Project Summary – CWT VIIb

Overview: The southern Appalachian forest biome is responding to a series of past and ongoing disturbances including increasing hydroclimate extremes, higher temperatures, lengthening growing seasons, and continuing exurbanization. A suite of experimental manipulations, observational studies, social science analysis, and regional modeling will be conducted to understand how ecosystem responses to increasing hydroclimate variability are mediated by interactions and indirect effects involving competition, the complex topography, disturbance, and land use. The manipulative Future Forest Experiments (FFEs), conducted at plot, stream-reach, and watershed scales, will anchor the research program and create targeted forest compositions to examine how the five core ecosystem processes differ among current and likely future forest conditions. Socioecological research will explore how social networks within and beyond the focal region influence environmental knowledge, land use decisions, and environmental governance. These two research endeavors together will provide mechanistic understanding of interactions to be examined at regional scales using the RHESSys model framework adopted by CWT in 2007. Interaction theory serves as the conceptual framework for examining ecosystem dynamics, and the analytical means for quantifying interactions and indirect effects among the factors under investigation. This research builds on long-term monitoring within and beyond the Coweeta Basin that includes >20 years of tree demographic data representing >350,000 tree-years, and diverse spatially extensive physical, biological, and socioeconomic data with some record lengths exceeding 100 years.

Intellectual Merit: The proposed research will make important contributions to understanding how shifting climate and disturbance regimes affect the North American biome supporting the highest diversity and endemism of amphibians, mollusks, fish, crayfish, millipedes, fungi, and trees. Our multi-decadal data for five core ecosystem processes, collected across diverse geographic and temporal scales, will allow us to resolve paradoxical responses to climate and disturbance that suggest shifts in ecosystem states will be mediated by interactions and indirect effects rather than through direct effects alone. A major contribution is to use joint species modeling combined with interaction theory to predict ecosystem responses probabilistically without need for specific indicator species. This will be a novel contribution to the fields of Ecosystem Ecology, Community Ecology and Landscape Ecology. The networks that bind humans together are key to understanding decision-making, policy implementation, and social connections to ecosystems. Our research contributes by examining the topology of networks and their relation to knowledge under conditions of rapid landscape change in relation to the governance of environmental management. This will be a novel contribution to the fields of Political Ecology, Rural Development, and Communication Science. Empirical work has documented changes in species distributions through time as functions of diverse and interacting physical, biotic, and anthropic factors, but we will undertake distributed ecosystem modeling to examine temporal and spatial ecosystem dynamics across scales. Integrating understanding of how fine-scale ecological processes interact across past, present, and future land-use will be accomplished through large-scale modeling that will advance the fields of Ecohydrology, Regional Modeling, and Conservation Biology.

Broader Impacts: Findings from this research will guide ecosystem restoration and management by land management agencies and NGOs and also the development of water quality policies at multiple levels of governance. For instance, the Mainsprings Land Trust developed their "Shade Your Stream" public campaign based on results from CWT research. The proposed research will create education, training and engagement opportunities for diverse scholars, undergraduate and graduate students, students from 5th through 8th grade, and various segments of society within the greater southern Appalachian biome, including the Eastern Band of the Cherokee. Our field-based middle-school education programs will serve ca. 1,500 students per year from 14 public schools in the study region. Our in-classroom support materials provide ecological content for teachers that meet state curriculum standards to benefit approximately 2,500 students per year. Between two and six undergraduates will be mentored each year in REU positions, while graduate students enrolled in the Integrative Conservation (ICON) PhD program at the University of Georgia, which operates across Anthropology, Ecology, Forest Resources, and Geography, will collaborate with practitioners in southern Appalachia to transform research into public outreach. Finally, the Coweeta Listening Project publishes a bi-weekly newspaper column in a regional newspaper that translates and communicates community-relevant CWT LTER science.

1.0 Project Overview, *CWT VIIb.* *LTER: Examining long-term southern Appalachian ecosystem dynamics through interactions and indirect effects*

1.1. Introduction

Understanding how shifting climate and disturbance regimes affect ecosystems is a priority for global change research (NRC 2013, Vose et al. 2016). These shifts can have both immediate and long-lasting effects on primary production and accumulation of organic matter, distributions of species, trophic structures, and nutrient cycling. *Ecological and social scientists increasingly recognize that responses to changing climate depend on how species, landscapes, disturbance legacies, and human activities interact*. With eight decades of long-term data and research on forest composition, hydrology, climate, and human-landscape interactions, the CWT LTER can now evaluate such interactions and determine how past events and projected changes will shape future ecosystems in the montane deciduous forest biome of the southern Appalachians.

The Coweeta long-term record shows a trajectory of increasing extremes in annual and seasonal precipitation (i.e., hydroclimatic variability). Our overarching goal is to understand the effect of such climatic change, concurrent with human and natural disturbances, on future southern Appalachian forests, which are among the most productive and biologically diverse in North America. Our previous studies demonstrate paradoxical responses to climate and disturbance, and suggest that shifts in ecosystem states will be mediated by interactions and indirect effects rather than through direct effects alone. We propose a suite of experimental manipulations, observational studies, social science analyses, and regional modeling exercises to evaluate how increasing hydroclimate variation interacts with biotic communities and ecosystem services. We will utilize a synthetic framework developed under previous NSF -- interaction theory -- to quantify interactions and indirect effects (Clark et al. 2014b, 2016c) involving competition, natural disturbances, topography, and human activities. Interaction effects will also be evaluated by hydrologic and biogeochemical modeling, hierarchical modeling, and conceptual analysis for environmental responses not amenable to current interaction models. Our proposed investigations will provide mechanistic understanding of interactions that determine regional impacts of hydroclimate variation.

Our proposal is guided by four objectives. We aim to:

1) Leverage long-term data with new measurements to determine how fine-scale ecological processes and human disturbance interact across past, present, and future land use to affect forest structure, hydrologic behavior, biogeochemical cycles, and environmental risk over larger geographies.
2) Conduct forest composition experiments to evaluate key interactions and indirect effects of plants, soils, and animals that will control future ecosystem states.
3) Determine the human migration and land use decisions that result from the interaction of ecological knowledge, local and regional culture, governance, and land values.
4) Maintain and extend dialogues and continue our educational program with local communities to understand and influence social dynamics and land management activities.

1.2. Background

The exceptional biodiversity and productivity of the southern Appalachian biome is the product of orogeny, erosion, species radiation, and changing climate over geological time scales. The southern Appalachians feature the highest rainfall and water yield among the eastern United States biomes, and topographic complexity has given rise to a diversity of habitats, including mesic mixed hardwood forests, cove forests, wet riparian complexes, xeric and historically fire-prone ridgelines, and high-elevation boreal conifer forests. The region supports North America's highest diversity of amphibians, mollusks, fish, crayfish, millipedes, fungi, and trees as well as its highest levels of endemism (Stein et al. 2000, Kozak and Wiens 2010, Duellman 1999, Jetz et al. 2012, Sheldon 1988, Neves et al. 1997). The breadth of habitats provided by interactions between climate and topography has been a focus of ecological research at least since the classical writings of Lucy Braun (1950) and Robert Whitaker (1956).

Human activities have induced change through a succession of disturbances including extractive logging, agriculture, introductions of non-native pests and pathogens, fire suppression and nitrogen pollution (Fig.

1). Climate and legacies of past disturbances continue to affect the hydrology (Bain et al. 2012, Brantley et al. 2014, Leigh, in press), biodiversity (Mitchell et al. 2002, Cecala 2012, Kirsch and Peterson 2014) and forest and stream community composition and food web structure (Elliott and Swank 2008, Ford et al. 2012, Meyer et al. 2014). Disturbances, such as high-elevation residential development, valley urbanization, and climatic extremes are new drivers of change (Cecala 2012, Kirsch and Peterson 2014). Consequently, ours is an ancient biome supporting a young, fragmented, and highly disturbed forest.

The Coweeta LTER (CWT) project was established with the first LTER cohort in 1980 to build an ecological understanding of biotic and physical interactions that shape the Nation's most diverse forested biome. The core study area lies within the 1600 ha undeveloped USDA Forest Service Coweeta Hydrologic Laboratory which has been collecting long-term data since 1934. The regional component, added in 1994, extends studies to the surrounding rural and exurbanizing landscape. An overarching question has guided all CWT research: *How do natural disturbances, topography, climate variability, and human activities interact with ecological processes and ecosystem states in temperate montane deciduous forests?* Each funding cycle has emphasized different themes within this question (Fig. 1).

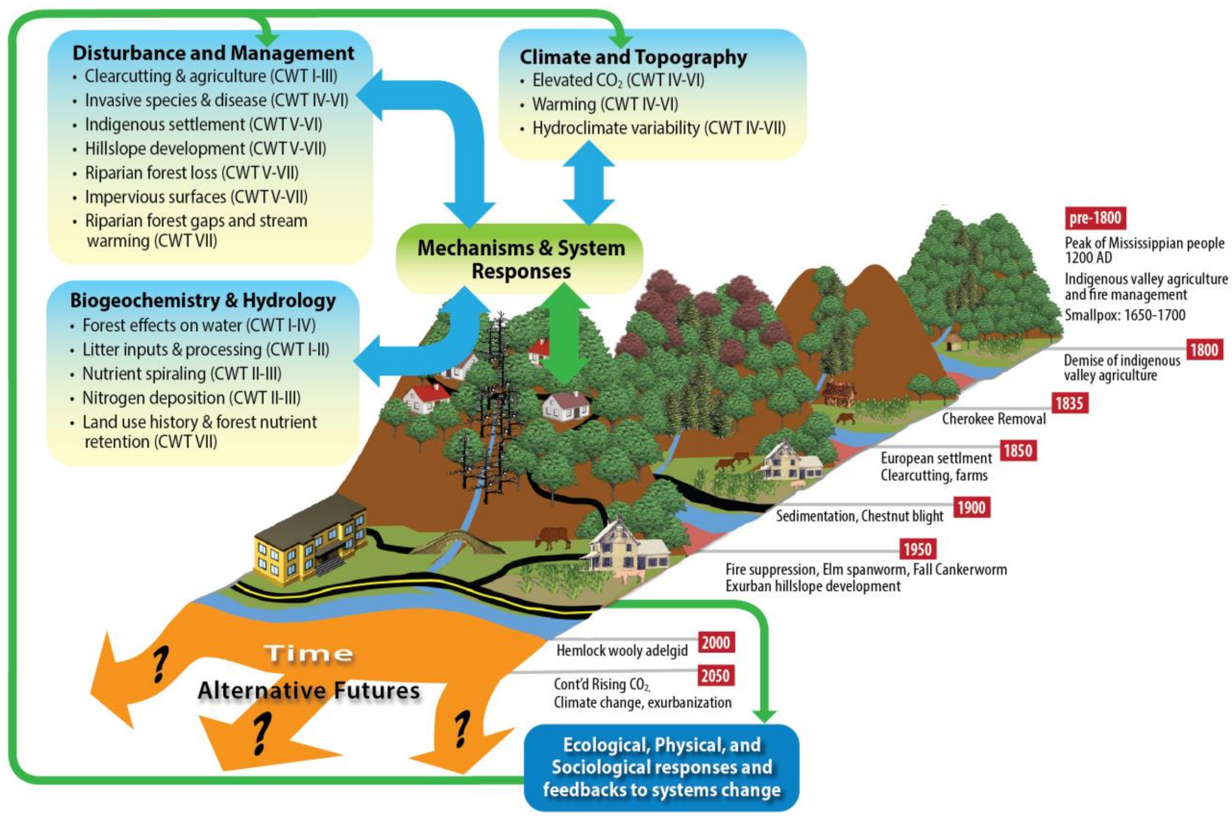


Figure 1**. **Conceptual framework guiding CWT LTER research. *Southern Appalachian ecosystems are unique in their antiquity, temperate biodiversity, high ecosystem productivity, and steep natural environmental gradients that have been continually modified by human disturbance. For 34 years, CWT has sought to understand how these historic and current human activities affect populations, biodiversity, biogeochemical cycling and other ecosystem processes and patterns. Early efforts determined the effects of forest clearing and agriculture on biogeochemistry, productivity, and hydrology (CWT I through III) (e.g. Swank and Webster 2014). Continuing research expanded our investigations of anthropogenic disturbances, to span the Holocene (CWT IV, V). Our long-term data sets have allowed us to analyze ecosystem response rates to disturbances and climate change and to discover surprises in the records (CWT VI). All of our work builds on the long-term observations of system behavior, but our research portfolio also includes short-term mechanistic and gradient studies that explicitly recognize the dominance of human activities over many states and processes, and the corresponding social and economic drivers (CWT V through VII).*

During its 35-year history as an LTER project, CWT has contributed to our understanding of climate, disturbance, and human impacts, from individual species and fine-scale processes to regional biodiversity and biogeochemistry, while accumulating some of the discipline's most important long-term data sets (Table 1, at bottom of document). Below we highlight key CWT findings that motivate our proposed work.

Historical agriculture and silviculture continue to have direct and indirect effects on terrestrial and aquatic ecosystems. The southern Appalachian biome has been transformed by millennia-long socioecological interactions, including valley bottom agriculture over the 19th century and extractive commercial forestry in the early 20th century (Fig. 1) (Gragson and Bolstad 2007, Gragson et al 2008, Bolstad and Gragson 2008). Past agricultural practices have decreased soil infiltration (Price et al. 2010) and increased the spatial heterogeneity of soil nutrients (Fraterrigo et al. 2005). In turn, these effects have altered soil microbial communities (Fraterrigo et al. 2006a), reduced forest herb density (Fraterrigo et al. 2006b, c) and increased overland flow (Price et al. 2010). Forest conversion to agriculture simultaneously reduces stream organic matter inputs and increases light, sediment and nutrient concentrations (Davis et al. 2010, Gulis and Suberkropp 2003, Gulis et al. 2004, Suberkropp et al. 2010, Harding et al. 1998, Webster et al. 2012a, Jackson et al. 2015), thereby reducing invertebrate diversity (Wallace et al. 1999). Even 40 years after agricultural abandonment, in-stream macroinvertebrate assemblages remain altered.

CWT's first large-scale ecological experiment demonstrated that forest logging can fundamentally change the nitrogen cycle. After 40 years of recovery, during which leaf area, aboveground biomass (Swank and Webster 2014) and forest water use (Ford et al. 2011b) returned to pre-treatment conditions, nitrogen export remains high, suggesting the transition from a biologically-controlled, nitrogen-retentive ecosystem to a hydrologically-controlled, nitrogen-saturated ecosystem (Webster et al. in press, Adams et al. 2014). This change to nitrogen cycling is likely due to inputs from black locust, a nitrogen-fixing species that dominated the ecosystem during early stages of recovery (Boring et al. 2014). Thus, our long-term studies on historical agricultural and silvicultural practices demonstrate strong and lasting effects of terrestrial ecosystem disturbance on aquatic biodiversity (Harding et al. 1998) and water quality.

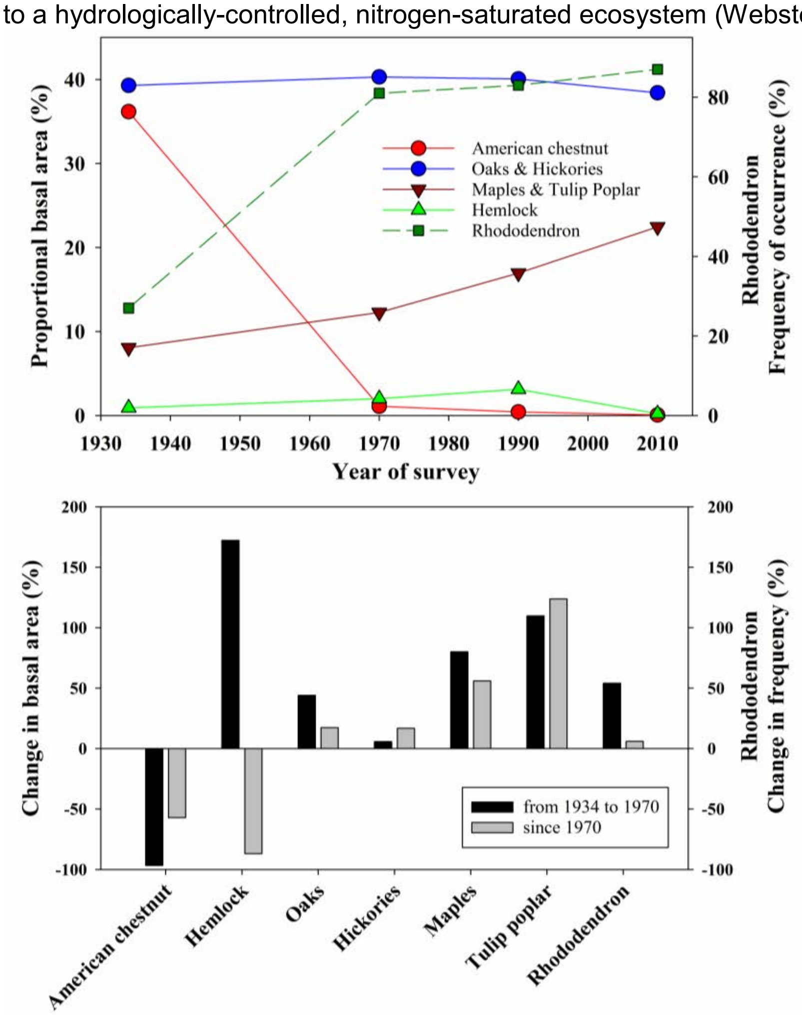


***Figure 2. Compositional changes for the dominant species grouped by functional type**. A) Proportional basal area for American chestnut, all oaks, all maples plus tulip poplar, and eastern hemlock on left y-axis; and frequency of occurrence for Rhododendron maximum on right y-axis (Elliott and Vose 2012). Only presence-absence data were available for rhododendron for the survey in 1934. B) Changes in basal area for the dominant species from 1934 to 1970 following the chestnut blight pandemic (Elliott and Swank 2008), and additional changes since 1970.*

Pest and pathogen-induced tree mortality has long-lasting effects on mass and energy flows throughout the ecosystem. In the 1920s–30s, chestnut blight fungus (*Endothia parasitica* (Murr.) P.J. And. & H.W.) led to widespread mortality of American chestnut (*Castanea dentata* (Marsh.) Borkh.) in eastern North America. Following mortality of this foundation species, mid-century southern Appalachian forests were dominated by xerophytic *Quercus* spp. but are now dominated by drought-intolerant, mesophytic species [e.g., red maple (*Acer rubrum* L.), and tulip poplar (*Liriodendron tulipifera* L.)] (Meyer 1927, Day and Monk 1974, Bauerle et al. 2006, Ford et al. 2011a, 2011b, Brantley et al. 2013, Caldwell et al., in review) (Fig. 2). These changes in species composition have coincided with declines in deep soil carbon (Fig. 3, Knoepp et al. 2014) and water yield (Caldwell et al. in review). Woody debris, a critical habitat and substrate for secondary stream production (Wallace et al. 1999), remains dominated by American chestnut 60 years later (Mattson et al. 1987) due to its slow decomposition. Stream woody inputs will eventually be dominated by mesophytic species that decompose rapidly (Wallace et al. 2001, Mattson et al. 1987).

