázquez et al. 2011), forest conversion resulted in an increase in NO_3^- export, as we had anticipated, perhaps because of differences in soil age, soil nutrient status (Lohse and Matson 2005), or land-use practices. In one of the earliest studies in which land-use effects on tropical river chemistry were detected, McDowell and colleagues (1995) found that watershed NO_3^- losses increased with human population density and with the extent of agricultural land use in upland Caribbean catchments. Export of NO_3^- was two to four times greater in the most densely populated catchment, despite that area's having less than half the total runoff.

In coffee-growing landscapes, agroforest conversion resulted in an increase in soil solution NO_3^- fluxes (figure 5b). We suggest that this is because of management practices—largely, the addition of fertilizer nitrogen: In a recent study by Tully and colleagues (2012), total inorganic nitrogen (NO_3^- plus ammonium) soil losses from conventional coffee monoculture were threefold greater than from coffee agroforest, a difference that they attributed to the combined effects of increased fertilizer input and reduced shade tree biomass in conventional monoculture farms.

Implications for watershed management in the high-elevation tropics

The success of PWS programs depends on the ability to predict the impacts of land change on water resources (Brauman et al. 2007), but many programs lack information linking land use and land cover to hydrologic service provision. As a result, managers in tropical regions are likely to rely on assumptions rather than on empirical relationships (Farley et al. 2011) or, alternatively, on relationships derived from studies in temperate ecosystems. However, at high altitudes, tropical and temperate regions differ in fundamental ways that affect hydrologic connectivity. For example, ecosystems located near the equator have yearlong growing seasons and, therefore, continuous water use by vegetation. Except at the highest elevations (approximately 5% of tropical mountain areas), snow does not persist for more than a few hours on tropical mountains (Rundel et al. 1994); as a result, vegetation effects on seasonal snow-cover dynamics are less important than in temperate regions. Human influences on tropical mountains are also quite distinct. Tropical mountains are blanketed by a spectrum of land-use and land-cover types over a broad range of elevations, as was first described by Humboldt, whereas land-use diversity is narrower in temperate zones (figure 1). A smaller area and proportion of land in tropical highlands is under formal conservation protection (Chape et al. 2008). In addition, most high-elevation tropical landscapes receive lower levels and different proportions of nitrogen input from wet, fog, and dry deposition (Weathers and Ponette-González 2011), which suggests that NO_3^- responses to land change may be dampened relative to those in temperate regions.

Land change at high elevations in LAC and Hawaii therefore results in hydrologic and NO_3^- responses (figure 6) that differ from those expected on the basis of principles developed in temperate mountain ecosystems (figure 3), which limits their usefulness in tropical PWS initiatives. The effect of land change on ET is of particular significance within the context of PWS because of long-standing debates about the nature of the relationships among land cover, ET, and water yield (Bosch and Hewlett 1982, Farley et al. 2005, Ellison et al. 2012). Similar to temperate regions, ET from forested ecosystems has been shown to be greater than that from grasses in seasonally water-limited tropical montane environments (figure 4a; Brauman et al. 2012). However, at very wet sites affected by fog and characterized by high relative humidity, there is evidence that ET can be similar or greater in grassland than in forest (figure 4a; Ataroff and Rada 2000). Clearly, the extent to which forest cover (or a lack thereof) affects water yield in high-elevation tropical regions depends on whether hydrologic processes are more strongly governed by atmospheric (i.e., climate) or vegetation (i.e., plant water use) controls or by interactions between the two (Brauman et al. 2012).

