ABSTRACT

REYES SANDOVAL, WILMER MISAEL. Landscape Heterogeneity and Complexity: Implications for Terrestrial Carbon and Water Cycles. (Under the direction of Dr. Ryan E. Emanuel).

Heterogeneity and complexity are ubiquitous phenomena in terrestrial landscapes. Landscape processes and patterns are governed by biotic and abiotic interactions that arise from and lead to both heterogeneity and complexity over wide ranges of spatial and temporal scales. Thus, different parts of a landscape may behave differently, resulting in diverse carbon and water dynamics across the landscape with the potential to alter not only water and carbon cycles but also other ecosystem processes and behaviors. Improving our understanding of these phenomena, and their consequences for natural resource sustainability is relevant for the scientific community and for society in general. Chapter two includes a literature review on landscape heterogeneity and complexity, which synthesizes classic and recent work on these topics, providing rigorous definitions of the terms and discussing implications for water and carbon cycling in terrestrial ecosystems. The review highlights opportunities for moving forward in both conceptual understanding and modeling. Chapter three synthesizes datasets from the AmeriFlux tower network to evaluate relationships between terrain complexity and responses of ecosystem carbon fluxes to temperature and precipitation. Analyses show that different characteristics of terrain mediate responses of daily carbon fluxes to temperature and annual carbon fluxes to precipitation. The fourth chapter characterizes the water balance of a tropical landscape characterized by heterogeneous land use and rapid environmental change. Analyses are aimed at a broader discussion of complex human-environment interactions in tropical landscapes. Overall, chapter two shows that, by affecting several factors and ecosystem processes, heterogeneity

and complexity can lead to a wide range of carbon and water dynamics across the landscape, which need to be accounted for in carbon and water modeling approaches. Chapter three demonstrates that terrain complexity can give rise to a broad spectrum of carbon fluxes responses to climate at multiple temporal scales, including linear, nonlinear, and bidirectional. Finally, chapter four finds that climate, soil water storage and complex human-environment interactions converge to influence tropical eco-hydrological systems. Taken as a whole, this work helps to improve our conceptual understanding of the roles of heterogeneity and complexity in terrestrial carbon and water cycling.

Landscape Heterogeneity and Complexity: Implications for Terrestrial Carbon and Water Cycles

by
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DEDICATION

To my beloved wife Yeni and children María, Emily, and Jimena, whose unconditional and endless love and support drive my life. Thanks for being the main reason for my existence.

To my parents, Pedro Adan and Enma Esperanza, who with their unwavering hardwork, love, and sacrifice are largely responsible for all that I am and have accomplished.

Papito:

Como quisiera que estuvieras aquí conmigo compartiendo este nuevo logro. Gracias por estar siempre presente en mi vida y por ser mi mayor fuente de inspiración.

"Daddy: I wish you were here with me sharing this new accomplishment. Thanks for being always present in my life and for being my major source of inspiration"

To my mother in law Maria, who has always supported every step we have given as a family.

To my brothers and sisters for their permanent encouragement

BIOGRAPHY

Wilmer was born and raised in San Marcos de Colon, a small city in southern Honduras. He completed his early education there and received a BS in Agricultural Engineering from the National Agricultural University of Honduras (UNA) in 1999, and a Master's degree in Integrated Watershed Management from the Tropical Agricultural Research and Higher Education Center (CATIE) in Costa Rica (2003). In 2011, Wilmer was awarded a Fulbright Fellowship for doctoral studies at NCSU and joined the Ecohydrology and Watershed Science's lab in Fall 2012. Wilmer was awarded a Russell E. Train Fellowship from the World Wildlife Fund in 2014, and a Global Change Fellowship from SE Climate Science Center (DOI-NCSU) in 2016. Wilmer is currently a professor at UNA. His academic and research interests include the study of biophysical factors and processes regulating spatial and temporal variability of water, CO_2 and nutrient fluxes in terrestrial ecosystems. Wilmer is particularly interested in using eco and sociohydrologic approaches to address issues related to water scarcity, global warming, ecosystem services and food security.

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LIST OF ABBREVIATIONS AND ACRONYMS

AET	Actual Evapotranspiration
AMSL	Above Mean Sea Level
AWC	Available Water Content
BFI	Base Flow Index
EP-ITCZ	Eastern Pacific Intertropical Convergence Zone
ET	Evapotranspiration
EVI	Enhanced Vegetation Index
GEP	Gross Ecosystem Production
GPCC	Global Precipitation Climatology Centre
GPP	Gross Primary Production
ICF	Instituto de Conservación Forestal
InVEST	Integrated Valuation of Ecosystems Services and Tradeoff
LAI	Leaf Area Index
MODIS	Moderate Resolution Imaging Spectroradiometer
NDVI	Normalized Difference Vegetation Index
NEE	Net Ecosystem Exchange
NEP	Net Ecosystem Production
NPP	Net Primary Production
PAR	Photosynthetically Active Radiation
PET	Potential Evapotranspiration
PFT	Plant Functional Type
RA	Autotrophic Respiration
RE	Total Ecosystem Respiration
RH	Heterotrophic Respiration
RS	Soil Respiration
SANP	Sierra de Agalta National Park
SAVI	Soil Adjusted Vegetation Index
SOC	Soil Organic Carbon
TRI	Topographic Ruggedness Index
TRMM	Tropical Rainfall Measuring Mission
UAA	Upslope Drainage Area
UNA	Universidad Nacional de Agricultura
UNESCO	The United Nations Educational, Scientific and Cultural Organization
USA	United States of America
USGS	United States Geological Survey

CHAPTER 1: INTRODUCTION

Climate change poses unequivocal and unprecedented risks for human and natural systems on Earth [*IPCC*, 2014]. The carbon and water cycles are intimately coupled to each other at multiple spatio-temporal scales, and they are two central components of the Earth system [*Rodríguez-Iturbe and Porporato*, 2005; *Lohse et al.*, 2009; *Smith et al.*, 2012]. The importance of these cycles to society, their high climate sensitivity, and their potential feedbacks to the Earth's climate all motivate a growing interest in characterizing and understanding global water and carbon cycles under current and future climatic conditions [*Mu et al.*, 2011; *Arora et al.*, 2013; *Bernacchi and VanLoocke*, 2015; *Clark et al.*, 2015]. Despite significant progress, how water and carbon cycles will affect and be affected by future climate remains highly uncertain [*Allen and Ingram*, 2002; *Booth et al.*, 2012; *Friedlingstein et al.*, 2014; *Clark et al.*, 2016]. Lack of full understanding of these cycles in terrestrial ecosystems, including their responses to future climate and human-induced disturbances, underpins some of the most urgent scientific and societal challenges of our times such as climate change.

Understanding water and carbon cycles in terrestrial ecosystems is challenging in part because of their heterogeneous and complex nature. They are made up of multiple components, and complex biotic and abiotic interactions and processes, that arise from and lead to heterogeneity and complexity over a wide range of spatiotemporal scales [*Gleason*, 1917; *Levin*, 1998; *Chapin et al.*, 2011]. This ubiquitous heterogeneity and complexity can influence many ecological processes that represent parts of both cycles [*Green and Sadedin*, 2005; *Turner and Gardner*, 2015]. Heterogeneity and complexity can lead to high variability in water and carbon status and fluxes over wide ranges of spatio-temporal scales [*McDonnell* *et al.*, 2007; *Troch et al.*, 2009; *Borchard et al.*, 2015]. Moreover, heterogeneity may give rise to complex processes and emergent properties which have the potential to alter not only water and carbon cycles, but other ecosystem processes behaviors [*Levin*, 1998; *de Haan*, 2006; *Green et al.*, 2006].

Our understanding of water and carbon cycles becomes even more challenging in highly disturbed terrestrial ecosystems such as tropical regions. Several factors and dynamics such as deforestation, land-use change and urbanization are important sources of heterogeneity and complexity and may dramatically alter water and carbon cycles [*Melillo et al.*, 1996; *Hutyra et al.*, 2014; *Tang et al.*, 2014; *Lawrence and Vandecar*, 2015]. Yet our ecological knowledge of these complex systems is extremely limited [*Malhi and Grace*, 2000; *Ogden and Harmon*, 2012; *Wohl et al.*, 2012]. Consequently, field-based knowledge of hydrological and carbon processes in tropical landscapes has emerged as a critical research need [*Wohl et al.*, 2012; *IPCC*, 2014].

This dissertation is organized around three related chapters that builds on existing scientific knowledge gaps, and aims to improve our conceptual understanding of the roles of heterogeneity and complexity in terrestrial carbon and water cycling. A growing body of literature has begun to address the influence of landscape heterogeneity and complexity on aspects of water and carbon cycling in terrestrial ecosystems. However, little review or synthesis work has been conducted on the topic. Chapter 2 reviews the scientific literature addressing landscape heterogeneity and complexity in terrestrial ecosystems, and examines the implications for terrestrial carbon and water cycles. Chapter 2 has two main goals: (i) review the general scientific background on landscape heterogeneity and complexity, providing helpful definitions, terminology, and metrics for discussing heterogeneity and complexity, (ii) discuss some of the underlying causes of landscape heterogeneity and complexity in terrestrial ecosystems and how they influence carbon and water cycles at local and larger scales.

Case studies demonstrate that complex terrain, which accounts for more than 50% of Earth's land surface, can affect ecological processes associated with land-atmosphere carbon fluxes. However, no study has addressed the role of complex terrain in mediating responses of land-atmosphere carbon fluxes to climate. Chapter 3 synthesizes 178 site-years of data from 30 AmeriFlux network sites to evaluate relationships between terrain complexity and responses of ecosystem carbon fluxes to temperature and precipitation. The overarching hypothesis tested is that terrain variables correlate with the responses to temperature and precipitation among tower sites, but only for sites situated in complex terrain, where landscapes exhibit more internal topographic heterogeneity than in flat (i.e., non-complex) terrain.

Unprecedented, rapid environmental changes in the tropics are altering hydrologic cycles and related earth system processes, with potential global environmental impacts, yet our understanding of these processes and their implications is limited in many tropical regions. Chapter 4 combines field-based monitoring and remote sensing data to investigate the water balance of a complex landscape: a tropical watershed in Honduras. The chapter discusses implications for water resources and ecological dynamics locally and in the broader context of Honduras as a model for developing tropical regions in general. The research addresses the following questions: (i) How well can we characterize the water balance of a tropical headwater watershed given limited science infrastructure, data availability, and difficult logistics of this remote, developing region? (ii) What are the key uncertainties in components of the water balance, and how might they be overcome in ways that are useful for research and management? (iii) What are the implications of this work for water management in Honduras and other tropical regions? Chapter 5 summarizes main results and draws more general conclusions from the three preceding chapters.

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CHAPTER 2: HETEROGENEITY AND COMPLEXITY OF TERRESTRIAL ECOSYSTEMS AND IMPLICATIONS FOR TERRESTRIAL CARBON AND WATER CYCLES: A REVIEW OF OUR CURRENT STATE OF KNOWLEDGE.

Abstract

Landscape heterogeneity and complexity are increasingly important for understanding ecological processes in terrestrial ecosystems. A better understanding of these phenomena will improve our ability to represent processes within terrestrial carbon and water cycles at landscape scales and larger. The objective of this chapter was to review the scientific literature addressing landscape heterogeneity and complexity in terrestrial ecosystems, and to discuss the implications for terrestrial carbon and water cycles. Despite an abundance of literature on landscape heterogeneity and complexity, ambiguous definitions and inconsistent use of terminology reflect unsettled conceptual and methodological issues, which hinder both understanding and application of the concepts. We provide rigorous, technical definitions for both terms and discuss their interrelated nature. Heterogeneity and complexity influence multiple aboveground and belowground factors and processes that determine storage, distribution, and exchanges of carbon and water with the atmosphere, potentially leading to a wide range of carbon and water dynamics across the landscape. Failure to adequately account for these effects at scales finer than those represented by many spatially distributed ecosystem models can introduce significant uncertainty or inaccuracy into their results. We discuss recent work showing that explicit incorporation of local scales heterogeneities and complexities into models can improve their overall performance and their ability to represent ecological processes.

2.1 Introduction

Terrestrial ecosystems are intrinsically heterogeneous and complex. Ecosystems and the broader landscapes that they occupy are made up of multiple components, and the processes and patterns contained within them are governed by complex biotic and abiotic interactions that arise from and lead to heterogeneity and complexity over a wide range of spatiotemporal scales [*Gleason*, 1917; *Jenny*, 1941; *Levin*, 1976, 1992, 1998; *Chapin et al.*, 2011]. Understanding heterogeneity and complexity, and their consequences for ecological patterns and processes, remains a research priority in the environmental sciences [*McDonnell et al.*, 2007; *Chapin et al.*, 2011; *Kitanidis*, 2015; *Turner and Gardner*, 2015].

Terrestrial ecosystems influence Earth's system through wide ranging physical and biogeochemical processes [*Foley et al.*, 2003; *Field et al.*, 2007; *Fisher et al.*, 2014], particularly through key roles in the water and carbon cycles. Ecosystems store large amounts of water and carbon, and mediate and sustain exchanges of energy and mass between Earth's surface and it atmosphere [*Schimel et al.*, 2001; *Foley et al.*, 2003; *Bonan*, 2008; *Heimann and Reichstein*, 2008; *D 'Odorico et al.*, 2010; *Pan et al.*, 2011]. Understanding water and carbon cycling in terrestrial ecosystems is challenging in part because of their heterogeneous and complex nature. Through processes associated with storing, transforming, or transporting water and carbon, terrestrial ecosystems both cause heterogeneity and are influenced by myriad heterogeneities over a wide range of spatial and temporal scales [*McDonnell et al.*, 2007; *Troch et al.*, 2009; *Bradford et al.*, 2010; *Borchard et al.*, 2015].

Heterogeneity also arises from and produces complex processes and emergent properties, which have the potential to alter not only water and carbon cycles but other ecosystem processes and behaviors [*Levin*, 1998; *de Haan*, 2006; *Green et al.*, 2006]. For example, changes in water stores and fluxes have the potential to influence nearly all processes along the soil-vegetation-atmosphere continuum, including soil water content (SWC), vegetation composition and structure, nutrient cycling, and climate feedbacks [*Vitousek et al.*, 1997; *Gerten et al.*, 2008; *Clark et al.*, 2015]. In turn, these ecosystem changes may affect water and carbon cycling and subsequent feedbacks with the atmosphere and with other components of the Earth system [*Friedlingstein et al.*, 2006; *Arora et al.*, 2013; *Govind and Kumari*, 2014].

A growing body of literature has begun to address the influence of landscape heterogeneity and complexity on aspects of water and carbon cycling within individual terrestrial ecosystems [*Lovett et al.*, 2006a; *Risch and Frank*, 2006; *Anderson et al.*, 2009b; *Troch et al.*, 2009; *Tan et al.*, 2010; *Emanuel et al.*, 2011; *Govind et al.*, 2011; *Belshe et al.*, 2012; *Riveros-Iregui et al.*, 2012; *Turner et al.*, 2013; *Melton and Arora*, 2014]. To date, however, little review or synthesis work has been conducted on the topics of heterogeneity and complexity associated with water and carbon cycling in terrestrial ecosystems. Here, we review research from ecology, global change, hydrology and related disciplines to provide a comprehensive synthesis of landscape heterogeneity and complexity in terrestrial ecosystems and their implications for terrestrial carbon and water cycles. We begin by reviewing the general scientific background on landscape heterogeneity and complexity, providing standardized definitions, terminology, and metrics for discussing heterogeneity and complexity. Next, we discuss some of the underlying causes of landscape heterogeneity and complexity in terrestrial ecosystems and influences on carbon and water cycles at local and larger scales.

2.2. Methods

We conducted this review through four research steps following the systematic approach [*Higgins and Green*, 2011]. First, we defined the goals of the review. Particularly we focused on four major aspects, (1) scientific background, (2) conceptualization and metrics, (3) influences of landscape heterogeneity and complexity on carbon and water cycles, and (4) implications for carbon and water modeling. Second, we identified relevant work using the Web of Science database (https://webofknowledge.com). We searched for peer-reviewed papers published annually from the 1960 through 2016 addressing landscape heterogeneity and complexity. The search codes were: for heterogeneity, TS = ("landscape heterogeneity" OR "heterogeneous landscape*" OR "ecological heterogeneity" OR "environmental heterogeneity" OR "heterogeneous environment" OR "ecosystem heterogeneity" OR "heterogeneous ecosystem*") AND LANGUAGE: (English) AND DOCUMENT TYPES: (Article). Result: $N_{heterogeneity}$ = 5892 papers. Most of the retrieved articles were related to ecology (72%), environmental sciences (11%) and forestry and water resources (7%).

For complexity, TS = ("landscape heterogeneity" OR "heterogeneous landscape*" OR "ecological heterogeneity" OR "environmental heterogeneity" OR "heterogeneous environment" OR "ecosystem heterogeneity" OR "heterogeneous ecosystem*") AND TS = (complex OR complexity)) AND LANGUAGE: (English) AND DOCUMENT TYPES: (Article). Result: $N_{complexity}$ = 905 papers. Predominant scientific areas studying landscape complexity included ecology (56%), environmental sciences (13%), remote sensing (13%), and forestry and water sciences (9%). Third, we subset to all studies with explicit definitions of heterogeneity and complexity (N = 65), those related to carbon and water cycles specifically (N =132), and to those including modeling work (N = 38). Finally, we extracted concepts, summarized findings or data from each relevant article, and made major conclusions for all aspects identified in step one. Figure 2.1 shows the overall review flow.

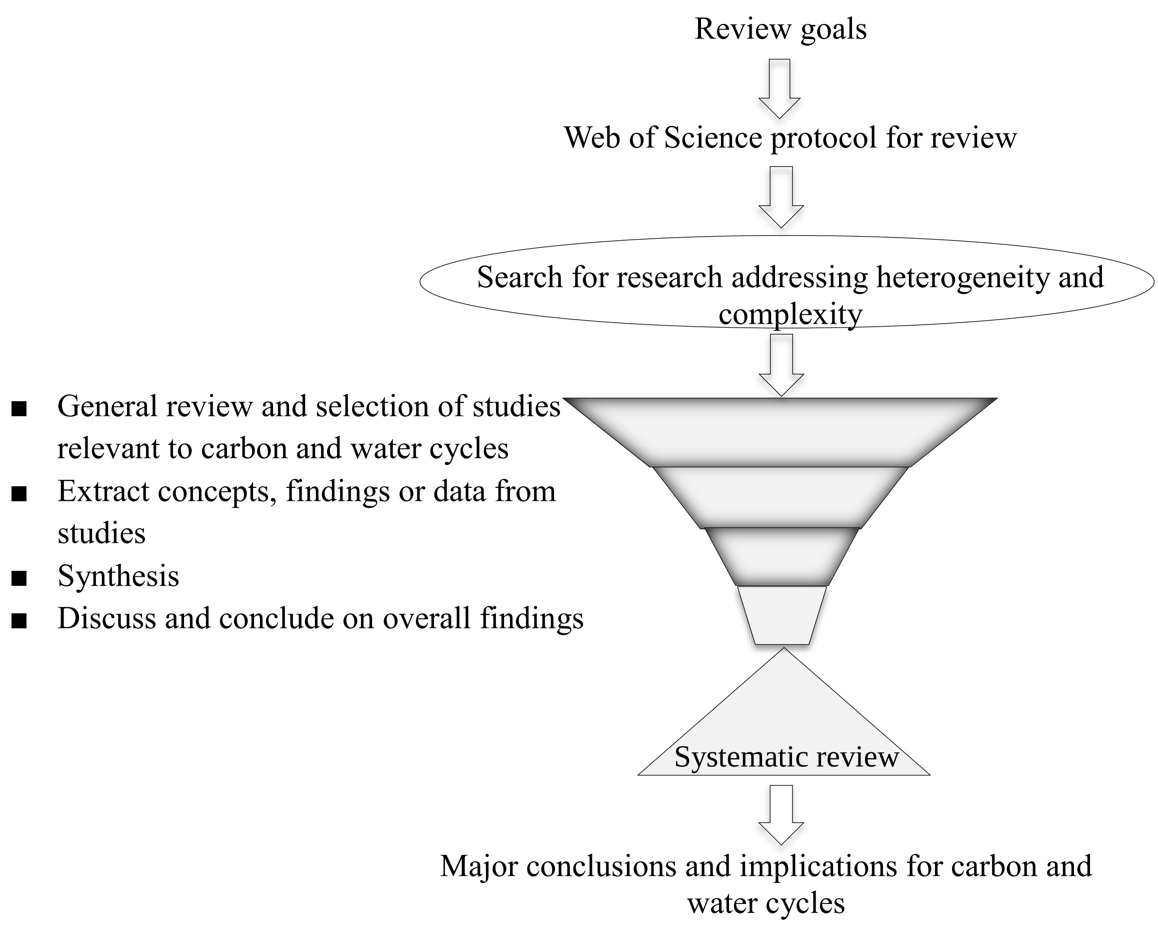

Figure 2.1 Research review process flowchart. Based on systematic review approach [*Higgins and Green*, 2011]

2.3 Heterogeneity and Complexity in Terrestrial Ecosystems

2.3.1 Scientific background

Landscape heterogeneity has been defined in various ways [*Kolasa and Pickett*, 1991; *Hutchings et al.*, 2000; *Farina*, 2006]. From the existing literature, we may synthesize a general definition of landscape heterogeneity as the dissimilitude and uneven distribution of components within a landscape or ecosystem [*Forman*, 1995; *Holderegger and Wagner*, 2006; *Farinaci et al.*, 2014; *Turner and Gardner*, 2015]. Scientists have long recognized that landscape heterogeneity is important for terrestrial ecosystem functions [*Cooper*, 1913; *Gleason*, 1917, 1926; *Jenny*, 1941; *Watt*, 1947; *Levin*, 1976; *Kolasa and Pickett*, 1991]. Most recently, understanding the causes and consequences of landscape heterogeneity in terrestrial ecosystems has become integral to the discipline of landscape ecology, and this topic has received much attention in related fields such as global change and hydrology [*McDonnell et al.*, 2007; *Chapin et al.*, 2011; *Turner and Gardner*, 2015].

The last two decades, in particular, have seen an explosion in research focusing on landscape heterogeneity, as demonstrated by a rapid increase in the annual number of peer-reviewed publications (Figure 2.2). It is now well established that heterogeneity is ubiquitous in the soil, vegetation, climate, and topography of landscapes, and it can exhibit high degrees of variability in both space and time [*Jenny*, 1941; *Townsend et al.*, 2008; *Savenije*, 2010; *Chapin et al.*, 2011]. This spatial and temporal variability can lead to strong environmental gradients that consequently mediate a wide range of physical and biogeochemical ecosystem processes [*McDonnell et al.*, 2007; *Troch et al.*, 2009; *Chapin et al.*, 2011].

Existing literature also offers several formal definitions of landscape complexity [*Maurer*, 1999; *Cadenasso et al.*, 2006; *Érdi*, 2008; *Parrot and Lange*, 2013]. We can define complexity in general terms as the level of difficulty required either to observe or explain a process or phenomenon emerging from multiple interactions among individual components of an ecosystem [*Michener et al.*, 2001; *Smithwick et al.*, 2003; *Green et al.*, 2006; *McDonnell et al.*, 2007; *Érdi*, 2008]. The degree of complexity exhibited by a terrestrial ecosystem generally depends on the number of biotic and abiotic components, the heterogeneity of these components, and the number and nature of interactions and functional relationships between components [*Jørgensen*, 1995; *Naveh and Carmel*, 2002; *Jensen and Arcaute*, 2010].

Terrestrial ecosystems are often described as complex systems [*Levin*, 1998; *Limburg et al.*, 2002; *Anand et al.*, 2010; *Parrott et al.*, 2012], in part because they are characterized by self-organization, non-linearity, and emergent behaviors occurring at multiple spatial and temporal scales [*Costanza et al.*, 1993; *Levin*, 1998; *Liu et al.*, 2007; *Ryan et al.*, 2007]. These characteristics may cause ecosystems to behave unpredictably when viewed in comparison to the behavior of their individual system components [*Green and Sadedin*, 2005; *Green et al.*, 2006; *Parrott and Meyer*, 2012; *Turner and Gardner*, 2015]. Acknowledging the complex nature of terrestrial ecosystems has become increasingly important for understanding their behavior [*May*, 1973, 1976; *Allen and Starr*, 1982; *Maurer*, 1999; *Wu and Hobbs*, 2002; *Green et al.*, 2006]. Seminal books [*Allen and Starr*, 1982; *Maurer*, 1999; *Green et al.*, 2006], international journals (*Ecological Complexity*), national research initiatives (e.g., NSF/USA biocomplexity program), and a growing number of peer-reviewed publications (Figure 2.2) all emphasize this increasing recognition. In summary, in this section we have shown that heterogeneity and complexity are well-known ecological phenomena, there is a widespread consensus about their importance for ecosystem functions and processes, and there is rapidly growing body of literature addressing the subject.

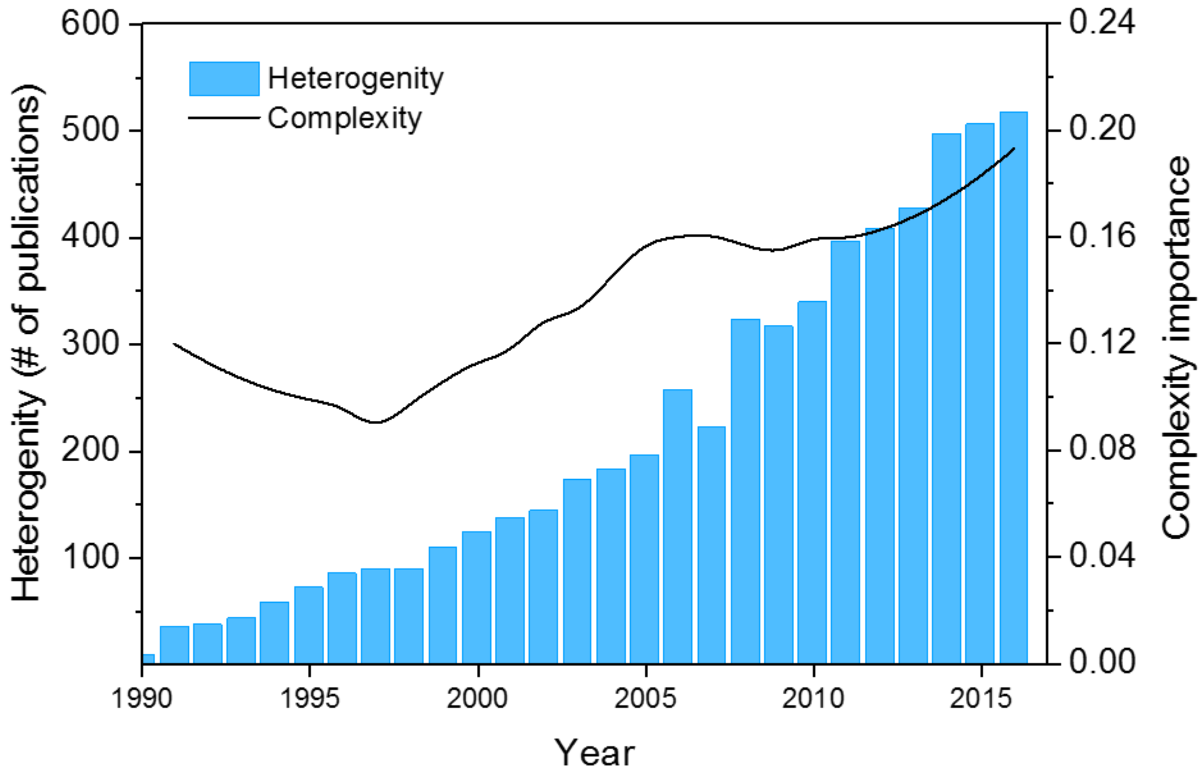

Figure 2.2 Number of peer-reviewed papers published annually (through 2016) addressing landscape heterogeneity and complexity (blue). Complexity importance was defined as the proportion of heterogeneity publications that include complexity as a keyword (i.e., $N_{complexity}/N_{heterogeneity}$). Data were obtained from the Web of Science; codes used are shown in section 2.2. $N_{heterogeneity}$ = 5892 studies (includes 70 articles published before 1990), and $N_{complexity}$ = 905 studies.