Following the decline of American chestnut, Eastern hemlock (*Tsuga canadensis* L.) expanded substantially in riparian areas (Woods and Shanks 1959, Elliott and Swank 2008), but declined precipitously at the turn of the 21st century as a result of the hemlock woolly adelgid (*Adelges tsugae* Annand) invasion (Fig. 2). The mortality of hemlock now appears to favor the growth and density of rhododendron (*Rhododendron maximum* L.) over other woody species (Ford et al. 2012, Elliott unpublished data). While the loss of riparian hemlock has had direct effects on stream ecosystem woody debris, light transmittance, and temperature variation (Webster et al. 2012), the longer-term effects of hemlock loss on both terrestrial and aquatic ecosystems will likely depend on the interactions and indirect effects that manifest from the expansion of rhododendron (see below).

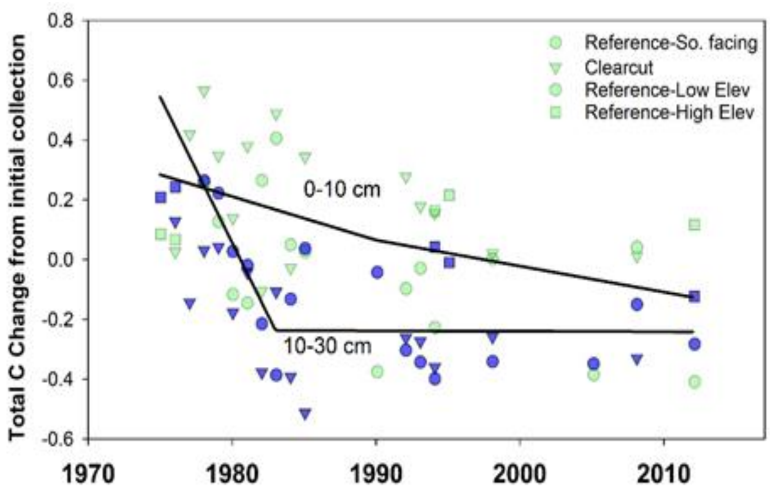


Figure 3 Long-term total carbon loss from both surface soil (0–10 cm or A horizon) (light symbols) and subsurface soil (10–30 cm or B horizon) (dark symbols). *Data represent proportional change from initial sample collection for all long-term watershed scale sample collections beginning in the 1970s. Watersheds include: south-facing low elevation reference (●, WS2, 1977–2008); south-facing clear-cut (▼, WS7, 1977–2008); north-facing low elevation reference (♦, WS18, 1970–2012); north-facing high elevation reference (■, WS27, 1974–2012).*

The CWT long-term record demonstrates warming and increases in hydrologic extremes. Our analysis identified the rise in hydroclimate variability (Ford et al. 2011), now recognized as a national threat (Vose et al. 2016b). Since 1975, CWT air temperatures increased 0.4 °C per decade, with minimum temperature rising earliest and most quickly compared to average or maximum temperature. Year-to-year variability in precipitation is increasing (Fig. 4). Rainfall seasonality has changed, declining in summer with more intense storms in autumn (Laseter et al. 2012). Warmer temperatures and drier summer conditions may expose regional forests to higher vapor pressure deficits, and greater atmospheric water stress (Hwang et al. 2011a and b, 2014). The region faces a future of increased hydroclimate extremes due to global shifts in temperature and atmospheric circulation, natural climate variability and teleconnections, and climate effects of regional urbanization (Li et al. 2012, NOAA 2013).

Although oak and hickory have been projected to dominate future forests, long-term CWT data demonstrate increasing dominance of maple and tulip poplar. General circulation models project that the region will experience warmer temperatures and more frequent and severe drought, trends consistent with our long-term climate data (Laseter et al. 2012). These climate trends would suggest a shift towards an oak-hickory (OH) forest (McEwan et al. 2011), in agreement with vegetation models (Iverson et al. 2004). However, trends in our long-term data contrast with these projections, and are more consistent with the proliferation of mesophytic species such as red maple and tulip poplar (MP) (Elliott and Vose 2012, McEwan et al. 2011, Caldwell et al. in review, Fig. 2), henceforth mesophication (*sensu* Nowacki and Abrams 2008). The reason for the lack of alignment between long-term records and climate models is unclear. While oaks are dominant in the region, their regeneration over the last century is lower than that of red maple and other mesophytic species (McEwan et al. 2011). Fire exclusion could explain recent decline in oaks (Abrams 1992, 1998, 2003). In the Coweeta Basin, tree recruitment has also been suppressed by the expansion of rhododendron, a consequence of American chestnut and hemlock loss.

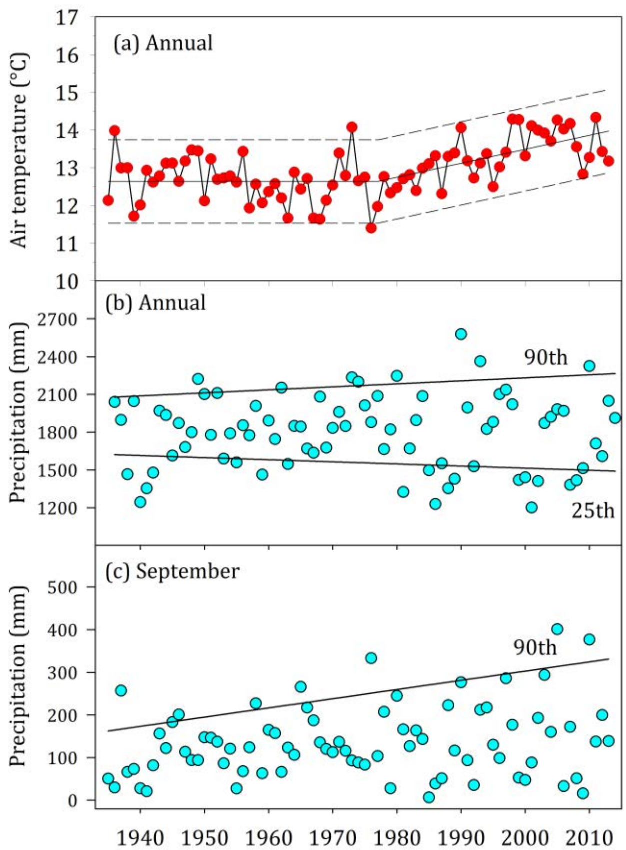


Figure 4. Select CWT climate trends. *CWT air temperatures have increased over time with minimum, average and maximum temps increasing in that order. Calculated from 1975, 1977, or 1987, temperatures have been increasing at the same rate of 0.4 degrees C per decade. No trend in the average precipitation over time is evident, but precipitation is becoming more variable over time, with wet years becoming wetter and dry years becoming drier. Summer months are becoming drier over time, while the fall months are becoming more wet. In September, only the most extreme part (>85%) of the distribution increased over time due to an increase in high intensity, shorter duration storm events, such as tropical storms, as opposed to an increase in the number of storms per month. (Laseter et al. 2012).*

Evergreen understory shrubs are expanding in the region at the expense of canopy tree regeneration. CWT research shows that the dense rhododendron subcanopy strongly attenuates light (Clinton 2003), suppresses herbaceous plants and tree seedlings (Clinton et al. 1994, Beckage et al. 2000, HilleRisLambers and Clark 2003), and reduces nitrogen availability in the soil mineral and organic horizons (Wurzburger and Hendrick 2007, 2009). Our long-term forest demography data suggest that a chain of disturbances -- starting with widespread logging in the 19th century, the loss of American chestnut, and finally the hemlock woolly adelgid invasion -- led to a cascade of overstory, midstory, and soil responses that permitted an expansion of rhododendron (Fig. 2). Therefore, the response of future forests to hydroclimatic extremes may depend on these tree-shrub interactions that manifest through disturbance legacies and indirect effects.

Ecosystem services of the region will depend on the interactions of climate, species, topographic position and land use. The 23-year long-term forest demographic (LTFD) network has demonstrated that drought effects manifest through indirect effects and interactions. Thus, interaction theory was developed to evaluate such climate-competition connections (Clark 2010, Clark et al. 2010). Drought appears to benefit oak species in ridge sites due presumably to reduced water use from less drought tolerant species (Clark 2010, Clark et al. 2010, 2011b, 2012b, Dietz and Clark 2008). The negative effects of drought via interactions and indirect effects are amplified in areas of high light and moisture, such as cove habitats. Thus the effects of warmer temperatures and increased likelihood of drought are expected to differentially impact tree communities based on their topographic position. At the basin and regional scales, these species responses may give rise to different patterns in water yield.

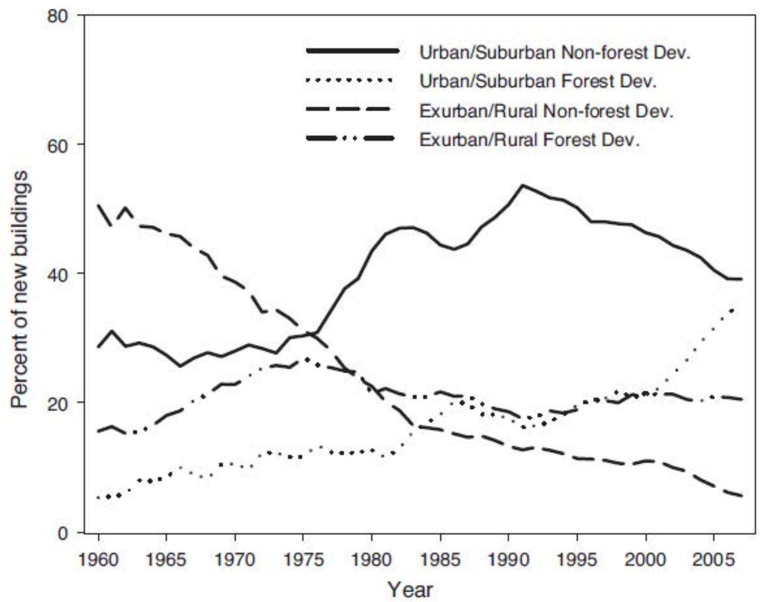


Fig. 5. Development type of new buildings in Macon County, NC, 1960–2007. *Non-forest development indicates new building in areas <70% forested, while forest development denotes new buildings in areas 70% forested. All values are smoothed 5-year moving averages. (Kirk et al. 2012).*

Mixed environmental knowledge affects land use, environmental governance, and landscape vulnerabilities. Over the last 40 years, exurban development in forested areas has steadily increased in our study area (Fig. 5). Half of all new construction now occurs in forested areas (Kirk et al. 2013) with many new residents moving to the region to enjoy environmental amenities. Migration and development not only directly contribute to amenity degradation but indirectly mitigate their effects. The mixing of local and extra-local environmental knowledge leads to changes in governance that place pressure on local policy makers to increase environmental regulations to preserve environmental amenities (Burke et al. 2015a, Rice et al. 2015). However, they also affect local efforts to adapt to climate change by redistributing vulnerability to ecological hazards (floods, landslides, fire) across the region (Gustafson et al. 2014, Verco et al. 2014, Rice et al 2015).

In summary, two major themes emerge from our long-term work and motivate our current research interests: *i*) hydroclimate extremes now represent the dominant climate transition for this region, and *ii*) anticipating the impacts of such effects requires a synthetic effort across scales that captures interactions and indirect effects of climate, topography, disturbance, and human activities.

1.3. Results of Prior Support, CWT-VI and CWT VIIa, 2008–2016, 2009–2015 products highlighted

CWT-VI (2008–2014) and CWT-VIIa (2015–2016) involved 28 Project Investigators and 12 Affiliated Investigators from nine institutions. During this period, we published 354 peer-reviewed publications, one book, 11 additional book chapters, and 44 theses and dissertations. In the review below, we highlight ten signature publications (*italicized*) reflecting project breadth. Supplement-supported activities are denoted by (S*). Our cumulative total from 1980 through 2015 is 1308 publications along with 268 theses and dissertations. Leveraging to support the CWT-VI and VIIa awards came from NSF, NASA, PUF, USDA, USGS, and our participating units.

Our CWT-VI and VIIa studies employed a regional geographic scope to evaluate how water quantity, water quality, and biodiversity were affected by a) changes in temperature, precipitation, and streamflow; b) interactions involving land use and climate and their effects on biodiversity and ecosystem processes; and c) transitions in land uses from wildland to urban and peri-urban. We conducted long-term data synthesis and scaled integration of ecosystem knowledge through the Regional Hydro-Ecologic Simulation System (RHESSys) modeling framework. Here we synthesize our 2009–2015 results as they motivate our current work, emphasizing how paradoxical responses are understood through a focus on interactions and indirect effects.

Long-term Climate and Flow Analysis: Eighty-five years of climate and streamflow records revealed increasing air temperature, and increasing precipitation and streamflow variability since 1980 (*Ford et al. 2011b*, Laseter et al. 2012),. Hydrologic modeling indicates that current trends will lead to reduced soil moisture in summer and fall at both low and high elevations, uncertain changes in summer streamflow, and increased streamflow in winter (Wu et al. 2011, 2012). These observations, combined with past CWT projects on disturbance, biogeochemistry, and populations, show interactions may govern ecosystem response to land use and climate changes and motivate our new research directions.

Land Use Change and Climate Change Impact Ecosystem Processes and Biodiversity: Our long-term watershed 7 study (*Swank and Webster 2014*) demonstrated that forest disturbance and succession can produce long-term changes in biogeochemical regimes. Road construction and logging in this watershed exported more than 70 metric tons of sediment (*Swank and Webster 2014*). To understand the larger biome, we needed regional data to put these findings in perspective. CWT VI research advanced our knowledge of how development patterns and practices affect water quality. For example, increasing steep-slope development disproportionately increases stream nitrate levels (*Webster et al. 2012b*), urban development increases debris flow, runoff and erosion hazard (*Kirk et al. 2012*), and forest conversion to agriculture has reduced infiltration, soil storage, and hence baseflow (Price and Leigh 2006a, b, Leigh 2010, *Price et al. 2010*, 2011).

Land use legacies and contemporary landscape patterns interact to affect invasion biogeography and understory herb diversity (Albright et al. 2009, Anderson et al. 2013, *Kuhman et al. 2013*), which can accelerate soil carbon loss (Bradford et al. 2012, Strickland et al. 2010, 2011). Spatial heterogeneity in disturbance and resource availability affects the dispersal, persistence, and abundance of native and non-native plants (Fraterrigo et al. 2009a, 2009b). For example, past agricultural land use supports the largest populations of invasive plants (Kuhman et al. 2011). Invasibility is high in areas with thin leaf litter, high soil moisture, and abundant tulip poplar (*Kuhman et al. 2013*). One of the common invaders, non-native Japanese stiltgrass (*Microstegium vimineum* (Trin) A. Camus), accelerates carbon cycling and soil carbon loss via priming effects (Bradford et al. 2012, Strickland et al. 2010, 2011). However, increased nitrogen availability associated with intensive land use can reverse this pattern, and lead to soil carbon accretion by suppressing exoenzyme activites (Craig et al. 2015).

Climate change is shifting interactions between biotic and abiotic processes within ecosystems**.** Such interactions include plant species responses to temperature, drought, and competition for light and moisture. Spring leaf-out is occurring earlier than in previous decades due to warmer spring temperatures. Leaf senescence arrives earlier following growing season droughts at rates that depend on elevation (Hwang et al. 2011a and b, *2012*, 2014). These temperature-moisture interactions have impacts that vary widely between tree species and size classes. 2012).