That tropical forest-to-grassland transitions do not always enhance watershed NO_3^- export (figure 6) is also important, given concerns over land-change effects on downstream water quality. Our results support the emerging view that some tropical montane forest watersheds share more characteristics with lowland tropical (e.g., high rates of nitrogen mineralization and nitrification and phosphorus limitation) than with montane temperate watersheds (Matson et al. 1999). For example, in a survey of streams draining 61 montane forest sites across Central America and the Caribbean, Brookshire and colleagues (2012) attributed substantial hydrologic NO_3^- losses to microbial nitrification, which suggests that the replacement of forest with grassland has the potential to lower nitrogen cycling rates and streamwater losses (Neill et al. 2006, Chaves et al. 2009). However, as was shown by Homeier and colleagues (2012), phosphorus—or nitrogen and phosphorus combined—often limits forest ecosystem processes in tropical highlands. This heterogeneity (*sensu* Townsend et al. 2008) suggests that land change in the high-elevation tropics is likely to result in a broader set of linked biogeochemical responses than might be expected in highland temperate regions.

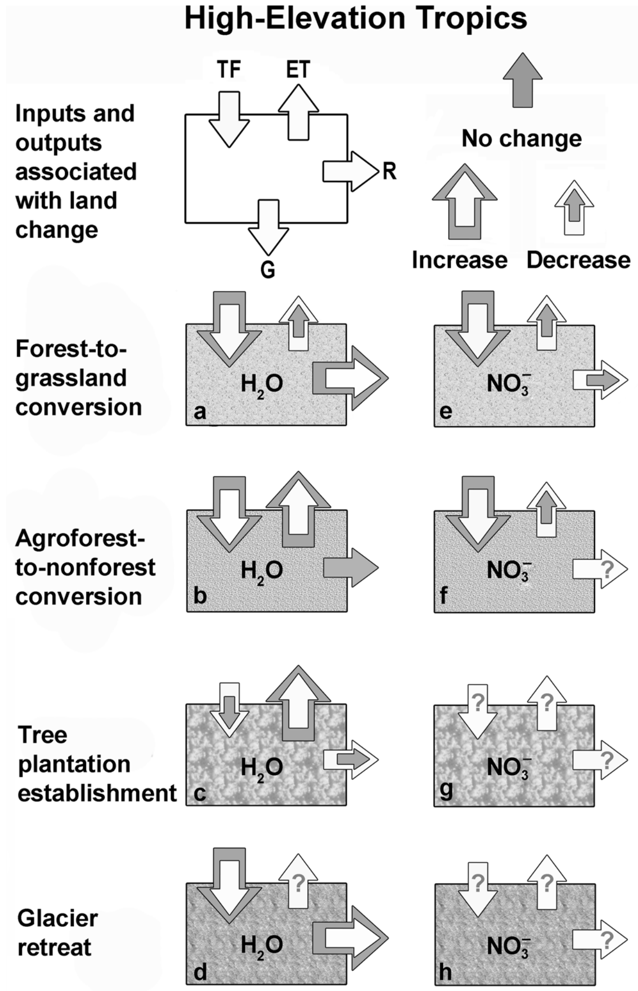


Figure 6. The predicted influence of forest-to-grassland conversion, agroforest-to-nonforest conversion, tree plantation establishment on nonforest land, and recent glacier retreat on the direction of change in water (H_2O; a–d) and nitrate (NO_3^-; e–h) inputs and outputs to ecosystems based on studies for the high-elevation tropics. Land-change affects water and nitrate fluxes across ecosystem boundaries, including inputs in throughfall (TF) and outputs as evapotranspiration (ET), runoff (R), and groundwater flow (G). The white arrows represent fluxes in the initial land cover, and the gray arrows represent those in the replacement land cover; land change can increase (gray larger than white), decrease (white larger than gray), or have a neutral effect (gray and white the same size) on any of these fluxes. For relative magnitudes of change, see the text.

Future research needs for improved water management in tropical highlands

All mountain systems, whether temperate or tropical, perform a pivotal function in the distribution and redistribution of water and materials across landscapes. As Humboldt observed, the uniqueness of tropical mountains lies in the breadth of climatic conditions, soil types, and associated land-use and land-cover types that is unparalleled at higher latitudes (figure 1). The heterogeneity in hydrologic and biogeochemical responses to land change that results represents a major challenge for managers of water resources and connectivity in the high-elevation tropics, especially in the context of a changing climate, altered species distributions, and increasing human pressures. Therefore, there is a need to better understand how diverse land transitions affect hydrology and biogeochemistry in these regions (Wohl et al. 2012).

