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The Graduate School  
College of Earth and Mineral Sciences

**CLIMATE CHANGE IMPACTS ON FORESTS:  
MODELING RELATIONSHIPS BETWEEN  
STATIC LANDSCAPE PATTERNS AND DYNAMIC VEGETATION RESPONSES**

A Dissertation in  
Geography  
by  
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## ABSTRACT

The Appalachian Mountains are home to remarkable diversity compared to other temperate climates. Paleoecological and contemporary ecological and biogeographical investigations have contributed considerably to our understanding of vegetative adaptation to climate change over geologic time and today. Some of these investigations have pointed to intrinsic characteristics of the mountains that helped plant species adapt to change over geologic time scales. In this dissertation, the geography of Appalachian forests is reviewed (Chapter 1) and the role of topography in supporting migratory adaptation is explained, qualitatively and quantitatively (Chapter 2). Geographic factors supporting dispersal, establishment, and regeneration are combined and analyzed using a network approach to identify critical habitat pathways for plant migration (Chapter 3). Forest fire regimes under historical and future climate conditions are analyzed and vegetation and carbon storage effects are evaluated (Chapter 4). The preponderance of the evidence presented here support the conclusion that, at large spatial extents, long temporal scales, and high biotic levels, Appalachian forests are relatively resilient to the scope of stressors anticipated in the coming century, although interactions between stressors can not be ruled out (Chapter 5). The predicted degree of temperature and precipitation in this region will have very noticeable effects on species composition and ecosystem processes, but this research highlights aspects of the Appalachians that support adaptation to climatic change. The complex topography provides a high diversity of microclimates that can support biodiversity through global warming and with small investments in land conservation to improve connectivity natural migratory adaptation may be successful in many places. This research predicts an increase in wildfire frequency and extent, with a consequent decrease in severity. These shifts in fire regimes have the potential to lower carbon storage and change species dominance slowly by selecting more fire-adapted species.

## TABLE OF CONTENTS

List of Tables.....	vi
List of Figures.....	vii
Acknowledgements.....	viii
Chapter 1. Appalachian Forests: Past, Present, and Future .....	1
Introduction .....	2
Study area – physical geography.....	4
Study area – biogeography .....	10
Study area – human geography .....	17
Dissertation Motivation .....	24
References .....	26
Chapter 2. Topographic complexity explains tree diversity with implications for climate adaptation.....	34
Introduction .....	35
Methods .....	38
Results .....	45
Discussion .....	47
References .....	49
Acknowledgements .....	52
Chapter 3. Dispersal vectors and site suitability influence migration networks .....	53
Abstract.....	54
Introduction .....	54
Methods.....	58
Results .....	61
Discussion .....	66
References .....	69
Chapter 4. MAPSS CENTURY DISTRIB: A hybrid model approach to understanding potential feedbacks between climate, fire, and species composition .....	73
Introduction .....	74
Methods.....	78
Results .....	83
Discussion .....	92
References .....	96
Chapter 5. Resilience in Appalachian Forests .....	100
References .....	115
Appendix A: Supplementary Figures, Methods, and Results (Chapter 2) .....	120
Appendix B: High Elevation Species Information (Chapter 3).....	142
Appendix C: Description of Circuitscape (Chapter 3) .....	143

Appendix D: MC1 command line options (Chapter 4) ..... 144

Appendix E: MC1 parameterization (Chapter 4) ..... 146

Appendix F: Program to calculate fire index from MC1 fire output variables (Chapter 4) ..... 149

Appendix G: Species scores for vulnerability to fire and regeneration after fire (Chapter 4) ..... 153

Appendix H: Program to calculate adjusted importance values for each cell based on fire index  
(Chapter 4) .....159

## LIST OF TABLES

Table 2.1: Descriptions of topographic metrics including methods, tools, relevance, and literature	40
Table 3.1: Network permeability datasets . . . . .	60
Table 3.2: Data preparation steps . . . . .	60
Table 3.3: Results for network simulations. . . . .	65
Table 4.1: Fire regime results historical and future . . . . .	85
Table 4.2: Fire regime results by test domain . . . . .	87
Table 4.3: Fire and climate effects on vegetation . . . . .	90
Table 5.1: Carbon storage by biome globally (adapted from Watson) . . . . .	103

## LIST OF FIGURES

Figure 1.1: Conceptual diagram of scale context . . . . .	3
Figure 1.2: Appalachian topography . . . . .	5
Figure 1.3: Lithotectonic map of Appalachian Orogen . . . . .	7
Figure 1.4: Ecomap provinces . . . . .	13
Figure 1.5: Ecoregions (Omernik) . . . . .	14
Figure 1.6: MC1 potential vegetation classes . . . . .	15
Figure 1.7: Forest types mapped by the USFS Tree Atlas. . . . .	16
Figure 1.8: Fire regime map . . . . .	22
Figure 1.9: Scott and Burgan Fire Behavior Fuel Models Map . . . . .	23
Figure 2.1: Map of tree species diversity . . . . .	42
Figure 2.2: Map of species richness . . . . .	43
Figure 2.3: Map of species dominance . . . . .	44
Figure 2.4: Map of terrain metrics . . . . .	46
Figure 3.1: Permeability based on wind, elevation, and forest cover . . . . .	62
Figure 3.2: Permeability based on wind speed, elevation, forest cover, and pH between 12 source and sink habitats over 1300 ft elevation . . . . .	64
Figure 3.3: Results of priority conservation areas by Anderson Clark and Sheldon (2012) . . . . .	68
Figure 4.1: Appalachian biogeography and test domain locations . . . . .	80
Figure 4.2: Fire and climate relationships between simulations . . . . .	82
Figure 4.3: Example vegetation type map and temporal dynamics . . . . .	91
Figure 4.4: Ecosystem carbon under historical and future climate . . . . .	95