Clark et al. (*2013*) developed the dynamic inverse prediction framework for quantifying interactions among drivers and responses in complex high-dimensional systems, and this framework is a key conceptual and analytical foundation of our proposed research. *Clark et al.* (*2013*) used this framework to show that the most important variables for forest change at individual scales can be extended to explain patterns at continental scales (Zhu et al. 2012, Zhu et al. 2014). Ecological theory cannot explain high diversity of communities where competition is intense. Models predict low diversity, as the best competitors drive all others to extinction. Our work has revealed that high biodiversity can be maintained by interactions and indirect effects that involve temperature, drought, and local moisture availability (Clark 2010, Clark et al. 2010, 2011b, 2012b, Dietze and Clark 2008, Uriarte et al. 2012). Individual trees respond most like other trees of the same species, a mechanism that concentrates competition within species (Clark 2010, Clark et al. 2010, Clark et al. 2012a, b, c). Interactions involving climate and competition also control understory plant abundance, reproduction and growth across gradients (Warren 2009, Warren and Bradford 2010). Interactions between native and nonnative understory species vary systematically with climate (Fraterrigo et al. 2014). Cold-air drainage from high-elevation to valley bottoms can suppress temperature and increase net ecosystem productivity (Novick et al. *under review*). These findings motivate the regional observation network and Future Forest Experiments proposed below.

Land use change and climate change affect biodiversity of higher trophic levels. Increasing mountainside development reduces habitat for interior-forest neotropical migrant bird species (Lumpkin et al. 2012, Lumpkin and Pearson 2013). These species appear vulnerable to warming and increased nest predation, open forest canopies, and increases in predatory mammals common in residential areas. Fish, salamanders, and stream macroinvertebrates decline when riparian forest is removed (Cecala 2012, Kirsch and Peterson 2014, Frisch in press). Salamanders are the dominant vertebrate predators in headwater and first order streams, and they accelerate nutrient recycling through their effects on macroinvertebrate abundance and community composition (Milanovich et al. 2015, Kietzer and Goforth 2013a, b). Experimental small gaps in the riparian forest canopy create behavioral or abiotic barriers to in-stream movement (Cecala et al. 2014) that may reduce salamander abundance within developing watersheds. A shift in ant distribution to higher elevations is best explained by minimum temperature tolerance (*Warren and Chick 2013*). Community composition of herb species depends on interactions involving elevation, competition with other herbaceous species, the presence of ants, and land use legacies (Jackson et al. 2012).

Parcel- to Regional-level Land Use Change and Decision Making: The Piedmont Megapolitan region and its "Ring of Asphalt" (Shepherd et al. 2013) surrounding our biome is rapidly urbanizing (*Gustafson et al. 2014*) (S*). Former agricultural lands are fragmented by residential developments that increase surface runoff and stream sedimentation (*Price et al. 2010*, *Kirk et al. 2012*). Although landowners value healthy streams and regard "stream muddiness" as a pressing issue, they also regularly remove riparian vegetation and large woody debris from streams on their properties (S*) (Evans 2013, Jackson et al. 2015). Landowner activities thus narrow and simplify channels and decrease wood loading (Jackson et al. 2015, Jensen et al. 2014), which may exacerbate stream biogeochemical responses to increased nitrogen concentrations from agricultural and residential areas (*Webster et al. 2012b*, Evans 2013). Our work also addressed relationships among awareness of ecological services, risk, and community actions. A willingness-to-pay survey (Allen and Moore, in press) found 86% agreement among the Macon County population for "an ordinance to monitor mountain slope development"; however, the trade-offs of implementing such regulation remain unresolved (*Gustafson et al. 2014*, Vercoe et al. 2014). Private conservation increases land prices by creating amenity effects and removing land from a market that distinguishes between conservation in fee versus conservation in easement (Chamblee et al. 2011; Chamblee et al. 2015) (S*). A better understanding of how and where people will develop the landscape is crucial to the ongoing RHESSys modeling adopted by CWT in 2007.

Synthesis and Scaled Integration: Motivated by long-term work at the Harvard Forest LTER, we expected that rapid hemlock loss in southern Appalachian forests would lead to reduced watershed nitrogen retention (Elliott and Vose 2012, Ford et al. 2012). However, our long-term experiments show that soil nitrogen retention did not change as a result of hemlock mortality (Knoepp et al. 2011) even in high elevation stands that receive substantial nitrogen deposition (Block et al. 2012). Instead our studies revealed a decoupling of nitrogen deposition and ecosystem nitrogen fluxes, due in part to the indirect effects of increased growth by other tree taxa and an alleviation of phosphorus limitation (Ford et al. 2012, Block et al. 2013). In addition, while hemlock mortality initially caused declines in aggregate root respiration (Nuckolls et al. 2009), our ongoing long-term studies (10 years post-disturbance) show that increased belowground carbon allocation by the new forest accelerated soil carbon cycling and, non-intuitively, increased soil carbon storage in topsoils (Fraterrigo and Ream, unpublished data).

Our work has revealed cascading ecosystem effects of hemlock loss. Hemlock mortality reduced soil carbon pools and fluxes in the short-term (Nuckolls et al. 2009, Ford et al. 2012); caused initial reductions in forest water use followed by increases (Ford and Vose 2007, Brantley et al. 2013, 2014); reduced decomposition (Ball et al. 2008); and caused changes to nutrient cycling that were dependent on the presence of rhododendron (Knoepp et al. 2011, Block et al. 2012, 2013). Stream responses to hemlock loss are manifested through a cascade of forest species changes, which affect the quantity and quality of particulate organic carbon (POC, Wallace et al. 1997 Wallace et al. 2015), hydrology and stream chemistry (Knoepp et al. 2014, Qualls et al. 2014, Meyer et al. 2014), and stream production (Cross et al. 2007). Increases in riparian rhododendron growth and density after hemlock loss decreased microbial and invertebrate diversity and litter decomposition rates (Kominoski et al. 2009, Kominoski and Pringle 2009). Light incident on streams increased following hemlock loss, increasing trophic processing (Webster et al. 2012a) and shifting stream metabolism towards greater heterotrophy (Northington et al. 2013). Forests dominated by evergreen versus deciduous species have markedly different hydrologic responses to extreme precipitation, due to differences in species' sensitivity to climate variability (*Ford et al. 2011b*). This, plus work from previous LTER cycles (Wallace et al. 1997, HilleRisLambers and Clark 2003, Meyer et al. 2014) motivates our proposed riparian rhododendron manipulations.

Experimental nutrient additions revealed that litter breakdown depends on interactions between streamwater nutrients and litter quality (Manning et al. in press). Streamflows and water temperature interact with biogeochemical processes to affect carbon retention and breakdown rates of POC in streams (Rosemond et al. 2015, Manning et al. 2015). Flow and temperatures in turn depend on upslope forest composition and climate. These interactions among forest composition, leaf litter quality, stream nutrients, and stream processes motivate our proposed whole-watershed manipulation of forest cover in our Future Forest Experiments and the hillslope to basin-scale ecohydrological modeling.

Ecohydrological models provided new insight on dynamics of water, carbon, and nitrogen in watersheds of the Little Tennessee River Basin. The RHESSys model of hillslope hydrology, biogeochemistry, and productivity (Tague and Band 2004, Hwang et al. 2009) predicts the largest differences in hydrologic behavior among forested watersheds will occur in winter because high summer evapotranspiration disconnects hillslopes and streams (*Hwang et al. 2012*). A potential shift to more frequent landslide deposition into streams is exacerbated by recent increases in extreme precipitation events (*Band et al. 2012*) and expansion of rhododendron, which reduces net soil cohesion due to its weak root tensile strength and shallow root distributions (Hales et al. 2009). Coupling a stream metabolism model with RHESSys (Lin 2013) allowed us to integrate terrestrial and stream effects on timing and magnitude of water and nitrogen inputs. Nitrogen export is especially sensitive to in-stream processes when terrestrial inputs are low; whereas high nitrogen loading overwhelms in-stream processes (Lin and Webster 2013). This is consistent with our experimental observations from the long-term Watershed 7 manipulation (*Swank and Webster 2014, section 1.2*). We are extending the model to predict the effects of mountainside development on nitrogen export in the Little Tennessee River, and to evaluate the roles and interactions of residential development and buffer zone protection in nitrogen export (Lin 2013).

Education and Outreach: We developed educational activities in the Coweeta LTER Schoolyard program (S*) that met state curriculum standards and have created numerous opportunities for students and teachers. We have held 105 events since 2009 engaging 9,027 students from 17 schools across three states. Signature events included "Migration Celebration" and "Kids in the Creek", organized in partnership with Mainspring Conservation Trust, Southern Appalachian Raptor Research, USFWS, NC Natural Heritage Program, NC Wildlife Resources Commission, NC Division of Water Resources, Great Smoky Mountains National Park, Hiwassee River Watershed Coalition, and Watershed Association of the Tuckasegee River. Our Science Study Boxes, filled with science equipment and activities covering diverse topics, served over 13,000 students in western North Carolina and north Georgia. In coordination with the USDA Forest Service Coweeta Hydrologic Laboratory, we offered 282 tours and events to 3,780 people for a total of 1,293 contact hours. In October 2015 we held a 1-day workshop attended by 45 land managers from state and federal agencies on the experiment proposed in the current proposal to help restore forests affected by hemlock woolly adelgid (see section 2.2.B). During three summers, area high school teachers with RET funding (S*) worked with CWT LTER researchers on curriculum development and student activities. Six REU-funded University of Georgia students (S*) worked with CWT LTER researchers on projects examining salamander predation, climate effects on fauna, and citizen-science engagement in North Carolina, and an ILTER project in France. The Coweeta Listening Project (CLP), established in 2011, translates CWT science for diverse audiences. CLP publishes a bi-weekly column in a local newspaper under the by-line "Science, Public Policy, Community" to foster community connections and awareness of CWT research. The CLP helped create a partnership with Mainspring Conservation Trust to identify vulnerable streams for use in public education, and collaboratively developed the *Southern Appalachian Stream Visual Assessment Protocol* (saSVAP), a citizen science tool. A local high school student tested saSVAP through a summer RAHSS (S*).

Cross-site and Collaborative Activities: The *Long-term Forest Demographic (LTFD) Analysis* network was established in 1991 in the Coweeta Basin as part of CWT III (*Terrestrial Gradient Plots* see Facilities) to understand how climate and competition interact to control change in eastern forests (Clark et al. 1998, Clark et al. 2004). These plots were supplemented in 2002 with the *Gap Plots* in the Coweeta Basin (see Facilities), and the network now includes scientists from eight institutions, three LTER sites (CWT, HFR, LUQ), and other sites across eastern North America and Central America. Observations are made at member sites on natural variation in space and time that are combined with experimental manipulation of competitive environments. Analysis of LTFD data showed that tree populations are not migrating as rapidly as their putative climate envelope (Zhu et al. 2012, 2014). Large-scale experiments along CWT elevation and moisture gradients confirm that competition neutralizes effects of warming for potential migration (Ibanez et al. 2007, 2008, 2009). Competitive limitation of expansion is pervasive and strongest for abundant, not rare, species (Zhu et al. 2015).

CWT LTER scientists participated in the Lotic Intersite Nitrogen Experiment (LINX I and LINX II) with members of eight other LTER sites and demonstrated the role of streams in watershed nitrogen export (Mulholland et al. 2008, Hall Jr. et al. 2009, Mulholland et al. 2009, Bernot et al. 2010, Helton et al. 2010, Johnson et al. 2013). Cross-site research initiatives developed at the 2012 All Scientists Meeting in which CWT LTER scientists participated include: *Legacy Effects*, which quantified pre-instrumental signals in sediment and material flux from catchments across the LTER network (Bain et al. 2012); *QUEST*, which quantified sources of uncertainty in streamflow and chemistry across LTER and non-LTER sites (Yanai et al. 2015); and *Clim-Hydro*, which focused on social and ecological responses to climate change and land use effects on water availability across LTER sites (Jones et al. 2012, Creed et al. in 2014). The CWT LTER and GCE LTER Information Managers also partnered (S*) to document the use of the GCE Data Toolbox, and then hosted a training workshop for 15 information managers from 11 LTER sites (Chamblee et al. 2013). Now nearly half of the Information Managers across the LTER Network use the Toolbox for some aspect of information management at their site.

CWT-affiliated scientists are also engaged in a cross-site comparison with HBR involving the population ecology of long-distance migratory birds. Populations of many species of migratory birds with northern breeding distributions are stable at Hubbard Brook but declining at CWT, which is at or near the southern edge of their ranges. Food abundance (primarily caterpillars) and phenology differ between the two sites. As CWT experiences earlier leaf emergence and warmer, drier summers, we expect stronger effects of hydroclimate variability on tri-trophic interactions between trees, herbivorous insects, and insectivorous birds at CWT relative to HBR.

2.0 Proposed Research

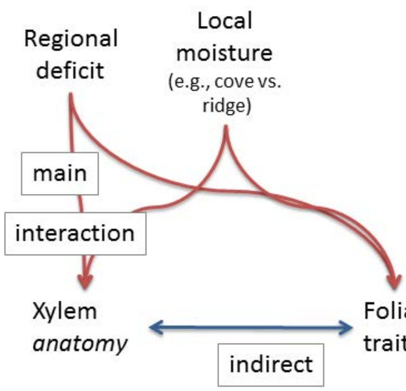
2.1. Introduction

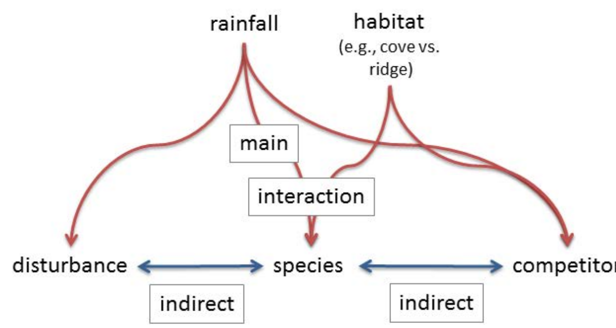
Building on past work, our proposed research focuses on how increasing hydroclimate extremes affect forests already shaped by human and natural disturbances (IPCC 2013, Melillo et al. 2014, Vose et al. 2016). More frequent and prolonged summer drought, with rainfall concentrated in fewer events, will impact the southern Appalachian biome at all levels. Our ecological understanding of ecosystem response to disturbances motivates our new research, where we propose to quantify key interactions and indirect effects that determine how hydroclimate extremes and human activities affect southern Appalachian forests. In Section 1.3 we discuss how interactions and indirect effects are implicated in every study, including human responses to hydroclimate variability. The three elements of our proposed research, Future Forest Experiments, Socioecological Interactions and the Regional Interactions Effort, each confront the challenges of multiple interacting forces.

Interaction theory, developed under previous funding, decomposes effects of climate variability into *direct* and *indirect* effects, the latter filtered through their influence on multiple response variables (Fig. 6). The interactive effects of two variables on a response can be hard to quantify, requiring that both predictors vary. The example of trait responses to regional climate and local moisture in Figure 6 are expected to include ***interactions***. For example, plant traits that confer drought tolerance might be widespread in dry climates, but limited to ridgelines in mesic climates. Quantifying the interaction requires that data sets include the relevant combinations, mesic and xeric sites in different climate settings. ***Indirect effects*** arise when the response of one variable depends on responses of others. If drought tolerance benefits both from ring-porous xylem anatomy and low foliar nutrient concentrations, then distributions of the two traits respond indirectly to each other. The strength of interaction theory comes from the joint decomposition of effects into main effects, interactions, and indirect effects for an arbitrarily large community of species or network of processes (Figs. 7 and 8). Formal inference through Generalized Joint Attribute Modeling (GJAM, Clark 2016 a, c, Clark et al. 2013, 2014b) allows for probabilistic prediction. Our proposed research will quantify indirect effects and interactions from long-term observational datasets, from the responses of manipulative studies, and through hierarchical modeling, ecohydrological modeling, and conceptual analysis for environmental responses not amenable to current interaction models.

Our proposed **Future Forest Experiments (FFEs)** consist of three manipulative studies that alter vegetation at different scales through targeted species removal and management practices. These experiments are designed to determine the consequences of future forest composition on species interactions within and across trophic levels, and ecosystem processes across the terrestrial-aquatic interface. Interactions and indirect effects play key roles in each component of our proposed research and create a predictive framework for how these local-scale processes give rise to patterns in biodiversity, productivity, and water quantity and quality at the regional scale.