Forest-to-grassland conversion is the most widely studied land transition with regard to its impact on water resources (table 1). Nonetheless, there are few measures of ET and stemflow—hydrologic processes that are key to understanding land-change effects on coupled water and element cycles (Levia and Frost 2003). Although there appears to be an increasing focus on hydrology in coffee-growing landscapes (Lin 2010), significant gaps remain in our understanding of nitrogen cycling within these systems (table 1). The extent to which land-use intensification alters hydrologically mediated NO_3^- loss is of crucial importance, given the prevalence of coffee agroforestry at middle elevations in tropical highlands and the potential landscape-level importance of agroforestry in mediating hydrologic connections between upland and lowland environments.

Grassland afforestation, especially for commercial timber plantations, is an increasingly important land-change pathway in the humid tropics (Van Dijk and Keenan 2007). Tree plantation establishment has been proposed as a mechanism to increase carbon sequestration in terrestrial biomass to mitigate the effects of climate change (Farley et al. 2005). However, the effects of tree plantations on hydrologic connectivity in the highland tropics are less well studied. We found very few measurements of ET and no empirical data on NO_3^- fluxes for this land-transition type, despite much debate over the influence of tree plantations on water yield (table 1; Ellison et al. 2012). Tree plantation establishment on nonforest land has been shown to reduce annual surface runoff by as much as 36% (Buytaert et al. 2007) and could therefore reduce watershed NO_3^- export by halving water yield.

At still higher elevations, glaciers are receding at an unprecedented pace (Thompson et al. 2006). In the Central Andes of Peru, home to 70% of all tropical glaciers, glaciers serve as environmental buffers, providing meltwater to downhill areas during seasonally dry periods (Bradley et al. 2006, Young 2009). With the exception of some research in the Cordillera Blanca of Peru, there remain few comparisons of glaciated and newly deglaciated terrain in terms of hydrologic function. Emerging work nonetheless suggests that hydrologic reorganization of headwater areas significantly affects water resources for downstream users (Mark et al. 2010, Bury et al. 2013). In addition to surface runoff, water quality is affected by chemical interactions of water with newly exposed bedrock, as was shown by Fortner and colleagues (2011), who found sulfide weathering that led to low pH values and concentrations of aluminum, iron, lead, and zinc in some streams of the Cordillera Blanca on par with those found in acid mine drainage. Furthermore, the chemical composition of water may change as it percolates through developing soil profiles on newly deglaciated surfaces (Schmidt et al. 2008). More research on all of these aspects of glacier retreat is essential.

Research focused on managing ecosystems for maintaining or restoring hydrologic connectivity does not yet exist for most high-elevation tropical landscapes. The heterogeneous responses of water quantity and quality to changes in land use and land cover revealed in our analysis of the available studies from tropical highland sites and a comparison with predictions based on data from temperate ecosystems provide evidence that additional targeted research is key for improving management outcomes and the success of PWS programs.

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Supplemental material

The supplemental material is available online at *www.bioscience.oxfordjournals.org*.

References cited

Aide TM, Clark ML, Grau HR, López-Carr D, Levy MA, Redo D, Bonilla-Moheno M, Riner G, Andrade-Núñez MJ, Muñiz M. 2013. Deforestation and reforestation of Latin America and the Caribbean (2001–2010). Biotropica 45: 262–271.

Ataroff V, Rada F. 2000. Deforestation impact on water dynamics in a Venezuelan Andean cloud forest. AMBIO 29: 440–444.

Babbar-Amighetti LI, Zak DR. 1995. Nitrogen loss from coffee agroecosystems in Costa Rica: Leaching and denitrification in the presence and absence of shade trees. Journal of Environmental Quality 24: 227–223.

Baraer M, Mark BG, McKenzie JM, Condom T, Bury J, Huh K-I, Portocarrero C, Gomez J, Rathay S. 2012. Glacier recession and water resources in Peru's Cordillera Blanca. Journal of Glaciology 58: 134–150.