2.3.2 *Definition and conceptual issues*

In section 2.3.1 we highlighted the existence of several formal definitions of landscape heterogeneity and complexity, and broadly defined these terms. Despite existing definitions, usage of heterogeneity and complexity remain unclear and ambiguous in the literature of environmental sciences with neither common definitions nor congruent interpretations emerging. In this section we show that much of the confusion surrounding these terms can be attributed to inconsistent terminology usage, and to the plurality in forms of heterogeneity and complexity.

Landscape heterogeneity and complexity are generally linked in terrestrial ecosystems, but there is some disagreement about how they relate to each other. Some authors use landscape heterogeneity and landscape complexity as interchangeable terms [*Strayer et al.*, 2003; *Miles et al.*, 2012], other describe heterogeneity as a function of complexity [*Li and Reynold*, 1994; *Bin Chen and Bing Xu*, 2015], and still others consider heterogeneity a descriptor of ecosystems complexity [*Cadenasso et al.*, 2006; *Papadimitriou*, 2010], with complexity often increasing with increasing heterogeneity [*Levin*, 2000; *Parrott*, 2002; *Wu and David*, 2002]. In some cases, heterogeneity has been regarded as both a cause and a consequence of complexity in terrestrial ecosystems [*Lovett et al.*, 2005; *Wu*, 2006]. Moreover, some authors describe landscapes as a two-dimensional space where the horizontal variation of components refers to heterogeneity and the vertical variation represents complexity [*August*, 1983; *Grelle*, 2003]. This conceptualization, however, has been contested by others [*Kolasa and Rollo*, 1991]. These competing, in some cases opposing, views have hampered our understanding of how landscape heterogeneity and landscape complexity relate to each other in terrestrial ecosystems.

Another source of confusion is that heterogeneity is often used synonymously with gradients [*Veech and Crist*, 2007; *Herndon et al.*, 2015; *Yang et al.*, 2015], variation [*Cambardella et al.*, 1994; *Resat et al.*, 2012; *Morbidelli et al.*, 2016], and diversity [*Malanson and Cramer*, 1999; *Perović et al.*, 2015], despite these terms having been differentiated from heterogeneity by others [*Kolasa and Rollo*, 1991; *Jobbagy et al.*, 1996; *Wagner et al.*, 2000; *Turner and Gardner*, 2015].

One additional difficulty in defining heterogeneity and complexity is that these properties can take multiple forms in ecological systems. Examples of different forms include spatio-temporal, structural, and functional heterogeneity and complexity [*Kolasa and Rollo*, 1991; *Wiens*, 2000; *Bolliger et al.*, 2005; *Lovett et al.*, 2005; *Farina*, 2006; *Pickett and Cadenasso*, 2008; *Papadimitriou*, 2010]. Moreover, complexity may take on additional forms including algorithmic, deterministic, and aggregate [*Manson*, 2001]. As a result, heterogeneity and complexity can be defined as a function of a system property (e.g., land cover), or it can be defined by a number of components, interactions, or ecological functions [*Naveh and Carmel*, 2002; *Green et al.*, 2006; *Bin Chen and Bing Xu*, 2015; *Turner and Gardner*, 2015; *MacFadyen et al.*, 2016]. This plurality in forms of heterogeneity and complexity has led to an overwhelming number of definitions in the literature, making the concepts of heterogeneity and complexity complicated to understand and apply.

Ambiguity in terminology and definitions makes it difficult to determine whether terms used in different studies refer to the same concept or not. For example, a landscape can be homogeneous (and non-complex) if heterogeneity is defined with respect to species diversity, but it may be highly heterogeneous or complex if described as a function of topography. The uncontrolled use of synonyms also hampers the comparability and synthesis of research on this topic because studies are not easily revealed in database searches. For instance, when we searched "landscape heterogeneity" in *ISI Web of Science* we recovered 958 papers. However, the number increased to about 5900 when three other commonly used terms to describe landscape heterogeneity were included as search keywords (Figure 2.2).

In addition, generalizations about heterogeneity and complexity without delimitation may significantly hurts the utility of the concepts and their implications. For instance, the use of "landscape heterogeneity" or "landscape complexity" instead of "soil heterogeneity" or "topographic complexity" can make sense as applied for a particular study or area (e.g., soil science or geomorphology), but it can make no sense for ecologist studying or modeling landscape composition and configuration. In conclusion, the inconsistent usage of terms, the plurality in forms of heterogeneity and complexity, and generalizations of the terms without delimitation have created misdirection and confusion in interpretation, which have hindered communication and application of the concepts.

2.3.3 *Metrics and modeling*

Interest in quantifying landscape heterogeneity and complexity has increased tremendously in recent decades [*Farina*, 2006; *Uuemaa et al.*, 2009; *Parrott*, 2010; *Kupfer*, 2012; *Leitao et al.*, 2012; *Turner and Gardner*, 2015]. As a result, metrics exist to quantify spatial, temporal and functional heterogeneity [*Kolasa and Pickett*, 1991; *Li and Reynold*, 1994; *Feagin*, 2005; *Farina*, 2006], and new statistical and spatial methods [*Wagner and Fortin*, 2005; *Fortin et al.*, 2012; *Leitao et al.*, 2012] and software tools have facilitated the proliferation of landscape metrics used to characterize heterogeneity [*McGarigal and Marks*, 1994; *Kupfer*, 2012; *Turner and Gardner*, 2015]. Much attention has been given to spatial heterogeneity, particularly from the perspective of landscape composition and configuration, and at multiple spatio-temporal scales. The former refers to the type of land cover present within a landscape and in what proportions in occurs. The latter describes its spatial arrangement [*Lovett et al.*, 2005; *Turner*, 2005]. Together, these two components are often assumed to represent the heterogeneity of the landscape [*Farina*, 2006; *Turner and Gardner*, 2015].

Although fewer in number than heterogeneity metrics, there are several approaches and methods for measuring landscape complexity as well. These approaches include metrics and methods for characterizing structural [*Bolliger et al.*, 2005; *Cadenasso et al.*, 2006; *Proulx and Parrott*, 2008], spatial [*Huaxing*, 2008; *Papadimitriou*, 2009], temporal [*Hauhs and Lange*, 2008; *Serinaldi et al.*, 2014], spatio-temporal [*Kaspar and Schuster*, 1987; *Parrott*, 2005] and functional components of complexity [*Papadimitriou*, 2013]. In addition, many of the same metrics used to describe heterogeneity are also used to characterize landscape complexity.

Table 2.1 presents a set of commonly used metrics to characterize heterogeneity and complexity in terrestrial ecosystems. Moreover, Table 2.2 lists common software tools used to compute and evaluate these metrics. A few studies have proposed quantification of heterogeneity and complexity integrating multiples biotic and abiotic landscape components [*Stein and Kreft*, 2015]. However, existing metrics remain limited to quantifying specific aspects or components of landscape heterogeneity and complexity. For example, the coefficient of variation of plant height, the number of species, or indices of species diversity (e.g., Shannon index) are frequently used to quantify vegetation structure and composition. Heterogeneity and complexity of land cover is often assessed as a function of composition (e.g., % of forest cover, # land cover types), and configuration (e.g., edge and patch density, edge contrast, or patch fractal dimension). Patch refers to a continuous and relatively homogeneous area in a landscape, and contrast is defined as a function of one or more attributes of interest. For example, hydrology, vegetation or soil [*McGarigal and Marks*, 1994]. The fractal dimension refers to the degree of shape and edge complexity based on a perimeter-to-area ratio [*O'Neill et al.*, 1988].

Examples of typical metrics for evaluating heterogeneity and complexity using abiotic components of terrestrial ecosystems include number of distinct soil types, standard deviation of elevation and mean slope or mean aspect for topography, and coefficient of variation and ranges for climate variables such as air temperature. Most of these metrics have been developed from landscape ecology, and their primary use in the last two decades have been concerning habitat and biodiversity analysis as well as landscape patterns and land use and land cover change. Further information about landscape heterogeneity and complexity metrics, including scientific background and examples of their applications to different themes may be found elsewhere [*Cale and Hobbs*, 1994; *McGarigal and Marks*, 1994; *Ritters et al.*, 1995; *Uuemaa et al.*, 2009; *Parrott*, 2010; *Leitao et al.*, 2012; *Turner and Gardner*, 2015].

Table 2.1 Selected set of commonly used landscape heterogeneity and landscape complexity metrics.

Landscape property	Metric	Units	Description	Reference
Heterogeneity	Patch density	#/km^2	Number of patches per unit area. It reveals aspects of landscape patterns. Greater values mean greater heterogeneity.	[*McGarigal and Marks*, 1994]
Heterogeneity	Class area proportion	0-1	Measure the proportion of the landscape composed of a particular land cover type.	[*Leitao et al.*, 2012]
Heterogeneity	Edge Contrast Index	%	Relative measure of the contrast between adjacent land cover patches.	[*Turner and Gardner*, 2015]
Heterogeneity	Area-Weighted Shape Index	> 1	Average perimeter-to-area ratio for a landscape, weighted by the size of its patches. Increases with heterogeneity.	[*McGarigal and Marks*, 1994]
Complexity	Contagion	%	Degree of aggregation and interspersion of patches in an area. Higher values indicate greater aggregation.	[*Li and Reynolds*, 1993]
Complexity	Landscape Shape Index (LSI)	> 1	Structural complexity. Values increase with either landscape shape irregularity or edge length within the landscape.	[*McGarigal and Marks*, 1994]
Complexity	Fractal dimension	1-2	Degree of shape and edge complexity based on a perimeter-to-area ratio. Values approaching 2 indicate greater complexity.	[*O'Neill et al.*, 1988]
Complexity	Shannon diversity and evenness index	> 1	The index increases (more complex) as the number of different patch types (i.e., patch richness) increases.	[*Romme*, 1982]

Table 2.2 Selected set of commonly used software tools for quantifying landscape heterogeneity and landscape complexity.

Landscape property	Software tool	Description	Reference
Heterogeneity	FRAGSTATS	Windows-based package that computes most of existing landscape metrics. It accepts inputs from many GIS software.	[*McGarigal and Marks*, 1994]
Heterogeneity	QRULE	FORTRAN-based program for the analysis of landscape pattern, generation of neutral models, and testing hypotheses relating process and pattern.	[*Gardner*, 1999] [*Gardner and Urban*, 2007]
Heterogeneity	Patch analyst	Extension to the ArcGIS® software system for spatial analysis of landscape patches and the modeling of attributes associated with patches.	[*Rempel et al.*, 2012]
Complexity	3D Metrics Toolbox	Collection of raster-based Matlab routines for 3-dimensional analysis (e.g., two spatial axes and 1 temporal axis). Tool includes composition and configuration metrics.	[*Parrott et al.*, 2008]

In section 2.3 we have shown that heterogeneity and complexity are widely used terms but suffer from ambiguous definitions in the ecology literature. In addition, the growing interest in quantifying heterogeneity and complexity has led to a proliferation of tools and methods; however, heterogeneity and complexity are often reduced to a single number or index for a given patch or stand which may not reflect heterogeneity or complexity fully. Moreover, no metric or method exist to quantify heterogeneity and complexity at the landscape level as a whole, but metrics quantifying specific landscape aspect or components.

2.4 Sources of Landscape Heterogeneity and Complexity and Influences on Carbon and Water Cycles

We began this review by noting that landscapes comprise multiple components, and their processes and patterns are governed by biotic and abiotic interactions that arise from and lead to heterogeneity and complexity over wide ranges of spatial and temporal scales. Different parts of a landscape may behave differently, resulting in diverse carbon and water dynamics across the landscape. In this section, we highlight four major sources of landscape heterogeneity: soils, topography, vegetation, and disturbance [*Jenny*, 1941; *Lovett et al.*, 2005; *Chapin et al.*, 2011; *Turner and Gardner*, 2015]. We first discuss the influence of each source of heterogeneity on carbon and water cycling in terrestrial ecosystems, then we discuss implications of heterogeneous carbon and water dynamics for emergent properties.

2.4.1 Landscape heterogeneity and carbon cycling

We begin by reviewing basic concepts used throughout the section. In terrestrial ecosystems, carbon is gained through photosynthesis and it returns to the atmosphere through respiration. The total amount of carbon uptake by plants expressed at the ecosystem scale is known as gross ecosystem production (GEP). Total ecosystem respiration (RE) includes autotrophic respiration (RA) of live tissues (e.g., roots, leaves), and heterotrophic respiration (RH) of soil microorganisms and other soil fauna. The belowground component of RE (i.e., RA_{root} + RH) is known as soil respiration (RS). Net primary production (NPP) refers to the difference between GEP and RA, and the balance between carbon gained by GEP and carbon loss from total RE is termed net ecosystem production, NEP, [*Emanuel et al.*, 2006; *Lovett et* *al.*, 2006b; *Chapin et al.*, 2011; *Hicke et al.*, 2012; *Chen et al.*, 2014; *Monson and Baldocchi*, 2014].

Soil properties and topography

Soils properties, including physical, biological and chemical properties, are highly heterogeneous [*Cambardella et al.*, 1994; *Hillel*, 2003; *Troch et al.*, 2009; *Schmidt et al.*, 2011; *García-Palacios et al.*, 2012; *Du et al.*, 2015], and they have substantial implications for the transformation and transport of carbon in terrestrial ecosystems [*Schlesinger*, 1999; *Martin and Bolstad*, 2009; *Monson and Baldocchi*, 2014]. Soil texture influences RE by controlling soil aeration, water holding capacity, and soil organic carbon [*Paul*, 1984; *Power and Prasad*, 1997; *Rice*, 2002; *Luo and Xuhui*, 2006]. Spatial variation in bulk density, porosity, and water availability generally drive the spatial variability of soil C fluxes [*Jassal et al.*, 2005; *Luan et al.*, 2011; *Riveros-Iregui et al.*, 2012], and overall NEP *[Emanuel et al., 2011; Borchard et al., 2015; Ehrenfeld et al., 2005; Krüger et al., 2013*].

Moreover, soil organic matter (SOM) is tightly linked to substrate, moisture holding capacity, and nutrient availability [*Hudson*, 1994; *Fontaine et al.*, 2003; *Luo and Xuhui*, 2006]. Thus, SOM controls the magnitude and variability of RS by influencing root and microbial activity and composition [*Raich and Tufekciogul*, 2000; *Schmidt et al.*, 2011; *Schuur and Trumbore, 2006; Scott-Denton et al., 2006*]. Variability in SOM can lead to differences in root density and litter distribution [*Jobbagy and Jackson*, 2000; *Knohl et al.*, 2008], distinct RS rates [*Manzoni et al.*, 2008; *Fan et al.*, 2015], and, consequently, to multiple root pools with different carbon turnover times [*Gaudinski et al.*, 2010].

Topography also has implications for carbon cycling in terrestrial ecosystems. Topographic variation (e.g., terrain slope, terrain aspect, drainage area, elevation) influences some of the major drivers of C fluxes [*Nemani et al.*, 2003; *Baldocchi and Valentini*, 2004; *Beer et al.*, 2010; *Mahecha et al.*, 2010; *Fisher et al.*, 2012], often leading to strong gradients in water, energy and nutrients throughout the landscape [*Kang et al.*, 2002; *Anders et al.*, 2006; *Lundquist and Cayan*, 2007; *Li et al.*, 2014]. These gradients, in turn, can result in significant variability in C pools and fluxes landscape-wide [*Bohn et al.*, 2013]. For example, SWC, a key carbon-mediating variable, is often correlated with topographic variables such as convergence [*Anderson and Burt*, 1978; *McGlynn and Seibert*, 2003], slope position, and drainage areas [*Jencso et al.*, 2009; *Pacific et al.*, 2011; *Riveros-Iregui et al.*, 2012]. These terrain features are associated with the topographically-driven lateral redistribution of water [*Beven and Kirkby*, 1979], which alters not only local moisture regimes [*Wigmosta et al.*, 1994; *Grayson et al.*, 1997; *Western et al.*, 1999], but also microbial community composition and activity [*Du et al.*, 2015], and nutrient availability [*Bronstert et al.*, 2005; *Wheeler et al.*, 2007].

Although the response of C fluxes to SWC varies widely among ecosystems [*Baldocchi and Valentini*, 2004; *Wolf et al.*, 2013], GEP generally increases with SWC but can be suppressed at near-saturation levels [*Frolking et al.*, 2002; *Porporato et al.*, 2002; *Chapin et al.*, 2011]. Similarly, RE often increases with SWC but can quickly decline under either very dry or very wet soil conditions due to RS limitation by water and CO_2 diffusivity, respectively [*Reichstein*, 2003; *Riveros-Iregui et al.*, 2007; *Govind et al.*, 2009].

The effect of topography on C fluxes via insolation is also well known [*Western et al.*, 1999; *Gómez-Plaza et al.*, 2001; *Broxton et al.*, 2009; *Riveros-Iregui and McGlynn*, 2009]. Terrain features such as slope and aspect strongly affect the amount and distribution of solar radiation intercepted by the landscape surface. Direct solar radiation generally increases with terrain inclination [*Yang*, 2005; *Zhang et al.*, 2010a], which has a direct impact on short-term GPP. Moreover, in the northern hemisphere, NPP on north and east aspects is generally higher than NPP on west and southwest aspects [*Desta et al.*, 2004]. In addition, differences in radiation often have significant impacts on air and soil temperatures [*Korkalainen and Laurén*, 2006; *Guan et al.*, 2013; *Liang et al.*, 2014] as well as on litter accumulation [*Stage*, 1976]. In turn, these changes in temperature and substrate control RE rates at multiple spatio-temporal scales [*Raich and Schlesinger*, 1992; *Granier et al.*, 2007; *Mahecha et al.*, 2010].

The influences of topographic variables on ecosystem C fluxes are not necessarily additive. These variables may combine interactively in complex ways, giving rise to unpredictable C behavior [*Davidson et al.*, 1998; *Epron et al.*, 2006; *Kang et al.*, 2006; *Webster et al.*, 2008; *Emanuel et al.*, 2011; *Riveros-Iregui et al.*, 2012]. In summary, heterogeneity in soil properties and topography may alter carbon storage and fluxes directly by creating gradients in water and energy throughout the landscape, and indirectly by altering key influencing factors of carbon fluxes such as plant-derived organic inputs, microbial activity and carbon turnover times.

Vegetation

Vegetation can alter carbon fluxes in different ways. Differences in forest composition, forest age, or changes in leaf area index imply differences in plant interception of energy and water, photosynthesis, carbon allocation strategies and respiration, all of which, in turn, alter the ecosystem level carbon pools, fluxes, and their spatio-temporal variability.

Vegetation exerts direct control on GEP and ER; thus, vegetation heterogeneity (i.e., composition and structure) can dramatically alter ecosystem-scale C pools and fluxes [*Schimel et al.*, 2001; *Piao et al.*, 2009; *Chapin et al.*, 2011; *Melton and Arora*, 2014]. For example, GEP is directly affected by disturbance-related forest fragmentation [*Paula et al.*, 2011], changes in leaf area index (LAI), or forest structure due to changes in albedo and photosynthetically active radiation (PAR) [*Ni-Meister and Gao*, 2011; *Kobayashi et al.*, 2012; *Chen et al.*, 2013a], or due to successional dynamics [*Emanuel et al.*, 2006]. In addition, GEP and NEP are often correlated to leaf aging and forest age [*Turner et al.*, 1995; *Kitajima et al.*, 1997]. In general, it is assumed that GEP and NEP decrease with forest age [*Gower et al.*, 1996; *Pregitzer and Euskirchen*, 2004]. For example, the high carbon storage and NEP in the Eastern US have been attributed to the forest regrowth after past large-scale clearing [*Pan et al.*, 2009]. Nevertheless, recent work demonstrates that old-growth forests also have a high GEP potential [*Carey et al.*, 2001; *Luyssaert et al.*, 2008], and lower interannual variability of GEP than younger forest, which may translate into a higher or at least more stable interannual NEP [*Musavi et al.*, 2017] .

Vegetation also has a significant influence on RE. For example, plant interception of energy and precipitation as well as soil water extraction via plant transpiration alter the soil energy and water balances [*Rutter and Morton*, 1977; *Raich and Tufekciogul*, 2000], which are major drivers of RE [*Reichstein*, 2003]. Variation in plant functional type (PFT) can further control RE in different ways. For example, fast-growing plant species are metabolically more active and have higher RE than slow-growing species, and both fast and slow growing plants have distinctive carbon allocation strategies [*De Deyn et al.*, 2008]. Moreover, the amount, quality, and distribution of SOM are directly influenced by PFT, which in turn control RS [*Berg*, 2000; *Reichstein*, 2003]. Vegetation also interacts with abiotic factors (e.g., topography, soil texture) to mediate soil temperature and moisture regimes, which determine C fluxes variability and spatial patterns [*Wullschleger et al.*, 2002; *Emanuel et al.*, 2011; *Vesterdal et al.*, 2012].

Disturbance

Natural or human-induced disturbances can influence the C balance dramatically, resulting in rapid or progressive changes in the magnitude and direction of carbon fluxes and carbon storage in terrestrial ecosystems. For example, disturbances such as fire or land-use change can release large amounts of carbon to the atmosphere, which influence carbon storage [*Bradford et al.*, 2008; *Chapin et al.*, 2011; *Turner and Gardner*, 2015]. Carbon losses from fire or land use change may drive a landscape to switch temporarily from a net sink to a net source of carbon. However, the carbon released after a fire can be regained once stands and landscape recover [*Kashian et al.*, 2006; *Campbell et al.*, 2012], so that the landscape may go back to the initial net carbon sink state. Other disturbances, including drought and disease, may also alter the carbon cycle. Droughts affect the terrestrial carbon balance by modifying both the rates of GEP and RE directly via direct impact on plant physiology, phenology, forest composition and soil microbial activity [*Meir et al.*, 2008; *Van der Molen et al.*, 2011; *Frank et al.*, 2015], or indirectly through controls on hydrocarbon allocation, soil temperature and water content [*Reichstein*, 2003; *Carbone and Trumbore*, 2007]. Moreover, NPP can decrease immediately and dramatically after a pathogen attack, but can recover the following years as a result of enhanced growth of surviving vegetation [*Hicke et al.*, 2012].

2.4.2 Landscape Heterogeneity and Water Cycling

Connections between landscape heterogeneity in terrestrial ecosystems and the storage and movement of water represent a central research focus in hydrology [*McDonnell et al.*, 2007; *Kitanidis*, 2015]. Landscape heterogeneity contributes to variability in hydrological processes and can influence flow and transport properties, water status and fluxes [*Troch et al.*, 2009].

Heterogeneity in vegetation characteristics can produce spatial heterogeneity in hydrologic processes, particularly evapotranspiration, interception, infiltration, and hydraulic redistribution. Vegetation controls ET directly by regulating stomatal conductance [*Jarvis and McNaughton*, 1986; *Jones*, 1998], and differences in landcover type may lead to large landscape-wide differences in water yield and ET [*Bosch and Hewlett*, 1982b]. Precipitation intercepted by canopies can account for 10-50% of annual precipitation [*Carlyle-Moses and Gash*, 2011], and this is highly variable across ecosystems [*Miralles et al.*, 2010]. Precipitation not intercepted by plant canopies passes through to soils as throughfall or stemflow. Ground cover and litter heterogeneity can facilitate or limit infiltration flow paths and influence water transmission to groundwater recharge [*Crockford and Richardson*, 2000]. Once in the soil, water can move in direction of potential energy (i.e., high to low water potential), or can be passively redistributed by roots from deeper and moister soil layers to drier and shallower regions in the soil profile [*Domec et al.*, 2010; *Prieto et al.*, 2012]. The latter process, termed hydraulic redistribution, has been found to increase the dry season ET over the Amazon forest in about 40% [*Lee et al.*, 2005].

Soil heterogeneity in key properties such depth, texture, hydraulic conductivity, and porosity can have a profound influence on subsurface hydrological processes. One clear example of soil heterogeneity influence on subsurface hydrology is preferential flow. Macropores generated by plant roots, soil structure, and animal can increase significantly effective hydraulic conductivities and hence infiltration and percolation through the soil profile [*Clapp and Hornberger*, 1978; *Beven and Germann*, 1982; *Flury et al.*, 1994]. At the hillslope scale, lateral preferential flow through high-permeability areas and interconnected macropores can lead to homogeneous or heterogeneous subsurface storm flow [*McDonnell*, 1990; *Band et al.*, 2014; *Hartmann*, 2016; *Jarvis et al.*, 2016]. Moreover, connectivity of the hillslope preferential flow network controls average subsurface flow velocity [*Anderson et al.*, 2009a]. Other factors such as bedrock type and geologic structure may greatly influence baseflow hydrology and subsurface flow patterns [*Al-Taj*, 2008; *Delinom*, 2009].

Topography is one of the greatest influences on hydrology processes at the landscape scale, particularly in mountainous areas. For example, topographic gradients control the rate at which soil water moves downslope, how much runoff flushes through channel networks, and how much water remains in soils following storms [*Price*, 2011]. As we discussed in

Section 2.4.1, topographic attributes such as slope, aspect, drainage area, and elevation impose strong heterogeneities in insolation and water. These energy and water gradients control SWC regimes [*Burt and Butcher*, 1985; *Grayson et al.*, 1997; *Western et al.*, 1999], snowmelt rate [*Jost et al.*, 2007], and subsurface water redistribution and hydrologic connectivity [*Güntner and Bronstert*, 2004; *Jencso et al.*, 2009; *Pacific et al.*, 2011]. In turn, these factors and processes help control soil water storage [*Hanna et al.*, 1982; *Lanni et al.*, 2011], baseflow dynamics [*Vivoni et al.*, 2007], evapotranspiration [*Govind et al.*, 2011], and the timing of hydrologic responses [*Nippgen et al.*, 2011].

In this section, we show that landscape heterogeneity generally results in high variability in water storage, lateral transport, and exchange with the atmosphere. Soil, vegetation, and topographic heterogeneities influence critical components of the water cycle, including evapotranspiration, interception, infiltration, and subsurface redistribution of water. These factors are essential for understanding how much water enters an ecosystem, how it is redistributed throughout the landscape, and how and how much water leaves, either through exchange with the atmosphere or through drainage.

2.4.3 Complexity and Emergent Ecological Behaviors

In section 2.4.1 and 2.4.2 we have shown that different sources of heterogeneity can influence several factors and processes that have a direct impact on carbon and water storage and fluxes. However, interactions between heterogeneous landscape components can increase complexity, which may lead to unexpected emergent behavior or complex patterns. For example, as discussed in section 2.4.1, RE often increases with SWC. However, it may not always be the case depending on landscape position. For example, research at a subalpine forest in central Montana documented bidirectional (opposite) behavior of soil respiration in response to inter-annual water availability [*Riveros-Iregui et al.*, 2012]. They found that locations with high drainage areas (i.e., lowlands and wet areas of the forest) had higher cumulative soil respiration in dry years, whereas locations with low drainage areas (i.e., uplands and dry areas of the forest) had higher cumulative soil respiration in wet years.

Similarly, empirical modeling shows that net carbon sources and net carbon sinks are clearly distributed across the landscape as a function of both topography and vegetation in a northern Rocky Mountain landscape, yet specific source and sink regions are apparent across the landscape only when considering both of these variables simultaneously [*Emanuel et al.*, 2011]. Moreover, in Chapter 3 of this dissertation we show that topographic variables can interact among them and with vegetation to give rise to a broad spectrum of ecological behavior. For example, GEP responses to annual precipitation was predominantly dependent upon upslope drainage area, yet the combined effects of terrain slope and drainage area elicited a bidirectional response of RE, in which greatest positive responses were associated with small upslope drainage areas and greatest negative responses associated with large drainage areas. Furthermore, these relationships between GEP and RE and the two terrain variables revealed a nonlinear response of NEP to terrain, in which annual NEP was greatest for low to intermediate slopes with intermediate to high upslope drainage areas. All these examples illustrate how interactions among heterogeneous landscape components can give rise to emergent ecological behavior not apparent when investigating effects of landscape component or factors separately.