Figure 6. Conceptualization of interactions and indirect effects. *Interaction theory quantifies direct effects and indirect effects, the latter requiring a joint distribution. At left, we illustrate main effects of drought and interactions and indirect effects with site characteristics, xylem anatomy, and foliar traits. Right, we consider main effects of hydroclimate and habitat on species and also indirect effects of competitors and disturbance.*





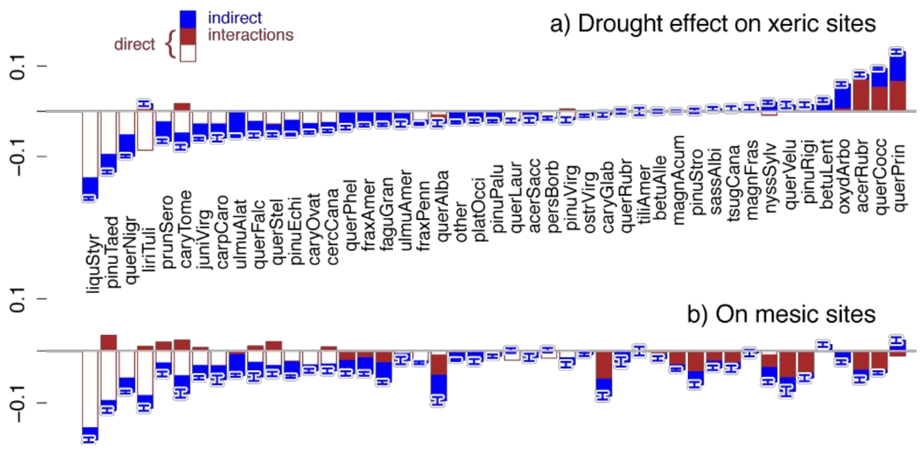


Figure 7. Effects of regional moisture deficits on the joint growth response (y axis) of 45 tree species (x axis) in the Southeast*, showing contributions of main effects (white bar), interactions (red bar), and indirect effects (blue bar) on a) xeric and b) mesic sites. To facilitate comparison, species are ordered by full effect. Ninety-five percent credible intervals are shown only for indirect effects to reduce clutter.*

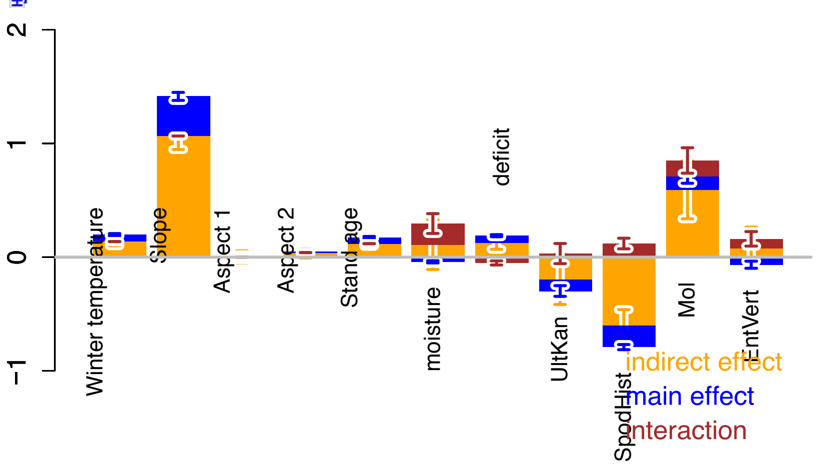


Figure 8. Example of interactions of environmental variables on growth of ring-porous xylem species*. Benefit of* ***moisture*** *comes from interactions (red) and indirect (yellow) effects. The* ***Slope*** *effect is main and indirect.*

The **Socioecological Interactions (SI)** will examine how people and places outside the focal region (i.e., extralocal linkages) interact with local belief systems and landscape processes to determine land use policies and practices. We will determine whether new immigrants and long-term residents acquire and use environmental knowledge in different ways. Our objective is to understand how human perceptions of increasing flood, drought, fire, and landslides affect landscapes indirectly, through the choices people make about where and how to live, work, and recreate. This work will also be used to inform the regional modeling efforts.

The **Regional Interactions Effort (RIE)** will utilize an array of data sources and observational networks to model ecosystem processes across space and time. This effort will incorporate CWT's long-term hydrologic, climatologic, and land use data, in conjunction with new data from the FFE. It will also expand the regional scope of these findings to determine whether the predictions from interaction theory, parameterized from experiments, are realized at regional scales.

The FFEs are critical for disentangling species-specific determinants of ecosystem functioning as well as predicting future ecosystem services. The Socioecological Interactions will provide necessary insight into how changing regional demographics affect the decision-making processes related to land use and ecosystem services. Together, FFEs and SI provide an empirical foundation for the Regional Interactions Effort that will integrate long-term and new observations on hydrology, climate, and land use with local-scale interactions to predict ecosystem services under climate and land use scenarios.

2.2. The Future Forest Experiments (FFEs)

Eighty years of research at Coweeta have documented fundamental changes in forest composition and structure, due to the irreversible loss of key species and the spread of an evergreen shrub understory. Not only are these forests still recovering from past disturbances, they are now responding to increasing hydroclimate extremes. Of particular interest are observations of forest composition change that do not match those predicted by coupled climate-vegetation models. Our proposed research is motivated by this discrepancy and seeks to understand contrasting alternatives in future forest composition, where many forest stands will be dominated by oak and hickory (**OH**), or by maple and tulip poplar (**MP**), with and without a rhododendron shrub layer. We expect that these future forest scenarios will result in interactions and indirect effects among soil microbiota, and trees and shrubs. These interactions and indirect effects will also play across higher trophic levels and ultimately manifest in divergent patterns in water dynamics and biogeochemical cycles. These effects, which originate from changes in the terrestrial ecosystem, will further affect water quality and quantity and downstream processes. The FFEs are designed to disentangle species-specific determinants of ecosystem functioning including their interactions and indirect effects, and allow for the prediction of ecosystem services under potential future forest scenarios.

We propose three FFE experiments, summarized next.

FFE1 will determine how alternative future forest composition will affect ecological, hydrological, and biogeochemical processes, by quantifying interactions and direct and indirect effects among hydroclimate variability, competition, and topography. We will alter the composition of reference forests by thinning overstory trees to produce forests composed of only oak and hickory species (**OH**), mesophytic species (**MP**), evenly thinned (**TH**), and unthinned (**C**) in a blocked, replicated, plot-level (2-ha) experiment (Fig. 9, top). This study will allow us to isolate the effects of tree species on localized, fine-scale relationships between plants and soils and resulting effects on biogeochemistry.

FFE2 will determine how rhododendron—which is expanding due to past disturbance—alters resources, tree recruitment and demography, trophic structure, and terrestrial and stream ecosystem productivity through its interactions with light, soil moisture and microbiota, and soil biogeochemistry. This manipulation, initiated in 2015, cut all *Rhododendron maximum* stems (spring 2015) and will remove the forest floor (soil O-horizon) (spring 2016) in a replicated plot-level (0.04-ha) experiment in riparian or cove forests, and along 300 m stream reaches. This study allows us to target effects of the shrub layer on terrestrial and aquatic processes and their potential interactions.

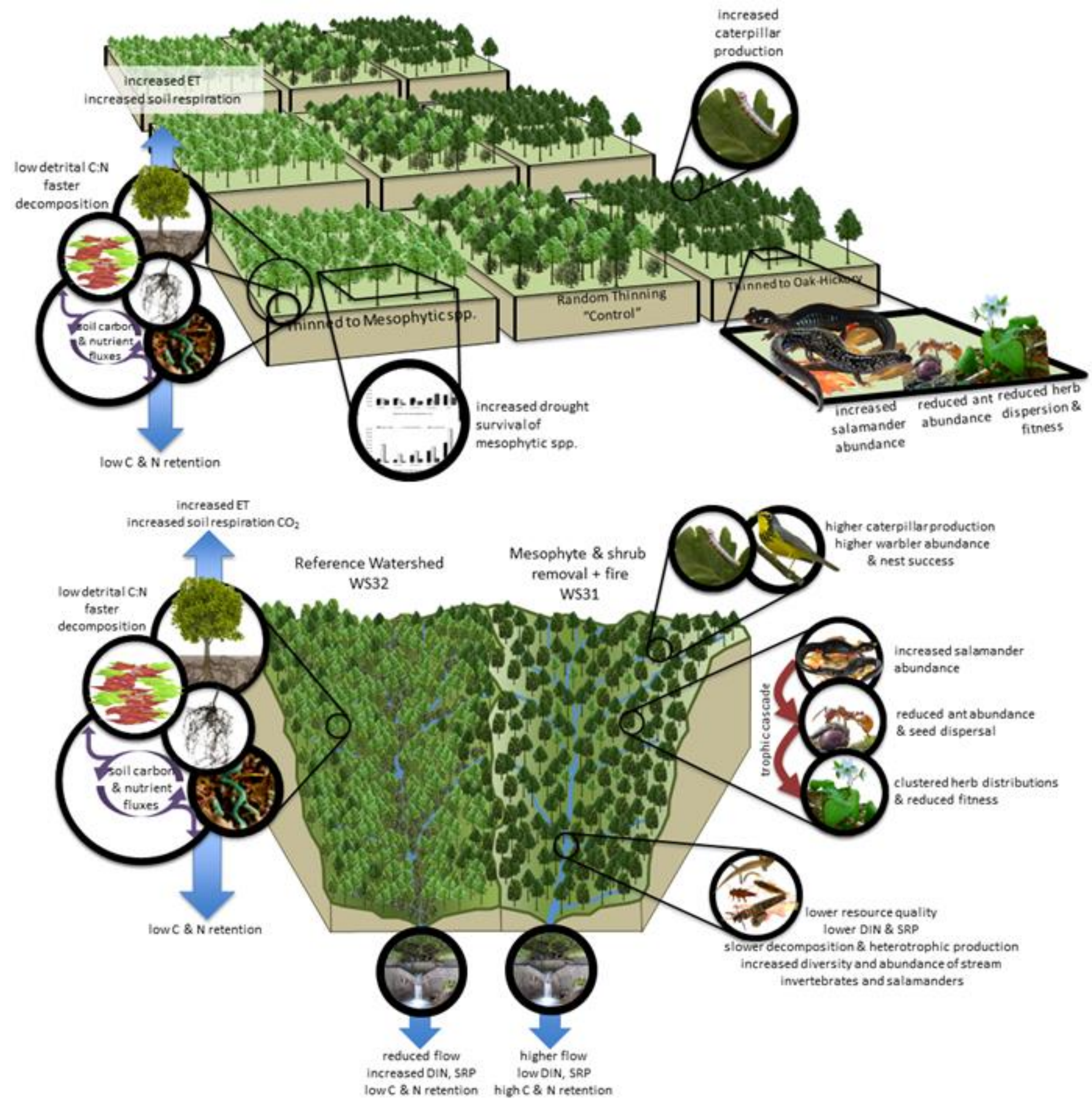


Fig. 9. FFE1 (above) and FFE3 (below) design and predictions. *Illustration of treatments, response variables, and predictions for the proposed FFE1 and FFE3 experiments.*

FFE3 will examine how future changes in forest composition might affect whole-system terrestrial and aquatic processes. This experiment represents a new, long-term paired watershed experiment with the goal of achieving an OH forest composition through management practices, while allowing the reference watershed to maintain its current trajectory of increasing mesophication (Fig. 9, bottom). This study allows for a powerful, long-term examination of the interactive effects of hydroclimatic variation and forest composition on watershed processes and fluxes, effectively linking small-scale mechanisms that govern patterns in FFE1 and FFE2 to ecosystem properties at a scale more relevant for regional upscaling.

2.2.A. FFE1, Plot-scale Forest Composition Manipulation: Following the loss of American chestnut, oak-hickory forests were expected to dominate the southern Appalachians (Keever 1953; McCormick and Platt 1980). The relative drought-tolerance of these species suggests that they will dominate a future characterized by increasing hydroclimatic variability (Iverson et al. 2004, Roman et al. 2015). However, our long-term vegetation data from across the Coweeta Basin show instead the expansion of red maple and tulip poplar. Potential explanations for this unexpected pattern include interactions involving climate, species loss and previous forest management (Abrams 2003, Nowacki and Abrams 2008, McEwan et al. 2011). While the mechanism is unknown, it is critical to understand how the current trajectory of forest communities (towards MP), and the predicted forest community (OH), may affect ecosystem services in different ways. These two alternative future forests are characterized by different plant traits that will directly and indirectly affect water use and productivity, biogeochemical cycling, competition dynamics, and trophic interactions. This experiment will address the following— **Will these alternative forest types differentially affect surface water supply, primary production and soil carbon storage? Do these forest types differ in their sensitivity to climate? And if so, how do competitive interactions in biodiverse forests offset the sensitivity of the ecosystem?**

We hypothesize that OH will exhibit lower water use, which leads to higher summer soil moisture than MP plots, with possible interactions and indirect effects among isohydric and anisohydric species in the TH plots. Ecosystem water cycling and primary production are largely determined by tree water use (Ford and Vose 2007, Bahari et al. 1985, Gholz et al. 1990). MP species are isohydric, closing stomates quickly during periods of hydrologic stress, but spending water at a high rate when it is available. Conversely, OH species are anisohydric and deeply-rooted (Bilan 1971, Abrams, 1990). They maintain open stomata during drought, and are conservative in their water use throughout the season. Anisohydric species (OH) may benefit from the reduced water uptake of their isohydric neighbors (MP) during periods of water limitation. Such effects may be amplified by variations in rooting depth and hydraulic redistribution (Dawson 1993, Nadezhdina et al. 2010). The ability of oaks to redistribute water from deeper to shallower soil (Ishikawa and Bledsoe 2000, Kurz-Bessen et al. 2006) may be of limited benefit in OH plots if soil moisture remains high, but may provide an important water subsidy to isohydric species in the TH and C plots.

We hypothesize that net primary productivity in MP will be more sensitive to hydroclimate variability than in other treatments. We expect net primary productivity to increase in all thinned plots (MP, OH, and TH), due to increased light availability and reduced competition for water. Since both tulip poplar and red oak have high potential for annual basal area growth, we do not expect differences in net primary productivity among treatments in wet years (Elliott et al. 2015). However, we expect prolonged periods of drought to reduce net primary productivity of isohydric species (MP) more than anisohydric species (OH) (Brzostek et al. 2015, Elliott et al. 2015) because anisohydric species can maintain higher stomatal conductance than isohydric species, allowing for greater carbon dioxide movement into leaves (Tardeau and Simonneau 1998, Attia et al. 2015).

We hypothesize that poor leaf litter quality and ectomycorrhizal fungal dominance will reduce rates of organic matter decomposition and heterotrophic respiration in OH relative to MP forests. Elemental cycling in these alternative forest communities may diverge due to different mycorrhizal associations, litter traits and microbial communities (Fig. 6, Phillips et al. 2013). OH tree species associate with ectomycorrhizal (**EM**) fungi, which produce extracellular enzymes that depolymerize soil organic matter and allow them to utilize organic nitrogen and effectively compete with decomposers for it (Orwin et al. 2011). By contrast, MP species have arbuscular mycorrhizal (**AM**) fungi, which scavenge mineral nitrogen and rely on, and even promote, the activity of decomposers (Cheng et al. 2012). In addition, EM tree species possess litter that is more recalcitrant than that of AM tree species. Differences with tree water use discussed above may complicate effects on soluble fluxes. Specifically, reduced water use by OH will increase hydrologic flux through the soil profile, thereby balancing the losses of soluble carbon and nitrogen in these two forest types. Thus, over the period of several years, the differences in the soil carbon balance may be more affected by the activity of decomposers than soluble fluxes in the two forest types.

We expect AM-tree seedling growth to be favored in AM-dominated stands (MP), and vice versa, because trees will promote favorable nutrient context for seedlings that rely on the same symbiotic associations. Communities with a mix of AM and EM fungi may favor the seedlings of species that can form both symbioses (i.e., oak species) buffering impacts of environmental change. Mycorrhizal symbioses will likely mediate tree seedling performance, depending on hydroclimatic conditions (*direct effect*) and mycorrhizal dominance of the forest community (*indirect effect*). For example, in contrast to EM seedlings, we expect AM-tree seedling growth and nitrogen acquisition to be more sensitive to drought because of their smaller mycorrhizal networks and strict dependence on free-living decomposers for mineral nitrogen. Indirectly, we expect tree seedling growth response to further depend on the mycorrhizal context of their community. We will conduct seedling censuses, manipulations, and measurements (described below) to test these ideas.

The contrast between predicted OH future and the observed MP trend suggests that canopy competition and its effects on recruitment could promote either future, depending on indirect effects. Competition will be studied within the canopy of treated stands, for its effects on understory species subjected to a treated canopy, and for its effects on recruitment, using both natural and planted seeds. Demographic evidence shows that growth and survival of oaks has been relatively insensitive to climate variation and local drainage (Clark et al. 2014a, Roman et al. 2015). However, during drought, oak mortality can be higher than many other species, particularly on xeric ridges (Clinton et al. 1993, 2003). Demographic rates of target individuals will allow us to quantify the direct and indirect effects of neighbor size and species identity, on growth, fecundity, and survival. We ask whether or not OH forests will be promoted by their ability to better compete with other OH species. Further, the direct and indirect effects of alternative canopies on recruitment could explain expansion of MP in the understory when most models predict shifts to OH. Similar understory light levels in OH and MP treatments, but higher moisture anticipated in OH, could benefit MP beneath not only MP, but also OH. However, despite slow growth, juvenile oaks tolerate shade. The interactions we will quantify include responses to low light, moisture, and drought—positive interactions would represent the type of amplification that can produce tipping points from forest to savanna (Clark et al. 2011a, 2012a). Indirect effects include responses of soil fungi that could release or inhibit oak seedlings/saplings and of canopy species, which use different amounts of water and have different mycorrhizal symbioses. The long-term forest demography plots (LTFD) provide an important reference for the FFE1 results, because they allow us to observe simultaneous year-to-year variation across gradients in elevation and moisture, with natural variation in OH and MP species.

We hypothesize that salamander abundance will decrease in forests dominated by fast-decomposition leaves (MP), and that declines in salamander abundance will increase ant abundance and herb seed dispersal. The food web response to alternative forest futures can be understood by focusing on the interactions among taxa that represent key trophic positions (Schmitz 2010). *Plethodon* salamanders are the most abundant and have the highest biomass of any predatory vertebrates (Semlitsch et al. 2014; Burton and Likens 1976; Hairston 1996), and they are extremely sensitive to changes in litter cover (Maerz et al. 2009, Pough et al. 1987). The primary prey of *Plethodon* are ants (*Aphaenogaster rudis*), which are the most abundant forest-floor insect (King et al., 2013) and the key seed dispersers of woodland herbs (Ness et al., 2009). Thus, differences in forest floor microclimate, litter quality and quantity, and leaf phenology will propagate to terrestrial trophic cascades that may feedback on the abundance and distribution of herb species.