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## **CHAPTER 1:**

### **Appalachian Forests: Past, Present, and Future**

## Introduction

Forests are valued worldwide for their wildlife habitat value, timber production, and increasingly for their role in the global carbon budget (Sedjo 1992; Turner et al. 1995; Goodale et al. 2002; Ryan et al. 2010). In many places, as along the Appalachian Trail, they also have recreational value (Willis & Benson 1989; Krieger 2001). Global climate change will cause a number of shifts in forests including species composition and phenology of the annual cycles (Walther et al. 2002; Parmesan & Yohe 2003; Parmesan 2007), and disturbance regimes like wildfire that affect stand age and biomass among other forest traits (Dale et al. 2001). The magnitude of change, and perhaps more importantly, the pace, may interfere with the role forests play in earth systems, interrupting the services other organisms rely upon. **This dissertation contributes to the understanding of migration and fire disturbance, both processes by which forest composition changes especially in response to climate change.**

The Appalachian Mountains provide an opportunity to study forest ecosystems along a latitudinal gradient from 35 to 46 degrees north latitude. However, this large spatial extent also presents a number of challenges that limit the kinds of research questions that can be attempted. Traditionally, ecological studies have been designed to hold key variables constant to simplify inferences about cause and effect. Variation in soil substrate, temperature and precipitation regimes, and land use history across the north-south Appalachian transect make these kinds of controlled studies nearly impossible at this continental scale (but see (Cogbill et al. 2002, Cogbill et al. 1997, S. K. Wisser 1998). Biogeographical approaches have much to offer, but “a general failure of ecological theory to deal adequately with geographical scale” continues to inhibit consensus on processes that explain spatial patterns of ecological communities at greater than landscape extents (Levin 1992; Whittaker, Willis, & Field 2001; Wiens & Donoghue 2004). Nonetheless, anthropogenic climate

change promises to provide a continental scale disturbance with complicated and cascading effects across scales (O'Brien, Sygna, & Haugen 2004).

Alongside the challenges of spatial scale, understanding dynamic responses to a nearly unprecedented rapid global climate change presents temporal challenges as well. Stommel diagrams provide scalar context for research projects and conceptual model development (Steele 1978; Urban, O'Neill, & Shugart 1987; Delcourt & Delcourt 1988; Peterson, Allen, & Holling 1998; Schneider 2001) (Fig. 1.1).

Much of what is known about biological responses to climate change over large spatial extents and geologic time scales is

drawn from the study of responses to Quaternary climate trends (Prentice, Bartlein, & Webb 1991).

These studies typically spanned large spatial and temporal scales, up to tens of degrees of latitude and thousands to a million years. The velocity of current climate change is rapid by comparison to the drivers of Quaternary climate change (Prentice et al. 1991; Loarie et al. 2009) calling for research at large spatial scales, but with responses expected over shorter time periods. Furthermore, biological scales ranging from species to biomes, are an equally important research context. Methods for defining biomes are wide-ranging and dependent upon research questions and spatial resolution and extent, thus scaling between them is complicated, at best (Williams et al. 2004). **In this**

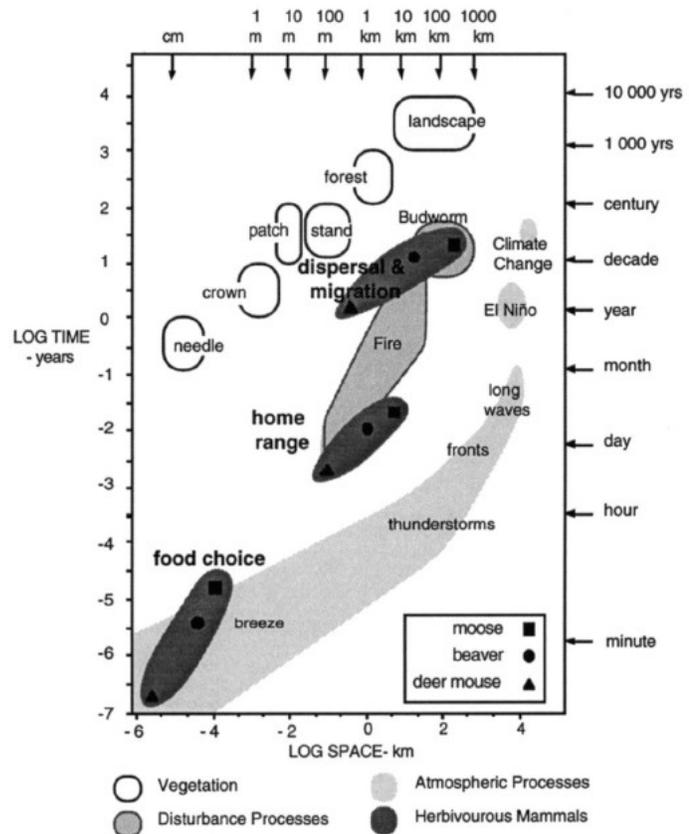


Figure 1.1. Stommel diagram to explain scale context for ecosystem processes. (Peterson et al., 1998)