In summary, in section 2.4 we have discussed implications of well-known causes of landscape heterogeneity (i.e., soil, topography, vegetation, and disturbances) for terrestrial carbon and water cycles. Altogether, the evidence presented shows that landscape heterogeneity affects multiple aboveground and belowground factors and processes that determine how water and carbon are stored, transformed, distributed within ecosystems, and exchanged with the atmosphere. This suggests that water and carbon dynamics (i.e., storage and fluxes) and related processes vary significantly across the landscape as a function of heterogeneity, potentially leading to a wide range of ecologically emergent behaviors.

2.5. Implications for Regional and Global Carbon and Water Dynamics

The myriad possible consequences of landscape heterogeneity and associated complexity for terrestrial carbon and water cycles have been highlighted by many [*McDonnell et al.*, 2007; *Townsend et al.*, 2008; *Fisher et al.*, 2014; *Jin et al.*, 2015; *Luo et al.*, 2016]. Comparisons between terrestrial ecosystem models and ground-based data show little agreement of water and carbon dynamics either regionally or globally [*Sitch et al.*, 2008; *Schaefer et al.*, 2012; *Piao et al.*, 2013; *Zhang et al.*, 2013; *Wieder et al.*, 2014a]. Failure to adequately account for landscape heterogeneities has been identified as a major source of uncertainty in terrestrial ecosystem models [*Belshe et al.*, 2012; *Bohn et al.*, 2013; *Piao et al.*, 2013; *Zhang et al.*, 2013; *Eliseev and Sergeev*, 2014; *Melton and Arora*, 2014; *Pappas et al.*, 2015]. In this section, we discuss the influence of landscape heterogeneity and complexity on water and carbon cycling in terrestrial ecosystems (Table 2.3) and highlight how local-scale heterogeneities, often ignored by terrestrial ecosystem models, influence water-carbon dynamics that may impact regional and global model results.

2.5.1 Heterogeneity in terrestrial ecosystem models

Most organisms in Earth do not experience environmental variations at the coarse scale of regional or global earth system models, but instead they experience and respond to variations at local scales [*Sears et al.*, 2011; *Potter et al.*, 2013]. Thus, regional and global estimates of water and carbon cycling should ideally account for such local heterogeneities, yet it is rarely done due to computational and other technical limitations [*Fisher et al.*, 2014; *Pappas et al.*, 2015; *Prentice et al.*, 2015; *Davison et al.*, 2016]. Although some models address this shortcoming through sub-grid parametrization (i.e., quantification of within-patch heterogeneity), a common assumption in modeling is that carbon and water dynamics can be modeled within homogeneous units at a given scale (e.g., canopy, catchment, patch), and these results may be aggregated linearly to predict regional and global dynamics [*Ghan et al.*, 1997; *Fisher et al.*, 2014; *Melton and Arora*, 2014; *Sood and Smakhtin*, 2014; *Hartmann*, 2016]. For example, water and carbon fluxes at the canopy level are often estimated using the “big leaf approach” [*Friend et al.*, 1997]. That is, the complex structure of canopy leaf area is often treated as a single, homogeneous unit with an area equal to the total leaf area of the canopy. However, this approach is unrealistic because leaf properties and their interaction with the environment are not uniform throughout the canopy.

At landscapes or regional levels, terrestrial ecosystem models represent vegetation in terms of plant functional types (PFTs). This representation assumes homogeneity in atmospheric forces and plants, and hence fixed (averaged) values are frequently assigned to physical environmental conditions (e.g., albedo, SWC, soil temperature) within the PFTs, which then are used for energy, water and carbon estimations and dynamics [*Fisher et al.*, 2014; *Melton and Arora*, 2014]. Yet, PFT grids (e.g., 1° or greater) can be extremely heterogeneous and complex in terms of vegetation composition and structure, soil, topography, geology, hydrology, and microclimates [*Ghan et al.*, 1997; *Arora et al.*, 2001; *Beven and Cloke*, 2012; *Eliseev and Sergeev*, 2014]. Ignoring or simplifying local-scale heterogeneities can have significant consequences for regional and global carbon and water estimations and dynamics [*Ke et al.*, 2013; *Pappas et al.*, 2015], which is now being documented by a growing body of research (Table 2.3).

Table 2.3 Summary of recent studies investigating landscape heterogeneities influences on the water and carbon cycle.

Location	Spatial scale	Heterogeneity evaluated*	Implications for	Main results	Reference
Central Ontario, CA	Watershed	Topography/SOC/SSC	Carbon cycle	Improved RS prediction (r^2: 0.47 to 0.80)	[*Lecki and Creed*, 2016]
Central Siberia	Region	Topography	Carbon cycle	Modes differences in elevation generate high gradients in CO_2	[*van der Molen and Dolman*, 2007]
Northern Alaska, US	Watershed	Topography	Carbon cycle	Highest GPP and RE found at highest permafrost thaw and ground subsidence areas	[*Belshe et al.*, 2012]
Central Switzerland	Landscape	Topography/hydrology/ Vegetation/climate/soil	Carbon cycle	Explicit representation of heterogeneities improved spatial and temporal prediction of GPP.	[*Pappas et al.*, 2015]
Great Britain	Country	Vegetation	Carbon cycle	Actual vegetation-based GPP, NPP and NEP significantly greater than aggregation-based vegetation	[*Quaife et al.*, 2008]
California, US	Landscape	Vegetation	Carbon cycle	3D canopy structure scheme improved PAR predictions, particularly during light-limited period.	[*Kobayashi et al.*, 2012]
Shanxi Province, China	Watershed	Vegetation/topography	Carbon cycle	Explicit representation of heterogeneities improved NPP prediction (r^2: 0.78 to 0.88)	[*Chen et al.*, 2013a]
NE Germany	Landscape	Landscape diversity	Carbon cycle	Small inland water play pivotal role in landscape-wide C balance	[*Premke et al.*, 2016]
Northern Wisconsin/Michigan, US	Region	Landscape composition	Carbon cycle	Small area (33%) dominated landscape C storage (>80%)	[*Buffam et al.*, 2011]
West Siberian	Region	Soil water content	Carbon cycle	Unsaturated wetlands (64%) of the region accounted for about 80% of NPP and RS	[*Bohn et al.*, 2013]

Table 2.3 Continued

Location	Spatial scale	Heterogeneity evaluated*	Implications for	Main results	Reference
Global	Global	Interacting climate, soil texture, vegetation	Carbon cycle	PFTs influenced vertical distribution of SOC. SOC controls switched with depth. Shoot/root allocations + vertical root distributions affected SOC with depth	[*Jobbagy and Jackson*, 2000]
Global	Global	Microbial processes	Carbon cycle	Explicit incorporation reduced prediction errors of soil carbon models by 26%	[*Fujita et al.*, 2014]
Saskatchewan, Canada	Watershed	Topography	Water cycle	Model incorporating depression heterogeneity better than lumped single storage approach. Streamflow prediction improved r^2: 71 to 79 and 80 to 91 on daily and monthly basis respectively	[*Mekonnen et al.*, 2016]
Georgia, US	Watershed	Interacting topography, vegetation, soil texture, precipitation	Water cycle	Large increase in the variability of soil water content due to topographic heterogeneity	[*Chaney et al.*, 2014]
Central Canada	Region	Vegetation	Water cycle	Clumped scheme forest structure reduced radiation at the underlying snow surface and thereby lowered the snowmelt rate	[*Ni-Meister and Gao*, 2011]
Central Pennsylvania, US and Gales, UK	Watershed	SOM	Water cycle	Concentration–discharge behaviors strongly impacted by the distribution of SOM matter and hydrologic connectivity	[*Herndon et al.*, 2015]
Norwegian mainland	Region	Ground temperatures	Water cycle	Modelled total permafrost area using sub-grid variability of ground temperature doubled area estimated using grid-cell average.	[*Gisnas et al.*, 2016]

Table 2.3 Continued

Location	Spatial scale	Heterogeneity evaluated*	Implications for	Main results	Reference
Lena River Delta, Siberia	Region	Ice-wedge polygonal tundra	Water cycle	Wet tundra and small water bodies represented about half of the total ET in summer. Sub-pixel water bodies increased total water surface area in about 7%.	[*Muster et al.*, 2012]
Europe	Continent	Drought-induced	Water/carbon	ET, GPP and RE decreased when SWC dropped below 0.4	[*Granier et al.*, 2007]
Catskill Mountain region, NY, US	Watershed	Topography	Water/carbon	Water routing increased water fluxes but decreased C fluxes	[*Tang et al.*, 2014]

*SOC=soil organic content, SSC = soil sorption capacity. Other abbreviations where defined earlier in this review.

2.5.2 Vegetation and topographic heterogeneity

A common assumption in modeling approaches is that carbon and water dynamics can be modeled within homogeneous units at a given scale (e.g., canopy, catchment, patch). However, in this section we show that such assumptions of homogeneity limit our understanding of the carbon and water cycles, which can significantly impact model results. For example, heterogeneous canopy architecture may lower albedo, through greater interaction between radiation and different canopy levels [*Rowe*, 1993], and hence control availability of photosynthetically active radiation [*Kobayashi et al.*, 2012]. These light-canopy interactions, in combination with other factors such as wind exposure or edge-induced, may give rise to a multitude of emergent behaviors at the leaf and canopy scale that cannot be resolved at regional and global scales using additive approaches [*Smithwick et al.*, 2003]. For instance, research in central Amazonia used a multilayer canopy approach to scale fluxes from leaf to canopy level photosynthesis, and used eddy covariance measurements for validation. Compared to the big leaf approach, they improved GPP estimates dramatically when explicit calculations of light interception at different canopy levels were incorporated [*Mercado et al.*, 2007].

Moreover, heterogeneities in canopy cover, canopy architecture, and tree age have a direct influence on canopy water storage capacity, direct throughfall fraction, and the ratio of evaporation to rainfall intensity [*Pypker et al.*, 2005; *Park and Cameron*, 2008]. These factors successively control water and carbon fluxes and storage [*Kelliher et al.*, 1993; *Baldocchi et al.*, 2002]. For example, a study in boreal systems in central Canada found that canopy structure had strong control over radiative energy at the forest floor, which resulted in large variation in snow cover and snowmelt rates [*Ni-Meister and Gao*, 2011]. Another study in northern Lower Michigan concluded that canopy structural complexity (3D heterogeneity) improved water use efficiency across aging forests and so increased above ground NPP compared to structurally simpler canopies in young forests [*Hardiman et al.*, 2013]. These two examples illustrate how canopy scale heterogeneities and its inherent complexity can affect water estimates and water use by plants.

The importance of landscape topography for water and carbon dynamics has been widely recognized, yet it is frequently neglected in modeling work. Water and carbon fluxes are generally predicted at points or grid cells under the assumption that vertical flux are generally dominant [*Fisher et al.*, 2014; *Sood and Smakhtin*, 2014], hence, lateral flows and patch interactions are rarely considered as explicit processes in models. However, as discussed in Section 2.4.1 and 2.4.2, topography influences several ecological processes by redistributing water, energy and nutrients throughout the landscape [*Grayson et al.*, 1997; *Kang et al.*, 2002; *Yeakley et al.*, 2003; *Rotach et al.*, 2007; *Pacific et al.*, 2011; *Adams et al.*, 2014]. Therefore, accounting for these effects can help to improve model results. For example, atmospheric CO_2 predictions over regions can be improved by incorporating elevation gradients into mesoscale or global models [*van der Molen and Dolman*, 2007]. Moreover, explicit representation of landscape topography has dramatically improved lumped approaches predictions of GPP [*Belshe et al.*, 2012], RE [*Belshe et al.*, 2012; *Lecki and Creed*, 2016], ET and NEP [*Tang et al.*, 2014], and stream flow [*Mekonnen et al.*, 2016] at multiple spatial scales. These studies highlight the need for the modeling community to account for topographic effects on carbon estimates and predictions.

In this section, we have shown the effect of landscape heterogeneity on carbon and water fluxes at different scales, from leaf to canopy to landscape. Specifically, we have presented evidence showing that explicit representation of different aspects of forest structure and composition, and topography, into terrestrial ecosystem modeling can significantly improve current lumped-based (i.e., fixed averaged values) estimates and predictions of carbon and water.

2.5.3 Heterogeneity in landscape composition and configuration

Water and carbon estimates in regional and global models should account for the entire mosaic of ecosystems types and configurations within the modeling grid. Some modeling studies have highlighted the risk of predicting regional water and carbon fluxes using lumped composite or mosaic approaches for a given PFT tile [*Ghan et al.*, 1997; *Ke et al.*, 2013; *Melton and Arora*, 2014], particularly in regions characterized by high landscape heterogeneity [*Shrestha et al.*, 2016]. For instance, a study in southeastern Michigan combined field data and an ecosystem model (BIOME-BGC) to demonstrate that within-patch heterogeneity and fragmentation had a strong control on carbon cycling and storage [*Robinson et al.*, 2009]. This control is due in part to differences in vegetation types, which can alter root and root litter distribution, transport processes, and nutrients [*Davidson et al.*, 2006; *De Deyn et al.*, 2008]. These differences can lead to strong gradients in SOC, NPP, and RS. For example, observations from 2700 soil profiles in three global databases showed that SOC followed a clear decreasing concentration gradient with depth [*Jobbagy and Jackson*, 2000], and was related to vegetation. After controlling for climate, SOC had deeper distribution in arid shrublands than in arid grasslands, and subhumid forests had shallower

SOC distribution than subhumid grasslands [*Jackson et al.*, 2000]. The explicit incorporation of such local heterogeneities into global models has dramatically improved GPP predictions [*Pappas et al.*, 2015].

The large impact of within-patch heterogeneity on hydrologic processes is also well documented. For example, a regional study in Norway evaluated the impact of sub-grid variability of ground temperatures on snow distribution. The total permafrost area, modeled with the sub-grid approach, was twice as large as the area obtained using grid-cell average [*Gisnas et al.*, 2016]. A similar study in Kansas and Oklahoma investigated the effect of sub-grid variability in precipitation, vegetation, and soil properties. Sub-grid variability in precipitation led to a doubling of surface runoff and a 15% increase in ET during summer. Subgrid variability in vegetation and soil properties also increased runoff and ET by the order 2.75 times and 15%, respectively [*Ghan et al.*, 1997].

Lumped approaches ignore the capacities of different ecosystems or PFTs within a patch to process and store water and carbon differently. For example, studies of integrated carbon budgets of aquatic and terrestrial components of landscapes found that more complex ecosystems contributed most to the carbon balance even though they occupied a small area of the landscapes [*Buffam et al.*, 2011; *Premke et al.*, 2016]. In addition, interactions between heterogeneous landscape components may lead to unexpected behavior or complex patterns. For example, empirical modeling shows that net carbon sources and net carbon sinks are clearly distributed across the landscape as a function of both topography and vegetation in a northern Rocky Mountain landscape, yet specific source and sink regions are apparent across the landscape only when considering both of these variables simultaneously [*Emanuel et al.*, 2011]. Research in the Little River Experimental Watershed in Georgia used an interactive modeling approach to assess the effects of multiple sources of landscape heterogeneity (i.e., soil texture, vegetation, topography, precipitation) on the spatial variability of SWC. The influence of precipitation on SWC was observed after each storm only, but such effects decreased rapidly. However, strong variability in SWC emerged when precipitation interacted with vegetation, especially during the summer months when vegetation actively modified the hydrologic cycle. When spatial heterogeneity of topography was added to the model, there was a large variation in SWC, mainly during the winter, when vegetation was dormant and the surface tended to be wetter [*Chaney et al.*, 2014].

The evidence presented in this section show that if we consider landscape configuration (i.e., types of ecosystem within-patch), and the interactions among landscape components, we may be able to reduce uncertainty in carbon and water storage and fluxes. Together, the examples and discussion presented here highlight the risk of predicting regional water and carbon fluxes using lumped composite or mosaic approaches, and they also show how explicit incorporation of local-scale heterogeneities, which are often ignored by terrestrial ecosystem models, can help improve current regional and global carbon and water cycle estimates and predictions. We have shown how these local scale heterogeneities are present and have implications for carbon and water cycles at multiple scales (e.g., leaf, canopy, landscape), and driven by multiple landscape components, including topography and vegetation. The research reviewed here highlights the need to represent not only spatial heterogeneities within-patches, but also aspects of configuration (i.e., types of ecosystems within-patches) and interactions, which can also produce complex, often-unexpected, landscape behaviors and patterns. These results show notable differences between carbon and water estimates using lumped and explicit approaches (more than twofold in some cases) and highlight the need for the modeling community to account for heterogeneity effects on carbon estimates and predictions.

2.6 Conclusion

Scholarly attention to landscape heterogeneity and complexity and their implications for ecological processes has, arguably, never been greater. A better understanding of these phenomena has been suggested as a critical research area to improve carbon and water cycle predictions, yet challenges remain related to conceptualizations of phenomena and metrics used to quantify them. The inconsistent use of terminology along with generalizations about heterogeneity and complexity sometimes produce ambiguity, which hinders progress. Existing metrics quantify specific aspects or components of landscape heterogeneity and complexity, but no metric or method currently exists to quantify heterogeneity or complexity for an entire landscape.

Landscape heterogeneity and complexity influence multiple aboveground and belowground factors and processes that determine the storage, distribution, and exchange of carbon and water with the atmosphere. Carbon and water dynamics and related processes may vary significantly across the landscape as a function of heterogeneity and complexity, potentially leading to unexpected, emergent ecological behaviors. Failure to adequately account for these effects can influence the accuracy of carbon and water cycle models at spatial scales of landscapes and larger. Recent studies highlight risks associated with predicting regional water and carbon fluxes using lumped composite or mosaic approaches, and they provide robust evidence showing that incorporation of local-scale heterogeneities can significantly improve model results. This review highlights several general ways in which heterogeneity and complexity could be incorporated into models. Still, important questions remain: What type of heterogeneity and complexity are more relevant for the carbon and water cycles? At which scales? How to link the impact of heterogeneity and complexity across spatial and temporal scales? These questions must be answered to move to science forward.

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CHAPTER 3: COMPLEX TERRAIN INFLUENCES ECOSYSTEM RESPONSES TO CLIMATE

Abstract

Terrestrial ecosystem responses to climate have major implications for the global carbon cycle. Case studies demonstrate that complex terrain, which accounts for more than 50% of Earth's land surface, can affect ecological processes associated with land-atmosphere carbon fluxes. However, no studies have addressed the role of complex terrain in mediating responses of land-atmosphere carbon fluxes to climate. We synthesized data from AmeriFlux towers and found that for sites in complex terrain, responses of ecosystem carbon fluxes to temperature and precipitation are organized according to terrain slope and drainage area, variables associated with water and energy availability. Specifically, we found that for tower sites in complex terrain, mean topographic slope and drainage area surrounding the tower explained between 51% and 78% of site-to-site variation in the response of carbon fluxes to climate depending on the time scale. We found no such organization among sites located in flat terrain, even though they exhibited similar ranges in their flux responses. These results challenge the prevailing conceptual framework that assumes terrestrial ecosystem carbon fluxes derive simply from vertical soil-plant-climate interactions. In addition to these interactions, we conclude that the terrain in which ecosystems are situated can significantly influence carbon responses to climate, suggesting a new path to look at the current uncertainty in the global carbon cycle and future climate responses. For the conterminous US alone, this work has implications for about 14% of the total land area, which is considered topographically complex and contributes to about 1.13 Gt of carbon sequestration per year.

3.1 Introduction

Uncertainty in the response of terrestrial carbon fluxes to climate dynamics remains a major challenge to predicting the future behavior of the global carbon cycle [*Piao et al.*, 2013; *Friedlingstein et al.*, 2014]. Discrepancies between carbon model predictions and ground-based observations has been attributed to landscape heterogeneities [*Sitch et al.*, 2008; *Schaefer et al.*, 2012; *Pappas et al.*, 2015], which are driven partly by terrain complexity. Terrain complexity, defined as the topography often found in hilly and mountainous terrain, produces strong heterogeneities and gradients in environmental variable (e.g., soil, radiation, temperature, precipitation), which influence interactions among topography, soil, microbial communities, vegetation, and climate [*Running et al.*, 1987; *Grayson et al.*, 1997; *Du et al.*, 2015]. These heterogeneities and gradients often produce emergent behaviors, meaning that landscape carbon dynamics behave in more complex and unpredictable ways than dynamics at finer scales [*Schimel et al.*, 2002; *Emanuel et al.*, 2011].

More than 50% of the world's terrestrial landscapes are situated in complex terrain [*Rotach et al.*, 2014], which include hilly and mountainous areas. These regions play a significant role in regional and global climatological, hydrological, and biogeochemical processes [*Whiteman*, 2000; *Viviroli and Weingartner*, 2004], and include some of the world's most climatically-sensitive ecosystems [*Seddon et al.*, 2016]. Moreover, many of these landscapes have been identified as significant terrestrial sinks for atmospheric CO_2 and play important roles in the regulation of Earth's climate system [*Pacala et al.*, 2001; *Schimel et al.*, 2002; *Piao et al.*, 2006]. Yet knowledge of carbon dynamics in these environments, including processes and factors influencing responses to climate, is limited [*Schimel et al.*, 2002; *Schimel and Braswell*, 2005; *Wohl et al.*, 2012a].

Ecosystem carbon fluxes such as gross ecosystem production (GEP) of carbon, ecosystem respiration (RE), and the net ecosystem production (NEP) of carbon, are sensitive to changes in local water, temperature, and energy conditions [*Nemani et al.*, 2003; *Running et al.*, 2004]. Site-specific studies highlight the influences of complex terrain on the redistribution of light, water, microbial activity and other resources [*Lyons and Halldin*, 2004; *Chen et al.*, 2013b; *Du et al.*, 2015], revealing the potential for terrain to mediate responses of carbon fluxes to climate variability. However, conceptual frameworks and models of land-atmosphere interactions assume that ecosystem carbon fluxes arise primarily from soil and plant interactions with climate, typically ignoring effects of terrain on heterogeneity within these ecosystems [*Running and Coughlan*, 1988; *Collins et al.*, 2006]. This assumption may suffice for relatively flat landscapes [*Rotach et al.*, 2014], but case studies demonstrate that topographic variability, as an internal characteristic of terrestrial ecosystems, influences both spatial and temporal dynamics of ecosystem-scale carbon fluxes [*Hwang et al.*, 2012; *Riveros-Iregui et al.*, 2012].

Unlike relatively well-developed conceptualizations of how complex terrain influences the atmospheric boundary layer and turbulent transport between complex terrain and the atmosphere [*Katul et al.*, 2006], no general framework exists for evaluating the impacts of terrain on the underlying biophysical fluxes, including GEP, RE, and NEP, despite increasing evidence that ecological behavior is influenced by terrain complexity [*Levin*, 1992; *Hwang et al.*, 2012; *Riveros-Iregui et al.*, 2012]. Apart from a few site-specific studies, no work has studied the effects of terrain complexity on ecosystem carbon fluxes in general. With this in mind, we evaluated relationships between terrain complexity and the response of ecosystem carbon fluxes to climate within the AmeriFlux tower network, evaluating responses of GEP, RE, and NEP to temperature (hereafter $\sum_{GT}$, $\sum_{RT}$, and $\sum_{NT}$, respectively) and precipitation (hereafter $\sum_{GP}$, $\sum_{RP}$, and $\sum_{NP}$, respectively) for sites located in both complex and simple terrain. We considered daily, monthly, seasonal, and annual responses for 30 tower sites covering a range of terrain conditions determined by geospatial analysis of topography surrounding each tower. We hypothesized that inter-site correlations between terrain and responses of GEP, RE, and NEP to temperature and precipitation would emerge only in complex terrain, where topographic heterogeneity drives the distribution of water and energy in ways not present in flat (non-complex) terrain. In the absence of controlled, landscape-scale experiments, such results would help to identify both landscapes and positions within the landscape that may be experiencing similar ecological behavior.

3.2 Methods

3.2.1 Carbon, Climate, and Terrain Data

Ecosystem fluxes (NEP, RE, GEP) and other climate data were obtained from the AmeriFlux network database (http://public.ornl.gov/ameriflux). We selected 30 eddy covariance tower sites with at least four years of quality-controlled daily data (i.e., Level 4) and covering a broad range of biomes, climates, and terrain conditions (Figure 3.1-3.2 and Table 3.1-3.2). Data were further screened to remove outliers [*Papale et al.*, 2006], and negative values of GEP were set to zero and transferred the flux to RE to maintain the observed NEP [*Schaefer et al.*, 2012]. If there were remaining gaps in the dataset, we used the following criteria: (1) gaps > 5 days in NEP and temperature data were filled by using mean values of the site-series for the same period; (2) gaps < 5 days were filled using the mean value in 15 points moving window. The NEP was computed from NEE observations integrated temporally (i.e., daily, monthly, seasonally, and annually) and inverted in sign so that positive NEP indicates a net carbon accumulation by the ecosystem, and negative NEP indicates net carbon release. The GEP and RE data that we obtained were derived following Reichstein *et al.* (2005). Missing meteorological data from tower sites were supplemented with data from the DAYMET database [*Thornton et al.*, 2014], which is publicly available at (http://daymet.ornl.gov/). Daily data were then aggregated into monthly, seasonal, and annual scales for further analysis.

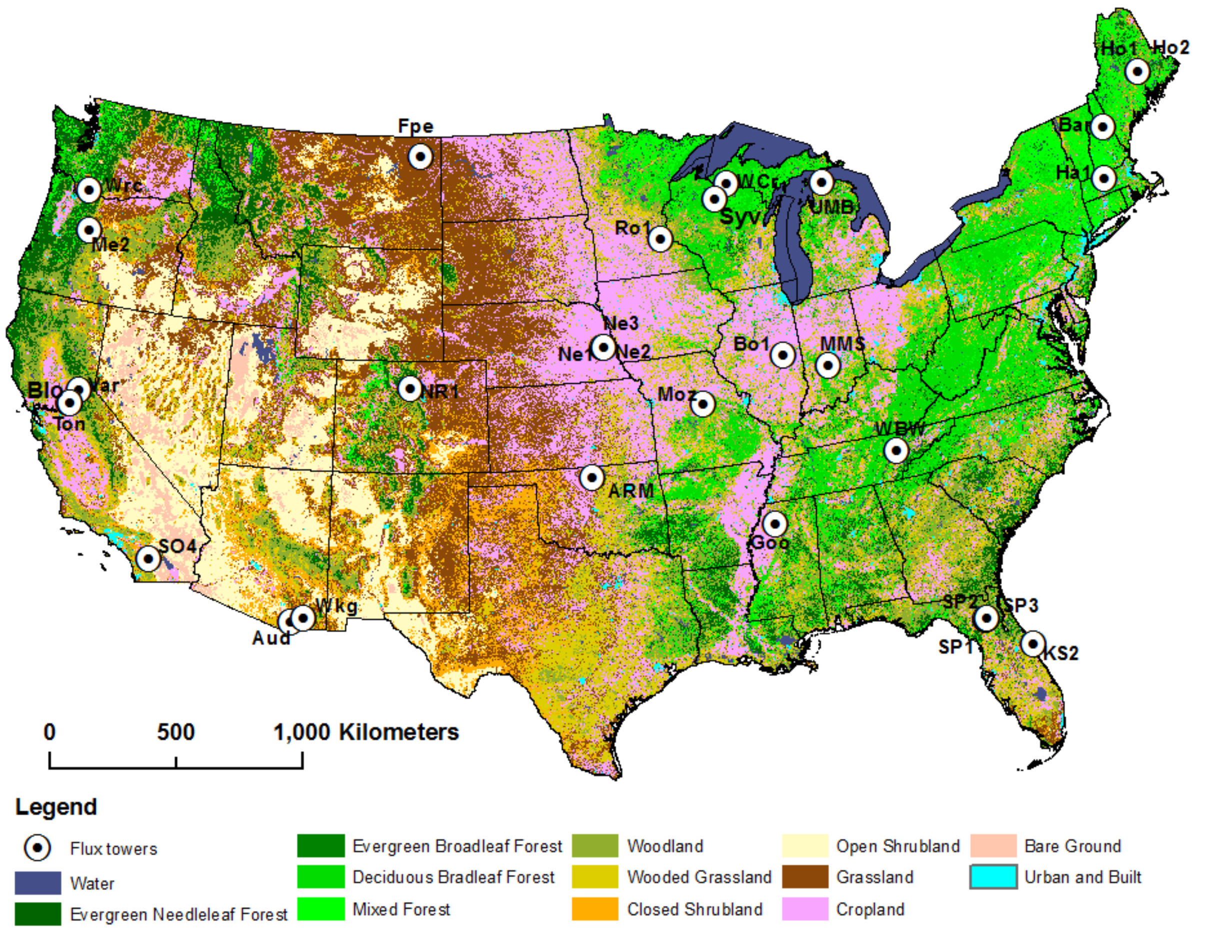

Figure 3.1 Location of AmeriFlux tower sites used in this study with land cover shown in the background. These sites cover a wide range of biomes as defined by the International Geosphere and Biosphere Programme (IGBP), including Closed Shrublands (2 sites), Cropland (5 sites), Deciduous Broadleaf Forests (7 sites), Evergreen Needleleaf Forests (9 sites), Grasslands (5 sites), Mixed Forests (1 site) and Woody Savannas (1 site). Complete description of sites and data used in this study presented in Table 3.1.