We hypothesize that the effects of future forest composition on the phenology and quality of basal resources will propagate up the food chain to impact herbivores and consumers. The different timing of leaf emergence among OH and MP forests may create interactions for breeding birds via tri-trophic relationships with trees and caterpillars. We expect to see indirect effects of changes in tree species composition on birds through effects on their caterpillar prey. For example, leaves of Coweeta Basin oaks emerge, on average, 5–9 days later than those of red maple (Prebyl, 2012). Migratory birds nest as soon as they arrive in the spring, but often too late to take advantage of the earliest caterpillar emergences. Therefore, more caterpillars should be available for nestlings in OH forests than MP forests. Also, changes in tree species will interact with changes in climate to influence caterpillar abundance and phenology (Townsend et al., 2016). Some bird populations also will be directly reduced from loss of rhododendron, an important nest substrate for some species (Stodola et al., 2013). Therefore, while the loss of nesting habitat and reductions in basal area may decrease bird abundances in OH forests, the birds that remain may benefit from the later emergence of caterpillars, which may better coincide with the period that they feed their young.

Design and Measurements: We will change the composition of present forests by cutting overstory and midstory trees of certain species to produce forests composed of mesophytic maple-poplar (MP) or oak and hickory (OH) in a blocked, replicated, plot-level experiment. We will establish three replicate 2-ha plots of each forest type by cutting non-target canopy species (OH or MP), applying herbicide to cut stumps and mid-story non-target species, and allowing for recruitment of target species (Loftis 2004, Lewis et al. 2006). Based on our long-term, basin-wide census data, we estimate these treatments will reduce basal area by 35-40%. We will remove stems in the growing season of year two. Thinned reference plots (TH) will be thinned to a basal area equal to the treatment plots by cutting a representative distribution of canopy and midstory species and treating cut stumps with herbicide as above. In subsequent years we will apply herbicide to control advance regeneration of non-target species and emerging stump sprouts. Control plots (C) will not receive any thinning or manipulation. All replicate plots will be located in mid-elevation forest communities. Treatments will be maintained for at least a decade. The OH treatment is designed to produce an oak-savanna community that has been predicted by species distribution models (Iverson et al. 2004) and dynamic global vegetation models (Bachelet et al. 2003).

Micro-climate and vertical soil hydrological and biogeochemical fluxes will be monitored to understand the dynamic nature of transpiration water sources. In each replicate plot (n = 12) we will measure canopy air temperature and relative humidity, throughfall, soil moisture and temperature, and incident radiation on the forest floor. For 12 trees representing up to four dominant species, we will measure tree water use in all replicated plots, and root hydraulic redistribution in lateral roots with sapflow sensors in one set of replicated plots (Ford et al. 2011a, Burgess et al. 2001). Soil and herbaceous evapotranspiration will be estimated using four subcanopy eddy covariance systems owned by the Forest Service, deployed in one set of treatment plots. Tension lysimeters and a shallow (2-m depth) groundwater well co-located with sapflow-instrumented trees will allow a one-dimensional water budget through measurements of stable isotope ratios in soil- and groundwater water, as well as water table. Tension and resin lysimeters will allow measurements of dissolved organic nitrogen and carbon (DON, DOC), and dissolved inorganic nitrogen (DIN) and PO_4^{2-} movement within the soil profile. Water use efficiency of canopy and sub-canopy leaves of each tree monitored for sap flux will be determined at least twice during each growing season using isotopic methods described in Farquhar 1982). These water use efficiency estimates will allow us to derive estimates of gross primary productivity in each treatment plot, and will permit a quantification of the extent to which regulation of water use efficiency decouples photosynthesis and transpiration in isohydric MP as compared to anisohydric OH stands.

Demographic measurements of germination, establishment, growth, survival, maturation, and fecundity of all tree species in the MP, OH, and TH treatments will be used to quantify fitness (Clark et al. 2010, 2014a). Germination and seedling growth responses will come from annual censuses from seeds on 50 2-m^2 plots. A new seed cohort will be added to each plot annually to provide age-by-year effects (Ibanez et al. 2015). Responses of trees > 2 m tall will be mapped and censused every two years for survival, diameter, height, and maturation status. Seed traps will be located with seed and seedling plots and used to quantify fecundity (Clark et al. 2010). Leaf area will be estimated from Coweeta-specific allometric equations (Martin et al. 1998), and from light interception measurements (LAI-2200). Analysis of transpiration, gross and net primary productivity, and soil moisture and soil water use by depth will address the questions posed above, and inform modification of the RHESSys model (Band et al. 2012) used in scaling, described in section 2.4.

To test how mycorrhizal identity and context influences tree seedling responses to hydroclimate variability, EM-associated seedlings (red oak, hickory, sweet birch, white pine) and AM-associated seedlings (red maple, tulip poplar, blackgum) will be planted in each plot. Four 16 m^2 subplots will be installed in each OH and MP plot, with half the area tarped after one year to impose drought in the upper soil layers. We have used this method successfully to reduce soil moisture by 50% in the 0–10 cm soil profile in other forested ecosystems (Refsland and Fraterrigo, unpublished data). We will measure soil moisture, whole-seedling and microbial biomass, root colonization, soil carbon and nitrogen content and isotopic composition, extracellular enzyme activities, carbon and nitrogen mineralization, soil carbon dioxide efflux, and mycorrhizal hyphal production.

Finally, we will measure *Plethodon* and *A. rudis* responses using repeated surveys of plots using a robust sampling regime for estimating demographic rates from unmarked populations (Chandler et al. 2011, Zipkin et al. 2014). We expect *A. rudis* to respond positively to declines in salamander abundance, and we will test for cascading effects on woodland plant seed dispersal and fitness. We will use counts of ants and seed removal at seed bait stations, and we will measure dispersion and fitness of plants within focal plots. Tri-trophic interactions among trees, birds and caterpillars will be examined by quantifying the treatment effects on bird community composition using standard spot-mapping techniques, and direct visual surveys of caterpillars according to standardized protocols we have used before (Stodola et al. 2013). Samples of 100 leaves from multiple saplings of selected tree species will be visually inspected five times during the breeding season, starting at leaf out and continuing every two weeks.

Joint analysis of demographic responses will follow the methods of Clark et al. (2014a), including interactions and indirect effects. These joint models are 'state-space' models, meaning that we include full uncertainty from parameters, model, and data, including correlation over time and between the different demographic rates (growth, reproduction, survival). Individual fitness is obtained by marginalizing the model over individuals and size classes. Sensitivity to drought, light, and competition and direct and indirect effects and interactions are available from the posterior distribution. Prediction makes use of the same posterior distribution.

2.2.B. FFE2, Rhododendron Manipulation at Plot- and Reach-scales: Rosebay rhododendron, a native evergreen ericaceous shrub, dominates the understories of mesic southern Appalachian forests. Until recently, Eastern hemlock commonly co-occurred with rhododendron in southern Appalachian forests (Elliott and Swank 2008); unlike most other tree species, the recruitment and growth of hemlock is little affected by rhododendron (Phillips and Murdy 1985). The expansion of rhododendron, combined with convincing evidence that rhododendron inhibits the recruitment and growth of canopy tree species (Fig. 10, Phillips and Murdy 1985, Clinton and Vose 1996, Beckage et al. 2000), has prompted land managers to suggest "aggressive management" (Vose et al. 2013). Future forests could have more or less rhododendron than today, depending on implementation of such management, with potentially significant effects on other biota and biogeochemical processes. Here we ask, **how does the presence or absence of this native shrub and its litter affect terrestrial and aquatic ecosystem processes?**

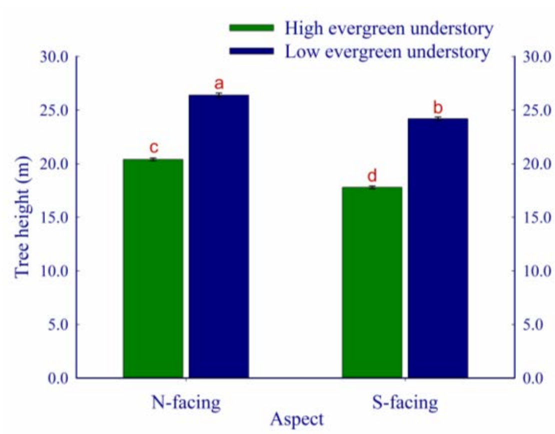


Fig. 10. Effects of rhododendron on overstory tree height. *Overstory tree canopy heights (leaf-on LiDAR) on sideslopes with north- or south-facing aspects, with high evergreen understory shrub density (green) and low evergreen understory shrub density (blue). Bolstad et al., in review.*

We hypothesize that rhododendron removal will increase nutrient biogeochemical cycling including soil nitrogen-mineralization, nitrification and leaf litter decomposition and nutrient transport into streams resulting in higher stream pH, acid-neutralizing capacity, and nitrogen and phosphorus concentrations. Rhododendron leaves are resistant to decomposition (Hoover and Crossley 1995), resulting in the development of a thick O-horizon under the rhododendron canopy where nitrogen and cations are bound in complex organic compounds (Wurzburger and Hendrick 2007, 2009), inhibiting nutrient availability to plants. Prior research has demonstrated that where rhododendron was present, the loss of hemlock had no effect on nitrogen availability (Knoepp et al. 2011), however, when rhododendron was absent, nitrogen availability increased after hemlock mortality (Block et al. 2013). Here we expect that in the long term, altered rates of carbon and nitrogen cycling along with increased overstory and understory vegetation biomass, will decrease total nutrient pools but increase cycling rates due to reduction of recalcitrant organic matter. Additionally, we predict that soil microbial communities will shift, with bacterial ammonium oxidizers outcompeting archaeal nitrifiers, following removal of rhododendron and consequent increases in pH and nutrient availability.

We predict that riparian plant growth, richness, and tree recruitment will be greater within a few years after rhododendron removal. Rhododendron tolerates shade, reduces light on the forest floor

(Clinton 2003), and suppresses herbaceous plants and tree seedlings growth and recruitment (Clinton et al. 1994, Beckage et al. 2000, HilleRisLambers and Clark 2003). Thus, we anticipate that the removal of rhododendron will increase plant growth and productivity and recruitment of herbaceous and tree species due to the direct effects of increased light and the indirect effect of increased nutrient availability.

We hypothesize that increases in light and nutrients reaching the stream after rhododendron removal will cause greater variation in stream temperature, a net increase in stream metabolism, and a seasonal shift from allochthony to autochthony due to multiple interacting effects. Rhododendron forms a dense canopy that maintains cool summer temperatures in soils (Clinton and Vose 1996) and presumably streams. Rhododendron leaves are highly refractory and of low resource quality (carbon:nitrogen ratios >100, compared to 45–70 for hardwood species: Kominoski et al. 2007, Kominoski and Pringle 2009), resulting in slow in-stream decomposition rates (Webster and Benfield 1986) and thus their year-round presence in streams. Removal of rhododendron will increase the average lability of leaf resources; coupled with increased temperature and nutrient availability, we predict the autumnal input of leaf resources will decompose in streams by mid-summer, resulting in a deficit of allochthonous carbon (see, e.g., Rosemond 2015). Increased light availability will permit algal production to increase, potentially replacing this lost carbon with an authochthonous source.

We predict increases in grazing aquatic macroinvertebrate species and their predators and declines in salamanders after rhododendron removal. The particular effects of rhododendron presence or absence on stream and riparian animals have not been examined, and responses will depend on a complex interplay of increased light and alterations in basal resources and habitat structure. The long residence time of rhododendron leaves in streams, coupled with year-round inputs, results in "resource islands" during the summer (Schofield et al. 2001), providing food and habitat for key stream taxa such as crayfish (Huryn and Wallace 1987, Schofield et al. 2001), Lepidostoma caddisflies (Whiles et al. 1993), and several salamander species. This work will examine how the presence/absence of riparian rhododendron affects the demographics of aquatic macroinvertebrates and top consumers, specifically crayfish and salamanders.

Design and Measurements: Rhododendron and O-horizon removal treatments will be applied in riparian or mesic forests in a replicated large plot-scale experiment and along stream reaches within riparian forests. All forests have experienced recent hemlock mortality. Research involves terrestrial measurements within both the plot-scale and the stream-reach-scale experiments to identify cascading effects on properties and processes within and between terrestrial and stream ecosystems. Four factorial rhododendron removal (2 levels; removal/no removal) (implemented spring 2015) and O-horizon removal (2 levels; removal/no removal) (scheduled spring 2016) treatments will be applied to both plots and stream reaches: (1) control (no removal of rhododendron or O-horizon); (2) removal of both rhododendron and O-horizon; (3) rhododendron removal but no O-horizon removal; and (4) no removal of rhododendron but removal of O-horizon. Removal of rhododendron was achieved by cutting individual stems and herbicide application to cut stumps, to prevent sprouting. Removal of the O-horizon will be achieved by prescribed burning in spring 2016 (conditions were unsuitable for burning in 2015).We worked closely with the Nantahala National Forest to design rhododendron and O-horizon removal protocols that could be implemented on a landscape scale in efforts to restore sites with high hemlock mortality and a dense rhododendron subcanopy. Previous prescribed burning studies conducted on National Forest lands have shown minimal and short-lived increases in soil, soil solution, and stream nutrient concentrations under the low-to-moderate severity fire prescriptions in this region (Knoepp et al. 2004, 2009, Elliott et al. 2012). Because of these negligible effects of prescribed fire on site productivity and water quality, it has been suggested that prescribed burning can be a useful tool for maintaining and restoring ecosystem services (Vose 2003, Vose and Elliott 2016).

Within the Coweeta Hydrologic Laboratory, sixteen 0.04-ha plots were established for intensive measurements with the same four rhododendron and O-horizon removal factorial treatments as the stream reaches. Eight of the sixteen plots have been monitored as part of the "Intensive Hemlock Woolly Adelgid Experiment" for vegetation dynamics, carbon and nutrient pools and fluxes, and soil solution chemistry since 2004 (referred to in Nuckolls et al. 2009, Knoepp et al. 2011, and Ford et al. 2012a). These plots provide the long-term response to hemlock mortality of vegetation, total mineral soil and O-horizon carbon and nitrogen pools and rates of biogeochemical cycling. Rhododendron and O-horizon removal treatments were randomly applied for a total of four replicates of each treatment. Intensive plot measurements include continuous microclimate (air temperature, soil temperature, photosynthetically-active radiation, soil moisture), vegetation dynamics (growth and recruitment of overstory species, diversity of herbaceous species, shrub layer), soil nitrogen mineralization and nitrification rates, soil microbial community (identification of autotrophic and heterotrophic nitrifier populations using DNA methods), extracellular enzyme activity, biogeochemistry (canopy throughfall and soil solution chemistry) and available and total nutrient and carbon pools in soil surface subsurface layers and O-horizon, and litterfall fluxes (quarterly litterfall collections and analyses for total carbon and nutrients).

Four 300 m stream reaches were selected on 2nd to 3rd order perennial streams (670–1000 m elevation) in the White Oak Creek Watershed in Nantahala National Forest located 21 km north-northwest of the Coweeta Hydrologic Laboratory. Imbedded within each stream reach are 12 0.04-ha plots (12 plots per treatment; total n = 48). Annual measurements of vegetation (herbaceous layer, shrub layer, and overstory), forest floor mass and chemistry, and soil chemistry are being made on all imbedded plots. Measurements in stream reaches include weekly precipitation and stream water chemistry sampling, algal standing crop, leaf litter standing stock, stream nutrient uptake, insect community composition, stream salamander and crayfish occupancy/abundance and bird abundance. All pre-treatment measurements were made in 2014; measurements continue during the treatment years (2015–2016) and will be made 1–2x annually post-treatment. Additional *in situ* manipulations of top-down control by stream macroconsumers were conducted in stream reaches in 2014 and 2015 and will be repeated in 2016 and every 2 years thereafter.

We will impart fine-scale lessons learned from the FFE1 and FFE2 manipulations to better understand hydrological and biogeochemical responses to changing tree species composition at larger scales. Observations from the FFE1 and FFE2 plots will inform a spatially explicit understanding of watershed-scale processes under the RHESSys modeling framework (section 2.4). Because many watershed biogeochemical processes cannot be captured at plot scales, we are also motivated to conduct the watershed-scale forest composition manipulation described below to better inform our regional models.

2.2.C. FFE3, Watershed-scale Forest Composition Manipulation: At the watershed-scale, we expect that a shift toward a more open and water-use-efficient OH forest will increase streamflow, produce more recalcitrant and lower quality leaf litter, and decrease stream nitrogen concentrations, with attendant effects on stream and forest animals. This watershed-scale experiment allows us to examine aspects of biogeochemical cycling, water and nutrients fluxes, and habitat responses that are not possible at the plot-scale. In FFE3, we will implement a long-term, paired watershed manipulation to move the treatment watershed (WS 31) toward an open OH forest using selective cutting, herbicides, and prescribed burns (standard silvicultural practices) starting in year three. We will cut all understory evergreen shrubs (rhododendron and mountain laurel, *Kalmia latifolia*), herbicide stumps, allow material to dry so that fire can carry, and implement a prescribed burn with moderate intensity over the entire watershed. A moderately intense fire will consume the downed shrub layer, damage or kill some of the dominant tree species with thin bark (e.g., red maple, Bova and Dickinson 2005, Hengst and Dawson, 1994), and promote a more open canopy allowing oak and hickory species to regenerate after each scheduled burn (Arthur et al. 2015). Midstory competitors will be manually stem injected with herbicide as needed to allow oak species to recruit into the canopy (Loftis 2004). We will implement a prescribed burn on a three-yr return interval, with the desired future condition of a moderately open woodland dominated by oak and hickory tree species with no evergreen shrub layer (Arthur et al. 2015). The treatment watershed (WS31) is an east-facing, mid-elevation (869–1141m) watershed, 37.8 ha in area, with streamflow and chemistry recorded sub-hourly or weekly, respectively, since 1981. The reference watershed (W32) is similar in aspect (east-facing), elevation (920–1236m) and area (41.3 ha); and it also has a longer record depth (streamflow since 1941 and chemistry since 1976). QA/QC protocols and equipment for all measurements and data acquisition will follow established protocols (Laseter et al. 2012) except where noted below. This experiment allows us to ask the question, **how would an oak-hickory future forest affect hydrological and biogeochemical fluxes at the watershed-scale?**

We expect that silvicultural and prescribed fire treatments will preferentially reduce mesophytic (MP) species, resulting in decreased forest water use and increased watershed yield, but not

changing nutrient or sediment export. Our long-term data show that water yield in unmanaged, forested reference watersheds in the southern Appalachians decreased by up to 22% between the mid-1970s and 2013; changes from xerophytic to mesophytic species alone decreased water yield by as much as 18% in a given year since the mid-1970s (Caldwell et al. in review). Forest mesophication has contributed to the long-term changes in water yield, as mesophytic species have a diffuse-porous xylem anatomy and more functional sapwood area than do xerophytic species with a ring-porous xylem anatomy, allowing mesophytic species to transpire up to four times more water for a given diameter (Ford et al. 2011a, b). Low- and moderate intensity prescribed fires in the southern Appalachians do not remove all of the forest floor humus layer and thus prevent changes in nutrient and sediment export following fires (Clinton and Vose 2007, Knoepp et al. 2005).