Bellanger B, Huon S, Velasquez F, Vallès V, Girardin C, Mariotti A. 2004. Monitoring soil organic carbon erosion with $\delta^{13}C$ and $\delta^{15}N$ on experimental field plots in the Venezuelan Andes. Catena 58: 125–150.

Bosch JM, Hewlett JD. 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. Journal of Hydrology 55: 3–23.

Boy J, Valarezo C, Wilcke W. 2008. Water flow paths in soil control element exports in an Andean tropical montane forest. European Journal of Soil Science 59: 1209–1227.

Bradley RS, Vuille M, Diaz HF, Vergara W. 2006. Threats to water supplies in the tropical Andes. Science 312: 1755–1756.

Brauman KA, Daily GC, Duarte TK, Mooney HA. 2007. The nature and value of ecosystem services: An overview highlighting hydrologic services. Annual Review of Environment and Resources 32: 67–98.

Brauman KA, Freyberg DL, Daily GC. 2010. Forest structure influences on rainfall partitioning and cloud interception: A comparison of native forest sites in Kona, Hawai'i. Agricultural and Forest Meteorology 150: 265–275.

———. 2012. Potential evapotranspiration from forest and pasture in the tropics: A case study in Kona, Hawai'i. Journal of Hydrology 440–441: 52–61.

Brookshire ENJ, Hedin LO, Newbold JD, Sigman DM, Jackson JK. 2012. Sustained losses of bioavailable nitrogen from montane tropical forests. Nature Geoscience 5: 123–126. doi:10.1038/ngeo1372

Brown AE, Zhang L, McMahon TA, Western AW, Vertessy RA. 2005. A review of paired catchment studies for determining changes in water yield resulting from alterations in vegetation. Journal of Hydrology 310: 28–61.

Bruijnzeel LA. 2004. Hydrological functions of tropical forests: Not seeing the soil for the trees? Agriculture Ecosystems and Environment 104: 185–228.

Bruijnzeel LA, Mulligan M, Scatena FN. 2011. Hydrometeorology of tropical montane cloud forests: Emerging patterns. Hydrological Processes 25: 465-498.

Bücker A, Crespo P, Frede H-G, Breuer L. 2011. Solute behavior and export rates in Neotropical montane catchments under different land-uses. Journal of Tropical Ecology 27: 305–317.

Bury J, Mark BG, Carey M, Young KR, McKenzie JM, Baraer M, French A, Polk MH. 2013. New geographies of water and climate change in Peru: Coupled natural and social transformations in the Santa River watershed. Annals of the Association of American Geographers 103: 363–374.

Buytaert W, Célleri R, De Bièvre B, Cisneros F, Wyseure G, Deckers J, Hofstede R. 2006. Human impact on the hydrology of the Andean páramos. Earth-Science Reviews 79: 53–72.

Buytaert W, Iñiguez V, De Bièvre B. 2007. The effects of afforestation and cultivation on water yield in the Andean páramo. Forest Ecology and Management 251: 22–30.

Cannavo P, Sansoulet J, Harmand J-M, Siles P, Dreyer E, Vaast P. 2011. Agroforestry associating coffee and *Inga densiflora* results in complementarity for water uptake and decreases deep drainage in Costa Rica. Agriculture, Ecosystems and Environment 140: 1–13.

Chape S, Spalding M, Jenkins M, eds. 2008. The World's Protected Areas: Status, Values and Prospects in the Twenty-First Century. University of California Press.

Chaves J, Neill C, Germer S, Gouveia Neto S, Krusche AV, Castellanos Bonilla A, Elsenbeer H. 2009. Nitrogen transformations in flowpaths leading from soils to streams in Amazon forest and pasture. Ecosystems 12: 961–972.

Clark KL, Nadkarni NM, Schaefer D, Gholz HL. 1998. Atmospheric deposition and net retention of ions by the canopy in a tropical montane forest, Monteverde, Costa Rica. Journal of Tropical Ecology 14: 27–45.