**dissertation, the research questions and the methodological approaches were designed to address the spatio-temporal and trophic scales most relevant to questions of forest management during a period of rapid climate change.**

Methods and perspectives from a wide range of fields can help resolve these multi-scalar challenges (Meentemeyer 1989). Quantitative metrics for characterizing topography have been developed by geomorphologists outside the context of ecological research questions (Thompson 1941; Hurtrez, Sol, & Lucazeau, 1999; Hoechstetter et al. 2008; Lu 2008; Dinesh 2009), but these metrics, like hypsography and fractal dimension, capture patterns that may be very relevant to ecology. Graph theory (network theory) has been conceived as a useful tool for analyzing ecological relationships (spatial and hierarchical) but application has been limited (Harary 1969; Urban & Keitt 2001; McRae et al. 2008). **In this research I develop and evaluate geomorphological and network approaches to understand migratory opportunities as an adaptation response to climate change at the broad extent of the Appalachian Mountains.**

My research is rooted in literature drawn from biogeography, geology, meteorology, forestry, and ecology. The literature specific to the methods, approaches, and assumptions of each of the chapters is reviewed in the chapter introductions. Here, I focus instead on a strong description of the study area's past, present, and future, summarizing the work of others who have also chosen to study the Appalachian forests. This background information provides an important foundation for the prediction of forest response to climatic change.

### **Study area – physical geography**

The mountains of the Appalachian range stretch from Alabama through Maine in the eastern United States and continue north through the Gaspé Peninsula of Quebec in Canada to

Newfoundland – a distance of 3000 km and 15° latitude (Brooks 1965; Constantz 1993; Graham 1999) (Fig. 1.2). The mountain range has cycled through periods of orogeny and erosion.

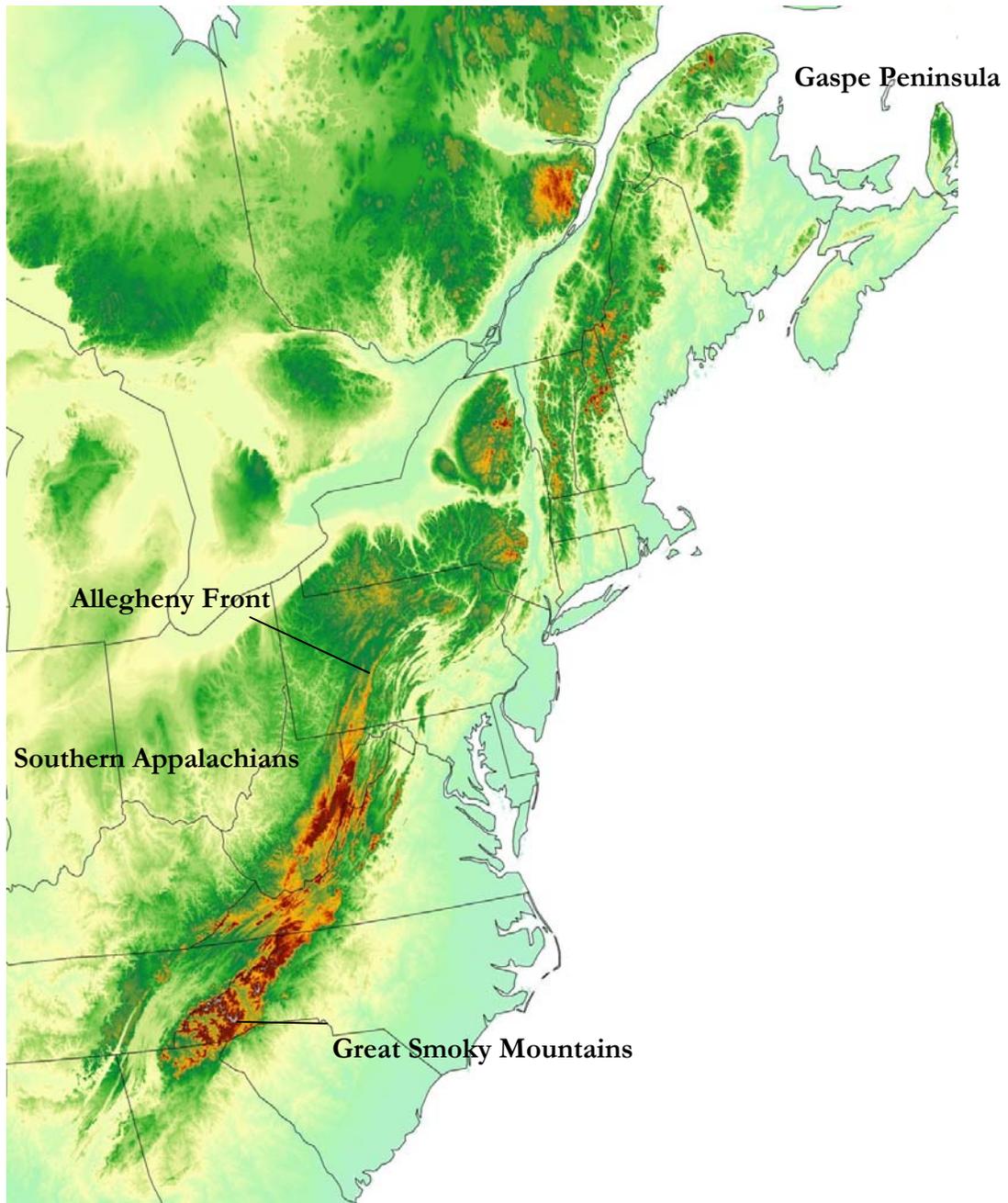


Figure 1.2. Appalachian topography. High elevations are shown in red, transitioning down to low elevations through green.