We hypothesize that hydroclimate and forest composition will interact to affect stream ecosystem carbon and nutrient retention, macroinvertebrate diversity, and energy flow pathways to vertebrate predators. Whole-stream nutrient addition experiments show that streamwater nutrients interact with litter quality and differentially affect breakdown rates (Manning et al. in press). In addition, forest-derived inputs affect stream ecosystem processes, as when the quantity and quality of particulate organic carbon (POC) affect macroinvertebrates (Wallace et al. 1997, 2015). Production and composition of stream-dwelling organisms are strongly controlled by fluxes of nitrogen, phosphorus and carbon that ultimately derive from POC and can be affected by anthropogenic nutrient sources (Cross et al. 2007). Hydrology and temperature regimes also affect carbon retention and breakdown rates of POC in streams (Rosemond et al. 2015, Manning et al. 2015). Direct effects here include increased solar radiation input and stream water temperature due to the removal of rhododendron and reduction of mesophytic tree species in the riparian zone. Indirect effects include changes in forest-derived litter input.

We hypothesize that rhododendron removal will increase Lepidopteran density on host trees, but not overall population numbers. Several bird species rely on rhododendron for nesting sites. While we might expect decreases in breeding bird populations and fecundity due to the direct effect of removing rhododendron, increases in canopy foliar nitrogen will increase bird's caterpillar food resources, and may, via indirect effects, increase bird success. Habitat changes towards OH (WS31) or MP (WS32) dominated systems should also drive changes in insectivore bird communities as part of the tri-trophic relationship described above for FFE1. However, in addition to examining indirect and interactive effects on caterpillars, we will rigorously survey birds on the larger experimental units of FFE3 (watersheds) with the goal of estimating community composition and demographic parameters of selected species. We will also be able to directly assess the tri-trophic relationships via an exclosure experiment, in which we will measure predation of insects by birds and herbivory by caterpillars.

Design and Measurements: All overstory and herbaceous vegetation will be measured annually, along with mortality before (July 2016) and after the first and second (July 2017, 2018) growing season fires using established protocols (Elliott et al. 1999a). Long-term climate from a station located on the southern boundary of the treatment watershed will provide measurements of air temperature and relative humidity, total solar radiation, photosynthetically active radiation, wind speed and direction at five-minute intervals that will aid in the interpretation of changes in vegetation water loss (i.e., evapotranspiration due to the treatment). A nearby long-term recording rain gauge will be used to provide measurements of precipitation volume and intensity. Existing weirs located at the outlets of WS31 and WS32 will be used to measure streamflow (*Q*) according to Swank and Crossley (1988). Weekly grab stream samples will provide measures of NO_3^-, NH_4^+, SO_4^{-2}, PO_4^{-3}, Cl^-, DOC, pH, base cations (Ca^{+2}, Mg^{+2}, K^+, Na^+), and total suspended solids to assess the impact of the treatment on ambient water quality. Automatic samplers (SIGMA 900MAX, Hach, Inc., Loveland, CO) will be installed to collect flow proportional samples during storm events. Datasondes (600R, YSI, Inc.) will be installed to measure pH, temperature, electrical conductivity, and dissolved oxygen *in-situ* at five-minute intervals. All water samples will be analyzed at the Coweeta Hydrologic Laboratory Analytical Chemistry Lab according to established protocols (Miniat 2014). In each watershed, we will establish two locations to instrument micrometeorology and sap flux stations, one at an up-slope/ridge position and one at a lower-slope/cove position, and three locations will measure soil moisture. Insight from these plots and from FFE1 will be used to parameterize models of tree water use and productivity (i.e., RHESSys, TREES). These parameterized models will then be run at the watershed scale. Differences in model performance at plot and watershed scales should highlight important processes and interactions as forests transition from current to future states.

Litterbag studies of 4 litter types (tulip poplar, red maple, oak species and rhododendron) will be conducted in the FFE streams to separate the effects of and test interactions among litter quality from other aspects of watershed and hydroclimate control on discharge, temperature and soluble carbon and nutrients on litter breakdown rates. Leaf litter from these four species will provide contrasts among species assemblages expected with climate change and incorporate those species endpoints included in the FFE1 and FFE2 manipulations. Quantitative analyses of salamander diet composition will be used to test how hydroclimate and forest composition affect prey utilization by top predators. Salamander assemblage composition, biomass and growth rates of certain salamander taxa will be used to link forest change to stream productivity and ultimately consumer performance, abundance, and diversity (e.g., Johnson et al. 2006, Bumpers et al. 2015, Trice et al. 2015).

Lepidopteran and bird surveys will be performed throughout the breeding season, as will the exclosure experiment. Five caterpillar surveys will be performed at randomly selected points as described above (Stodola et al. 2013), starting approximately with leaf-out and repeated every two weeks. Bird community composition will be assessed using point counts, a standard procedure (Ralph et al. 1995), repeated three times at randomly selected points at least 50m from the edge of each area. In addition, we will use constant-effort mist netting to assess productivity, survival and abundance of selected bird species in each area (Ralph and Dunn 2004). Bird exclosures will enclose a sapling and will be paired with an uncaged sapling following Zehnder et al. (2010). Exclosures will allow us to examine the strength of the bird predation effect on caterpillar numbers and herbivory on red maples and red oaks in forests of different condition, following previous exclosure experiments we have performed in these forests (Zehnder et al. 2010). Finally, results from plot and watershed scale analyses will be used to inform parameterization of RHESSys modeling used to explore these processes at larger spatial and temporal scales, as highlighted in the following sections. The parameterization of RHESSys will be informed by mechanistic- and individual-scale observations from FFE1.

2.3. Socioecological Interactions (SI).

Human activity has exerted strong influences on southern Appalachian ecosystems since pre-Colonial times; however, long-term demographic changes have resulted in dramatically different patterns of land use and management of natural resources. Legacies of past practices such as fire management and agriculture continue to affect land cover, material flows, and biodiversity of the region (Gragson and Bolstad 2007, Gragson et al 2008, Bolstad and Gragson 2008, McEwan et al 2011). Furthermore, more recent demographic mixing of recent in-migrants, seasonal residents, and multi-generational residents (Fig. 11) is driving new patterns of human decision-making about land use and landscape change. As an example, in-state residents own nearly 60% of valley bottom homes in the region, but they own only 33% of houses near the ridgetops above 3500 feet elevation (Gustafson et al. 2014). Here we ask**, how are patterns of migration, social networks, and feedbacks from environmental risks influencing governance as expressed in land use activities, policies, and ordinances** (Vercoe et al. 2014, Evans 2013)? A paradox of the region is that trends in development and land use practices threaten the aesthetic and environmental amenities that attract newcomers. We expect that human activity will have direct effects on the landscape, such as land use change, and also indirect effects, such as changes in behaviors resulting from interactions among individuals. We will focus our socioecological predictions about landscape change as affected by interactions among demographic diversity, governance structures, social values and perceptions, regional social networks, and environmental risks. The primary objectives of the socioecological investigations are to: (1) develop a spatially explicit model predicting both where development pressures will be greatest and the demographic characteristics of the people who will be living there; (2) characterize the sources of knowledge about land use and environmental management among different demographic groups; and (3) describe the social networks within the region and determine how these are likely to affect land use decisions and environmental governance.

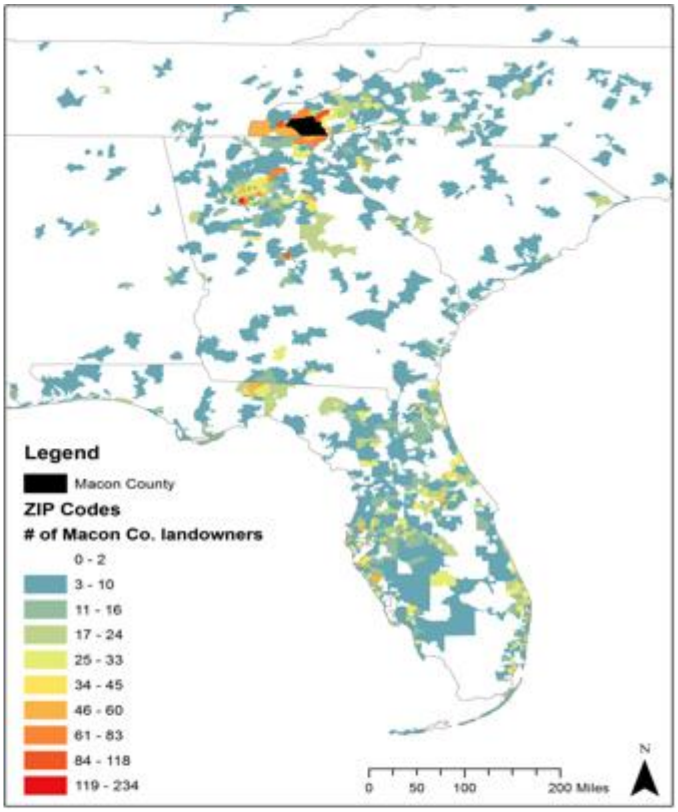


Figure 11. Evidence of extralocal influences on land management and governance. *County-level mapping of zip codes of Macon County landowners across the SE US. (Gustafson, 2014).*

2.3.A. Modeling Land Use Change and Exurban Disturbance. ***We expect that increasing demographic diversity and changes in governance structure will increase land use regulation with effects on development patterns.*** Changing economic conditions over the last several decades have driven migration, second home ownership, exurbanization and urban intensification across the southern Appalachian biome. Trends show some rural areas becoming increasingly depopulated while urban and exurban economic centers have shown population growth (Castells 2010, Florida 2014). However, some rural areas are experiencing population increases. In many cases, former agricultural lands have been rezoned for residential use (Angelo and Wachsmuth 2015, Woods 2009). Immigrants to these areas tend to live in houses on steeper slopes, at higher elevations, further from existing settlement clusters and closer to National Forest lands than multi-generational residents (Kirk et al. 2012, Gustafson 2014, Vercoe et al. 2014). Many of these immigrants are second-home owners with primary residence in urban areas (Fig. 11). They have higher incomes and more education on average than multi-generational residents (Gustafson 2014, Vercoe et al 2014), factors that are expected to affect their land use decisions. Our ability to predict not only where new development is likely to occur, but also who will be living in these areas, is critical for our ability to understand how these trends will directly and indirectly affect ecosystem processes.

We will combine historical land use data from our core data sets (Table 1) with U.S. Census and tax parcel data, land pricing, home location and governance characteristics to carry out a regional analysis of migration patterns and refine existing land use change models (e.g., Sohl and Sayler 2008; Terando et al. 2014, Wear 2011, Cho et al. 2003). The spatial information contained in these data sets will be integrated using geospatial procedures to allocate human footprints to ecologically meaningful boundaries (such as sub-watersheds) from 1970 to the present (Hepinstall-Cymerman et al. 2009, Hepinstall-Cymerman 2013). We will derive development classes similar to Waddell (2002), but focused on slope location (e.g., valley bottom, mid-slope, upper slope) combined with demographic characteristics and migration history of residents along with key landscape attributes relevant to ecohydrological modeling (e.g., percent impervious area, road density, forest canopy cover) (Hepinstall et al. 2008). An ethnographic survey will be used to gather observations on land use and resident characteristics not available through existing data sets to generate future scenarios from economic storylines (e.g., low, moderate, or high income exurban migrants) and habitat change (future forests, OH versus MP, see section 2.2).

2.3.B. Citizen Knowledge and Governance Interactions. ***We hypothesize that socioecological interactions will drive governance of and response to changes in flow regimes and hazards (e.g., floods, landslides, fire).*** Humans directly integrate various forms of environmental knowledge (e.g., scientific, lay, experiential) into individual decisions about residential location, development type, and land management practices, and indirectly, into the creation of governance regimes for environmental management (Raymond et al. 2010). Our prior research demonstrates that experiential forms of environmental knowledge (e.g., perception, observation) are particularly important for influencing the priorities expressed by southern Appalachian residents (Rice et al. 2015). However, little is known about the values and knowledge of residents or organizational decision-makers (e.g., county commissioners and employees) that lead to environmental policy. Additionally, changing demographics in this region are expected to alter the environmental knowledge base. In southern Appalachia, as elsewhere in the Southeast, most land (~87%) is privately owned, and most owners are families (~57%) rather than corporations (Wear and Greis 2002, Butler 2008, Smith et al. 2009). Thus, an increasingly diverse set of individuals and closely connected groups of individuals will be making land use decisions that affect the region. Local and regional governance will also be an important factor affecting land use, and these decision-makers will be responding not only to demographic and land use shifts, but to changing climate and species compositions. Our objective in this section is to develop a model for how different forms of knowledge and governance interact to produce ecologically sound land use practices (Ogden et al 2013).

We will determine 1) how knowledges of long-term vs. recent residents produce new forms of environmental management and regulatory outcomes, and 2) what the interactions and feedbacks are between these knowledge-governance systems and processes of exurbanization and environmental change (Adger 2006; Hilhorst and Bankoff 2004; Roncoli 2006). We will examine these knowledge-governance interactions and their effects on ecological outcomes using semi-structured interviews, participant observation, and focus groups with elected officials, county employees, members of environmental organizations and local residents, including members of the Eastern Band of the Cherokee Indians (EBCI). We will analyze how government representatives understand their environmental management missions, how they employ particular types of knowledge and values, and how they think about policy instruments to mediate human modification of the landscape, both historically and at present. We will also determine the ways in which environmental change motivates citizens to respond or not respond to various decision-making activities (e.g., land use activities, residential location, social organizing, individual actions). We will use these results in our Regional Interactions Effort described next (section 2.4) to understand how exurbanization processes drive vulnerability (Kirk et al. 2012, Hansen et al. 2005, Wenger et al. 2011, Band et al. 2012).

2.3.C. Multi-Scale Human Population Drivers of Land Values and Management Practices. ***We hypothesize that the strength of local and extralocal social networks will affect ecological values and knowledge, with resulting effects on environmental governance.*** Theory developed from ecology has provided insight into the strength and diversity of interactions in a community that may subsequently affect ecosystem function including attributes such as redundancy, robustness and dependency (Bascompte et al. 2003, Blüthgen et al. 2007, Devoto et al. 2012). Within the human realm, social networks are related to individual and community wellbeing (Falcon 1995, Putnam 2000, Benkler 2006). Social networks are built through processes of social interaction and collective action, but there are key differences between networks of socially homogenous groups and networks of socially heterogeneous groups (Poortinga 2006, 2012, Granovetter 1973, Burt 1992). The topology of these networks can inform whether outcomes span social divides. Nevertheless, little is known about how social networks may help to mitigate the negative impacts of rapid landscape change (Tylianakis et al. 2008). More specifically, we are interested in whether networks among homogeneous and heterogeneous groups can develop to promote ecologically focused, voluntary land use practices and regulations that address issues such as steep slope development and riparian protection (Günerlap et al. 2013, Meyfroidt et al. 2013).

We will first use spatially explicit logistic and standard regression analyses of multi-decadal county-to-county migration flow data, individual-level Public Use Microdata Sample (PUMS) data that include migration and commuting variables, and parcel-level municipal records (Ellis et al 1999) to examine relevant social networks. Specifically, we will examine: (1) influences including gender, age, race, income and education; (2) local context including site characteristics and local governance structures; and (3) extralocal effects reflecting connections within and beyond the region. Results will define the long-term pattern and structure of extralocal linkages via (a) migration, (b) long-distance commuting, and (c) second homeownership (Paasi 2004, Nelson 2004). The findings will be used to guide subsequent ethnographic data collection to define bridging and bonding networks. We will interview informants about sources of knowledge and resources for land management, names of communities they belong to, and participation in government to assess civic engagement. Bonding within homogeneous networks and bridging between heterogeneous networks are understood as points along a continuum, and we will calculate k-cores and cut-points (supplemented with demographic information on members) to determine the structure of social networks (Crowe 2007, Ramirez-Sanchez and Pinkerton 2009). A k-core represents the minimum number of individuals linked to individual "A" within the network, while a cut-point is identified when by removing an individual a network fragments into sub-networks with no connections. A community with high k-cores and low cut-points has a strong, densely bonded network, while a community with low k-cores and low cut-points is a bridging network. Results will be integrated with those from FFEs to assess how the strength of bonding and bridging networks among residents interacts with vegetation, vertebrate and invertebrate biodiversity.