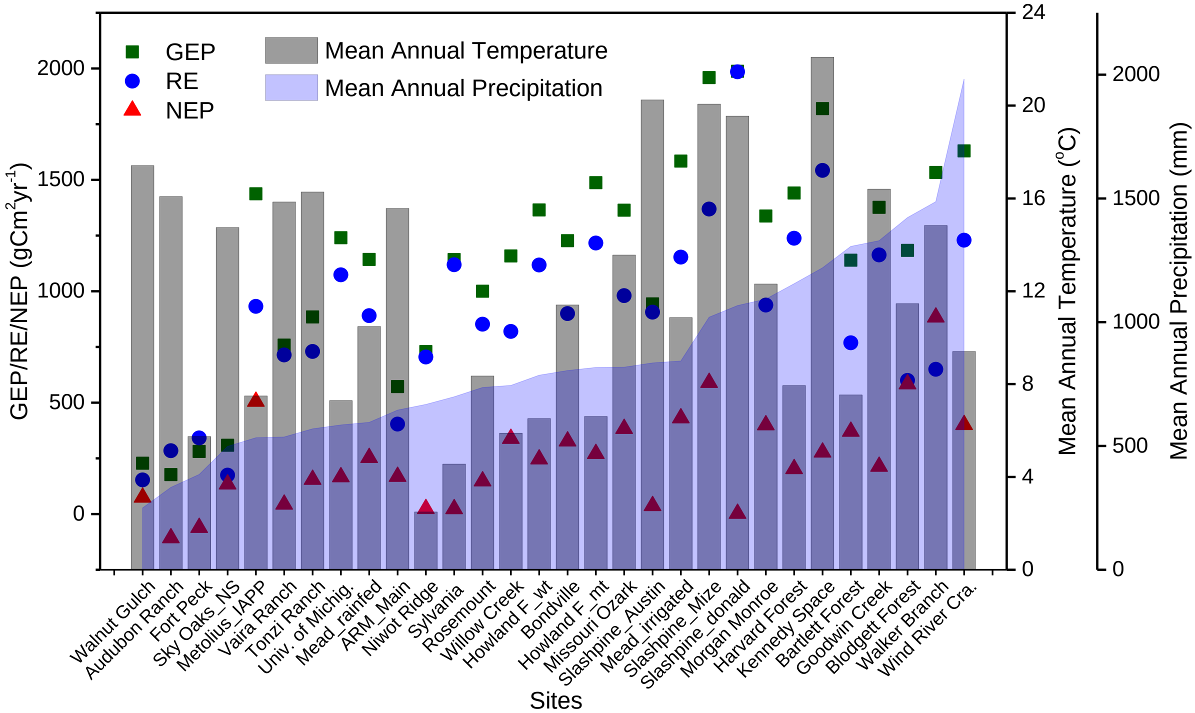

Figure 3.2 Mean values of precipitation, air temperature, and carbon fluxes across AmeriFlux sites evaluated. Sites are organized by increasing precipitation. Further information about the sites is shown in Table 3.1.

Table 3.1 Description of sites and data years used in this study.

ID	Name	Years of data	LAT	LONG	IGBP[1]	ELEV[2]	MAT[3]	MAP[4]	Reference
ARM	ARM-Lamont	2003-2006	36.6	-97.5	Cropland	314	14.8	843	*Fischer et al.,* 2007
Bar	Bartlett Forest	2004-2007	44.1	-71.3	Deciduous Broadleaf Forests	272	5.6	1246	*Jenkins et al.* , 2007
Blo	Blodgett Forest	1999-2006	38.9	-120.6	Evergreen Needleleaf Forests	1315	11.1	1226	*Goldstein et al.,* 2000
Bo1	Bondville	1997-2006	40	-88.3	Cropland	219	11	991	Hollinger et al., 2005
Fpe	Fort Peck	2001-2006	48.3	-105.1	Grasslands	634	5.5	335	*Wilson and Meyer* , 2007
Goo	Goodwin Creek	2003-2006	34.3	-89.9	Grasslands	87	15.9	1426	*Wilson and Meyer,* 2007
Ha1	Harvard Forest	1992-2006	42.5	-72.2	Deciduous Broadleaf Forests	340	6.6	1071	*Urbanski et al.,* 2007
Ho1	Howland Forest (MT)	1996-2004	45.2	-68.7	Evergreen Needleleaf Forests	60	5.3	1070	*Hollinger et al.* , 1999
Ho2	Howland Forest	1999-2004	45.2	-68.7	Evergreen Needleleaf Forests	91	5.1	1064	*Richardson and Hollinger* , 2005
KS2	Kennedy Space Center	2001-2006	28.6	-80.7	Closed Shrublands	3	21.7	1294	*Powell et al.,* 2006
Me2	Metolius-intermediate	2002, 2004-2007	44.5	-121.6	Evergreen Needleleaf Forests	1253	6.3	523	*Thomas et al.* , 2009
Ne1	Mead – irrigated	2002-2005	41.2	-96.5	Cropland	361	10.1	790	*Verma et al.,* 2005
Ne3	Mead - rainfed	2002-2005	41.2	-96.4	Cropland	363	10.1	784	*Verma et al.,* 2005
Ro1	Rosemount	2004-2007	44.7	-93.1	Cropland	260	6.9	806	*Griffis et al.,* 2008
SP1	Slashpine-Austin Cary	2001, 2003, 2005, 2006	29.7	-82.2	Evergreen Needleleaf Forests	50	20.1	1310	*Clark et al.,* 1999
SP2	Slashpine-Mize	2000-2004	29.8	-82.2	Evergreen Needleleaf Forests	50	20.1	1314	*Bracho et al.,* 2012
SP3	Slashpine-Donaldson	1999, 2001-2004	29.8	-82.2	Evergreen Needleleaf Forests	50	20.3	1312	*Bracho et al.,* 2012
Syv	Sylvania Wilderness	2002-2006	46.2	-89.3	Mixed Forests	540	3.8	826	*Desai et al.* , 2005
Ton	Tonzi Ranch	2002-2007	38.4	-121	Woody Savannas	177	15.7	559	*Ma et al.* , 2007
UMB	Biological Station (UoM)	2000-2006	45.6	-84.7	Deciduous Broadleaf Forests	234	5.8	803	*Gough et al.,* 2013
WCr	Willow Creek	1999-2006	45.8	-90.1	Deciduous Broadleaf Forests	520	4	787	*Cook et al.* , 2004
Wrc	Wind River Crane	1999-2002, 2004, 2006	45.8	-122	Evergreen Needleleaf Forests	371	9.5	2452	*Harmon et al.,* 2004
Aud*	Audubon Ranch	2002-2005	31.6	-110.5	Grasslands	1469	14.9	438	*Wilson & Meyer,* 2007
MMS*	Morgan Monroe Forest	1999-2006	39.3	-86.4	Deciduous Broadleaf Forests	275	10.9	1032	*Dragoni et al.,* 2007
Moz*	Missouri Ozark Site	2005-2008	38.7	-92.2	Deciduous Broadleaf Forests	219	12.1	986	*Gu et al.,* 2006
NR1*	Niwot Ridge Forest	1999-2005, 2007	40	-105.5	Evergreen Needleleaf Forests	3050	1.5	800	*Monson et al.,* 2002
SO4*	Sky Oaks	2004-2006	33.4	-116.6	Closed Shrublands	1429	14.8	498	*Luo et al.,* 2006
Var*	Vaira Ranch	2001-2007	38.4	-121	Grasslands	129	15.9	559	Ma et al., 2007
WBW*	Walker Branch	1995-1999	36	-84.3	Deciduous Broadleaf Forests	283	13.7	1372	*Wilson and Meyers,* 2001
Wkg*	Walnut Gulch Kendall	2005-2008	31.7	-109.9	Grasslands	1531	15.6	407	*Scott et al.,* 2010

[1]IGPP: The International Geosphere–Biosphere Programme land cover classification [*Loveland and Belward*, 1997]
[2]Elevation (m), [3]Mean annual temperature, [4]Mean annual precipitation.

Table 3.2 Mean annual gross ecosystem productivity (GEP), ecosystem respiration (RE), net ecosystem productivity (NEP), and mean terrain variables for all sites used in this study.

ID	GEP (gCm^2yr^{-1})	RE (gCm^2yr^{-1})	NEP (gCm^2yr^{-1})	Drainage area (m^2)	Terrain slope (%)	Terrain aspect (Degrees)
ARM	571.7	403.7	168	850	1.83	182
Bar	1139.2	768.7	370.5	1066	6.15	142
Blo	1183.3	599.8	583.5	884	4.38	196
Bo1	1226.9	899.7	327.2	868	1.22	237
Fpe	280.7	341.7	-61	909	2.36	120
Goo	1376.3	1163.1	213.2	755	5.37	199
Ha1	1440.8	1237.8	203	989	6.12	151
Ho1	1487.3	1216.6	270.7	947	1.4	150
Ho2	1364.7	1117.9	246.8	896	1.59	157
KS2	1819.8	1542.3	277.5	728	1.47	139
Me2	1437.3	932.2	505.1	881	3.29	169
Ne1	1584.1	1153.2	430.9	778	0.47	79
Ne3	1142.9	890.2	252.8	694	0.51	93
Ro1	1000	852.1	147.9	759	0.63	136
SP1	943.2	906.3	36.9	792	1.03	181
SP2	1987.2	1985.1	2.1	762	0.46	91
SP3	1958.9	1369	589.9	721	0.84	197
Syv	1142.3	1119.1	23.2	836	3.1	145
Ton	884.8	729.8	154.9	919	3.8	210
UMB	1240	1073.7	166.3	947	2.4	170
WCr	1158.3	819.5	338.8	1002	2.7	168
Wrc	1630	1229.2	400.8	1055	5.18	128
Aud*	176.8	284	-107.2	814	9.25	149
MMS*	1337.4	938	399.4	880	13.87	183
Moz*	1363.8	980.1	383.7	865	15.3	169
NR1*	729.1	705	24.1	958	12.05	91
SO4*	308.4	174.5	133.9	834	10.64	215
Var*	758.1	714.3	43.8	901	9.3	202
WBW*	1533	649.4	883.6	854	16.34	189
Wkg*	228	153.2	74.8	812	9.13	217

* Sites identified as having complex terrain, see methodology in main paper for further details.

We used a 10 m USGS digital elevation model (https://viewer.nationalmap.gov/basic) to derive terrain variables within a flux tower footprint. These variable included upslope drainage area [*Seibert and McGlynn*, 2007], terrain slope and topographic ruggedness index [*Riley et al.*, 1999]. Initially, all terrain variables were derived for each site for a circle with 5 km radius (approximately 78.5 km^2), with the flux tower situated at the center. This large radius ensured accurate calculation of non-local variables (i.e., drainage area) in the vicinity of the tower. The gridded terrain data were then clipped to a standardized footprint comprising a 1 km radius surrounding each tower to provide a uniform estimate of the terrain within the typical flux tower footprint. We computed both the mean and variance of terrain values within the 1 km radius for each site.

3.2.2 Data Analysis

Stepwise multiple and simple least square linear regressions were used to assess relationships between climate variables and carbon fluxes across sites and temporal scales (daily, monthly, seasonal, and annual). These analyses enabled us to determine when and at which temporal scale GEP, RE and NEP were monotonic functions of either temperature or precipitation, and when and at which temporal scale both climate variables contributed significantly to the response of carbon fluxes among sites. We tested correlations between climate (temperature and precipitation) and carbon fluxes for daily, monthly, seasonal, and annual scales, and computed the responses for all time scales. The flux response to climate ($\sum$) is defined as the slope of the linear least-squares regression between an ecosystem flux and a climate variable at a particular time scale (e.g., the response of annual GEP to annual precipitation, annual $\sum_{GP}$).

We determined the degree of terrain complexity for each site using the topographic ruggedness index (TRI) and the variance of upslope drainage area. The TRI and the variance of upslope drainage area were used as grouping criteria for an unsupervised K-means cluster analysis [*Hartigan and Wong*, 1979]. The analysis objectively placed each AmeriFlux site into one of two clusters. The centroids of the two clusters confirmed that they represented less complex terrain and more complex terrain.

We tested global correlations (i.e., correlations among all sites) between $\sum$ and terrain variables, and also between $\sum$ and potential confounding factors including mean site elevation, mean annual temperature and mean annual precipitation. For each cluster we performed stepwise multiple linear regression to determine significant terrain variables influencing carbon flux responses at each time scale. Once significant terrain variables were identified at all time scales, we computed the correlation between terrain variables and carbon flux responses by linear regression. We used multiple regression analysis to identify the codependence of carbon flux responses to annual precipitation on both terrain slope and upslope drainage area.

To place our results in a broader context, we used data from the MODIS GPP/NPP (MOD17) dataset [*Zhao et al.*, 2005] to calculate the contribution of complex terrain to the annual carbon sequestration for the conterminous US. We used bivariate frequency distributions to identify areas having similar terrain slope and upslope drainage area to the AmeriFlux sites evaluated in this study. All statistical and geospatial analyses were performed using Matlab R2015b and ArcGIS 10.3.

3.3 Results

We analyzed a total of 178 site-years of data (Table 3.1), and we found that responses of carbon fluxes to temperature and precipitation varied considerably across temporal scales and among sites (Table A1 in Appendix A). The unsupervised k-means cluster analysis of terrain variables identified eight sites as occupying complex terrain and placed the remaining 22 sites in the cluster of non-complex terrain (Table 3.1). Complex sites included grasslands (GRAS, 30%), deciduous broadleaf forests (DBF, 30%), shrublands (SCH, 20%), and evergreen needleleaf forests (ENF, 20%). The non-complex sites cluster included Croplands (23%), GRA (14%), DBF (18%), EFN (32%), CSH (4%), mixed forests (4%), and woody savannas (4%).

For the eight sites situated in complex terrain, we found that topographic slope and upslope drainage area explained between 51% and 78% of site-to-site variation in the response of fluxes to climate depending on the time scale. Specifically, mean topographic slope of the surrounding landscape was correlated with temperature responses $\sum_{GT}$, $\sum_{RT}$, and $\sum_{NT}$ at each of the time scales that we tested (Table 3.3), but daily correlations were strongest between temperature responses and terrain slope (Figure 3.3a-c). In other words, as terrain became steeper, GEP, RE, and NEP became more responsive to diel temperature fluctuations.

Among towers in complex terrain, we also found that mean upslope drainage area was correlated with annual precipitation responses, $\sum_{GP}$, $\sum_{RP}$, and $\sum_{NP}$ (Figure 3.3d-f). The two constituent fluxes, GEP and RE, responded linearly, both became less responsive to annual precipitation as mean drainage area of the landscape increased (Figure 3.3d, e). However, the relationship between annual $\sum_{NP}$ and upslope drainage area was non-monotonic, with peak response occurring at a mean upslope drainage area of approximately 900 m^2. For complex sites with mean upslope drainage areas below this threshold, $\sum_{NP}$ increased with drainage area, but above this threshold the flux response decreased with upslope drainage area (Figure 3.3f).

Multiple regression analysis between terrain variables and carbon flux responses to annual precipitation showed that $\sum_{GP}$ was predominantly dependent upon upslope drainage area (Figure 3.4a). On the other hand, the combined effects of terrain slope and drainage area on $\sum_{RP}$ elicited a bidirectional response (Figure 3.4b), in which greatest positive responses were associated with small upslope drainage areas and greatest negative responses associated with large drainage areas. Relationships between $\sum_{GP}$ and $\sum_{RP}$ and the two terrain variables revealed a nonlinear response of $\sum_{NP}$ to terrain (Figure 3.4c). Annual $\sum_{NP}$ was greatest for low to intermediate slopes with intermediate to high upslope drainage areas. The 22 tower sites located in flat (i.e., non-complex) terrain exhibited very weak or nonexistent relationships between terrain variables and the responses of carbon fluxes to temperature and precipitation (Table 3.3).

Table 3.3 Regression analysis between carbon fluxes responses to climate and terrain variables for complex and non-complex sites across temporal scales. Responses not shown at certain temporal scales (e.g. GEP to Ta at annual scale) were found to be statistically not significant.

Response	Terrain variable	Scale	Regression results			
			Intercept	Slope	R^2	p-v
Complex terrain sites						
GEP to P	Slope	Daily	0.09	-0.008	0.59	0.02
GEP to T_a*	Slope	Daily	-0.42	0.044	0.67	0.01
GEP to T_a	Slope	Monthly	-16.4	1.74	0.7	0.009
GEP to T_a	Slope	Seasonal	-47.4	5.04	0.67	0.01
RE to T_a	Slope	Daily	-0.19	0.02	0.51	0.04
NEP to T_a	Slope	Daily	-0.32	0.032	0.78	0.04
NEP to T_a	Slope	Monthly	-13.27	1.3	0.79	0.003
NEP to T_a	Slope	Seasonal	-38.24	3.83	0.8	0.003
GEP to P	UAA	Daily	7.25	-0.008	0.67	0.013
RE to P	UAA	Annual	6.84	-0.007	0.51	0.04
NEP to P	UAA	Annual	-40.40	b1:0.093 b2:-5.2E-5	0.76	0.02
Non-complex terrain sites						
GEP to P	Slope	Seasonal	1.8	-0.34	0.26	0.01
NEP to P	Slope	Monthly	0.49	-0.11	0.19	0.04
RE to P	Slope	Daily	0.05	-0.01	0.32	0.004
RE to P	Slope	Monthly	0.65	-0.11	0.34	0.003
RE to P	Slope	Seasonal	1.02	-0.18	0.28	0.009

*T_a = Air temperature, UAA is Upslope drainage area and P is precipitation. RE, GEP, NEP are total ecosystem respiration, gross ecosystem production, and net ecosystem production respectively.

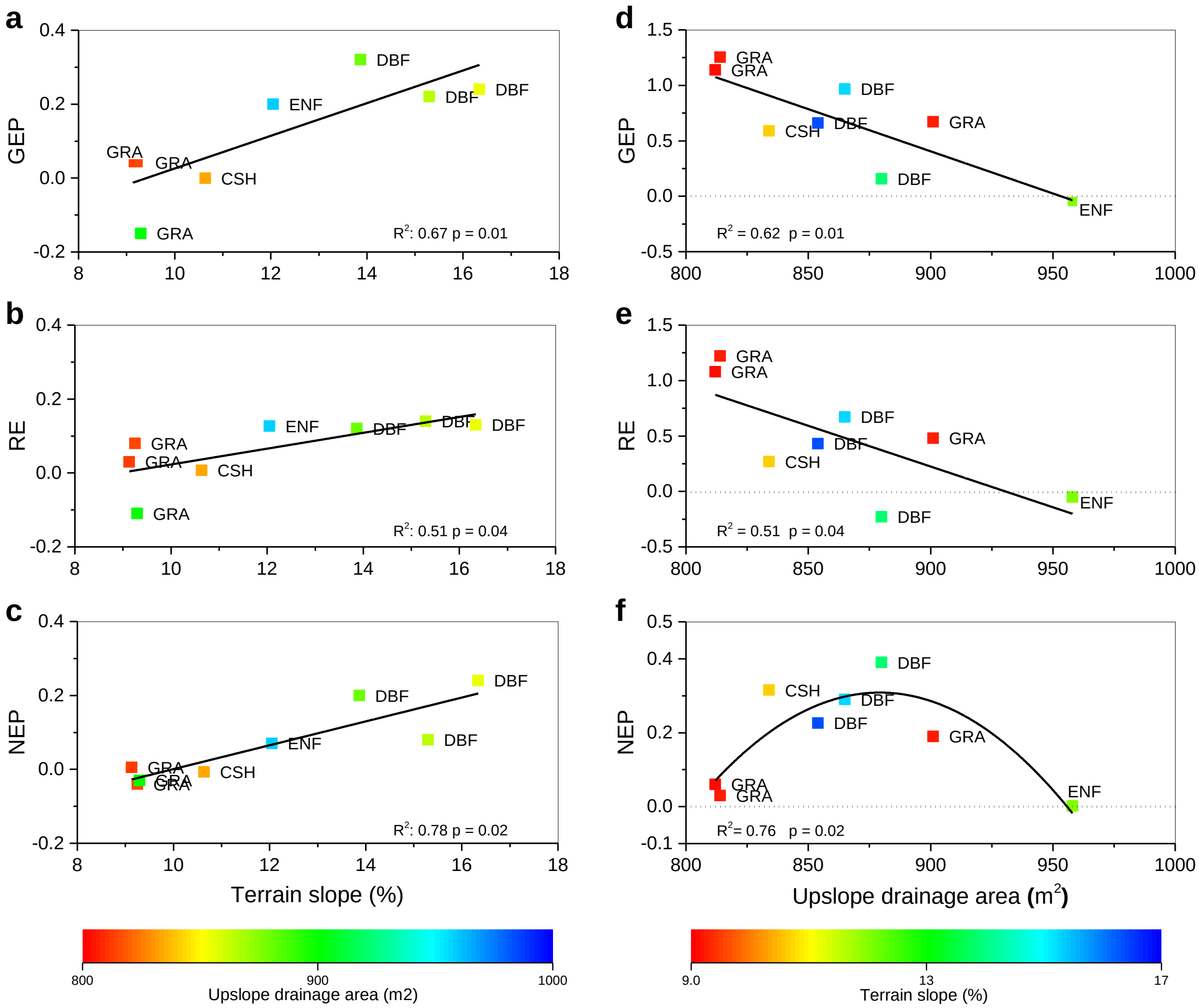

Figure 3.3 Relationships between the response of carbon flux to climate and terrain variables for sites situated in complex terrain. (a-c) show daily temperature response (g C m^{-2} day^{-1} / °C), and (d-f) show annual precipitation response (g C m^{-2} yr^{-1}/ mm). Dotted line on panels (d-f) is Y = 0. Labels indicate the type of ecosystem as defined by The International Geosphere–Biosphere Programme: GRA (Grassland), DBF (Deciduous Broadleaf Forests), ENF (Evergreen Needleleaf Forests), and CSH (Closed Shrublands).

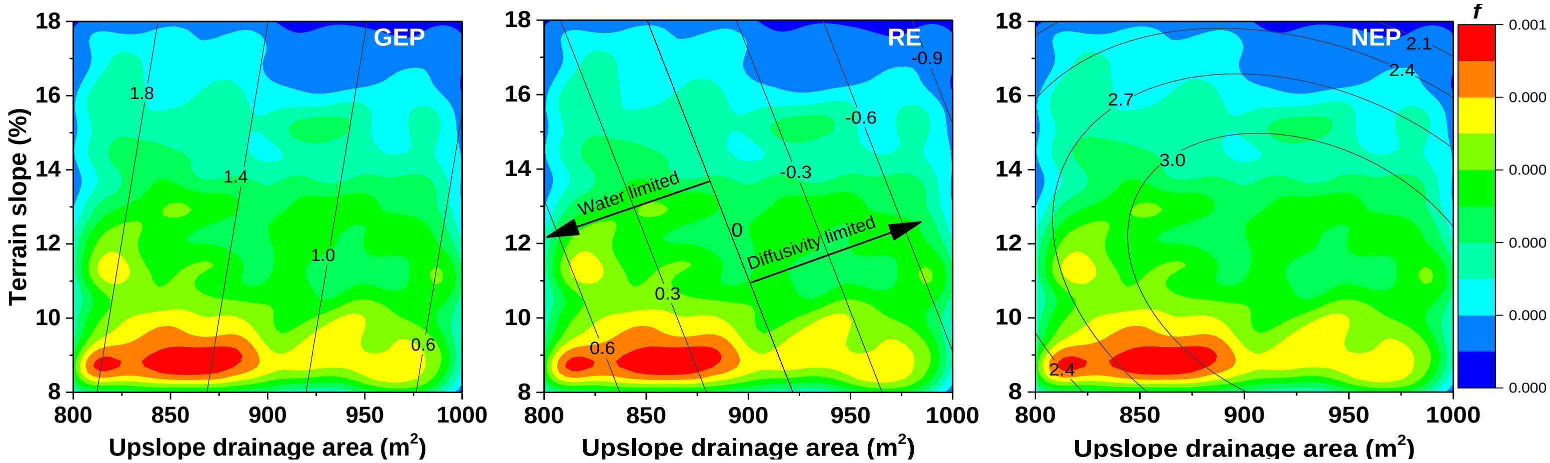

Figure 3.4 Codependence of carbon flux responses to precipitation on both terrain slope and drainage area. Black contour lines are annual responses to precipitation (g C m^{-2} yr^{-1}/mm) derived from multiple regression analysis. Colored contours in the background are bivariate frequency distributions of complex terrain in the conterminous US (i.e. Figure 3.5a). Arrows show potential limitation of ecosystem respiration by water availability or gas diffusivity in soils.

3.4 Discussion

3.4.1 Influences of Terrain on Carbon Fluxes

The results presented here show that ecosystem carbon assimilation and respiration are responsive to diel temperature fluctuations in complex terrain but not in simple terrain. Sites in complex terrain had mean terrain slopes in excess of approximately 9%, and above this threshold daily flux responses to temperature increased linearly with increasing terrain slope (Figure 3.3a-c). This phenomenon is likely related to the influence of topographic slope on local energy and water balances, because direct solar radiation and soil dryness generally increase with terrain inclination [*Hanna et al.*, 1982; *Zhang et al.*, 2010a]. Ecosystems in steep terrain receive more photosynthetically active radiation and may be exposed to greater air and soil temperatures than similar ecosystems in flat terrain. These elevated temperatures may enhance short-term carbon assimilation and belowground respiration rates [*Kang et al.*, 2003]. These findings span multiple ecosystem types and climate regimes, and we identified no confounding effects of mean elevation, mean temperature, or mean precipitation on these results (Table 3.1; Figure A1-A2 in Appendix A).