Orogeny is an important context for understanding regional climate and vegetation history. The Appalachian Mountains formed at the eastern edge of Laurentia during the Neoproterozoic and Paleozoic eras (Hibbard, Van Staal et al. 2007; Hibbard 2009). Approximately 550 million years ago (Ma) - 750 Ma rifting along the axis of the Grenville orogen opened Iapetus, a proto-Atlantic ocean, breaking up the supercontinent of Rodinia. This initial event was followed by the Taconic orogeny (490-450 Ma), the result of Laurentia's collision with a chain of islands or microcontinents in the Iapetus, that had been separated from Laurentia by the Taconic Seaway (Hibbard, Van Staal, & Rankin 2007). The Taconic orogeny took place along the entire range, from present-day Alabama to Newfoundland (Hibbard 2009). Some have speculated that a collision with South America happened at this time, while others remain unconvinced (Dalziel 2005; Hibbard et al. 2007). The Cherokee orogeny in the Southern Appalachians, occurred between 460-430 Ma and involved collisions with land masses associated with Gondwana (Hibbard, van Staal, & Rankin 2010). Just after this, the Salinic and Acadian orogenies (440-420 and 420-380 Ma) in the northern Appalachians attached Ganderia and Avalonia to the Appalachian Range (Hibbard 2009), and the new continent is called Laurasia. Around 370-350 Ma, some believe the Fammenian event attached Meguma (Nova Scotia) to the northern Appalachians and Suwanee in the deep south (Hibbard 2009). Finally, the Alleghanian orogeny from 335-260 Ma marks the collision of Gondwana with North America forming the super continent Pangaea (Hibbard 2009). Uplift of the current eroded mountain range occurred 20-30 Ma. These most recent major orogenic events are probably responsible for much of the topographic structure of the mountains we observe today, particularly the ridge and valley province.

The rock formations composing the Appalachian Mountains are native to Laurentia (the Laurentian Realm), rocks that were formed in the basin of the Iapetus ocean (Iapetus Realm), and rocks that formed in microcontinents in the vicinity of Gondwana (the peri-Gondwanan Realm)

(Hibbard, van Staal et al. 2006) (Fig. 1.3). Each of the orogenic events described above are associated with uplifting the native rocks or bringing the non-native rocks from the site of their genesis to their current locations in the Appalachian Mountain Range. The result is two provinces: the Appalachian Plateau and Valley and Ridge Provinces underlain by Paleozoic sedimentary rocks, and the Blue Ridge, Piedmont and Northern Appalachian Provinces underlain by Precambrian and Early Paleozoic metamorphic and igneous rocks.

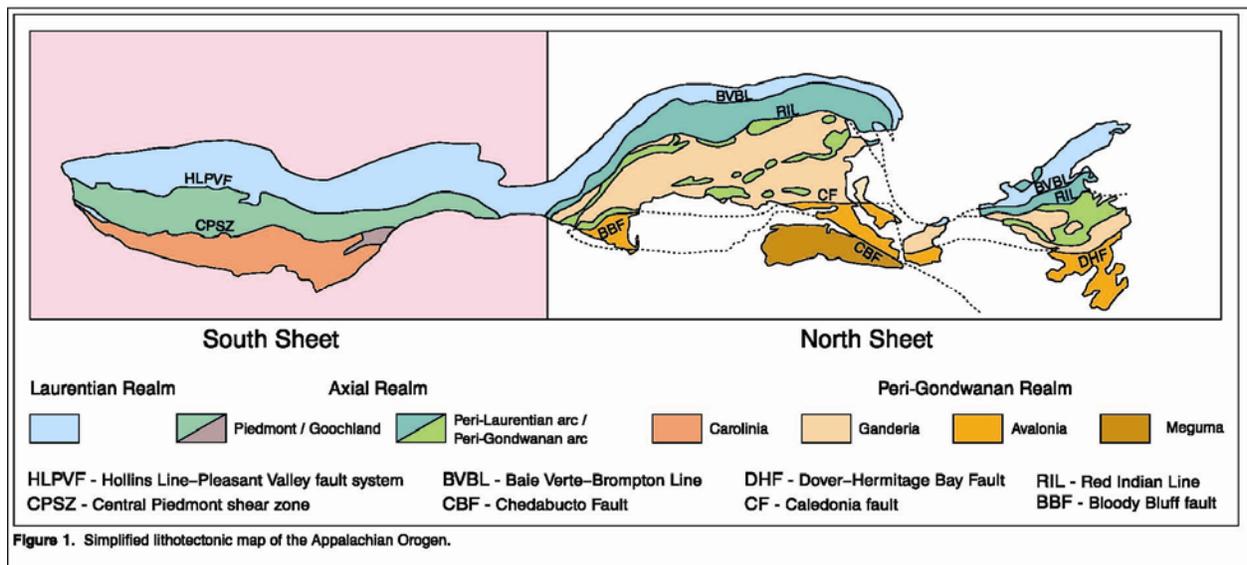


Figure 1.3. Lithotectonic map of the Appalachian Orogen. Hibbard, van Staal et al. 2006.