Crespo PJ, Feyen J, Buytaert W, Bücker A, Breuer L, Frede H-G, Ramírez M. 2011. Identifying controls of the rainfall-runoff response of small catchments in the tropical Andes (Ecuador). Journal of Hydrology 407: 164–174.

De Almeida AQ. 2012. Dinâmica Hídrica em Microbacias Cultivadas com Eucalipto e Pastagem no Leste de Minas Gerais. PhD dissertation. Federal University of Viçosa, Viçosa, Brazil.

Ellison D, Futter MN, Bishop K. 2012. On the forest cover-water yield debate: From demand- to supply-side thinking. Global Change Biology 18: 806–820.

Farley KA, Jobbágy EG, Jackson RB. 2005. Effects of afforestation on water yield: A global synthesis with implications for policy. Global Change Biology 11: 1565–1576.

Farley KA, Anderson WG, Bremer LL, Harden CP. 2011. Compensation for ecosystem services: An evaluation of efforts to achieve conservation and development in Ecuadorian páramo grasslands. Environmental Conservation 38: 393–405.

Fleischbein K, Wilcke W, Goller R, Boy J, Valarezo C, Zech W, Knoblich K. 2005. Rainfall interception in a lower montane forest in Ecuador: Effects of canopy properties. Hydrological Processes 19: 1355–1371.

Fortner SK, Mark BG, McKenzie JM, Bury J, Trierweiler A, Baraer M, Burns PJ, Munk L. 2011. Elevated stream trace and minor element concentrations in the foreland of receding tropical glaciers. Applied Geochemistry 26: 1792–1801.

Fowler D, Cape JN, Coyle M, Flechard C, Kuylenstierna J, Hicks K, Derwent D, Johnson C, Stevenson D. 1999. The global exposure of forests to air pollutants. Water, Air, and Soil Pollution 116: 5–32.

Galloway JN, Townsend AR, Erisman JW, Bekunda M, Cai Z, Freney JR, Martinelli LA, Seitzinger SP, Sutton MA. 2008. Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. Science 320: 889–892.

Goldman-Benner RL, Benitez S, Boucher T, Calvache A, Daily G, Kareiva P, Kroeger T, Ramos A. 2012. Water funds and payments for ecosystem services: Practice learns from theory and theory can learn from practice. Oryx 46: 55–63.

Harmand J-M, Ávila H, Dambrine E, Skiba U, de Miguel S, Renderos RV, Oliver R, Jiménez F, Beer J. 2007. Nitrogen dynamics and soil nitrate retention in a *Coffea arabica—Eucalyptus deglupta* agroforestry system in Southern Costa Rica. Biogeochemistry 85: 125–139.

Homeier J, et al. 2012. Tropical Andean forests are highly susceptible to nutrient inputs—Rapid effects of experimental N and P addition to an Ecuadorian montane forest. PLOS ONE 7 (art. e47128). doi:10.1371/journal.pone.0047128

Huddleston B, Ataman E, de Salvo P, Zanetti M, Bloise M, Bel J, Franceschini G, d'Ostiani LF. 2003. Towards a GIS-Based Analysis of Mountain Environments and Populations. Food and Agricultural Organization of the United Nations. Environment and Natural Resources Working Paper no. 10.

Huss M, Farinotti D, Bauder A, Funk M. 2008. Modelling runoff from highly glacierized alpine drainage basins in a changing climate. Hydrological Processes 22: 3888–3902.

Kagawa A, Sack L, Duarte K, James S. 2009. Hawaiian native forest conserves water relative to timber plantation: Species and stand traits influence water use. Ecological Applications 19: 1429–1443.

Latrubesse EM, Stevaux JC, Sinha R. 2005. Tropical rivers. Geomorphology 70: 187–206.

León Peláez JD, González Hernández MI, Gallardo Lancho JF. 2010. Rainfall distribution in three high Andean forests in the Central Cordillera of Colombia. Revista Facultad Nacional de Agronomía Medellín 63: 5319–5336.