The decline in GEP response to precipitation with increasing upslope drainage area (Figure 3.3d) likely reflects increased availability of soil water in landscape positions with greater drainage areas. As upslope drainage areas increase, lateral redistribution of soil water allows soil water storage to increase in volume and persist for longer periods [*Tenhunen et al.*, 2001], leading to less vegetation water stress [*Emanuel et al.*, 2010] and decreased response of GEP to precipitation variability at wetter sites [*Hwang et al.*, 2012]. Soil water availability may similarly explain the decline in $\sum_{RP}$ with upslope drainage area (Figure 3.3e). In a given climate, landscapes with small upslope drainage areas tend to be drier than landscapes with larger drainage areas, and small precipitation inputs have greater potential to enhance both below and aboveground respiration in these drier landscapes [*Riveros-Iregui et al.*, 2012]. As upslope drainage area increases, water availability increases due to greater and longer duration of water supplied by lateral soil water redistribution [*Grayson et al.*, 1997]. Eventually, these landscapes may experience reduced RE due to limitations in oxygen availability and gas diffusivity [*Riveros-Iregui et al.*, 2012]. These factors likely contribute to the changing sign of annual $\sum_{RP}$ observed among sites in complex terrain (Figure 3.3e).

The observed non-monotonic relationship between the annual $\sum_{NP}$ and upslope drainage area (Figure 3.3f) reflects the combined response of both GEP and RE to increasing water availability. For landscapes with small upslope drainage areas, GEP and RE are highly responsive to precipitation, whereas for landscapes with large upslope drainage areas, GEP and REP are less responsive to precipitation. Similar response magnitudes but opposite directions of fluxes result in minimally responsive $\sum_{NP}$ at sites where the mean upslope drainage area is either very high or very low. At intermediate upslope drainage areas, the response of GPP is greater than RE, resulting in a higher positive $\sum_{NP}$.

Multiple regression analysis revealed that $\sum_{GP}$ was largely a function of upslope drainage area (Figure 3.4, GEP), confirming the strong dependence of $\sum_{GP}$ on soil water availability [*Huxman et al.*, 2004]. The observed bidirectional response of $\sum_{RP}$ to the combined effect of terrain slope and drainage area (Figure 3.4, RE) is consistent with known landscape-scale limitations of RE by water availability at dry landscape positions (i.e., small drainage area), and by gas diffusivity limitations at wet landscape positions -i.e., large drainage areas- [*Riveros-Iregui et al.*, 2012]. Likewise, greatest annual $\sum_{NP}$ (Figure 3.4, NEP) corresponds to areas of the landscape where soil water is expected to accumulate and persist following storms or snowmelt [*Beven and Kirkby*, 1979], but not to the extent that excess soil water limits the responsiveness of carbon fluxes to changes in annual precipitation. These results help to clarify interactions among terrain characteristics that give rise to ecological behavior not apparent when investigating effects of slope and drainage area separately.

Relationships between terrain variables and the responses of carbon fluxes to temperature and precipitation were weak or nonexistent in flat terrain (Table 3.3). Results from flat landscapes are consistent with the prevailing conceptual framework, which asserts that energy and water balances arise primarily from soil and vegetation characteristics, and that vertical interactions among soils, plants, and the atmosphere dominate landscape-scale behavior [*Running and Coughlan*, 1988; *Collins et al.*, 2006]. Our results suggest that carbon fluxes in flat terrain are less likely to be influenced by lateral redistribution of water and other resources across the landscape. These topographically simple sites lack combinations of slope and drainage area found in more complex terrain and therefore lack the accompanying spatial heterogeneity in water and energy found in complex environments. Although both flat and complex sites share similar ranges of variability in responses of carbon fluxes to climate, only complex sites exhibit clear organization of this variability with respect to terrain variables.

Altogether, these results suggest that above certain thresholds of terrain complexity, responses of carbon fluxes to climate vary predictably with terrain characteristics. These patterns are independent of other landscape features such as mean climate conditions or ecosystem type. We found that much of the complex terrain in the conterminous US corresponds with high response of annual carbon fluxes to precipitation (Figure 3.4, NEP colored contours). We conclude that overlooking the terrain dependence of these variations in ecosystem responses to climate may result in inaccurate estimates of carbon fluxes, with profound impacts on larger-scale carbon budgets.

3.4.2 Modeling implications

Land surface components of earth system models are central in representing the interactions between the terrestrial biosphere and the atmosphere [*Fisher et al.*, 2014; *Davison et al.*, 2016]. Realistic representation of land surface heterogeneity is fundamental for predicting key land processes such as GPP and RE [*Ke et al.*, 2013]. Particularly, sub-grid heterogeneity in vegetation and topography can significantly influence the estimates of energy and mass fluxes. These sub-grid heterogeneities are often ignored in land surface models [*Fisher et al.*, 2014; *Melton and Arora*, 2014; *Prentice et al.*, 2015], or they are parameterized separately, with few exceptions [e.g., *Leung and Ghan*, 1998]. Although this parameterization approach helps to provide more realistic representations of biogeochemical processes within a land surface model pixel, it may not capture emergent behavior arising from interactions between landscape components such as topography and vegetation, or between terrain characteristics such as slope and drainage area.

The results presented here support the assertion that interactions between vegetation and terrain may lead to emergent behavior in carbon fluxes. As discussed in 3.4.1, variability in carbon responses to temperature and precipitation was clearly organized according to terrain slope and drainage area, but only for sites with mean topographic slope greater than approximately 9% (Figure 3.3, Table 3.3). This result suggests that in complex terrain, topographic variables interact with each other and with vegetation in different ways to influence carbon cycling. These interactions can produce linear (Figure 3.3a-e), bidirectional

(Figure 3.4, RE), or nonlinear responses of carbon fluxes to climate (Figure 3.4, NEP). Current approaches to parameterizing landscape components in land surface models may not capture these types of behaviors. Representing these types of interactions and emergent behaviors in models of the carbon cycle will take careful thought to balance process representation with computational demands, but doing so may help to address uncertainties that remain in models of the terrestrial carbon cycle [*Piao et al.*, 2013; *Friedlingstein et al.*, 2014].

Our results underline the importance of accounting for the effects of complex terrain on the redistribution of resources that are directly linked to ecosystem carbon cycling (e.g. water and light). Likewise, our findings emphasize the need for models to recognize the heretofore unparameterized interactions between terrain and other sources of heterogeneity in driving ecological responses at spatial scales that are typically considered “subgrid resolution” by regional and global carbon models [*Collins et al.*, 2006].

This work has implications for about 14% of the total conterminous US that is considered topographically complex according to our previously identified threshold of 9% terrain slope. In total, these areas are responsible for about 1.13 Gt of carbon sequestration per year [*Zhao et al.*, 2005] (Figure 3.5a). A much smaller sub-area of about 2,800 km^2 within the conterminous US falls within the exact ranges of slopes and drainage areas represented by AmeriFlux towers that we identified as occupying complex terrain (Figure 3.4b). Although small in total area, these landscapes are widely dispersed across the conterminous US (Figure 3.5b). About 30% of this area experiences very high NEP response to annual precipitation (Figure 3.5c). These large NEP responses derive, at least in part, from interactions between terrain and ecological processes that directly influence the response of

GEP and RE to precipitation. Our results provide the first evidence that complex terrain mediates the climate response of carbon fluxes across a range of ecosystems. Given the prevalence of complex terrain worldwide and its potential to influence the terrestrial carbon cycle in such landscapes, this work adds to our understanding and provide insights to how the biotic and abiotic components of terrestrial ecosystems function within the global carbon cycle.

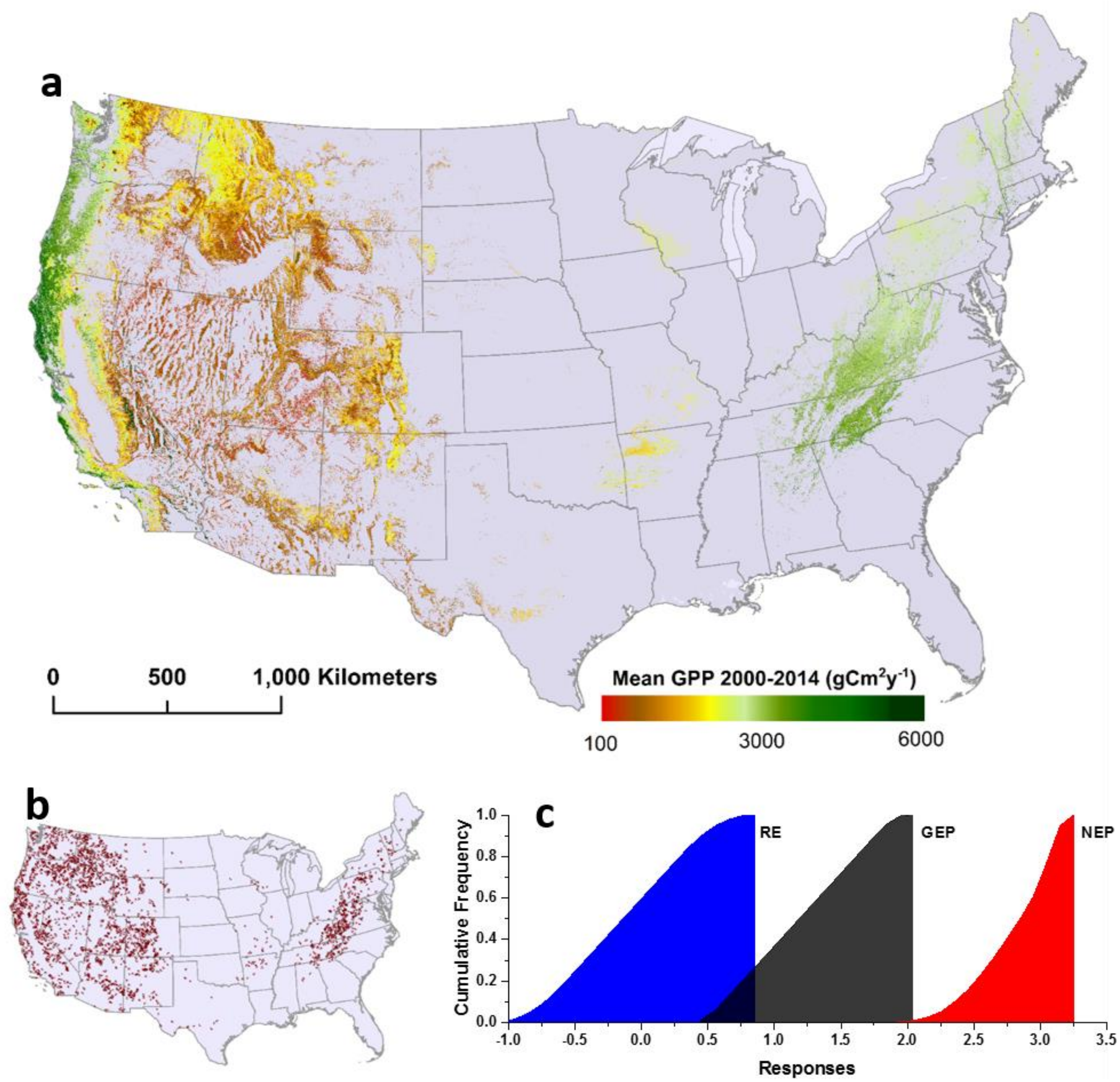

Figure 3.5 Implications of complex terrain for the total US annual carbon sequestration. (a) Complex terrain in the conterminous US accounts for 14% of the territory and 1.13 Gt of carbon uptake per year. (b) US complex terrain within the same range of terrain values identified in our study (i.e. 8 to 18 % in terrain slope, and 800-1000 m^2 of drainage area) constitutes about 2,800 km^2. (c), Cumulative frequency distribution of carbon responses to annual precipitation ($g\ C\ m^{-2}\ yr^{-1}$/mm) for complex terrain in the conterminous US. Sign in the response of RE indicates potential limitations by diffusivity (negative values) and by water (positive values). Area above a threshold of 3 for NEP exhibited high response to annual precipitation.

3.5 Conclusions

The results presented here demonstrate that in terrestrial ecosystems the responses of carbon fluxes to temperature and precipitation can be influenced by topography in complex terrain. These results are fundamentally different from prior studies, which have focused on the ability of complex terrain to modify the atmospheric boundary layer and drive advective flows. Our work shows that terrain slope and drainage area, which are often associated with water and energy availability, impact daily responses of carbon fluxes to temperature (in the case of slope) and annual responses of carbon fluxes to precipitation (in the case of drainage area). These topographic variables interact with vegetation and soils in complex ways to give rise to a broad spectrum of responses to climate. We found no such influences in flat terrain, suggesting that the traditional conceptualization of vertical soil-vegetation-atmosphere dynamics holds for these systems. The terrain impacts identified in this work have implications for approximately 14% of the total land area of the conterminous US, an area which sequesters more than 1 Gt of carbon annually. Prevailing conceptual frameworks and models may not be able to capture these terrain-derived responses, and our results highlight new opportunities to improve conceptual understanding and models of ecosystem carbon dynamics.

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CHAPTER 4: ECOHYDROLOGY OF A TROPICAL LANDSCAPE: HYDROLOGIC REGIMES AND IMPLICATIONS FOR WATER RESOURCES AND ECOLOGICAL DYNAMICS IN THE TALGUA WATERSHED, HONDURAS

Abstract

Tropical landscapes are highly heterogeneous and complex both in terms of their natural characteristics and human dimensions. Unprecedented, rapid environmental changes in the tropics are altering hydrologic cycles and related earth system processes, yet our understanding of these processes and their implications is limited in many tropical regions. Honduras, located within the Mesoamerican region, is one such location. A combination of rapid land use change, natural disasters susceptibility, poor access to drinking water, and poverty place Honduras among the most environmentally vulnerable countries in the world. These same factors create an ideal scenario for understanding complex human-environment interactions and their effects on tropical ecohydrological systems. To this end, we combined field-based monitoring and remote sensing to characterize the water balance for the upper Talgua River, a forested, montane catchment in the headwaters of Honduras' Patuca River. The annual water includes 1720 mm of rainfall, 451 mm of streamflow, and 1158 mm of evapotranspiration. We estimate closure of the annual water balance within 6% comprised changes in storage and error terms. We found that strong seasonality in climate variables and soil water storage combine with spatial patterns of land use to create a scenario of very low streamflow conditions. Water scarcity could become an even more serious threat in the future as a result of continued land use change and projections of drier future conditions for this region. These results have direct implications for water resources management in the Talgua watershed, but they also illustrate how the heterogeneous land use patterns of tropical areas, along with environmental vulnerability and complex coupled human-environment

interactions, influence tropical ecohydrological systems, and hence highlight the need for more and wider field-based research throughout the tropics.

4.1 Introduction

Tropical landscapes are extraordinarily heterogeneous and complex in terms of ecological and hydrological processes, and in terms of human activities that modify these landscapes. Tropical landscapes exhibit substantial heterogeneity in geology, topography, soil, and climate [*Landon*, 1991; *Richter and Babbar*, 1991; *Dirzo and Raven*, 2003; *Townsend et al.*, 2008; *Brauning*, 2009], and they are characterized by high biological diversity, exceptional biogeochemical heterogeneity, and an extraordinary number of complex interactions between species, and among ecosystems [*Townsend et al.*, 2008; *Fayle et al.*, 2015; *Levine et al.*, 2015]. Moreover, increasing human influences within tropical regions introduces yet another layer of complexity to these landscapes. Human activities limit the ability to predict basic ecological functions and processes due to heterogeneous and sometimes unexpected behavior [*Gibson et al.*, 2011; *Ponette-González et al.*, 2014; *Lewis et al.*, 2015]. Understanding the ecological consequences of heterogeneity and complexity in tropical landscapes is particularly important given the global significance of the tropics for climate regulation, biodiversity conservation, and the carbon and water cycle [*Bruijnzeel*, 2004; *Lewis*, 2006; *Wohl et al.*, 2012; *Edwards et al.*, 2014; *Malhi et al.*, 2014].

The tropics represent about 40% of the Earth's land surface and play a central role in the regulation of the water cycle [*Lewis*, 2006], storing and cycling more water than any other region of the world [*Wohl et al.*, 2012; *Lewis et al.*, 2015]. Unprecedented and rapid environmental changes in the tropics are altering hydrologic and other earth system processes, with potential global environmental impacts [*Lewis*, 2006; *Lawrence and Vandecar*, 2015; *Mohtadi et al.*, 2016]. However, field-based knowledge of hydrological processes in tropical areas remains limited compared to extra-tropical regions [*McDonnell* *and Burt*, 2015]; thus, present understanding of hydrological dynamics in the tropics relies heavily on modeling and remote sensing rather than field-based research [*Wohl et al.*, 2012; *Washington et al.*, 2013; *Ponette-González et al.*, 2014]. The current situation is particularly problematic given that hydrological models and remote sensing products used in tropical areas are often constructed and parameterized based on insight from temperate regions that may not adequately represent processes in tropical regions [*Winsemius et al.*, 2008; *Steenhuis et al.*, 2009; *Ogden and Harmon*, 2012; *Ponette-González et al.*, 2014].

The gap in hydrological knowledge in the tropical world is due partly to economic disparities between tropical countries and wealthier nations, which tend to be located in temperate regions of the world [*Sachs*, 2001]. Many tropical countries lack the basic infrastructure for hydrological monitoring, analysis, and data management [*Wohl et al.*, 2012; *Washington et al.*, 2013; *Deblauwe et al.*, 2016]. This not only hinders advances in basic understanding of these systems, but it also limits the capacity of tropical countries to pursue sustainable and scientifically informed management of their water resources. As a result, even tropical countries where water is considered to be abundant often suffer from severe water shortages [*World Water Council*, 2006; *Mejia*, 2014]. Moreover, many tropical countries are also considered to be natural disaster hotspots, particularly water-related disasters [*The World Bank*, 2005]. These countries are also among the world's most vulnerable to climate change [*Sönke et al.*, 2015] because their hydrologic cycles are expected to be modified substantially under future climate conditions [*Collins et al.*, 2013]. Field-based hydrological research in the tropics is essential for helping scientists, managers, and decision-makers understand how environmental change in the tropics may alter hydrologic cycles at different spatial and temporal scales [*Oki et al.*, 2006; *Dai et al.*, 2009;

Trenberth, 2011; *National Research Council*, 2012; *Wohl et al.*, 2012; *Burt and McDonnell*, 2015].

Honduras, located within the Mesoamerican region (Figure 4.1), is one of the world's least-studied countries in terms of hydrology. Few field-based studies have been conducted in the country [*Hanson et al.*, 2004; *Caballero et al.*, 2012, 2013], and only five research studies on Honduras have ever been published in the top ten hydrology journals, as ranked by the Web of Science [ISI, 2017]. Like many tropical countries, Honduras has a high rate of deforestation [*FAO*, 2009], and suffers frequently from a range of water-related natural disasters, including drought, floods, and landslides. Given the frequency of natural disasters, the degree to which human activities impact water quantity and quality, and poor infrastructure throughout the nation, Honduras has been ranked as the most environmentally vulnerable country in the world [*Sönke et al.*, 2015].

Despite vulnerability to environmental impacts in general, and vulnerability to water-related impacts in particular, Honduras has poor environmental monitoring infrastructure. The country has one of the lowest densities of weather stations in the Western Hemisphere, and only a few streamflow records are available nationwide [*Bolster*, 2014]. A combination of rapid land use change, poor access to drinking water, relatively frequent hurricanes, droughts, and floods, and projected decreases in overall precipitation, produces significant challenges for the country in terms of water resources sustainability [*Thattai et al.*, 2003; *Aguilar et al.*, 2005; *World Bank*, 2009; *USAID*, 2013; *Marengo et al.*, 2014]. The lack of field-based monitoring infrastructure exacerbates these challenges. Remote sensing increasingly offers water-related insight to help address these challenges [*Xie and Arkin*, 1997; *Huffman et al.*, 2007; *Zhang et al.*, 2010], but without ground-based observations to validate or complement remote sensing science, uncertainty or inconclusiveness associated with these studies may hinder their usefulness to managers and decision-makers. Thus, Honduras serves as an extreme example of the challenges faced by many tropical nations in terms of hydrological monitoring, analysis, and translation of science to decision-makers, managers, and stakeholders. We present the results of a watershed-scale hydrological analysis conducted from June 2015 through July 2016 in Honduras, but relevant to many parts of the tropics where complex natural and human processes intersect with implications for ecohydrology.

This study contributes to fundamental understanding of tropical ecohydrological processes using a combination of field-based monitoring and remote sensing to evaluate the water balance of a forested, headwater watershed. The study watershed is representative of highly disturbed landscapes found throughout Central America, and it is typical of the rural hillside system of subsistence agro-forestry upstream balanced against water quantity and quality requirements by humans and natural ecosystems within the watershed and downstream. This setting creates an ideal scenario for understanding complex human-environment interactions and their effects on tropical eco-hydrological systems. We address the following questions: (1) How well can we characterize the water balance of a tropical headwater watershed given limited science infrastructure, data availability, and difficult logistics of this region? (2) What are the key uncertainties in components of the water balance, and how might they be overcome to provide scientific information that is useful to managers and decision makers? We also discuss the implications of this work for water management in Honduras and in tropical regions more generally.

4.2 Methods

4.2.1 Site Description

The Talgua River watershed is a 79 km^2 forested, montane headwater area within the Patuca River basin of Honduras, which drains into the Caribbean Sea. The Patuca basin is the largest (23,898 km^2) river basin in Honduras, and it is the third largest basin in Central America [*ICF*, 2013; *UNAH*, 2014]. The Patuca river flows through three large land reserves: Patuca National Park, Tawahka Biosphere, and the UNESCO world heritage site Rio Platano Biosphere. Rapid anthropogenic land use change in the upper watersheds, including the Talgua watershed, makes the Patuca basin the second largest source of terrestrial sediment to the Mesoamerican Reef [*Burke and Sugg*, 2006]. The Talgua watershed itself is located within the Sierra de Agalta National Park (SANP), a land reserve established by the federal government for biodiversity conservation and wildlife protection. The core zone of the SANP has the most extensive cloud forest remaining in Honduras, which sustains rich biodiversity that is rarely seen elsewhere in the country [*Portillo*, 2013] (Figure 4.1).

Elevations within the watershed range from 450 to 2350 m AMSL, and the terrain is steep with a mean slope of 56%. Soils watershed-wide are Rendzina formed on sedimentary siliciclastic (92%) and plutonic (8%) parental material [*IGN*, 1956; *Simmons*, 1969]. Soils in the area are mostly clay and clay loam with smectitic type mineralogy, and can develop deep cracks (1 to 2 m deep) during the dry season [*Hanson et al.*, 2004]. The geology is dominated by the Cretaceous-Tertiary intrusive rocks with a small amount of shale, sandstone and coal [*IGN*, 1956].

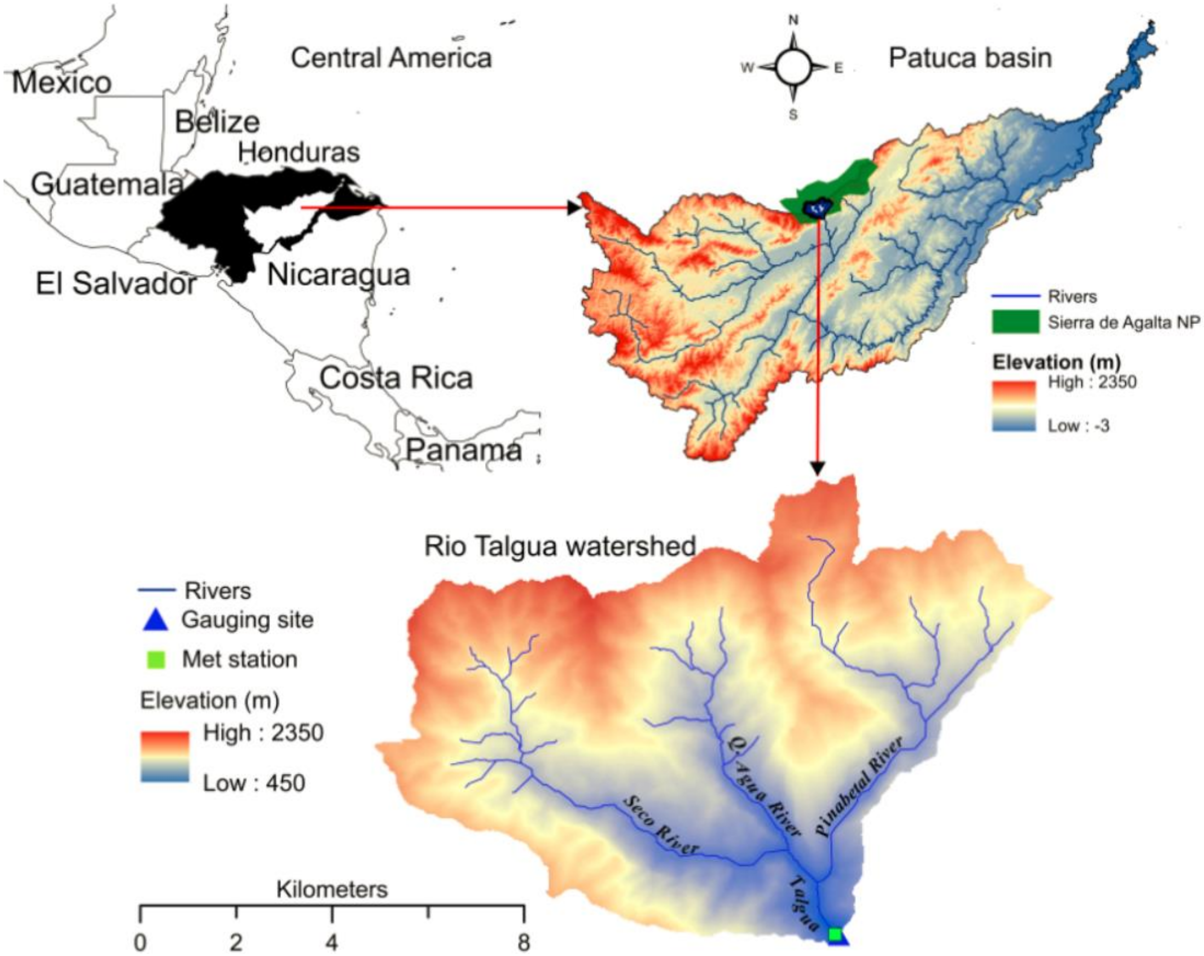

Figure 4.1 Geographic location of the Talgua watershed, Honduras. The Talgua River is a headwater catchment flowing into the Patuca River, northeastern Honduras, a major drainage to the Caribbean Sea. The watershed is also within the Sierra de Agalta National Park.

The Talgua watershed is dominated by primary humid broadleaf forest (72%), followed by cropland and pasture (21%), including a small number of coffee plantations (Figure 4.2). The climate is characteristic of the Central America Isthmus, which is alternatively controlled by the Eastern Pacific Intertropical Convergence Zone (EP-ITCZ), the Northern Hemisphere summer monsoon, and the north Atlantic subtropical anticyclone [*Hastenrath*, 2002; *Guswa et al.*, 2007]. The region has distinctive wet and dry seasons. The wet season extends from late May through October, and accounts for approximately 90% of annual precipitation. A significant reduction in wet-season rainfall between mid-July and mid-August [*Magaña et al.*, 1999; *Curtis*, 2002; *Hastenrath*, 2002] is known as the *Veranillo or Canícula* (translated as mid-summer drought) and is a phenomenon unique to Central American and southern Mexico [*Magaña et al.*, 1999; *Curtis*, 2002; *Small et al.*, 2007]. The dry season begins in November and continues through May. Mean annual precipitation, calculated from Tropical Rainfall Measuring Mission (TRMM), was estimated as 1271 mm for the 2000 – 2015 period. Mean annual temperature is 24.7 ºC [*World Weather*, 2016]. Other ecological and geomorphological characteristics are presented in Table 4.1.