Soils in the Southern Appalachians and eastward on the piedmont and coastal plains are classified as Ultisols, almost exclusively Udults, which are well-drained and low in organic matter (Soil Survey Staff 1999). The soils are associated with mixed forests but have been cleared for use as cropland with soil amendment. The soils in the high elevations in the Southern Appalachians and the Allegheny Plateau are Inceptisols, primarily Udepts, which are well drained and commonly support forest vegetation but are also used for cropland or pasture. In the northern Appalachians large areas of Spodosols, mostly Orthods, support forests. These soils are well-drained but have a moderate accumulation of organic matter. The Alfisols to the west of the Appalachians also occur to

a limited extent along the ridges and in the mid-Atlantic states (Udalfs), and very small patches of Entisol are also present in the region (various suborders).

The Appalachian Mountains are nearly continuous from north to south, even though the elevations are not comparable throughout and spatial topographic patterns vary. Higher maximum elevations are found in the southern Appalachians. The highest peak, Mount Mitchell in North Carolina, reaches an elevation of 2,037 m. Base elevations are also higher in the southern Appalachians than the northern Appalachians so elevation range (relief) is comparable between the southern and northern Appalachians. The mid-Atlantic, particularly northern Pennsylvania, has the weakest relief as the base elevations are relatively high and the maximum elevations are low.

A number of authors have proposed boundaries for the Appalachians based on topography or geology. Nearly all authors agree that the southern extent falls in northern Alabama or Georgia. A very well-defined transition from piedmont hills to much steeper mountains defines the southern tip and eastern edge of the range over most of its length. The northern boundary is defined variously in the vicinity of Maine (Constantz 1993), the Gaspé Peninsula (Brooks 1965), or where Newfoundland meets the Atlantic Ocean (Weidensaul 1994; Hibbard et al. 2006). The western extent is not easily defined on the basis of topography because the adjacent land is also high elevation. However, the western edge of the range might be defined by relief because land to the west becomes much flatter and does not have “mountain flavor” (Constantz 1993).

Climate varies on a continental scale, but also on local and regional scales. In general the southern end of the range has warmer temperatures, longer growing seasons, and less precipitation. Lower elevations generally have warmer temperatures and longer growing seasons but less precipitation. The entire range is classified as Humid Temperate.

Warmer temperatures characterize the southern extent of the range as compared with the northern extent of the range and the lower elevations as compared to the higher elevations. For example, average high temperatures in Blairsville, GA, elevation 584 m, are warmer than Pinkham Notch, NH, elevation 610 m, by an average of 13 °C in the winter (November-April) and by an average of 8 °C in the summer (May – October). In general, higher elevations are colder than nearby lower elevations. High temperatures on Mt. Washington, NH, (elevation 1906 m) are colder than Pinkham Notch, NH, (elevation 610 m) by an average of 10 °C throughout the year. Within Great Smoky Mountains National Park Clingman’s Dome, TN (elevation 2025 m) is colder than Gatlinburg, TN (elevation 622 m) by an average of 11 °C.

Consistent with these temperature trends, southern regions and lower elevations have longer growing seasons and higher minimum temperatures as compared to northern regions and high elevations. Blairsville, GA has low temperatures above freezing for almost 9 months while Pinkham Notch, NH, has low temperatures above freezing for just 6 months. Southeast and south-facing slopes are warmer and drier than other aspects.<sup>1</sup> Higher elevations generally have more precipitation. For example, Clingman’s Dome, TN, (elevation 2025 m) records 208 cm of precipitation while nearby Gatlinburg, TN (elevation 622 m) records 137 cm.<sup>2</sup>

In general, the entire Appalachian range is expected to become warmer in the future, with greater changes in the northeastern U.S. than the southeastern U.S. Based on the results of 16 general circulation models presented by the Nature Conservancy through the Climate Wizard Browser, by the 2080’s under a low emission scenario (B1), temperatures are expected to increase by 1.5-2 °C, with some models predicting just 1 °C of warming and some predicting more than 3 °C of warming. Under a high emissions scenario (A2), predicted increases in temperature range from 3 °C

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<sup>1</sup> [http://www.fs.fed.us/colormap/ecoreg1\\_provinces.conf?679,220](http://www.fs.fed.us/colormap/ecoreg1_provinces.conf?679,220) accessed on November 8, 2008

<sup>2</sup> <http://www.nps.gov/grsm/planyourvisit/weather.htm#wc> accessed on November 8, 2008

warmer in the south to 4 °C warmer in the north, by the 2080s, with some models predicting as little as 1.5 °C warming in the south or as much as 5 °C warming in the north. In the low emissions scenario, in the same time frame, precipitation is expected to increase slightly throughout the region, by roughly 5%, although some models (INM-CM3.0, IPSL-CM4, and MIROC3.2 (medres)) predict up to 10% less precipitation in the south. Predictions for the high emissions scenario show the same trends, increases in precipitation of roughly 10% throughout the region although the same three models predict less precipitation in the southern U.S. by up to 25% (MIROC3.2(medres)). Warming trends in the 20<sup>th</sup> century and biological responses consistent with these trends have already been observed (Beckage et al. 2008).

### **Study area - biogeography**

Despite forest fragmentation due to human development, especially within the energy sector, forest cover remains dominant (Fry et al. 2011). The Appalachian forests have relatively high biodiversity (255 bird species, 78 mammals, 58 reptiles, and 76 amphibians) considering the temperate climate (Graham 1999; Mittermeier et al. 2003). The Great Smoky Mountains alone is home to over 30 species of salamanders and more tree species than all of Europe (Mittermeier et al. 2003). The assemblages of species in any given place are determined by the combined effects of climate, topography, soils, topographic aspect, fire, timber harvest, insect pest, and land use history, factors that vary across space and through time. The notion of equilibrium has all but been discarded and species are known to respond individually (Prentice et al. 1991; Williams et al. 2004).