Levia DF Jr, Frost EE. 2003. A review and evaluation of stemflow literature in the hydrologic and biogeochemical cycles of forested and agricultural ecosystems. Journal of Hydrology 274: 1–29.

Lin BB. 2010. The role of agroforestry in reducing water loss through soil evaporation and crop transpiration in coffee agroecosystems. Agricultural and Forest Meteorology 150: 510–518.

Lindquist EJ, et al. 2012. Global Forest Land-Use Change: 1990–2005. Food and Agriculture Organization of the United Nations. FAO Forestry Paper no. 169. (9 September 2013; *www.fao.org/forestry/fra/remotesensingsurvey/en*)

Likens GE, Bormann FH, Johnson NM, Fisher DW, Pierce RS. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook Watershed-Ecosystem. Ecological Monographs 40: 23–47.

Lohse KA, Matson P. 2005. Consequences of nitrogen additions for soil losses from wet tropical forests. Ecological Applications 15: 1629–1648.

Mark BG, McKenzie JM. 2007. Tracing increasing tropical Andean glacier melt with stable isotopes in water. Environmental Science and Technology 41: 6955–6960.

Mark BG, McKenzie JM, Gómez J. 2005. Hydrochemical evaluation of changing glacier meltwater contribution to stream discharge: Callejon de Huaylas, Peru. Hydrological Sciences Journal 50: 975–987.

Mark BG, Bury J, McKenzie JM, French A, Baraer M. 2010. Climate change and tropical Andean glacier recession: Evaluating hydrologic changes and livelihood vulnerability in the Cordillera Blanca, Peru. Annals of the Association of American Geographers 100: 794–805.

Matson PA, McDowell WH, Townsend AR, Vitousek PM. 1999. The globalization of N deposition: Ecosystem consequences in tropical environments. Biochemistry 46: 67–83.

Matson PA, Lohse KA, Hall SJ. 2002. The globalization of nitrogen deposition: Consequences for terrestrial ecosystems. AMBIO 31: 113–119.

McClain ME, Naiman RJ. 2008. Andean influences on the biogeochemistry and ecology of the Amazon River. BioScience 58: 325–338.

McDowell WH, Lugo AE, James A. 1995. Export of nutrients and major ions from Caribbean catchments. Journal of the North American Benthological Society 14: 12–20.

Molina A, Govers G, Vanacker V, Poesen J, Zeelmaekers E, Cisneros F. 2007. Runoff generation in a degraded Andean ecosystem: Interaction of vegetation cover and land use. Catena 71: 357–370.

Mulligan M. 2011. Modeling the tropics-wide extent and distribution of cloud forest and cloud forest loss, with implications for conservation priority. Pages 14–38 in Bruijnzeel LA, Scatena FN, Hamilton LS, eds. Tropical Montane Cloud Forests. Cambridge University Press.

Neill C, Piccolo MC, Cerri CC, Steudler PA, Melillo JM. 2006. Soil solution nitrogen losses during clearing of lowland Amazon forest for pasture. Plant and Soil 281: 233–245.

Pace M. 2013. Revisiting the ecosystem concept: Important features that promote generality and understanding. Pages 181–190 in Weathers KC, Strayer DL, Likens GE, eds. Fundamentals of Ecosystem Science. Academic Press.

Pérez-Suárez M, Fenn ME, Cetina-Alcalá VM, Aldrete A. 2008. The effects of canopy cover on throughfall and soil chemistry in two forest sites in the Mexico City air basin. Atmósfera 21: 83–100.

Ponette-González AG, Weathers KC, Curran LM. 2010a. Water inputs across a tropical montane landscape in Veracruz, Mexico: Synergistic effects of land cover, rain and fog seasonality, and interannual precipitation variability. Global Change Biology 16: 946–963.

———. 2010b. Tropical land-cover change alters biogeochemical inputs to ecosystems in a Mexican montane landscape. Ecological Applications 20: 1820–1837.

Pringle CM. 2001. Hydrologic connectivity and the management of biological reserves: A global perspective. Ecological Applications 11: 981–998.