2.4. The Regional Interactions Effort (RIE)

The Regional Interactions Effort will integrate long-term and new observations on hydrology, climate and land use with stand and hillslope interactions within the RHESSys ecohydrological framework adopted by CWT in 2007. Regional investigations will focus on the inter-connected responses of land use and land cover, canopy structure (species composition, leaf area index), hydrology (soil moisture, transpiration, and streamflow) and carbon and nitrogen cycling (primary productivity, soil and stream nitrogen availability) to climate change and land use. We emphasize these variables because they are key ecosystem services, are vulnerable to change, and are primary drivers of many ecosystem processes and populations. In addition to drawing on long-term data in the Coweeta LTER archives (Table 1), the proposed research will synthesize findings from the FFEs (section 2.2), SI (Section 2.3) as well as from new measurements of soil, plant, climate, and hydrologic variables obtained through the Coweeta regional observation network (Fig 12). Our overarching goal is to achieve an improved understanding of the spatially explicit responses of land use and forest change over a range of geographic and time scales. We will specifically quantify the relative importance of variables governing water, energy, carbon and nutrient flows, and the relative vulnerability of ecosystems to future climate and land use changes along the broad disturbance gradients observed in the region (Fig. 12). Critical questions addressed include: **How do hydrologic, carbon, and nitrogen cycles differ under isohydric vs. anisohydric species compositions? How have hydrologic and dependent biogeochemical cycles been altered in forests recovering from agricultural abandonment? And, how will future development and climate influence hydrologic risk at regional scales?**

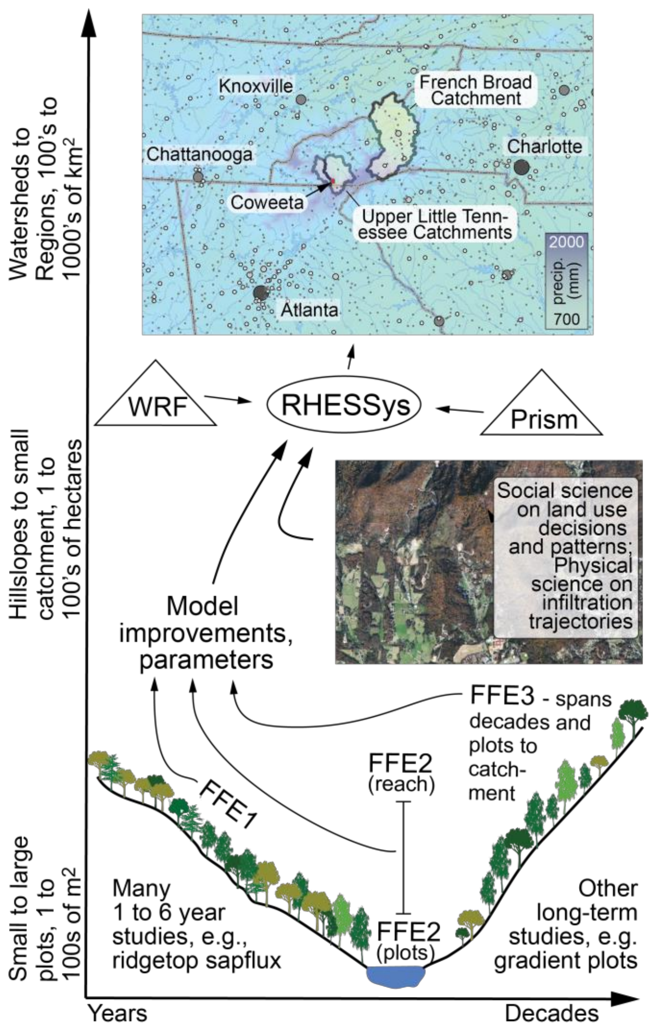


Fig. 12. Integration and scaling of field data to larger spatial and temporal scales through regional land cover data and models*.* *Research is proposed across a range of time and space scales, integrating past and present research of annual to decadal durations, across physical, biological, and social sciences. The aim is to discover and quantify processes at small scales (e.g., root, leaf, tree) and investigate their consequences from patch to regional scales*

2.4.A. Multi-scale Processes in Ecohydrology. ***We hypothesize that the sensitivity of water and carbon cycles to hydroclimate variability will depend on interactions between species composition and topography.*** The complex set of interactions between hydroclimate, topography, and species composition across the southern Appalachian landscape creates a challenge for predicting ecohydrologic responses under future conditions (Fig. 6). Currently, species composition covaries with topographic position, such that mesophytic tulip poplar are abundant in coves but nearly absent on ridges. Widespread dominance of MP or OH in southern Appalachian forests would create an unprecedented combination of conditions with unknown ecohydrological consequences. Results from the FFEs will provide a mechanistic understanding of ecohydrological responses to species composition changes within a relatively constrained spatial scale. Translating plot- and watershed-scale processes to the broader landscape requires accounting for variability in species level responses to factors like drought sensitivity, which varies with topographic position (Fig. 8). Here we seek to answer two related questions: first, **how does the spatial distribution of isohydric/anisohydric species affect ecosystem water use and carbon cycling at the patch and hillslope scale; and second, how does the species spatial distribution influence catchment level streamflow?** To our knowledge, no landscape-level model has incorporated the spatial arrangement and interactions between anisohydric/isohydric behavior, nor tested changes in hydrologic cycling under changing composition and pattern. We will extend RHESSys to incorporate isohydry/anisohydry and will test model skill in predicting key landscape variables critical to terrestrial and aquatic ecosystems. We will focus specifically on soil moisture patterns, streamflow, leaf area, and aboveground net primary productivity. We expect that interaction between hillslope positions will be most important during drought. This is when partial cavitation in the sapwood of anisohydric species or mortality in isohydric species can lead to long-term reductions in transpiration as well as increased proportional flow to downslope patches.

Design and Measurements: We will compare RHESSys estimates to: 1) observed coupled water, carbon and nitrogen cycling and transport; 2) changes in plant hydrologic fluxes quantified on the FFE1 and FFE2 plots; and 3) streamflows and soil and stream chemistry on the FFE3 sites. We will test model skill against an existing CWT network of 26 soil moisture stations distributed across elevation and topographic position, and against aggregate hydrologic response on the 11 long-term catchments in the LT and FB basin. We will also install nine synoptic soil moisture cove-to-ridge-transects within the gaged watersheds, incorporating regional observation network plots and sampling soil moisture monthly on seven to nine sites from cove to ridge. Canopy composition, biometry, and leaf area index will be mapped on these transects using the methods of Bolstad et al. (1998) and Elliott et al. (1999b). Model runs across years will provide response estimates to input variables for regional analysis in the next section.

RHESSys will generate estimates of transpiration, soil moisture, streamflow and carbon budgets in 11 representative, long-term measurement watersheds (70 to 110 year flow record) in the Little Tennessee (LT, Coweeta, USGS) and French Broad River Basins (FB, USGS, Asheville Water Supply). Multiple realizations of land use and climate change scenarios will be used to assess potential trajectories of these ecohydrological variables from past through present, and over the next several decades. Model outputs will be tested against various observations, while model skill in predicting soil moisture and streamflow across landscape positions and catchments will be diagnosed using standard metrics (e.g. Nash-Sutcliffe efficiency, spatial pattern metrics). Results will be compared to our existing regional satellite record (CWT-VI) and the regional observation network plot measurements to evaluate RHESSys predictions of leaf area and other canopy patterns.

2.4.B. Time and Space Scales of Land Use Change and Hydrologic Recovery. ***We hypothesize that soil properties relevant to hydrologic behavior recover on decennial to centennial timescales after forest reversion from agriculture, creating a legacy impact on patch to catchment level water balances.*** Our previous research shows that following agricultural abandonment, leaf area recovers within a decade (Ford et al. 2011, Boring et al. 2014), yet hydrologic recovery occurs over much longer time-scales (Kelley et al. in press). After precipitation, vegetation is the primary control on total water yield, but soil hydraulic properties appear to control the partitioning between baseflow and peakflow. Forested catchments previously under agricultural land uses show reduced baseflow and higher peak flows (Price and Leigh 2006a, b, Leigh 2010, Price et al. 2010, 2011), driven by increased overland flow and decreased water transmission times to stream networks (Hewlett et al., 1957; Leigh 2010; Price et al. 2010, 2011; Wang and Leigh 2012). Hence, the lagged recovery of forest soils from past agricultural practices is expected to continue to affect local soil moisture and downstream aquatic ecosystems. Accurately predicting future ecohydrological processes will require accounting for the rate of recovery of soil properties after agricultural abandonment. Interactions between land use history, vegetation, and hydrology will become increasingly important with the intensification of summer precipitation events (Fig. 4). Here we propose to quantify the lagged responses of soil properties that govern hydrologic behavior following land use change, and use this to parameterize RHESSys for soil effects following land use change.

Design and Measurements: We will use data collected from past experiments, new samplings at regional observation network sites, and existing data collected throughout the region by the USDA Natural Resources Conservation Service (NRCS). We will revisit sites to examine temporal changes in soil properties. Recovery response will be modeled as a function of landscape and use characteristics, and incorporated into RHESSys. Model comparisons with time-variant vs. time-invariant soil hydraulic properties will reveal their importance at the plot, stream, small catchment, and regional scales.

2.4.C. Interactive effects of regional development, hydroclimate trends, and changing forest composition on environmental risks. We hypothesize that continued development, changes in land use patterns and practices, altered forest composition, and regional hydroclimate trends will interact to affect streamflows, water quality, and environmental risks (floods, droughts, and landslides). Human activity across the southern Appalachian region will have direct and indirect effects on hydrological and biophysical processes. Continued alteration to the region may lead to unintended consequences, ironically affecting amenities that may have attracted in-migration to the region. Regional urbanization as well as hillslope development are expected to increase risks to human life and property through increased flood magnitude and landslide frequency and via development within high-risk zones. We also expect that mesoscale climate, particularly warm season convective storms, will be affected by rapid regional urbanization. Here we ask: ***How will future land use patterns interact with hydroclimate change to affect environmental risks?*** We will address this question by using long-term core landcover and new spatial data to estimate regional risks of landslides, flooding, and drought under changing climate, land use patterns, and forest composition. We will integrate ecosystem hydraulic architecture and response (FFE1 &3), species/landscape composition from 2.4.A, B, and C., and improved RHESSys from 2.4.B to estimate responses from past through future climate, population and development scenarios.

Many newcomers to the region, both landowners and developers, are unaware of the high landslide and flood risks inherent due to the steep topography and high rainfall (Wooten et al. 2008, Band et al. 2012). As an example, the developer of a major new mountainside subdivision in the study area went into foreclosure after landslides rendered the road system unusable (Smoky Mountain News, 9/28/2011). Landslides are common during tropical storms (Furmann et al. 2008), often causing loss of life and property damage (New York Times 9/20/2004, Wooten et al. 2016). Improved identification of landslide-prone areas, understanding of vegetation-landslide interactions, and identification of flash-flood prone areas are continuing needs (Hales et al. 2009, Liao et al. 2011, Tao and Barros 2013).

We hypothesize that increased urbanization within the region and the surrounding "ring of asphalt" will enhance local and downwind warm season convective precipitation activity. Long-term climate trends observed at Coweeta (Fig. 4) may be exacerbated by effects of urbanization in the region (Shepherd et al. 2010a,b, 2011). Recent results from the Coweeta LTER (Shepherd et al. 2013, Gustafson et al. 2013) have identified regional urban signals that could enhance the depth, intensity, and frequency of summer thunderstorms. Such changes would have direct effects on environmental risks and interactions with co-occurring changes in forest composition and land use.

We expect interactions among land use, climate, and species composition to strongly influence hydrological processes and landslide initiation. Flood risks increase with forest conversion to agriculture due to reduced transpiration rates and reduced soil infiltration rates (Price et al. 2010). Among forested landscapes, changes in tree species composition also affect the magnitude and timing of transpiration fluxes (Ford et al. 2011b), altering initial conditions for storm events. Following the loss of hemlock, peakflow after the biggest storm events increased by 20% (Brantley et al. 2015). Landsliding in the region is also affected by species composition. Roots reinforce soils against shallow landslide initiation by increasing apparent cohesion. The magnitude of the reinforcement provided by roots depends on the number, the size distribution, and the elastic properties of roots that cross potential failure planes. In forested landscapes, the variability in belowground properties poses a challenge in predicting root reinforcement at the hillslope scale. Expansion of rhododendron in the region has potentially decreased soil cohesion, as rhododendron has thinner, weaker, and more shallowly-distributed roots than most of the overstory trees in the Coweeta Basin (Hales et al. 2009). Stronger roots are also found in drier soils (Wooten et al. 2015, Hales and Miniat accepted). This suggests a positive feedback may exist on a hillslope where precipitation-driven increases in saturated soil depth both increase pore pressures and decrease root reinforcement exacerbating promoting potential slope instability. A key goal therefore will be to incorporate combinations of likely future climate, forest, and land cover scenarios into a modeling framework to estimate potential responses of floods, landslides, and extreme low flows (a water supply and water quality issue). Landslide risks vary with hillslope position, soil properties, soil moisture, and root strength, and are ideally addressed through a distributed ecohydrological model such as RHESSys. (Hwang et al. 2015).

Design and measurements: We will use the World Research Climate Program's Coupled Model Intercomparison Project Phase 5 (CMIP5) monthly and daily temperature and precipitation projections, at roughly 12 km spatial resolution, to project future climate. These daily datasets have been downscaled using Bias Correction with Constructed Analogues (BCCA), described by Maurer et al. (2010). Daily maximum temperature and daily precipitation rate from 2025–2034 model ensembles, generated with representative concentration pathway (RCP) scenarios 4.5 and 8.5, will be used as pseudo-base cases for extrapolation and simulation of local climate, and resulting water and carbon budgets with RHESSys. Impacts of local land use change and urbanization on hydroclimate will be conducted for the Little Tennessee and French Broad river basins. The Weather Research and Forecasting (WRF) model, coupled with the NOAH Land Surface Model, will be applied in sensitivity experiments to evaluate land use land change in and around the basins from the early 1900s to the present, with an emphasis on the growth of the Asheville urban area. WRF-NOAH will be mechanistically downscaled by progressive nesting from CMIP5 simulations. Appropriate statistical techniques will quantify the hydrometeorological response to different and increasingly complex land use land change configurations. We will test the impacts of these changes on patterns of forest ecosystem water balance and stress by adjustment of spatial rainfall patterns.

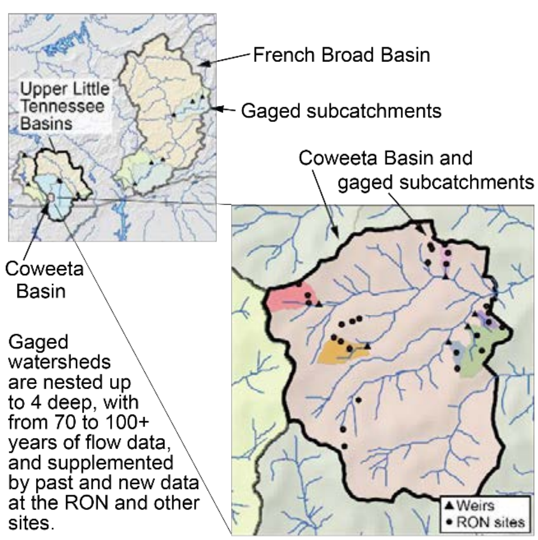


Fig 13. **Field data and model relations**. *Hydrolologic and biogeochemistry modeling will be informed by data and analysis in 11 nested watersheds, spanning long-term and current plot studies on the Coweeta sub-basins to field and spatial data collected over the LT and FB large catchments.*

U.S. Census Bureau county-level human population estimates will be downscaled to sub-watersheds based on relationships identified in 2.3.A, with and without slope ordinances using current floodplain delineations. In a set of the 11 representative watersheds (2.4.A) we will develop alternative scenarios of combined climate/development sets to be used as input to RHESSys to estimate changes to place-based ecosystem and human vulnerabilities to landslide and flooding risks (enabled by RHESSys modules developed in CWT-VI). Scenarios will be constructed consistent with results of downscaled climate and regional urbanization impacts on mesoscale weather patterns, and migration/development scenarios. Key taxonomic, biogeochemical, and social indicator responses will be estimated on decadal intervals through 2050 on the 11 test watersheds at 10 m resolution, and for larger regional watersheds in the Little Tennessee and French Broad basins at 30 m resolution (Fig. 13).

Response variables will include mean daily low and high flow frequencies in 1st through 5th order streams, overstory species composition, ecosystem net primary productivity, canopy leaf area index, and above ground biomass, soil drought frequency, and occurrence of critical slope saturation, pore pressures and slope stability metrics (e.g., factor of safety). Landslide (with RHESSys) and flood inundation extent (estimated with recent North Carolina stage/flood HEC-RAS simulations) will then be used to identify altered risk to communities downslope/downstream. We expect species composition to affect hillslope hydrology and change flood and landslide vulnerabilities (Fig. 14). We will include specific factorial tests of the hydrologic and landslide risk change associated with changing climate, overstory disturbance, and proposed policies of rhododendron removal over whole-catchments, integrating previous work (Hales et al. 2009, 2012, in revision, Band et al 2012, Hwang et al 2015, Wooten et al. 2016). RHESSys runs across hydroclimate conditions will identify ecosystem conditions (canopy and root density and strength) indicating landslide and flooding susceptibility, how forest overstory/understory structure affects these events, and whether current economic or policy systems integrate any changes in risk.