An example of the interaction of these controlling variables lies in comparisons of species composition of Northern Hemisphere forests. North America, Europe, the Middle East, and the Far East have experienced similar trends in climatic conditions over geologic time, but differences in topography (in large part as a climatic control) and human land use have resulted in different

vegetative compositions and patterns (Graham 1999). In Europe, the gymnosperm, broad-leaved deciduous forest disappeared after being caught between an advancing Fennoscandian ice sheet from the north, glaciers on the east-west trending Pyrennes-Alp range to the south around the beginning of the Quaternary period (Graham 1999). What refuge populations remained were unsuccessful in reforesting the region due to agricultural expansion or later arid conditions (Graham 1999). These constraints in Europe did not apply in eastern North America or east Asia where temperate forests with *Quercus-Acer-Betula-Picea* south to north gradients persist today (White 1983).

The description of species distributions in the eastern North American deciduous forests was based initially on observed species inventories ((Braun 1950) provides a very thorough description). But palynological techniques developed throughout the 1980's revised theories of migration based on fossil pollen from sediment cores taken from lakebeds and wetlands throughout the eastern U.S. (Delcourt 1979; Davis 1983; Prentice et al. 1991) These studies revealed northward range shifts of plants as the Laurentide glacier, which extended south to 39 degrees N approximately 18-20 thousand years before present (Davis 1981), receded. This fossil pollen data suggested species had completely retreated to the southern United States (outside of the Appalachians) during glaciation (Soltis et al. 2006), and migration routes and rates in response to climatic warming were then inferred by comparing these deep southern populations with their current distributions. Northward range expansion rates based on palynological evidence are on the order of 100-400 m/year (Davis 1981). But some saw an inconsistency with known seed dispersal mechanisms (Clark et al. 1998), while others found plausible explanations for long distance dispersal events (Clark 1998). With the development of genetic tests to distinguish populations having originated from different places, an entirely new assessment of phylogeography revealed that small isolated populations survived further north than previously assumed reducing the required dispersal rates to just 50 m<sup>2</sup> yr<sup>-1</sup> (McLachlan, Clark, & Manos 2005). Dispersal rates derived from the variety of phytogeography approaches are

not fast enough to keep pace with the anticipated rapid climatic warming over the next century (Davis & Shaw 2001; McLachlan et al. 2005).

Regardless of how these species distributions came to be, a number of ecological classification schemes provide a useful way to describe unique features of ecosystems. In general, these systems incorporate climate, plant functional groups or sometimes species, and representation of form (e.g. forest, woodland, and grassland). In the US Forest Service's 2007 update of the 1994 Ecomap based on the climatic classification of the United States (Bailey 1976; McNab & Avers 1994) (Fig. 1.4), the Appalachians are hierarchically classified as Humid Temperate (domain level), spanning the Subtropical, Hot Continental, and Warm Continental climate divisions (division level), and bridging five forest types (province level) from south to north: Southeastern Mixed Forest, Central Appalachian Broadleaf Forest-Coniferous Forest, Eastern Broadleaf Forest, Northeastern Mixed Forest, and the Adirondack-New England Mixed Forest--Coniferous Forest—Alpine Meadow. At a slightly more detailed level than Ecomap's provinces, Omernik classifies Appalachian ecoregions (level 3) in 11 categories (Fig. 1.5): Piedmont, Blue Ridge, Ridge and Valley, Central Appalachians, western Allegheny Plateau, Northern Piedmont, North Central Appalachians, Northern Appalachian Plateau and Uplands, Northeastern Highlands, Eastern Great Lakes and Hudson Lowlands, Laurentian Plains and Hills (Omernik 1987). The MAPSS biogeography module follows this standard approach, first classifying a pixel on the basis of climate, then carbon in biomass (forest, savannah, or grassland) and then by plant functional group. Nearly the entire Appalachians map as temperate forest, ranging from warm mixed in the south, through deciduous broadleaf, with cool mixed to the north (Neilson 1995) (Fig. 1.6).