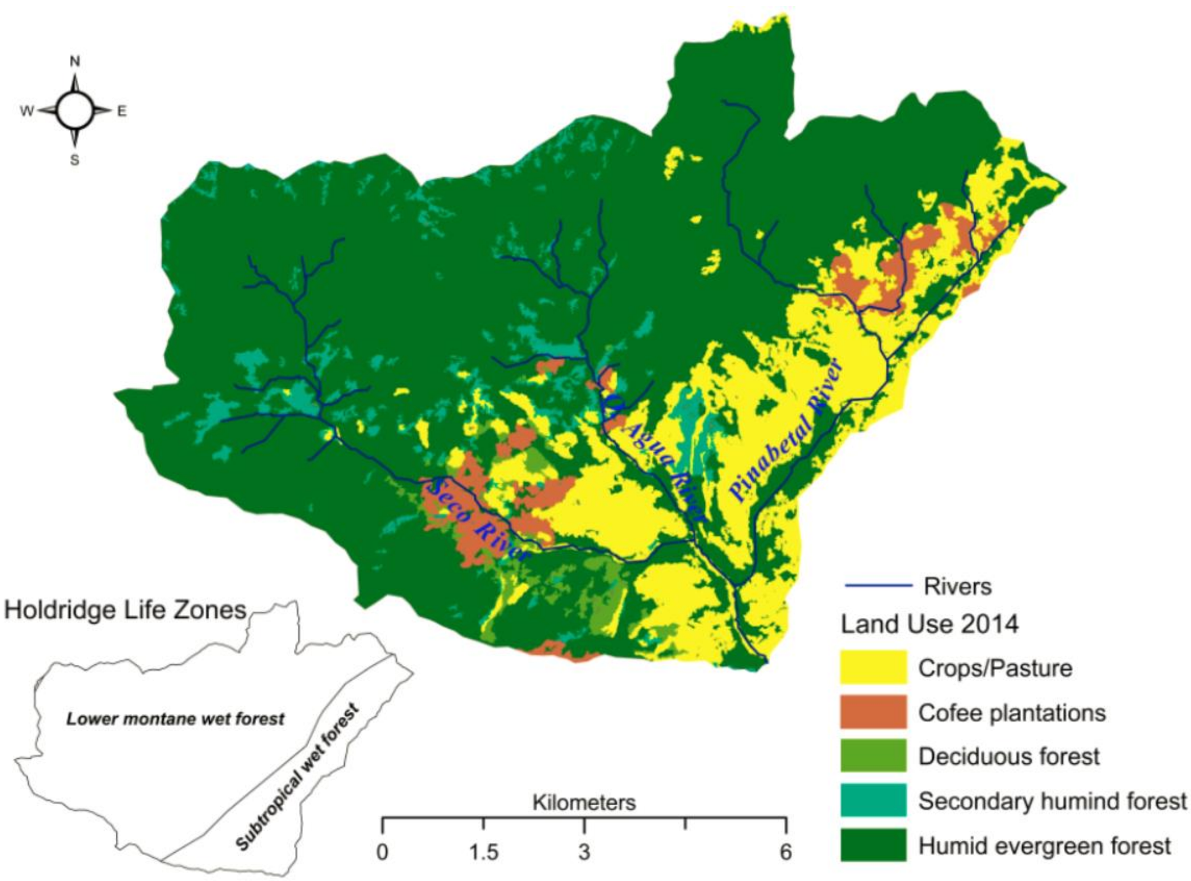

Figure 4.2 Landuse and Holdridge Life Zones in the Talgua River catchment**.**

Table 4.1 Main characteristics of the Talgua watershed.

Watershed characteristics			
Variable		Variable	
Population (n)	1400	Mean aspect (deg.)	162
Climate koopen	Tropical monsoon (Am)	Main stream length (km)	51
Holdridge Life Zone	Lower Montane Wet Forest	Drainage density (km/km^2)	0.64
Drainage area (km^2)	79.12	Geology (bedrock formation)	Sedimentary
Mean elevation (m)	1386	Elevation at gauging site (m)	454
Elevation range (m)	450 - 2350	Elevation at weather station (m	460
Mean slope (%)	56	Forest cover (%)	72

4.2.2 Hydrometeorological Measurements

In May 2015, we installed a weather station and stream gaging station at the watershed outlet of the Talgua River (Figure 4.1). The weather station comprised a temperature and relative humidity probe (Model HMP60, Vaisala, Inc., Louisville, Colorado, USA), a propeller anemometer (Model 5103, R.M. Young, Inc., Traverse City, Michigan, USA), an all-season solar pyranometer (Model SP-230, Apogee Instruments, Inc., Logan, Utah, USA), and a 203 mm (8” nominal) diameter tipping bucket rain gauge (Model TR-525USW, Texas Electronics Inc., Dallas, Texas, USA). Sensor outputs were recorded to a datalogger (Model CR206X, Campbell Scientific, Logan, Utah, USA), which averaged 5 minute observations every 15 minutes. The system was powered by a 12 VDC battery charged by a 20W solar panel. The weather station was installed on a vertical pipe with an instrument boom situated approximately 2 m above the ground. The station was sited in a clearing on small banana plantation near the watershed outlet. Vegetation growth was controlled mechanically within a 5-10 m radius of the station.

We established a stream gaging station on the Talgua River near the weather station. The gaging station was sited following standard recommendations for stream cross-section and reach morphology [*Holmes et al.*, 2001; *Turnipseed and Sauer*, 2010]. It was located in a reach with a natural bedrock control, located approximately 70 m downstream from the confluence of two third-order streams that form the fourth-order Talgua River. Early measurements included stage, conductivity and temperature of streamflow (Model AquaTROLL 200, Fondriest Environmental Inc., Fairborn, Ohio, USA) as well as turbidity (Model OBS-3+, Campbell Scientific). Stream observations were recorded at 15 minute intervals using a datalogger and power system identical to the system used at the weather station. Manual discharge measurements were collected every day at 0600 local time for a 14 month-period by a trained stakeholder who lives and farms in the watershed. Discharge measurements were made following the mid-section method [*Turnipseed and Sauer*, 2010] using an electromagnetic current meter (Model Marsh-McBirney FloMate 2000, Hach Company, Loveland, Colorado, USA) attached to a custom-made wooden wading rod. Baseflow was separated from total runoff using the WHAT online tool [*Kyoung et al.*, 2005].

Datalogger files were downloaded periodically by a collaborator at the National Agricultural University of Honduras (UNA), located approximately 15 km away from the field site. The UNA collaborator also photographed hand-written discharge notes and conductivity measurements from the stakeholder's field book. Weather data were recorded every fifteen minutes from June 2015 through July 2016. Instrumentation problems at the stream gage limited our stage, conductivity, temperature and turbidity to only a few weeks, but daily measurements of discharge continued throughout the entire study period. For days when streamflow was too great to safely enter the river (n =5 days), discharge was estimated using linear extrapolation between the last value before the gap and the first value after it.

Apart from our weather station, there were no additional surface measurements of meteorological variables in the area. Therefore, we assumed that rainfall measured at our weather station was representative of watershed-wide conditions. We tested this assumption by comparing annual estimates of precipitation to long-term satellite-derived estimates from the Tropical Rainfall Measuring Mission (TRMM). Remotely-sensed datasets of monthly and annual rainfall are available from TRMM (Product 3B43 v7) from 2000 through 2015, and these data are publicly available from NASA (https://pmm.nasa.gov/trmm). Monthly TRMM data are calculated by combining 3-hourly merged high-quality estimates with monthly accumulated Global Precipitation Climatology Centre (GPCC) rain gauge analysis, and have a 0.25° by 0.25°spatial resolution [*Huffman et al.*, 2007]. To match annual TRMM precipitation with our study period, long-term rainfall was calculated based on a calendar from June (one year) through May (following year).

4.2.3 Water Balance Calculations

The watershed monthly water balance was calculated as

$$P = Q - AET - \Delta S \tag{1}$$

where *P*, *Q*, *AET*, and ΔS are precipitation, runoff, actual evapotranspiration, and monthly soil water storage respectively, all in mm. Daily *P* and *Q*, measurements were aggregated to determine monthly, seasonal and annual values. Monthly actual evapotranspiration (*AET*) was estimated using the Priestley–Taylor Jet Propulsion Laboratory model (PT-JPL) [*Fisher et al.*, 2008], where *AET* is given by the sum of canopy transpiration (AET_c), interception evaporation (AET_i), and soil evaporation (AET_s). The PT-JPL model takes a bio-meteorological approach for converting Priestley-Taylor radiation-based potential evapotranspiration (*PET*) [*Priestley and Taylor*, 1972] into rates of *AET* by using ecophysiological constraint functions. We selected this method because of its demonstrated success in the tropics [*Fisher et al.*, 2009]. The model requires five inputs: net radiation (R_n), normalized difference vegetation index (NDVI), maximum air temperature (T_{max}), minimum relative humidity (RH_{min}), and soil adjusted vegetation index (SAVI) or enhanced vegetation index (EVI). Equations, variables, and parameters we used for AET estimates are presented in Table 4.2. A complete description of the PT-JPL model and additional bibliography can be found in Fisher et al. (2008).

Net radiation (R_n) was calculated from incoming short wave radiation by multiplying by 0.78, a typical correction factor for tropical forests based on field experiments elsewhere [*Malhi et al.*, 2002; *Kumagai et al.*, 2005; *Fisher et al.*, 2011]. No data were available for watershed-wide estimates of R_n, therefore, we assumed that our computed R_n was representative of the whole watershed. Mean monthly NDVI and EVI across the watershed were computed from the Moderate Resolution Imaging Spectrometer (MODIS) MOD13A3 L3 products at 1-km spatial resolution, which are publicly available at the Land Processed Distributed Active Archive Center (https://lpdaac.usgs.gov/). Monthly watershed-wide evapotranspiration (*PET*) was calculated using T_a and R_n estimate from our weather station. Our *PET* estimates were based on the Priestley & Taylor (1972) radiation-based method

$$PET = \alpha \frac{\Delta}{\Delta + \gamma} \tag{2}$$

where α is the psychrometric constant ($kPaK^{-1}$), Δ is the slope of saturation-to-vapor pressure curve ($kPaK^{-1}$), and γ is the Priestley & Taylor constant (1.26). More detail can be found in Table 4.2. We selected this method for two reasons: (1) to be consistent with the selected *AET* method, (2) because radiation-based methods have been found more reliable for tropical areas [*Fisher et al.*, 2011]. We compared our *AET* and *PET* results to long-term (2000-2014) watershed-wide *AET* and *PET* estimations based on MODIS-16A2/A3 (ftp://ftp.ntsg.umt.edu/pub/MODIS/NTSG_Products/MOD16/) [*Mu et al.*, 2007], and to mean long-term Hargreaves-based [*Zomer et al.*, 2006] , available at (http://www.cgiar-csi.org/).

Table 4.2 Equations and parameters used for *AET* calculations. For parameters with superscript (1) reference is [Allen et al., 1998], otherwise *Fisher et al.*, (2008).

Parameter	Description	Equation or value
AET	Actual evapotranspiration	$AET_c + AET_i + AET_s$
AET_c	Canopy transpiration	$(1-f_{wet})f_g f_T f_M \alpha\left(\frac{\Delta}{\Delta+\gamma}\right)R_{nc}$
AET_i	Interception evaporation	$f_{wet}\alpha\left(\frac{\Delta}{\Delta+\gamma}\right)R_{nc}$
AET_s	Soil evaporation	$(f_{wet}+f_{SM}(1-f_{wet}))\alpha\left(\frac{\Delta}{\Delta+\gamma}\right)(R_{ns}-G)$
f_{wet}	Relative humidity	RH^4
f_g	Green canopy fraction	$f\mathrm{APAR} / f\mathrm{IPAR}$
f_T	Plant temperature constraint	$\exp(-((T_{max}-T_{opt})/T_{opt})^2)$
f_M	Plant moisture constraint	$f\mathrm{APAR} / f\mathrm{APAR}_{max}$
α	Priestley & Taylor constant	1.26
Δ	Slope of saturation-to-vapor pressure curve ($kPaK^{-1}$)	$(4098(0.6108exp(17.27\cdot T_{mean} / T_{mean}+237.3)) / (T_{mean}+237.3)^2$
γ	Psychrometric constant ($kPaK^{-1}$)	0.066
R_n	Net radiation	Data
R_{ns}	R_n to the soil	$R_n exp(-k_{Rn}LAI)$
k_{Rn}	Light extinction coefficient	0.6
LAI	Total leaf area index	$-\ln(1-f_c) / k_{PAR}$
k_{PAR}	LAI coefficient	0.35
R_{nc}	R_n to the canopy	$R_n - R_{ns}$
f_{SM}	Soil moisture constraint	$\mathrm{RH}^{\mathrm{VPD}/\beta}$

Table 4.2 (Continued)

Parameter	Description	Equation or value
VPD[1]	Actual vapor pressure deficit (kPa)	$(e_{(T\ min)}\left(RH_{max}/100\right)+e_{(T\ max)}\left(RH_{min}/100\right))/2$
$e_{(T\ min)}$ [1]	Saturation pressure deficit at T_{min}	$0.6108\,exp\left(\frac{17.27 \cdot T_{min}}{T_{min}+237.3}\right)$
$e_{(T\ max)}$ [1]	Saturation pressure deficit at T_{max}	$0.6108\,exp\left(\frac{17.27 \cdot T_{max}}{T_{max}+237.3}\right)$
β	Units placeholder for f_{SM} (kPa)	1
G [1]	Ground heat flux	$Gmonth_i = 0.07\ (Tmonth_{i+1} - Tmonth_{i-1})$
fAPAR	Fraction of PAR absorbed by green vegetation cover	$1.4 \cdot$ EVI-0.05
EVI	Enhanced vegetation index	Data
f_c	Fractional total vegetation cover	fIPAR
fIPAR	Fraction of PAR intercepted by f_c	$1.0 \cdot$ NDVI-0.05
NDVI	Normalized difference vegetation index	Data
$f\text{APAR}_{max}$	Maximum fAPAR	$max\ f$APAR
T_{mean}	Mean air temperature	Data
T_{max}	Maximum air temperature	Data
T_{opt}	Optimum plant growth temperature	T_{max} at max($R_n T_{max}$EVI/VPD)

4.2.4 Water Yield and Land Use

We used the Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) Water Yield model [*Sharp et al.*, 2015] to quantify the relative contribution of distinct landscape parcels and subwatersheds to the annual water yield of the Talgua watershed. Although InVEST model is neither designed to reproduce empirical observations nor to quantify actual generation of flow, the modeled potential of streamflow generation provides insight to help understand the effect of land use and management on water resources. For each pixel in the InVEST model, the annual average water yield is calculated as

$$Y(x) = \left(1 - \frac{AET(x)}{P(x)}\right) \cdot P(x) \tag{3}$$

where $AET(x)$ is the annual actual evapotranspiration and $P(x)$ is the annual precipitation for pixel x. The model assumes that all water not evaporated reaches the outlet of the watershed during the course of one year, and it makes no distinction between storm flow and baseflow. The model relates the evapotranspiration fraction of the water balance, $AET_{(x)} / P_{(x)}$, to PET using the Budyko framework [*Budyko*, 1961; *Fu*, 1981; *Zhang et al.*, 2004] as

$$\frac{AET(x)}{P(x)} = 1 + \frac{PET(x)}{P(x)} - \left[1 + \left(\frac{PET(x)}{P(x)}\right)^{\omega}\right]^{1/\omega} \tag{4}$$

where ω is an empirical parameter that characterizes the natural climatic-soil properties [*Donohue et al.*, 2012].

The InVEST model requires five inputs: average annual precipitation (mm), average annual *PET* (mm), root restricting layer depth (mm), volumetric plant available water content (AWC), and land use. We computed annual precipitation from TRMM and used 1 km resolution *PET* from the CGIAR-CSI Global-Aridity and Global-*PET* Database [*Zomer et al.*, 2006]. Root restricting layer depth and AWC were obtained from Regridded Harmonized World Soil Database v1.2 [*Wieder et al.*, 2014]. High resolution land use data (5x5 m) 2014 were acquired from the national forest authority of Honduras (Instituto de Conservación Forestal). These data can be requested online at http://icf.gob.hn/ or by contacting directly to info@icf.gob.hn . InVEST 3.2.0 and ArcMap 10.3.1 were used to run the model.

4.3 Results

Total rainfall during the study period (June 2015 to May 2016) was 1,720 mm (Table 4.3). Based on long-term TRMM data, spatially averaged mean annual rainfall (2000 to 2015) over the watershed was 1271 ± 209 mm, indicating that our study was carried out during a year with above-average rainfall. Comparable rainfall to our study year has only been observed during one other year (2009) during the TRMM period of record (Figure 4.3). As expected for many EP-ITCZ and monsoonal regions [*Magaña et al.*, 1999; *Hastenrath*, 2002; *Westerberg et al.*, 2010], the annual cycle of rainfall exhibited strong seasonality (Figure 4.4). Similar to other regions of Honduras, the wet season or *Invierno* extended from May through October, with peaks in June and September, on either side of the *Veranillo* [*Westerberg et al.*, 2011]. Wet season rainfall accounted for 96% of annual precipitation (Table 4.3). There was a decline in rainfall from mid-July through mid-August due to mid-summer drought [*Magaña et al.*, 1999; *Curtis*, 2002; *Small et al.*, 2007]. The average rainfall for rainy days was 8 mm/day, the maximum was 205 mm/day. Sixty percent of total rainfall occurred between 14:00 and 20:00 h (70% between 14:00 and 23:00 h). The maximum instantaneous rainfall intensity in a 15-minute time interval was 136 mm/h. Similar rainfall amounts and intensities were observed in the Choluteca River basin of central Honduras. In that watershed, rainfall average was 5.9 mm/day, and 5-minute time step maximum intensity was 115 mm/h [*Caballero et al.*, 2012].

Table 4.3 Water budget components and season contribution.

Season	Rainfall (mm)*	Runoff (mm)	Base Flow (mm)	*BFI*	*AET* (mm)
Dry	62 (4)	54 (12)	42 (15)	0.78	467 (40)
Wet	1660 (96)	397 (88)	243 (85)	0.61	691 (60)
Total	1722	451	285	0.68	1158

*Values within parenthesis are percentages of totals.
BFI = Base Flo Index = Baseflow/total runoff.
AET = Actual Evapotranspiration.

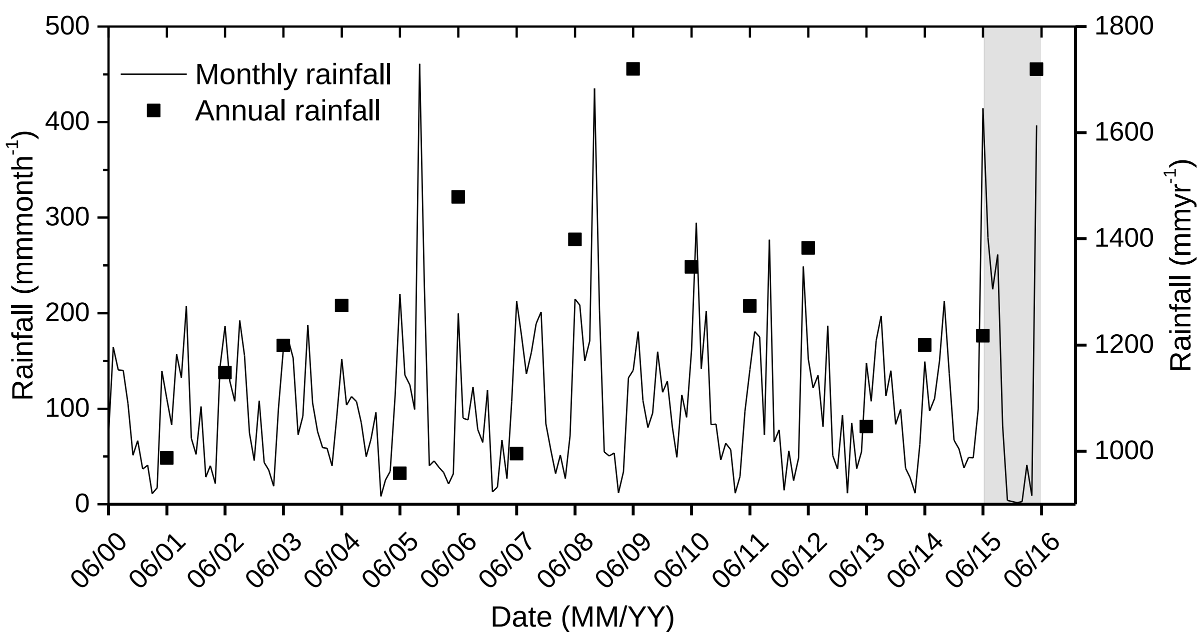

Figure 4.3 Long term TRMM precipitation for the Talgua Catchment. Shaded area is our study period.

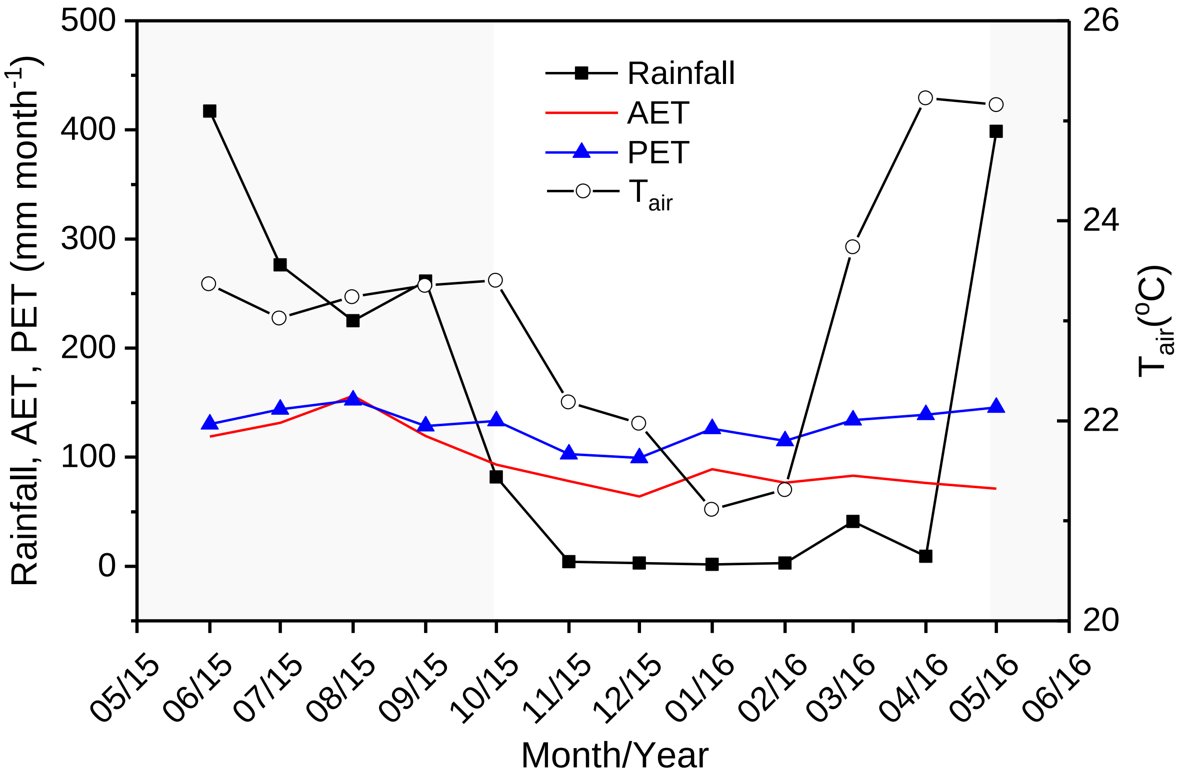

Figure 4.4 Monthly variation of main climate variables. Temperature, precipitation, and solar radiation were measured near the watershed outlet and used to compute monthly potential and actual evapotranspiration. Gray shading indicates wet season. AET and PET are actual and potential evapotranspiration respectively, and T_{air} is air temperature.

Daily total runoff and separated baseflow are presented in Figure 4.5. Mean discharge was 1.13 m^3s^{-1}, equivalents to an annual runoff of 451 mm and a runoff ratio (Q/P) of 26% for the study period. The lowest observed discharge was 0.06 m^3s^{-1} and the greatest observed discharge was approximately 7 m^3 s^{-1}. Streamflow seasonality followed overall the rainfall pattern, with 88% (397 mm) of the annual flow occurring during the wet season (Table 4.3). The highest monthly runoff occurred in June (126 mm), and it decreased steadily until reaching a minimum in April (4.5 mm), just before the onset of the next wet season (Figure 4.6). This cycle of annual runoff is consistent with the 25 years of simulated streamflow reported for the Tascalapa River watershed in Honduras, where climate, vegetation and geomorphological characteristics are very similar to our study watershed [*Luijten and Knapp*, 2007]. Our results are also similar to measured runoff (520 mm) from the Choluteca River basin of central Honduras, which is also highly forested [*Caballero et al.*, 2012].

Our streamflow separation results show that annual baseflow was 284 mm of total runoff, a baseflow index (*BFI*) of 63%. The BFI peaked at 0.88 near the beginning of the dry season (November) and reached its lowest value of 0.28 with the onset of rain during the wet season in May (Figure 4.6).

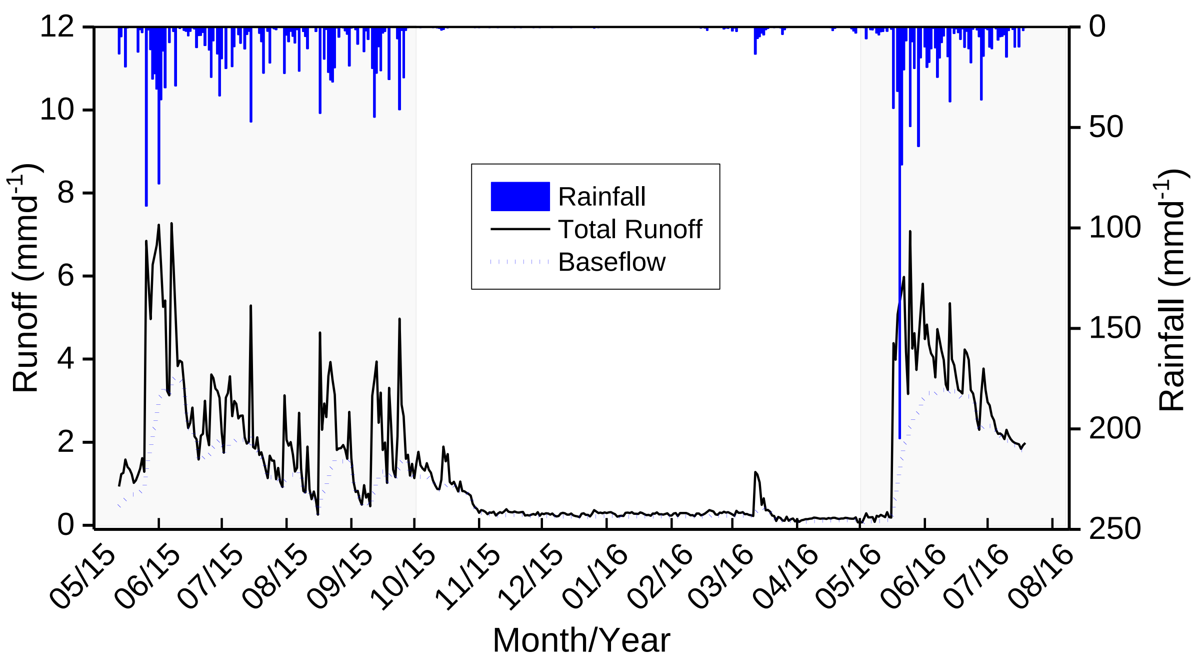

Figure 4.5 Daily variation of rainfall and runoff measured near the outlet of the Talgua River watershed. Baseflow is estimated using WHAT online tool (Kyoung et al., 2005). Gray shading indicates wet season.