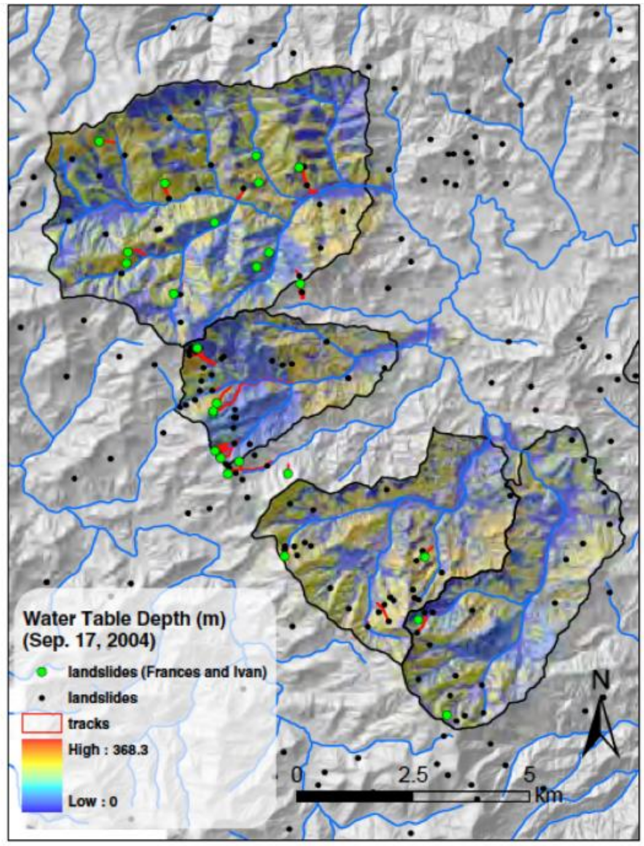


Fig. 14. Water table depths and landslide points and tracks modeled with RHESSys. *Mesophication may increase rhododendron density, increasing landslide risk due to reduced soil cohesion from lower root tensile strength of this shrub compared to trees. This may interact with development and hydroclimate variability.*

2.5. Synthesis

Our proposed research is motivated by an evolving conceptual model of southern Appalachian ecosystem dynamics informed by our long-term data and by shorter-term mechanistic studies. Using the past to predict the future, we can expect that the southern Appalachian forest biome will continue to change and evolve in response to increasing hydroclimate variability, new species invasions, and land use changes driven by exurbanization (Fig. 1). Certain trends and disturbances that we have documented affecting this biome are predictable; others are not. For instance, we have high confidence that increased hydroclimate extremes and lengthened growing seasons observed over the last 30 years will continue into the future (Fig 3.). We also expect that exurbanization of the southern Appalachians will continue as immigrants are drawn by the beauty of the landscape and the relative proximity of metropolitan areas. Conversely, sudden losses of key species, such as American chestnut and eastern hemlock due to pest and pathogens (Fig. 2), are unpredictable. The constant challenge for CWT is to conduct studies at multiple spatial and temporal scales across our complex landscape that inform our understanding of the region beyond the confines of the Coweeta Basin.

Our manipulative Future Forest Experiments will illuminate how ecosystem responses to increasing hydroclimate extremes are influenced by interactions and indirect effects involving the complex topography, competition, past disturbances, and human activities. The FFEs will create contrasting but likely future forest plant assemblages and observe how primary productivity, biogeochemical cycling, population dynamics, and hydrologic fluxes respond to altered canopy composition and structure under a changing climate. FFE1 and FFE2 will continue for at least 10 years to capture the effects of inter-annual climate variation and to allow time for soil biogeochemistry to respond to altered canopy or subcanopy conditions. FFE3 is a longer-term experiment that may require decades to capture altered biogeochemical fluxes. These experiments continue a rich CWT tradition of canopy manipulations including the original WS7 clearcut experiment (Swank and Webster 2014) and the stream litter exclusion project (Wallace et al. 1997, 1999).

Building on CWT's strong legacy of using social sciences to understand ecosystem change, our socioecological investigations seek a better understanding of place- and cultural-specificity of human decisions, behavior, and actions as they affect land use, environmental governance, and thus the southern Appalachian ecosystems. We will investigate interactions and feedbacks among extralocal cultural influences, long-term local culture, ecosystem processes, and land values as they affect land management decisions.

Together our ecological and social science field studies will provide mechanistic understanding of ecosystem and social changes that will inform our regional and long-term modeling of ecosystem dynamics described in Section 2.4. CWT adopted the RHESSys model in 2007 to synthesize our finer-scale ecological, hydrological, and social knowledge and apply it to larger spatial and temporal scales. In CWT VIIb, we continue to use this regional distributed hydrologic and biogeochemical modeling framework to predict spatial and temporal patterns in forest structure, plant water use, and hydrological and biogeochemical fluxes. To support and strengthen our regional analysis framework, we will collect new field data to improve our ability to model these processes and to quantify sources and propagation of uncertainty in our model. Our continued long-term data records and new research proposed here will improve our understanding and predictive capability of southern Appalachian ecosystem dynamics as affected by interactions and indirect effects.

3.0 Related Research Projects

CWT LTER research funded by NSF is strongly leveraged by USDA Forest Service work, and by a range of projects funded by other sources. CWT LTER and USDA Forest Service have an effective partnership that develops new information on forest ecosystem science that is then translated and demonstrated at diverse levels. USDA Forest Service scientists and technicians will be involved in all major proposed initiatives, and in particular the Future Forests Experiments (2.2). They will work with National Forest System land managers to coordinate project activities, in addition to continuing to sample the *Intensive Hemlock Plots*. They will also lead collection of core data extensively used in CWT LTER research including weekly grab samples from WS18 and WS27 for stream chemistry analysis; they will also maintain the station and calibrate sensors that serve to sample climate in the valley floor (CS01). Throughout the project, the USDA Forest Service will facilitate access to the Coweeta Hydrologic Laboratory field sites (see Facilities), as well as host a minimum of two meetings per year on-site for LTER project investigators and students to share findings of research, and to plan and coordinate research.

In *Consequences of Stand Age and Structure on Water Yield* (PI: Ford, 2012–2016), USDA-FS and CWT LTER investigators are examining how changing forest condition affect hydrologic processes in the southern Appalachian Mountains. The objective is to quantify the age and structural dependence of the hydrologic cycle in eastern deciduous forests by measuring the variation in hydrologic components across an early succession to old-growth hardwood chronosequence (i.e., shelterwood harvest site <2 years, 10 years, 30 years, 85 years, and >200 years). The 30-year old stand is located in Watershed 7, while the 85-year old stand is located in Watershed 5, both in the Coweeta Basin (see Facilities). The other three sites are in the Nantahala National Forest. Sites, measurements, and data from this project are central to activities in 2.4. After its completion, subcanopy eddy covariance/micrometeorology stations will be redeployed for campaigns in the FFE subplots (see Section 2.2) in order to quantify soil and herbaceous evapotranspiration.

The *Coweeta Eddy Flux Tower site* was initiated in 2011 to monitor the net ecosystem exchange of carbon and water in a mature, deciduous forest in the Coweeta Basin valley. Research here is led by USDA Forest Service with collaborators from CWT LTER (Novick, Bolstad) and external organizations (US EPA, NADP). At this site, above- and below-canopy eddy covariance measurements are coupled with measurements of ecosystem water balance (using sap flux, throughfall, soil and litter moisture, and streamflow), carbon dynamics (using vegetation surveys, soil and stem respiration measurements, and soil biogeochemical analysis), primary productivity (using leaf gas exchange and plant hydraulic measurements), canopy structure (using remotely sensed and ground-based measurements), and atmospheric pollution deposition (SO_2, HNO_3, NH_3, and O_3). This combination of activities will provide important information about ecosystem processes and produce specific parameters necessary for the scaling and modeling efforts (see sections 2.4).

The *Long-term Forest Demographic (LTFD) Analysis* network was established at the Coweeta Hydrologic Laboratory in 1991 (*Terrestrial Gradient Plots*) to understand how climate and competition interact to control change in eastern forests (Clark et al. 1998, Clark et al. 2004) and now includes a network of sites across eastern North and Central America. Early studies quantified basic demographic rates and introduced the hierarchical Bayes paradigm organized as state-space models (Clark 2005), while new modeling innovations have played a large role in quantifying the interactions between temperature, drought, and competition for light and moisture between species and size classes (Gelfand et al. 2013, Ghosh et al. 2013, Wu et al. 2012). Twenty-plus years of demographic data from 40,000 trees representing >350,000 tree-years serves a critical role in the activities described in 2.2.A.

Coweeta investigators are involved in collaborative activities with the NASA Integrated Precipitation and Hydrology Experiment (IPHEX) program to characterize the relationship between precipitation regimes and hydrologic processes in complex (mountainous) terrain. IPHEX includes two major activities: 1) development, evaluation and improvement of remote-sensing precipitation algorithms in support of the Global Precipitation Measurement Mission; and, 2) evaluation of Quantitative Precipitation Estimation products for hydrologic forecasting and water resource applications in the Upper Tennessee, Catawba-Santee, Yadkin-Pee Dee and Savannah river basins. Both activities have direct relevance to activities proposed in 2.4 as well as improving the predictive capacity of RHESSys.

In *Dynamics of Social Spaces and Mountain Environments* (PIs: Hautefeuille & Gragson, 2015–2019), French researchers and CWT LTER investigators are comparing the co-evolution of agropastoralism and soils across the French Pyrenees Mountains and the southern Appalachian Mountains. Multi-proxy evidence from bio-geoarchives, historical records, pedestrian survey, and ethnography are being used to develop millennial histories of the human transformation of mountain landscapes and in particular how management practices relate to soil fertility, pedogenic processes, and the stratigraphy of land parcels and small watersheds. Activities described in 2.4 are closely associated with this international collaboration.

In activity initiated at the 2012 ASM, investigators from the CWT, JOR and AND LTER sites are using the Coweeta Listening Project (CLP) model to meet the science needs of environmental managers, local environmental organizations and land owners. CWT and GCE LTER investigators are also using the CLP model in a partnership with Georgia Sea Grant and the Georgia Coastal Research Council to promote science-based management of Georgia coastal resources. These cross-site efforts are central to activities described in 2.3.

4.0 Education and Outreach Activities

We will continue ongoing educational and outreach activities described below while enhancing our ability to provide information to the general public, including the Eastern Band of Cherokee as described under future plans.

Educational Activities comprise field-based environmental education programs and in-classroom support for middle school students, and university student education and mentoring. Our field-based education targets 5th through 8th grade students and their teachers, and consists of four annual multi-day field trips that draw about 1,000 students/yr from 14 schools in North and South Carolina and Georgia. These trips involve collaborators from the US Fish and Wildlife Service, NC Natural Heritage Program, NC Wildlife Resources Commission, NC Division of Water Resources, Land Trust for the Little Tennessee and Southern Appalachian Raptor Research. Our main programs include **Migration Celebration**, **Kids in the Creek**, **Bird Monitoring**, **Biodiversity Day**, and **Invasive Species Awareness Day**.

We support environmental science in the classroom by providing **Science Study Boxes** that deliver ecological content for teachers to meet state curriculum requirements. This effort benefits approximately 2,500 students/yr. We additionally engage between three and six undergraduate research interns each year through REU and other funding. Our graduate students organize an annual symposium each summer at which they present results of their ongoing research. Many of those located at UGA are also involved in the Integrative Conservation (ICON) PhD program run jointly by Anthropology, Ecology, Forest Resources and Geography. Two CWT project investigators teach the core ICON seminar in which students collaborate with practitioners in southern Appalachia (e.g., Vercoe et al. 2014) to bridge research into public outreach.

Public Outreach. Our partner in outreach is the Land Trust for the Little Tennessee (LTLT), the leading non-profit conservation organization in the southern Blue Ridge. We support the LTLT in three areas. **Aquatic Biomonitoring** is a citizen-science program that has coordinated thousands of volunteers over the last 25 years to monitor freshwater fish across the upper Little Tennessee River. The CWT LTER website hosts the fish monitoring data that includes hundreds-of-thousands of observations on all known fish species in the watershed. The Coweeta Listening Project working with ICON students and LTLT science-practitioners developed the **Southern Appalachian Stream Visual Assessment Protocol** (**saSVAP**) to enable volunteers to document stream conditions in relation to land use, water quality, and habitat. The **Shade Your Stream** program incorporates CWT LTER results and educates landowners in the Little Tennessee watershed on the importance of riparian corridor integrity, and includes workshops to restore riparian areas through live staking.

Media Interactions. The Coweeta Listening Project engages the western North Carolina community in a process that links science, policy and management. One of the key activities to date has been a collaborative of CWT project investigators and graduate students who publish a bi-weekly newspaper column in the *Franklin Press* (first issue: January 2012) that translates and communicates community-relevant CWT LTER science. Our support for public outreach and media interactions materially contributed to the recent designation of the Little Tennessee River Basin as North America's first "Native Fish Conservation Area".

Future Plans. We will continue providing field-based environmental education for middle school students, in-classroom support for middle-school environmental science students and their teachers, summer undergraduate internships, and making publically available the Aquatic Biomonitoring data. Each year, a minimum of two REU students will be recruited and mentored by project investigators to develop independent, place-based research supporting the CWT LTER project. We will create a graduate certificate program in science communication in tandem with the ICON PhD and engage the Cooperative Institute for Climate and Satellites in Asheville, NC, using the bi-weekly newspaper column as an internship opportunity. We will help LTLT deploy and train users in the application of saSVAP, thus equipping students with tools to address grand challenges in global environmental change (Ledee et al. 2011). We will also support expansion of the Aquatic Biomonitoring and Shade Your Stream programs to the Tuckaseegee watershed.

Table 1: Key Long Term Data Sets Collected or Used by CWT. This table summarizes core long-term datasets that have shaped our knowledge of the study area and that are frequently used by CWT investigators and collaborators. Some data are hosted by LTER, some by the FS, and some by both. This is not a comprehensive summary of CWT long-term data sets.

Data collected or processed by CWT and the USDA Forest Service Coweeta Hydrologic Laboratory				
Description	**Duration**	**Resolution**	**Access (dataset)**	**Notes**
WS 7 streamflow	1971-present	5 min	FS	Used for WS7 experiment.
WS 7 chemistry	1971-present	Weekly	FS	Used for WS7 experiment. **
WS 18 streamflow	1936-present	5 min/Daily	FS/LTER (3033)	Undisturbed reference stream.
WS 27 streamflow	1946-present	5 min/Daily	FS/LTER (3034)	Undisturbed reference stream.
Gap plot tree demography (WS 18, 27, 28)	1991-present	1-2 years	LTER(1003) (1006)(1008), (1033) (1046)	Seedlings, seed rain, annual diameter, survival, crown status, reproductive status: 2 to 4 yr dendrometer bands

Gradient plot microclimate	1991-present	Hourly	LTER (1013)	Catalog and streaming data. (soil moisture, soil temperature, air temperature, RH)
Intensive Hemlock plot tree census	2004-2011	Yearly	LTER (1130)	Some being resumed.
Soil moisture, temperature network	2000 – 2015	Hourly	LTER (1040)	Four sites continuous soil moisture and temp., high and low elevation, ridge and cove
Regional telemetry sites climate data	2013-present	Hourly	LTER	http://coweeta.uga.edu/ultclimate
Buncombe County climate data	2004 – 2012	Hourly	LTER(4038)	Micrometeorology at multiple sites, subset of the regional telemetry network, above
CWT climate data (CS01, CS77)	1934-present	Daily	FS	http://www.srs.fs.usda.gov/coweeta/areas/long-term-research/
CWT precipitation data (SG31, SG19)	1936-present	Monthly	FS	http://www.srs.fs.usda.gov/coweeta/areas/long-term-research/
Holocene sedimentology	Holocene	from stratigraphy	LTER (4068)	From floodplain sediment profiles.
Leaf phenology	2003-2014	Weekly, in season	LTER(CWTREG1142)	Spring and fall leaf development and senescence
WS 53,54,55 macroinvertebrates	1984-2006	Yearly	LTER (3023)	CPOM exclusion study (Wallace).
Land cover (30m pixel, 15 class)	1986-2011	Every 5 years	LTER GIS data portal	S.App study region extent
Land cover (30m forest/non-forest)	1907 – present	Periodic	LTER GIS data portal	Macon County, forest/non-forest for 1907, approx.. each decade since 1950.
Building locations	1907 – present	Periodic	LTER GIS data portal	Macon County, building location time series since 1910
Interview and Focus Group Data	2009-present	Monthly		IRB protocol prohibits public access
Data collected by other agencies but frequently used by CWT				
Description	**Duration**	**Resolution**	**Access**	**Notes**
USGS stream data, 5 gages	From 1941 to present	Daily, hourly	USGS *	Flow, some water chemistry.
County census records	1790-2010	10 years	EcoTrends on the website	Population, economic activity, demographics.
Macon, Buncombe Co. parcel records	1910-present	Updated with transactions	Tax assessor websites	Real estate activity and value in space and time, parcel size.
LiDAR	2005, 2009	Periodic	North Carolina, NCALM**	Mid- (280 ha^{-1}) and high-resolution (60k returns ha^{-1}) discreet-return points.
Landsat, MODIS time series	1984-present, 2001-present	Annually, bi-weekly	USGS, NASA	Calibrated satellite image time series, 20+ year regional LAI and phenology time series

**Daily data on CWT website: http://coweeta.uga.edu/dbpublic/hydrologic_data.asp ** http://calm.geo.berkeley.edu/ncalm/ddc.ht*

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