Quintero M, Wunder S, Estrada RD. 2009. For services rendered? Modeling hydrology and livelihoods in Andean payments for environmental services schemes. Forest Ecology and Management 258: 1871–1880.

Rundel PW, Smith AP, Meinzer FC, eds. 1994. Tropical Alpine Environments: Plant Form and Function. Cambridge University Press.

Salemi LF, Groppo JD, Trevisan R, de Moraes JM, de Barros Ferraz SF, Villani JP, Duarte-Neto PJ, Martinelli LA. 2013. Land use change in the Atlantic rainforest region: Consequences for the hydrology of small catchments. Journal of Hydrology 499: 100–109.

Schmidt SK, et al. 2008. The earliest stages of ecosystem succession in high-elevation (5000 meters above sea level), recently deglaciated soils. Proceedings of the Royal Society B 275: 2793–2802.

Stanton T, Echavarria M, Hamilton K, Ott C. 2010. State of Watershed Payments: An Emerging Marketplace. Ecosystem Marketplace. (9 August 2012; *www.forest-trends.org/documents/files/doc_2438.pdf*).

Thompson LG, Mosley-Thompson E, Brecher H, Davis M, León B, Les D, Lin P-N, Mashiotta T, Mountain K. 2006. Abrupt tropical climate change: Past and present. Proceedings of the National Academy of Sciences 103: 10536–10543.

Townsend AR, Asner GP, Cleveland CC. 2008. The biogeochemical heterogeneity of tropical forests. Trends in Ecology and Evolution 23: 424–431.

Tully KL, Lawrence D, Scanlon TM. 2012. More trees less loss: Nitrogen leaching losses decrease with increasing biomass in coffee agroforests. Agriculture, Ecosystems and Environment 161: 137–144.

Valiela I, Barth-Jensen C, Stone T, Crusius J, Fox S, Bartholomew M. 2013. Deforestation of watersheds of Panama: Nutrient retention and export to streams. Biogeochemistry 115: 299–315.

Van Dijk AIJM, Keenan RJ. 2007. Planted forests and water in perspective. Forest Ecology and Management 251: 1–9.

Vázquez G, Aké-Castillo JA, Favila ME. 2011. Algal assemblages and their relationship with water quality in tropical Mexican streams with different land uses. Hydrobiologia 667: 173–189.

Vitousek PM, Farrington H. 1997. Nutrient limitation and soil development: Experimental test of a biogeochemical theory. Biogeochemistry 37: 63–75.

Vitousek PM, Gosz JR, Grier CC, Melillo JM, Reiners WA, Todd RL. 1979. Nitrate losses from disturbed ecosystems. Science 204: 469–474.

Von Humboldt A. 1817. De Distributione Geographica Plantarum: Secundum Coeli Temperiem et Altitudinem Montium, Prolegomena. Kessinger.

Von Humboldt A, Bonpland A. 2009 (1817). Essay on the Geography of Plants. Jackson ST, ed.; Romanowski S, trans. University of Chicago Press.

Weathers KC, Ponette-González AG. 2011. Atmospheric deposition. Pages 357–370 in Levia DF, Carlyle-Moses DE, Tanaka T, eds. Forest Hydrology and Biogeochemistry: Synthesis of Past Research and Future Directions. Springer.

Weathers KC, Simkin SM, Lovett GM, Lindberg SE. 2006. Empirical modeling of atmospheric deposition in mountainous landscapes. Ecological Applications 16: 1590–1607.

Wilcke W, Günter S, Alt F, Geißler C, Boy J, Knuth J, Oelmann Y, Weber M, Valarezo C, Mosandl R. 2009. Response of water and nutrient fluxes to improvement fellings in a tropical montane forest in Ecuador. Forest Ecology and Management 257: 1292–1304.

Wohl E, et al. 2012. The hydrology of the humid tropics. Nature Climate Change 2: 655–662. doi:10.1038/nclimate1556

Young KR. 2009. Andean land use and biodiversity: Humanized landscapes in a time of change. Annals of the Missouri Botanical Garden 96: 492–507.

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