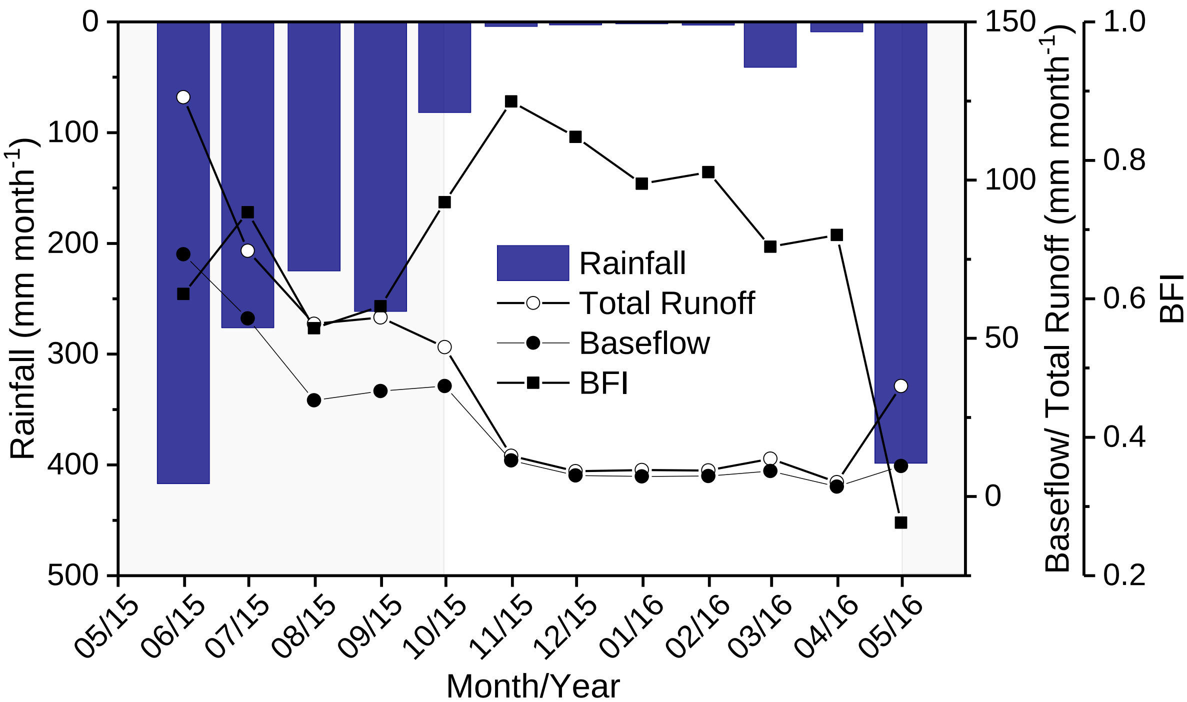

Figure 4.6 Monthly variation of water budget components. Strong precipitation seasonality and year-round atmospheric demand for moisture produce extreme wet and dry hydrologic regimes during the year. Gray shading indicates wet season.

Actual evapotranspiration (*AET*) was estimated at 1158 mm or 67% of total precipitation (Table 4.3). This value falls within the *AET* range of 1100-1300 mm yr^{-1} estimated for several tropical eddy covariance sites using the same *AET* method [*Fisher et al.*, 2009], but was about 17% lower that the long-term (2000-2014) watershed-wide annual *AET* estimate of 1400 mm yr^{-1} based on MODIS-16A2/A3 [*Mu et al.*, 2007]. Annual *PET* was 1547 mm, which also fall within the rage of PET estimates for similar tropical landscapes (Figure 4.7). For the larger Patuca River basin, to which the Talgua belongs, *PET* has been estimated at about 1500 mm yr^{-1} [*UNAH*, 2014]. Approximately 60% of annual *AET* occurred during the wet season, which also accounted for 44% of annual *PET* (Table 4.3). Neither *AET* nor *PET* followed monthly precipitation dynamics. Instead, these variables remained relatively static during the study period (Figure 4.4). Actual evapotranspiration and *PET* exceeded rainfall during the last month of the wet period and during the entire dry season. During the dry season, *AET* was considerably lower than *PET*, but the two were similar during wet season months (Figure 4.4).

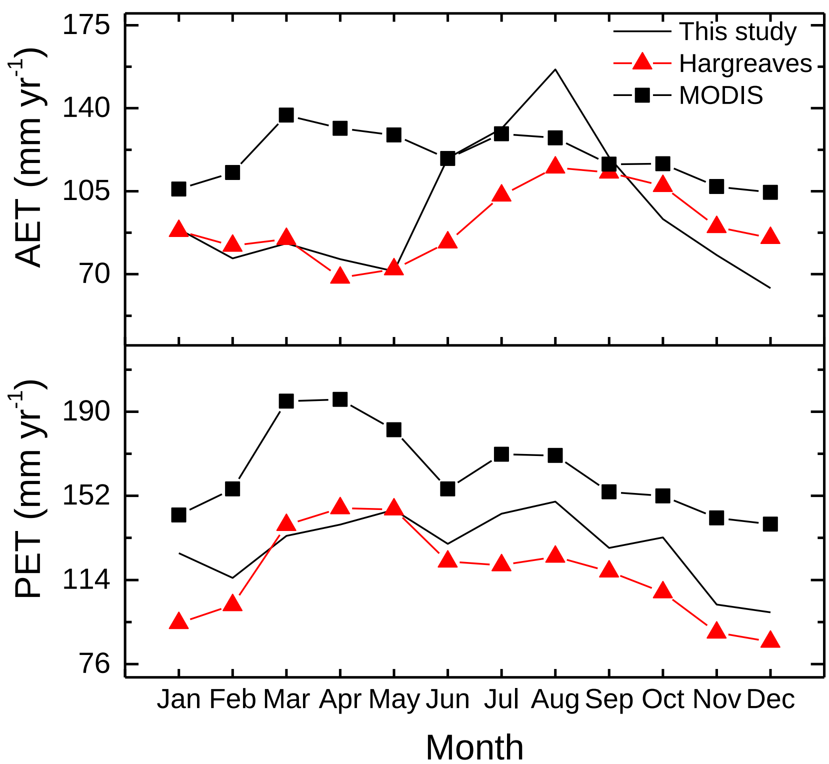

Figure 4.7 Comparison of estimated AET and PET to long-term MODIS (Mu et al., 2007) and Hargreaves-based estimates (*Zomer et al.*, 2006).

The relative change in monthly water storage (Δ*S*) at the watershed scale is presented in Figure 4.8a. Positive values indicate increasing water storage in soils and groundwater, and negative values indicate declining storage. Storage recharge and discharge were clearly linked to wet and dry season water balances. Most recharge occurred during the wet period (May to September) and this gained storage was lost to a combination of stream runoff and

ET beginning in the last month of the wet season (October) and extending through the entire dry season (November through April). The observed lower rate of storage in August was linked to a decline in precipitation during that month (Figure 4.4). Overall, the seasonal control of storage on baseflow demonstrates that rainfall stored during the wet season plays a critical role on sustaining the dry-period streamflow (Figure 4.8b).

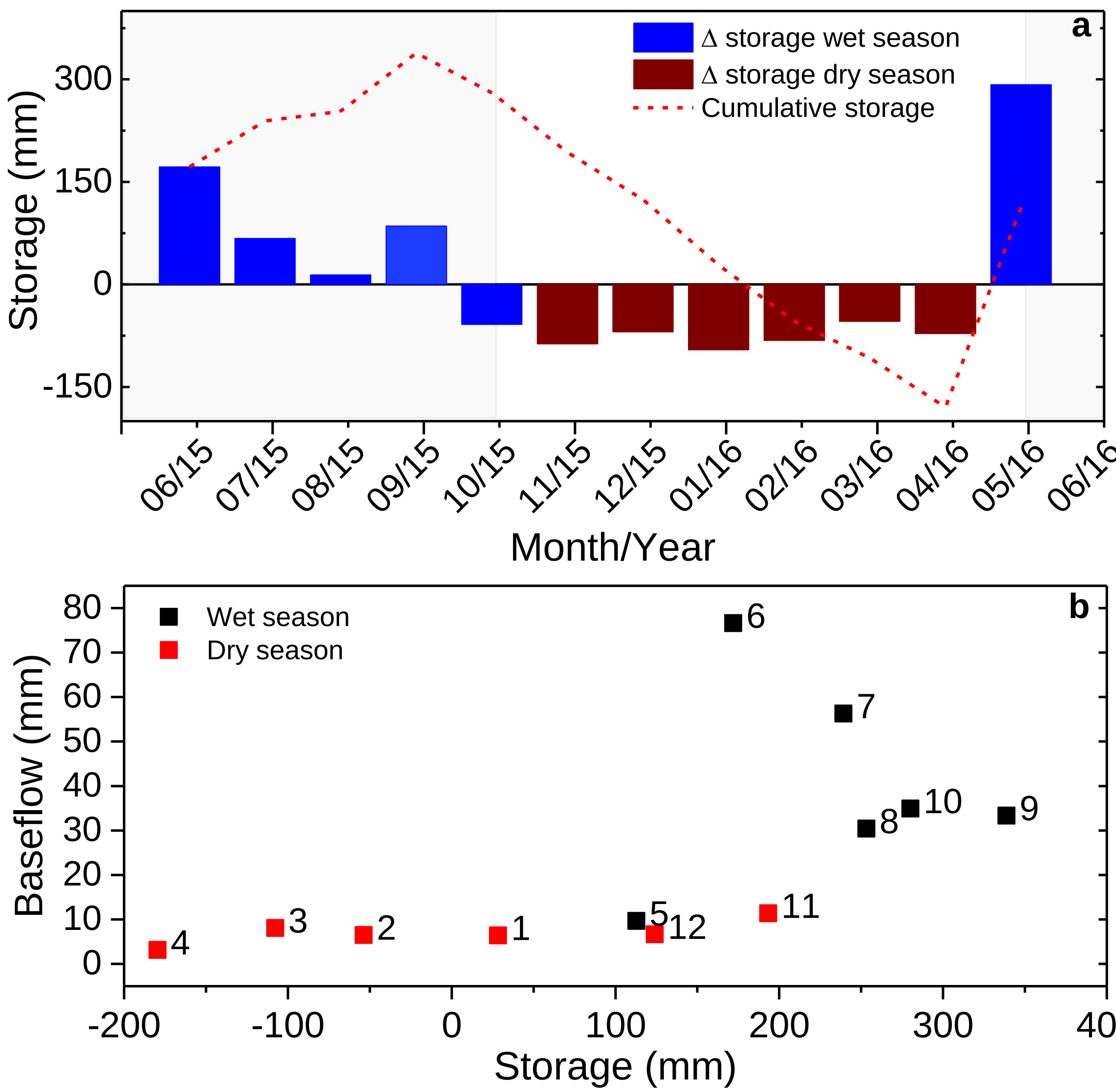

Figure 4.8 Monthly variation of relative water storage (a). Dotted line is cumulative relative water storage, and gray shading indicates wet season. Panel (b) shows the influence of soil water storage on monthly baseflow. Numbers in panel b indicate the month number in a year (i.e., 1 = January).

Annual water yields within the watershed derived from the InVEST model varied from 590 to 1030 mm depending on landscape position, with an average of 694 mm (40% of runoff ratio) (Figure 4.9). The InVEST model revealed landscape effects on potential water availability across the watershed. For instance, water yield from areas dominated by primary forest was 44% lower than water yields from croplands and pasture, and sub watersheds with lower forest cover and steeper terrain had higher water yields than those with higher forest cover and less steep slopes (Table 4.4).

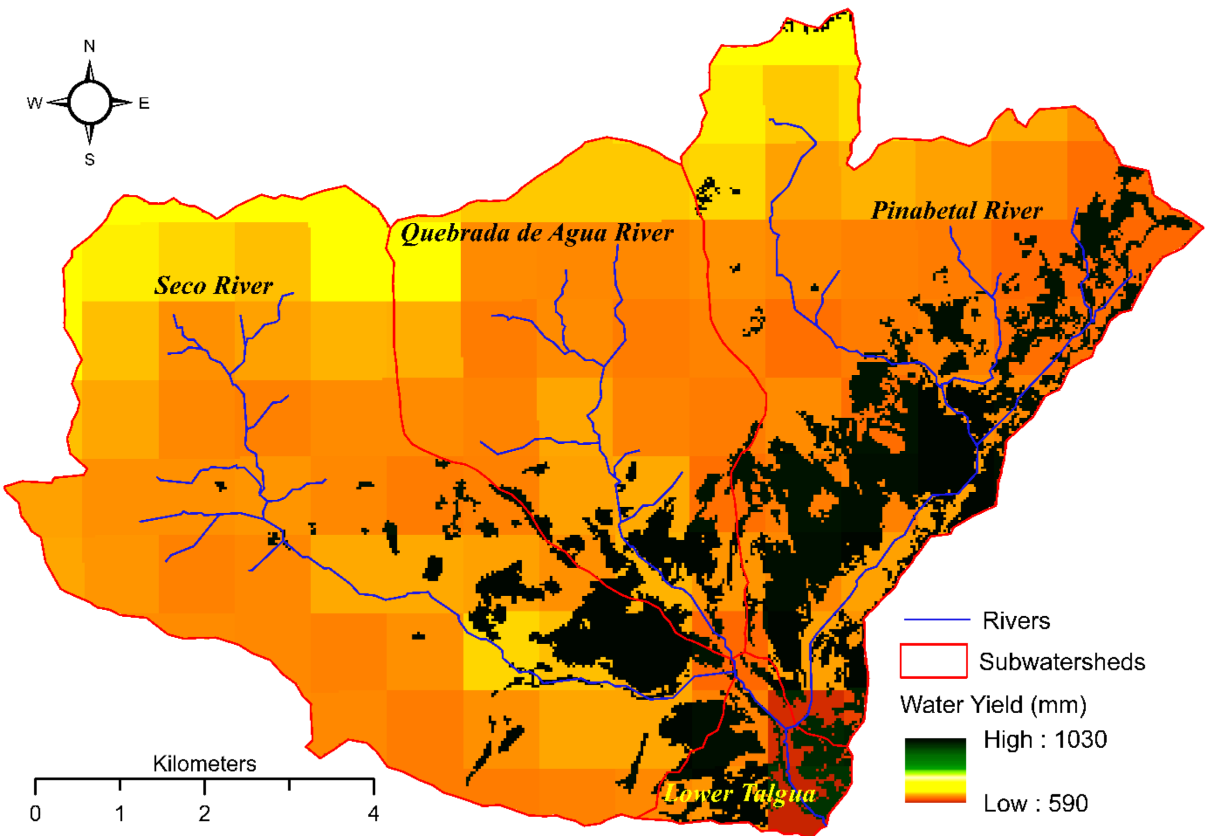

Figure 4.9 Spatially distributed water yield (mm) as modeled by InVEST. Water yield was modeled by subcathment and landcover.

4.4 Discussion

4.4.1 Uncertainties in the Annual Water Balance

Watershed-wide estimates of annual P, AET and Q for the study period were 1720, 1158 and 451 mm, respectively. Annual soil water storage was +111 mm, which is approximately 6% of precipitation, and includes the real annual storage plus any uncertainty in the water balance components. In addition to changes in annual water storage within the watershed, there are several additional sources of uncertainty in our water budget estimates. Atmospheric conditions (i.e., P, T_a, and R_n) measured at the weather station were assumed to represent the entire watershed. However, rainfall at this latitude tends to peak at about 1500 m AMSL and may decrease significantly at higher elevations within a given region [*Hastenrath*, 1991; *Rundel*, 1994; *Mölg et al.*, 2009]. Moreover, much of the watershed is considered montane cloud forest, with 77% of the watershed area falling into the Holdridge's Lower Montane Wet Forest category (Figure 4.2). Studies across the tropics show that cloud forest interception and other occult contributions to precipitation may range between 5 and 75% of total annual precipitation [*Bruijnzeel et al.*, 2011; *Clark et al.*, 2014; *Hu and Riveros-Iregui*, 2016]. This potential source of precipitation is not considered in our water balance, which means that our combined value of +111 mm for storage and uncertainty could be a conservative estimate.

Our annual AET estimate of 1158 mm likely represents an upper bound for the study area, although it was close to the mean of estimates from tropical eddy covariance sites [*Fisher et al.*, 2009], and from MODIS satellite products [*Mu et al.*, 2007]. The watershed is located within a region identified as energy limited [*Nemani et al.*, 2003]. We do not expect overall solar radiation to vary significantly watershed-wide, but R_n and T_a may differ due to differences and vegetation and topographic shading, which can lead to overestimate *AET*. During the dry season (6 months), for example, the predominant dry soil conditions and low vegetation coverage over non-forested areas increase albedo in those areas, which limit R_n and thus *AET* [*Shuttleworth*, 2012]. Particularly above 1300 m, there may be a reduction of *AET* in the cloud forest because reduced radiation and VPD combine to produce a lower atmospheric moisture demand [*McJannet et al.*, 2010; *Bruijnzeel et al.*, 2011; *Jarvis and Mulligan*, 2011; *Fahey et al.*, 2015]. Moreover, transpiration can be suppressed significantly due to fog [*Reinhardt and Smith*, 2008; *Alvarado-Barrientos et al.*, 2014; *Gotsch et al.*, 2014], although some cloud forest ecosystems may be adapted to maximize activity under diffuse light conditions [*Hu and Riveros-Iregui*, 2016]. The discharge value reported here for the Talgua watershed might be an underestimate. Early AM daily measurements may provide a conservative low estimate of annual runoff due to late evening hydrograph peaks following convective storms [*Magaña et al.*, 1999; *Westerberg et al.*, 2011], and five days where actual measurements were missed and required gap filling.

Despite these sources of uncertainty in the water balance, these monthly and annual estimates of water balance components are likely sufficient for answering important questions related to water availability and management in this region. Our analysis can support agricultural planning for water supplies during irrigation and planting periods, and it can support community planning for water collection and storage in advance of the dry season. Nevertheless, water balance estimates may be improved with additional effort. For example, watershed-wide meteorological observations can improve *P* and *AET* estimates. These observations can be acquired directly by adding additional weather stations or by employing terrain-based downscaling of global climate products [*Agnew and Palutikof*, 2000; *Clark and Slater*, 2006]. Automated, high-frequency stream stage measurements are helpful for capturing the diel variability in streamflow, and combining these measurements with our daily direct discharge measurements would minimize uncertainty due to rating curve assumptions and sub-daily streamflow variations. Finally, quantifying cloud forest contributions to total precipitation would help reduce uncertainty in estimates of water storage changes. These improvements in field observations would facilitate hydrological analyses related to hydrograph recession, storm responses, flood forecasting, and other processes that have implications for the human communities and natural ecosystems that depend on water resources in this watershed.

4.4.2 Water Yield: Implication for Water Storage and Management

The spatial distribution of the water yields emphasizes patterns induced by land use (Figure 4.2, Figure 4.9), and these patterns have substantial implications for water resources management. Water yield from cropland and pasture was about 44% greater than water yield from forests (Table 4.4), and this scenario has major implications for water availability and quality. A paired watershed study in Honduras has shown similar inverse relationships between forest cover and water yield [*Bonilla and Garay*, 2013]. Our results suggest that rainfall stored in the subsurface during the five-month wet season (May to September) sustained dry-period streamflow (Figure 4.8). Streamflow declined dramatically in the second month of the dry season (December) and reached a minimum value of 0.06 m^3s^{-2} before the rainy season began in April (Figure 4.6; Table B1 in appendices B). Increased water yields from agricultural lands may further decrease dry season water availability, given that agricultural lands are typically characterized by lower rates of infiltration and soil water recharge [*Bosch and Hewlett*, 1982; *Kosmas et al.*, 1997; *Nunes et al.*, 2011]. *Hanson et al.*, (2004) investigated the impact of soil degradation on surface water dynamics in the Talgua watershed and found that infiltration rates were > 840 mm/hr in primary forest, and 8-11 mm/hr in heavily-grazed pasture [*Hanson et al.*, 2004]. Given that maximum precipitation intensity observed in our study was 136 mm/h, we conclude that infiltration excess is very unlikely in forested areas of the watershed but highly likely to occur during intense storms in lands that have been cleared for grazing.

Table 4.4 Influence of land management on water yield by sub-watershed, and by landcover as modeled by InVEST.

Subwatershed	Spatial characteristics and watershed by subwaterhed				Water yield by land cover watershed-wide	
	Area (Km^2)*	Forest cover (%)	Mean Slope (%)	Water Yield (%)	Dominant Land cover	Water Yield (%)
Q. Agua River	17 (22)	91	59	39	Forest	39
Seco River	33 (41)	87	56	39	Coffee	38
Pinabetal River	26 (33)	67	51	43	Crops/pasture	56
Lower Talgua	3 (4)	51	60	48		

* Values in parentheses are % of the watershed total area.

The immediate effect of reduced infiltration capacity is an increase in surface runoff [*Bruijnzeel*, 2004]. This, in combination with steep terrain, leads to intensified hydrologic responses (i.e. higher and more rapid peak flows), and it can trigger landslides and flooding. All of these phenomena were major determinants of the devastation caused by hurricane Mitch in Honduras in 1998 [*Hellin and Haigh*, 1999; *Smith et al.*, 2002]. Runoff-related factors explain the high environmental vulnerability in the Talgua watershed [*Reyes et al.*, 2006]. Other effects of surface runoff amplified by land use change include more erosion and sediment transport into streams [*Gupta et al.*, 1975; *Bruijnzeel*, 1990; *Ogden et al.*, 2013]. Permanent vegetation maintains high infiltration capacities compared to other uses [*Hanson et al.*, 2004], plays an important role in reducing sediments, as well as increasing trapping or filtering other water pollutants [*Hicks et al.*, 1991; *Bruijnzeel*, 2004; *Neary et al.*, 2009]. This land use effect on sediment transport is particularly clear in the Patuca basin, in which the Talgua watershed is situated. Rapid anthropogenic land use change in the upper basin, including the Talgua watershed, has made the Patuca basin the second largest source of terrestrial sediment to the Mesoamerican Reef [*Burke and Sugg*, 2006].

The effects of land cover on water yields and baseflow are already well known [*Bosch and Hewlett*, 1982; *Ogden et al.*, 2013], and it is extremely important to evaluate site-specific implications for highly disturbed, populated landscapes such as the Talgua watershed and similar tropical regions. Talgua farmers, like farmers throughout Honduras and Latin America, often practice slash-and-burn shifting agriculture, experience extreme poverty, and rely on subsistence rainfall-fed agriculture [*Jansen et al.*, 2006; *Altieri and Nicholls*, 2008]. During the dry season, food production and drinking water supplies depend almost entirely on baseflow [*Jansen et al.*, 2006; *INE*, 2013]. For example, baseflow in this study accounts for 63% of total annual runoff of the watershed and represents 80% of the total dry season flow (Table 4.3). The mean *BFI* value for the Talgua River is lower than that reported by others for the Tascalapa and Choluteca watersheds (approximately 0.8), and it is also lower than values of 0.77 to 0.8, which were reported for forested watersheds in the Andes [*Crespo et al.*, 2011; *Clark et al.*, 2014]. Therefore, climate change may further exacerbate the already critical problems of water availability and quality, particularly during the dry season. For example, modeling work from the Lempa River basin (Guatemala, Honduras and El

Salvador), one of the largest river basins in Central America, found that future increases in evaporation and reductions in precipitation will likely lead to a 20% reduction in annual runoff [*Maurer et al.*, 2008]. Global climate models uniformly predict that Honduras will become substantially drier throughout the 21st century [*Christensen et al.*, 2007], and they project an earlier onset and intensification of the mid-summer drought [*Rauscher et al.*, 2008]. If land use change continues along its current trajectory, even more land will be converted to agriculture, likely reducing seasonal storage of water in soils and groundwater that can reemerge as baseflow during the dry season.

Knowledge about differences in water yields due to land uses within the watershed can be used by local stakeholders and policy makers for planning and prioritizing both management actions and intervention zones. For example, the Pinabetal River and the Lower Talgua subwatersheds have the highest water yields in the watershed and could be targeted for management. Low forest cover (51%) and steep slopes (>60%) make the Lower Talgua an especially interesting area for managers (Table 4.4, Figure 4.10). For example, planners and stakeholders may discourage further land use change in this subwatershed or promote conservation practices on degraded lands to regrow forest or at least prevent further expansion of agriculture within this area.

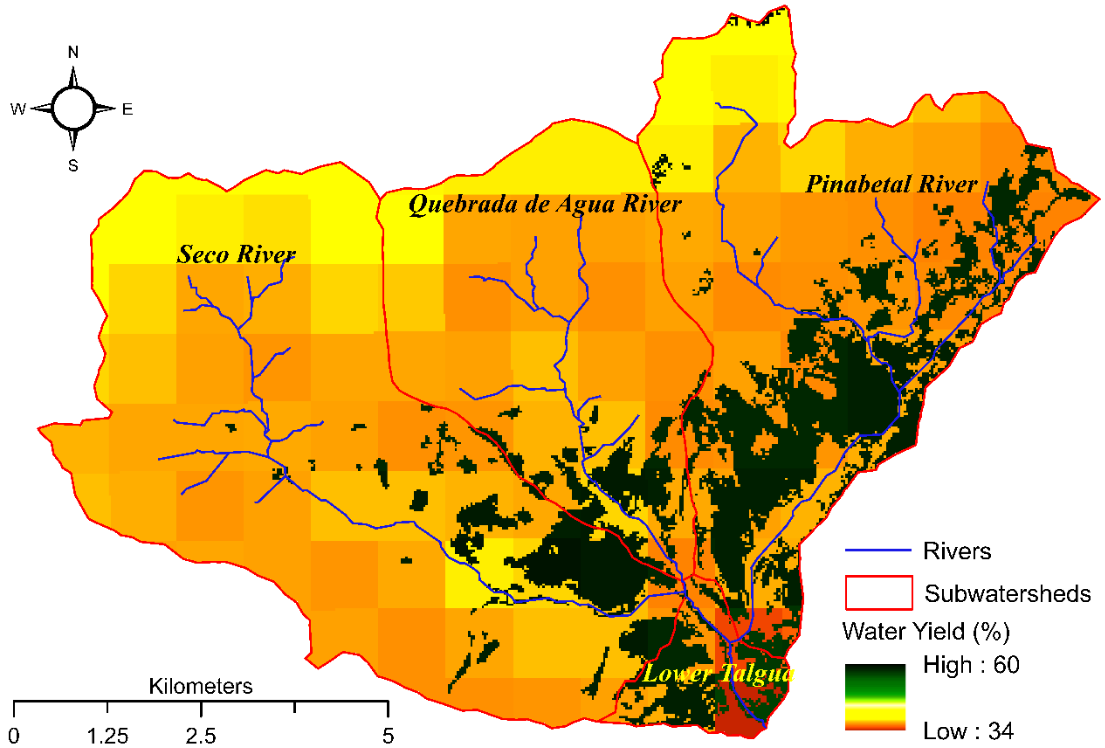

Figure 4.10 Spatially distributed water yield (%) as modeled by InVEST. Water yield was modeled by subcathment and landcover.

4.4.3 Complexity and Vulnerability of Tropical Landscapes: Challenges for Water Resources Sustainability

Hydrological behavior in tropical watersheds emerges from complex, coupled natural-human dynamics. We have discussed some of these dynamics earlier, including the impacts of land cover change on water sustainability, particularly during the dry season. Throughout Honduras, and particularly within the Talgua watershed, water management issues result from a combination of environmental factors, land management practices, chronic poverty, and policies not tailored to concerns of the region. For example, only about 15% of the Honduras's land territory is well suited for agriculture, yet the country's economy relies disproportionately on agricultural production [*Jansen et al.*, 2006; *INE*, 2013].

Most agricultural activities in Honduras are conducted by smallholder families living in mountainous terrain, which is typified by the Talgua watershed. These smallholder families constitute about 80 percent of Honduras's rural population [*Jansen et al.*, 2006]. Poverty is endemic on these communities; more than 90 percent of the inhabitants of these areas survive on less than US$1/day per capita [*Jansen et al.*, 2006; *INE*, 2013]. These populations have been forced to occupy mountainous areas due to limited access to arable land, which is already occupied by wealthier populations [*Pielke et al.*, 2003]. In many cases, these mountainous areas include protected lands with regulations restricting or prohibiting farming activities and private land ownership. For example, the Talgua watershed lies within the Sierra de Agalta national park, which is designated a "protected forest reserve." Under this category, agriculture activities and private farming are prohibited.