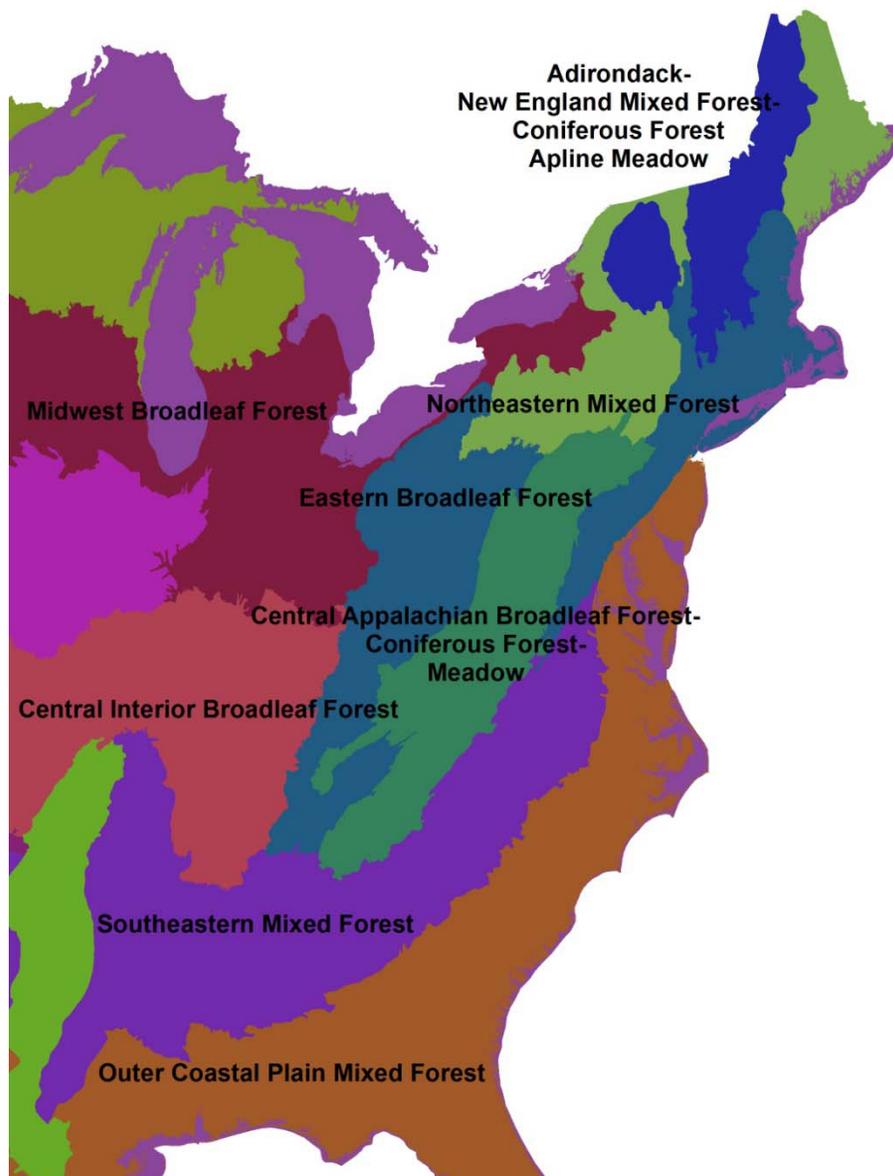


Figure 1.4. Ecomap provinces (Bailey 1976; McNab & Avers 1994)

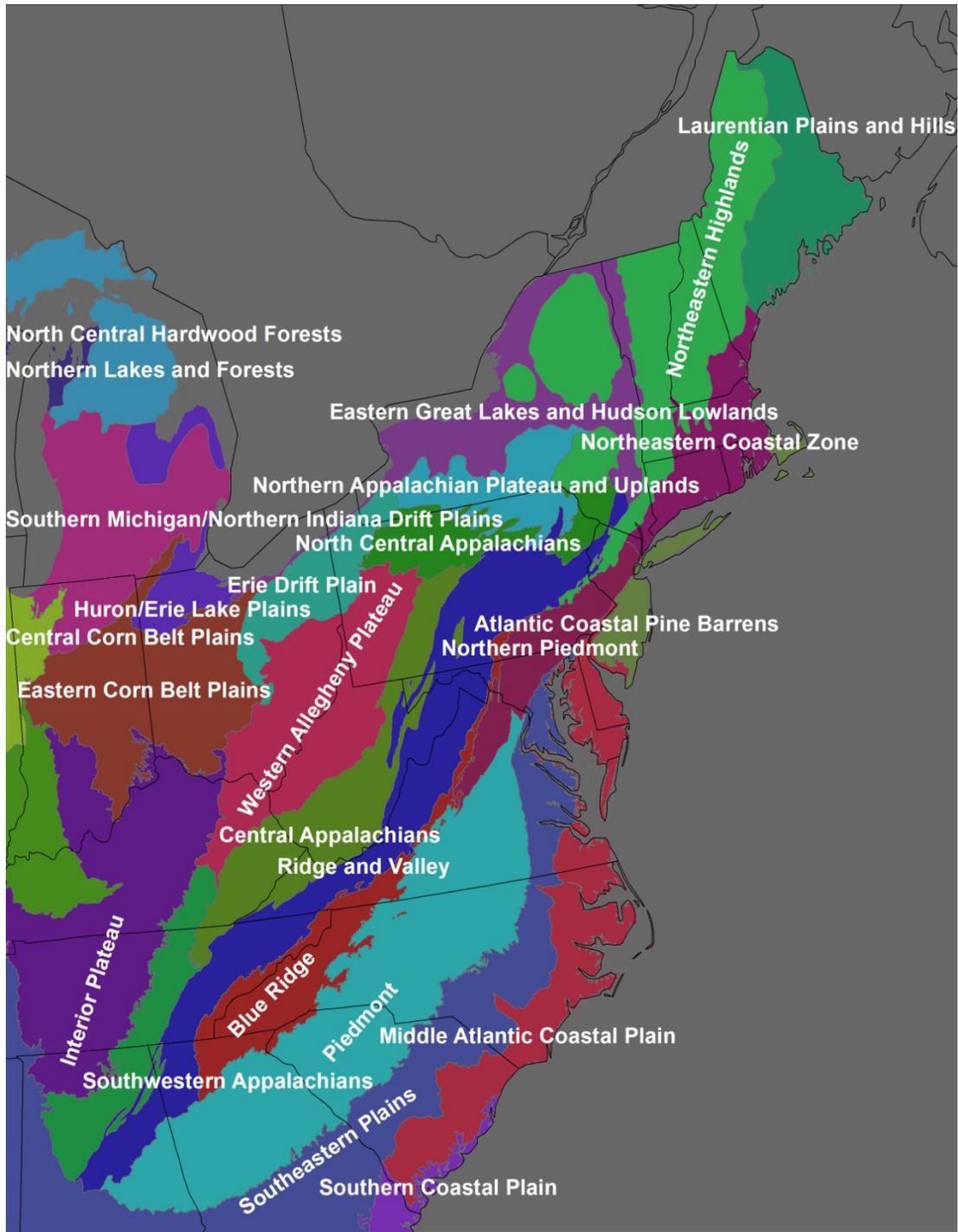


Figure 1.5. Omernik ecoregional classification (Omernik 1987)