However, about 1400 people live and farm within the watershed, and about 30% of the watershed's land area is under cultivation (Table 4.1). This situation poses difficulties for developing sustainable solutions to water management issues. Government support to these families for improved agriculture systems is limited due to economic constraints at the national level and due to legal restrictions that officially prohibit farming in protected areas. As a result, these hillside families practice subsistence agriculture, normally using primitive technology. Farmers experience very low crop productivity, and they exert disproportionately high environmental impacts on the landscapes due to lack of technological and economic resources needed to implement sustainable practices while maintaining sufficient yields for subsistence. The combination of human needs and policy inadequacies with a landscape that is susceptible to degradation and vulnerable to climate change creates a "limbo scenario" for smallholder families in the watershed.

Many other tropical countries experience similar scenarios to the situation described above, although Honduras may be considered an extreme example. Poverty, land inequality and high rates of deforestation are endemic to tropical regions [*Sachs,* 2001; *Hoffman and Centeno,* 2003; *Lawrence and Vandecar*, 2015]. However, heterogeneities in landscapes, climates, levels of disturbance, agriculture practices, human-natural resources interactions, and population dynamics [*Landon*, 1991; *Richter and Babbar*, 1991; *Dirzo and Raven*, 2003; *Townsend et al.*, 2008; *Brauning*, 2009; *YCU*, 2014], result in a broad spectrum of ecological dynamics that may limit the ability to generalize these results across the tropics [*Townsend et al.*, 2008; *Ponette-González et al.*, 2014; *YCU*, 2014; *Lewis et al.*, 2015]. For example, reductions in forest cover may significantly increase water yields in some areas [*Bosch and Hewlett*, 1982; *Bruijnzeel*, 2004; *Brown et al.*, 2005], but not in others [*Bruijnzeel*, 2004; *Salemi et al.*, 2013]. Moreover, other aspects such as the effect of land use change on water quality, or the hydrologic pathways within watersheds that are well established for temperate regions [*Likens et al.*, 1970; *Cirmo and McDonnell*, 1997], remain highly controversial for tropical watersheds [*U.S. DOE*, 2012; *Ponette-González et al.*, 2014]. Wider research throughout the tropics would improve understanding of ecological dynamics, particularly, how these heterogeneous and complex systems respond to rapid environmental changes and impact global ecological dynamics.

Water resources issues in tropical watersheds also highlight and emerge from the region's environmental vulnerability. Honduras, for example, is considered a hotspot for natural disasters [*The World Bank*, 2005], particularly due to its exposure and high vulnerability to water-related disasters, including storms, floods, droughts and rain-triggered landslides. These water-related disasters have killed more than 17,000 people and have caused economic losses to the country of about US$ 4.5 billion during the last two decades [*The World Bank*, 2010]. Increasing land degradation in mountainous terrain has been identified not only as the main driver of water-related disaster but also a major cause of Honduras' rural poverty and vulnerability of its water resources [*Ensor*, 2009; *The World Bank*, 2010]. For example, highly eroded mountainsides along with slash-and-burn agricultural practices generally render the soils unable to absorb excess water [*Hanson et al.*, 2004]. Consequently, high surface runoff and sediment transport overwhelm the natural carrying capacity of the stream network, increasing peak flood discharges, and resulting in catastrophic flooding and landslides [*Smith et al.*, 2002; *Ensor*, 2009]. As explained in section 4.4.2, these factors explained most of the devastation caused by hurricane Mitch in Honduras, including areas within the Talgua watershed.

Human activities in mountainous areas alter the quantity and quality of water resources, and hence these activities increase the vulnerability of communities within the watershed and communities downstream. In Honduras, like most tropical countries, water supplies in urban areas rely heavily on surface water generated in forested, mountain headwater regions [*Abell*, 2017]. During the rainy season or after a high precipitation event, high concentrations of suspended sediment in stream water creates drinking water shortages for urban populations given the lack the technology for water treatment. This is true of Catacamas, the city immediately downstream from our study site. Besides water shortages during high-sediment floods, urban dwellers may incur additional costs associated with purchasing purified water from private companies.

Small landholder in the Talgua watershed, on the other hand, are simply forced to drink polluted water as they draw water directly from the river. Their low income (US$1/day per capita) prevents them from buying water from private companies at all. Moreover, as we discussed in section 4.4.2, increased surface runoff during the wet season results in reduced seasonal storage of water in soils and groundwater, which diminishes baseflow and therefore water availability during the during the dry season. These reductions in dry season streamflow increase the likelihood of drinking water shortages for human populations, and they also increase the likelihood of water stress for ecosystems located within the watershed. Vegetation, both natural and cultivated, may die off during the summer period due to low soil water availability, which might have a negative feedback to the watershed system by decreasing ET. However, this death of vegetation, in combination with high summer temperatures, causes frequent wildfires in the area and may counteract or exceed the reduction of ET [*Obrist et al.*, 2003], and drives the watershed system into an even more vulnerable state.

The water resources vulnerability in the Talgua watershed, and in Honduras in general, could become more critical with projected drier conditions, which will result from less precipitation and streamflow, as well as an intensification of the midsummer drought period. A similar climate change trend is also throughout the tropics [*Christensen et al.*, 2007]. The examples and discussion presented in this section depict the complex human-nature dynamics that are prevalent in tropical areas. We show how inherent heterogeneity of the tropics, in combination with complex human-nature interactions, may lead to particular, in some cases unexpected, hydrological dynamics. Understanding the implications of these dynamics in the Earth's system will require more and wider field-based research throughout the tropic, which will be critical to improving the representation of tropical areas in Earth Systems models.

4.5 Conclusion

We used a combination of field-based monitoring and remote sensing to evaluate the water balance of a fourth-order forested, headwater watershed in Honduras. Despite limited science infrastructure, data availability, and difficult logistics of this region, we worked collaboratively with local stakeholders and local researchers to assess monthly, seasonal, and annual water balances. The annual water balance closure for the watershed was within 6%, with 1720 mm of rainfall, 451 mm was removed from the system as streamflow, and 1158 mm was lost through actual evapotranspiration. Sources of uncertainty in this water balance include errors from estimates of watershed-wide atmospheric conditions (P, T_a and R_n), and the potential influence of cloud forest on precipitation and evapotranspiration. We showed how strong seasonality in climatological variables and soil water storage combine with patterns of land use to create a scenario in which streamflow is currently very low, particularly during the dry season, but could become even lower in the future as result of continued land use change and the expected drier conditions for this region. These results have implications for water resources management in the Talgua watershed, but more importantly they highlight complex coupled natural-human interactions that determine ecological dynamics in tropical regions worldwide. These conclusions are relevant to many practical questions related to fresh water supply, water quality, and land-use management not only in the Talgua watershed, but in similar settings throughout the tropics.

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CHAPTER 5: SUMMARY

Motivated by the need to understand and predict better terrestrial ecosystem processes and behavior in a changing world, this dissertation has sought to improve our conceptual understanding of the roles of heterogeneity and complexity in terrestrial carbon and water cycling. With this in mind, three related studies were conducted. Chapter 2 reviewed the scientific literature addressing landscape heterogeneity and complexity in terrestrial ecosystems, and examined the implications for terrestrial carbon and water cycles. Chapter 3 synthesized data from 30 AmeriFlux network sites to evaluate relationships between terrain complexity and responses of ecosystem carbon fluxes to temperature and precipitation. Chapter 4 characterized the water balance of a tropical landscape characterized by heterogeneous land use and rapid environmental change.

Specifically, the second chapter synthesized classic and recent work on landscape heterogeneity and complexity, providing rigorous definitions of the terms, metrics, and discussing some of the underlying causes of landscape heterogeneity and complexity in terrestrial ecosystems and how they influence carbon and water cycles at local and larger scales. Chapter Two found that a better understanding of landscape heterogeneity and complexity is a critical research area to improve carbon and water cycles predictions, yet challenges remain related to conceptualizations of phenomena and metrics used to quantify them. The inconsistent use of terminology along with generalizations about heterogeneity and complexity sometimes produce ambiguity, which hinders progress. Existing metrics quantify specific aspects or components of landscape heterogeneity and complexity, but no metric or method currently exists to quantify heterogeneity or complexity for an entire landscape.

Landscape heterogeneity and complexity influence multiple aboveground and belowground factors and processes that determine the storage, distribution, and exchange of carbon and water with the atmosphere. Carbon and water dynamics and related processes may vary significantly across the landscape as a function of heterogeneity and complexity, potentially leading to unexpected, emergent ecological behavior. Failure to adequately account for these effects can influence the accuracy of carbon and water cycle models at spatial scales of landscapes and larger. Recent studies highlight risks associated with predicting regional water and carbon fluxes using lumped composite or mosaic approaches, and they provide robust evidence showing that incorporation of local-scale heterogeneities can significantly improve model results. This review highlighted several general ways in which heterogeneity and complexity could be incorporated into models, yet important questions remain: What type of heterogeneity and complexity are more relevant for the carbon and water cycles? At which scale? and how to link the impact of heterogeneity and complexity across spatial and temporal scales? These questions remain to be answered to move the topic forward.

The third chapter evaluated relationships between terrain complexity and the response of ecosystem carbon fluxes to climate within the AmeriFlux tower network, evaluating responses of GEP, RE, and NEP to temperature and precipitation for sites located in both complex and simple terrain. The study considered daily, monthly, seasonal, and annual responses for 30 tower sites covering a range of terrain conditions. In the absence of controlled, landscape-scale experiments, these results help to identify both landscapes and positions within the landscape that may be experiencing similar ecological behavior. Chapter three demonstrated that in terrestrial ecosystems, the responses of carbon fluxes to temperature and precipitation can be influenced by topography in complex terrain. These results are fundamentally different from prior studies, which have focused on the ability of complex terrain to modify the atmospheric boundary layer and drive advective flows. This work shows that terrain slope and drainage area, which are often associated with water and energy availability, impact daily responses of carbon fluxes to temperature (in the case of slope) and annual responses of carbon fluxes to precipitation (in the case of drainage area). These topographic variables interact with vegetation and soils in complex ways to give rise to a broad spectrum of responses to climate. We found no such influences in flat terrain, suggesting that the traditional conceptualization of vertical soil-vegetation-atmosphere dynamics holds for these systems. The terrain impacts identified in this work have implications for approximately 14% of the total land area of the conterminous US, an area which sequesters more than 1 Gt of carbon annually. Prevailing conceptual frameworks and models may not be able to capture these terrain-derived responses, and these results highlight new opportunities to improve conceptual understanding and models of ecosystem carbon dynamics.

The fourth chapter combined field-based monitoring and remote sensing to characterize the water balance for the upper Talgua River, a forested, montane catchment in the headwaters of Honduras' Patuca River. This watershed represents a common highly disturbed landscape in Central America, and typifies the complex rural hillside system of subsistence agro-forestry upstream balanced against water quantity and quality requirements by humans and natural ecosystems within the watershed and downstream. Therefore, the water balance and its implications for water resources sustainability were discussed in the context of complex human-environment interactions in this region of Mesoamerica.

Chapter four found that strong seasonality in climate variables and soil water storage combine with spatial patterns of land use to create a scenario of very low streamflow conditions. Water scarcity could become an even more serious threat in the future as a result of continued land use change and projections of drier future conditions for this region. These results have direct implications for water resources management in the Talgua watershed, but they also illustrated how the heterogeneous land use patterns of tropical areas, along with environmental vulnerability and complex coupled human-environment interactions, influence tropical ecohydrological systems, and hence highlight the need for more and wider field-based research throughout the tropics.

The work undertaken by this dissertation contributes to fill three important scientific knowledge gaps: Little review or synthesis work addressing the influence of landscape heterogeneity and complexity on aspects of water and carbon cycling in terrestrial ecosystems, lack of studies investigating the role of complex terrain in mediating responses of land-atmosphere carbon fluxes to climate, and poor understanding of complex human-environment interactions and their effects on tropical ecohydrological systems. Taken as a whole, this dissertation helps to improve our conceptual understanding of the roles of heterogeneity and complexity in terrestrial carbon and water cycling.

APPENDICES

Appendix A. Supplementary material for chapter III

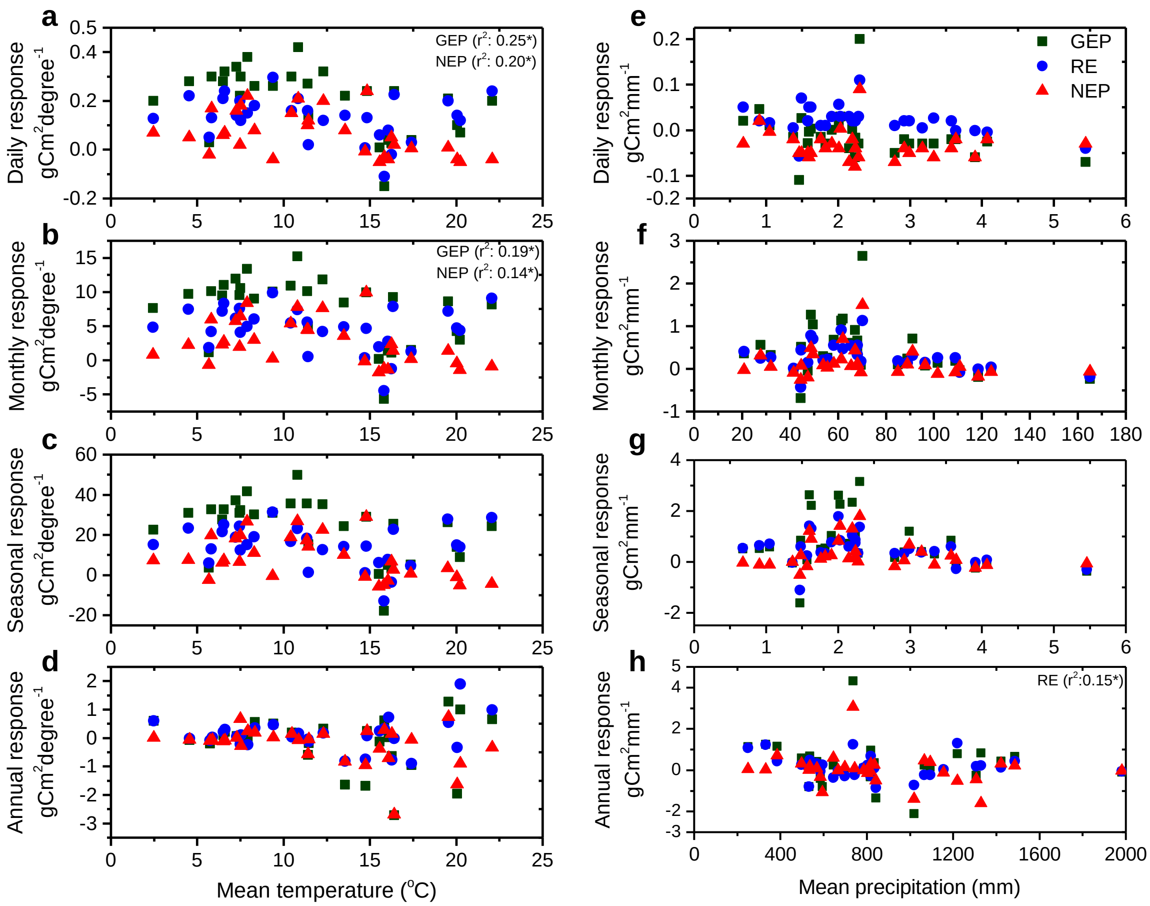

Figure A1 Relationship between mean climate and the response of carbon fluxes to climate (all sites). Carbon fluxes responses to climate were not explained by mean temperature and mean precipitation. Panels a-d are correlations between mean daily temperature and the responses of carbon fluxes at the daily scale. Panel e-h are the correlations between mean annual temperature and the response of carbon fluxes at annual scale.

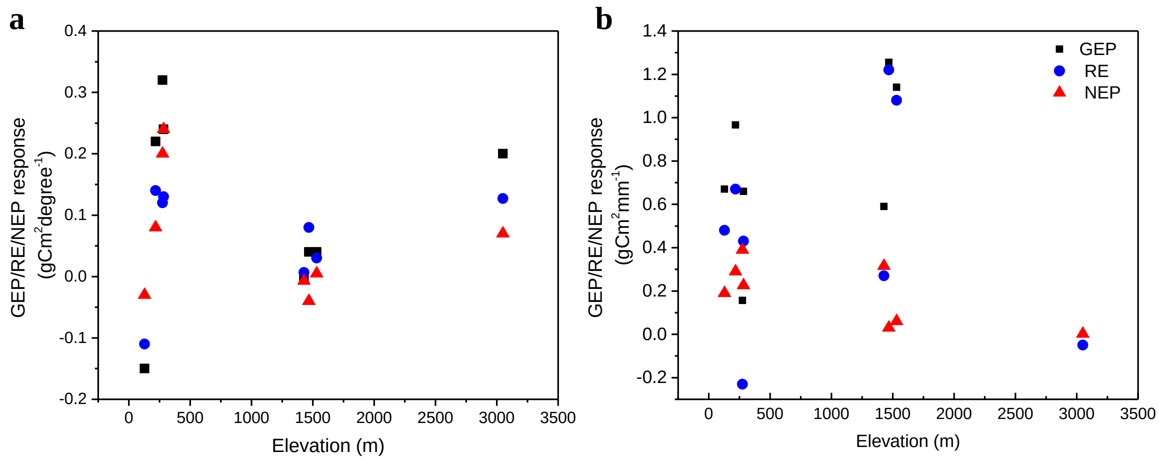

Figure A2 Relationship between mean elevation and the response of carbon fluxes to climate for complex sites. Carbon fluxes responses to climate were not explained by mean elevation. a, is the correlation between elevation and the responses of carbon fluxes to daily temperature; b, shows the correlation between elevation and the responses of carbon fluxes to annual precipitation.

Table A1 Carbon fluxes responses (regression slope) to air temperature and to precipitation for all sites across temporal scales. Units are (g C m^{-2} temporal scale^{-1}(e.g. day, yr.) / ^{o}C) for temperature, and g C m^{-2} temporal scale^{-1}/ mm.

ID	Response to temperature												Response to precipitation											
	Daily			Monthly			Seasonal			Annual			Daily			Monthly			Seasonal			Annual		
	GEP	RE	NEP	GEP	RE	NEP	GEP	RE	NEP	GEP	RE	NEP	GEP	RE	NEP	GEP	RE	NEP	GEP	RE	NEP	GEP	RE	NEP
Fpe	0.03	0.05	-0.02	1.14	1.83	-0.69	3.62	5.91	-2.3	-0.195	-0.09	-0.1	0.01	0.016	-0.004	0.32	0.267	0.05	0.585	0.7	-0.12	1.147	0.436	0.71
Me2	0.22	0.2	0.02	9.52	7.56	1.96	30.94	24.39	6.54	0.44	-0.23	0.67	-0.11	-0.057	-0.05	-0.69	-0.43	-0.26	-1.62	-1.11	-0.51	-0.807	-0.81	0.005
Ton	0.027	-0.02	0.05	1.12	-1.27	2.39	3.21	-3.62	6.83	-0.64	-0.78	0.14	-0.029	0.02	-0.05	-0.05	0.15	-0.2	0.07	0.24	-0.17	0.4	0.32	0.09
Ne3	0.3	0.16	0.15	10.88	5.46	5.41	35.64	16.74	18.9	0.19	0.04	0.14	0.003	0.05	-0.05	1.04	0.7	0.34	2.21	1.31	0.91	-0.8	0.265	-1.06
WCr	0.3	0.13	0.17	10.09	4.21	5.98	32.76	12.97	19.79	-0.057	0.02	-0.08	0.03	0.03	0.003	1.17	0.47	0.7	2.26	0.84	1.41	-0.14	-0.23	0.09
Ne1	0.42	0.21	0.21	15.23	7.41	7.82	49.95	23.14	26.81	0.08	0.16	-0.07	0.2	0.11	0.09	2.64	1.13	1.5	3.16	1.37	1.79	-1.36	-0.86	-0.5
UMB	0.34	0.14	0.16	11.91	6.16	5.75	37.15	18.85	18.3	0.06	0.05	0.011	-0.004	0.05	-0.06	1.27	0.78	0.49	2.63	1.42	1.21	-0.39	-0.06	-0.33
Ro1	0.26	0.18	0.08	9.04	6.02	3.01	30.12	19.02	11.1	0.55	0.36	0.19	0.017	0.056	-0.04	1.13	0.91	0.22	2.616	1.78	0.83	4.31	1.24	3.06
Syv	0.28	0.22	0.05	9.68	7.44	2.24	30.87	23.37	7.5	-0.08	-0.02	-0.06	0.0002	0.03	-0.03	0.68	0.55	0.12	1.03	0.77	0.26	-0.14	-0.285	0.14
ARM	0.008	0.06	-0.05	0.19	1.97	-1.78	0.52	6.61	-5.68	-0.13	0.24	-0.37	-0.015	0.01	-0.02	0.29	0.2	0.08	0.49	0.36	0.12	0.24	-0.357	0.6
Bo1	0.27	0.16	0.1	10.09	5.6	4.49	35.56	18.21	17.36	-0.606	-0.04	-0.57	0.002	0.02	-0.02	0.91	0.48	0.43	2.34	1.05	1.3	0.1	0.246	-0.14
Ho2	0.28	0.21	0.06	9.47	7.16	2.32	27.7	21.58	6.12	0.09	0.21	-0.11	-0.04	0.03	-0.07	0.61	0.54	0.06	0.72	0.59	0.14	0.096	0.11	-0.01
Ho1	0.32	0.24	0.07	11.02	8.34	2.68	32.65	25.2	7.42	0.21	0.3	-0.09	-0.06	0.02	-0.08	0.66	0.547	0.11	0.93	0.73	0.2	-0.32	-0.276	-0.04
Ha1	0.38	0.15	0.22	13.36	4.97	8.38	41.76	15.11	26.65	-7E-04	-0.24	0.24	-0.03	0.005	-0.04	0.075	0.15	0.08	0.39	0.367	0.39	-0.08	0.027	-0.11
Blo	0.14	0.02	0.12	4.95	0.54	4.41	15.39	1.23	14.16	-0.18	-0.13	-0.05	-0.06	-0.001	-0.06	-0.19	-0.009	-0.18	-0.25	-0.019	-0.23	0.43	0.12	0.31
Bar	0.3	0.12	0.18	10.54	4.08	6.46	32.24	12.47	19.77	-0.19	0.1	-0.28	-0.02	0.02	-0.04	0.18	0.26	-0.08	0.84	0.6	0.24	-0.26	0.18	-0.45
KS2	0.2	0.24	-0.04	8.17	9.09	-0.92	24.31	28.66	-4.36	0.66	0.99	-0.33	-0.03	0.026	-0.06	0.14	0.26	-0.12	0.3	0.41	-0.12	0.795	1.31	-0.52
SP1	0.07	0.12	-0.05	2.98	4.39	-1.41	8.96	14.06	-5.09	0.998	1.9	-0.9	-0.03	0.03	-0.06	0.09	0.17	-0.08	0.34	0.33	0.006	0.356	0.085	0.27
SP3	0.1	0.14	-0.04	4.26	4.73	-0.47	14	15.06	-1.06	-1.96	-0.33	-1.63	-0.05	0.01	-0.07	0.1	0.18	-0.07	0.16	0.33	-0.17	-2.1	-0.72	-1.39
SP2	0.21	0.2	0.008	8.59	7.2	1.39	26.26	27.76	3.5	1.28	0.54	0.74	-0.02	0.02	-0.04	0.24	0.14	0.1	0.38	0.32	0.06	0.23	-0.24	0.47
Goo	0.24	0.226	0.02	9.26	7.87	1.38	25.48	22.71	2.76	-2.71	-0.02	-2.69	-0.02	-0.001	-0.02	-0.037	-0.08	0.046	-0.206	-0.276	0.07	0.82	0.22	0.6
Wrc	0.26	0.296	-0.04	10.06	9.85	0.22	31	31.41	-0.42	0.5	0.47	0.02	-0.07	-0.04	-0.03	-0.24	-0.18	-0.06	-0.37	-0.32	-0.06	-0.098	-0.07	-0.03
Aud*	0.04	0.08	-0.04	1.37	2.75	-1.38	5.08	7.79	-2.71	0.027	0.73	-0.71	0.046	0.02	0.02	0.56	0.25	0.31	0.526	0.636	-0.11	1.255	1.22	0.03
MMS*	0.32	0.12	0.2	11.83	4.2	7.62	35.19	12.71	22.48	0.32	0.17	0.15	-0.03	0.02	-0.05	0.71	0.31	0.4	1.19	0.51	0.68	0.16	-0.23	0.39
Moz*	0.22	0.14	0.08	8.435	4.89	3.54	24.28	14.12	10.15	-1.64	-0.82	-0.83	-0.017	0.02	-0.04	0.39	0.33	0.06	1.27	0.86	0.41	0.966	0.67	0.29
NR1*	0.2	0.127	0.07	7.61	4.83	0.79	22.53	15.13	7.4	0.61	0.6	0.01	-0.03	0.01	-0.04	0.26	0.22	0.03	0.54	0.33	0.21	-0.05	-0.05	0.001
SO4*	-6E-04	0.0065	-0.007	0.2	0.36	-0.16	0.4	1.17	-0.76	-1.69	-0.75	-0.95	-0.015	0.005	-0.02	-0.076	0.01	-0.09	-0.056	-0.04	-0.01	0.59	0.27	0.31
Var*	-0.15	-0.11	-0.03	-5.68	-4.456	-1.23	-17.77	-12.85	-4.91	0.62	0.33	0.29	0.026	0.07	-0.05	0.51	0.44	0.07	0.84	0.59	0.25	0.67	0.48	0.19
WBW*	0.24	0.13	0.24	9.92	4.67	9.92	29.05	14.4	29.05	0.25	0.08	0.25	-0.025	-0.005	-0.02	-0.03	0.04	-0.07	-0.053	0.07	-0.13	0.66	0.43	0.23
Wkg*	0.04	0.03	0.005	1.49	1.3	0.19	5.22	4.57	0.65	-0.96	-0.9	-0.06	0.02	0.05	-0.03	0.36	0.4	-0.03	0.5	0.54	-0.04	1.14	1.08	0.059

* Sites identified as having complex terrain, see methodology in main paper for further details.

Appendix B. Supplementary material for chapter IV

Table B1 Monthly meteorological variables and water budget components.

Season	Year	Month	T_a (°C)	RH (%)	R_n (W/m^2)	Rainfall (mm)	PET (mm)	AET (mm)	Runoff (mm)	Baseflow (mm)	BFI
Wet	2015	6	23.4	89.5	142.9	417.1	130.3	118.9	126.2	76.6	0.6
Wet	2015	7	23.0	88.1	158.7	276.3	144.0	131.4	77.6	56.3	0.7
Wet	2015	8	23.2	88.5	164.1	225.0	149.4	156.3	54.6	30.4	0.6
Wet	2015	9	23.4	86.1	140.9	261.4	128.5	119.3	56.6	33.3	0.6
Wet	2015	10	23.4	65.2	145.9	81.9	133.2	93.2	47.2	34.9	0.7
Dry	2015	11	22.2	53.3	114.8	4.1	102.9	78.1	12.9	11.4	0.9
Dry	2015	12	22.0	49.7	111.3	2.8	99.4	64.1	8.0	6.7	0.8
Dry	2016	1	21.1	67.2	143.1	1.7	126.1	89.0	8.3	6.4	0.8
Dry	2016	2	21.3	68.4	130.0	2.9	114.9	76.7	8.3	6.5	0.8
Dry	2016	3	23.7	67.2	146.0	41.0	133.9	83.0	12.0	8.1	0.7
Dry	2016	4	25.2	66.2	148.5	9.0	139.0	76.3	4.5	3.1	0.7
Wet	2016	5	25.2	55.3	155.8	398.6	145.7	71.2	34.9	9.7	0.3
Mean/total			23.1	70.4	141.8	1721.8	1547.3	1157.7	451.2	283.4	0.7