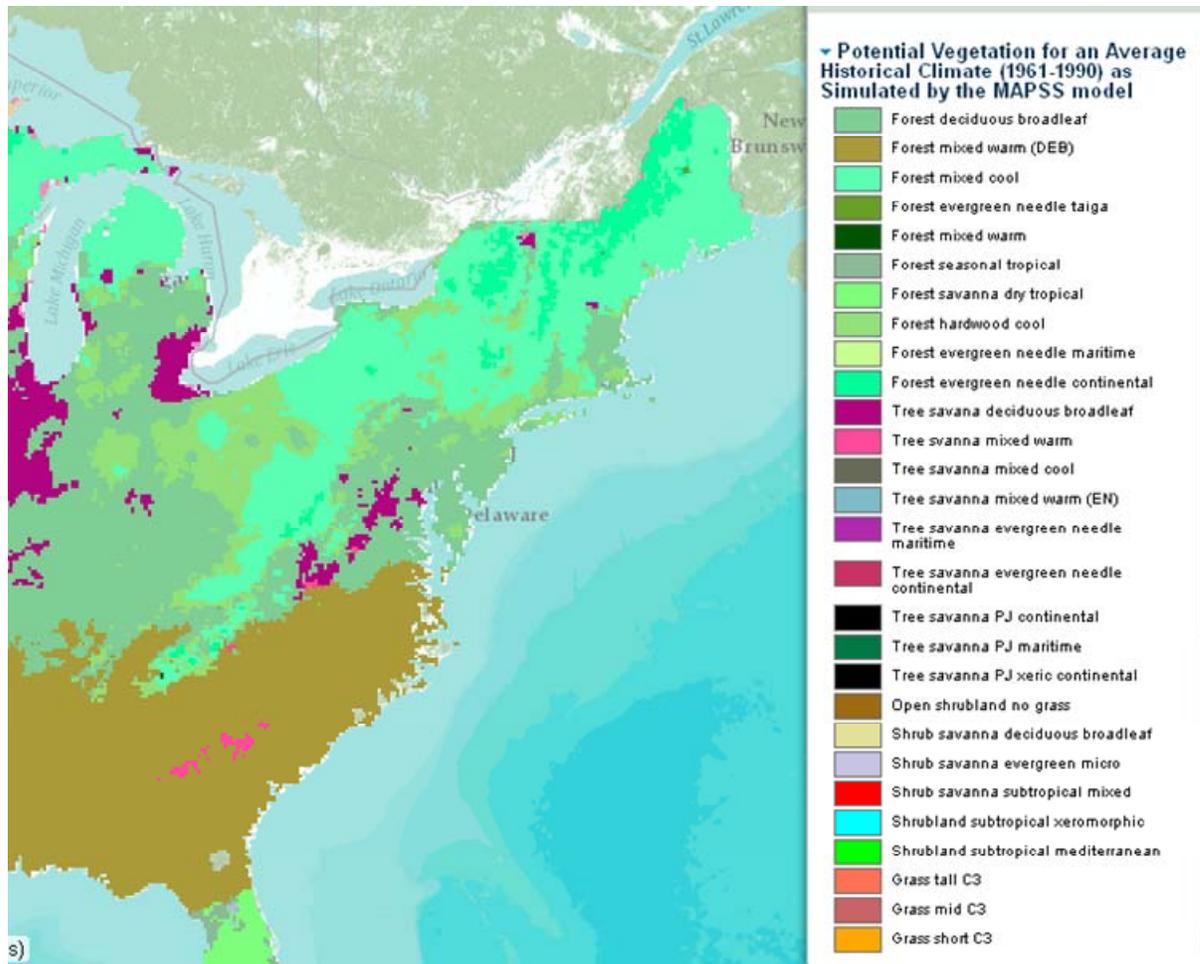


Figure 1.6. MC1 potential vegetation for a 30-year historical period (Neilson 1995).

The most complete picture of current species distributions is provided by the Forest Inventory Analysis Data, sampled by the USFS with a frequency of 5 years, in long term plots around the country (Bechtold, Patterson, & Editors 2005). These data have been mapped into seven forest types in the Appalachians (Prasad et al. 2007) based on earlier Society of American Foresters work (Eyre 1980) (Fig. 1.7). In the Southern Appalachians, “Oak-Hickory” dominates, but “Oak-Pine and Loblolly-Shortleaf Pine” extend into the mountains from the lower elevations. “Maple-Beech-Birch” is dominant in the highest elevations of the Mid-Atlantic and throughout New England, but “White-Red-Jack Pine” appears in Vermont and New Hampshire and “Spruce-Fir” becomes dominant in Maine.

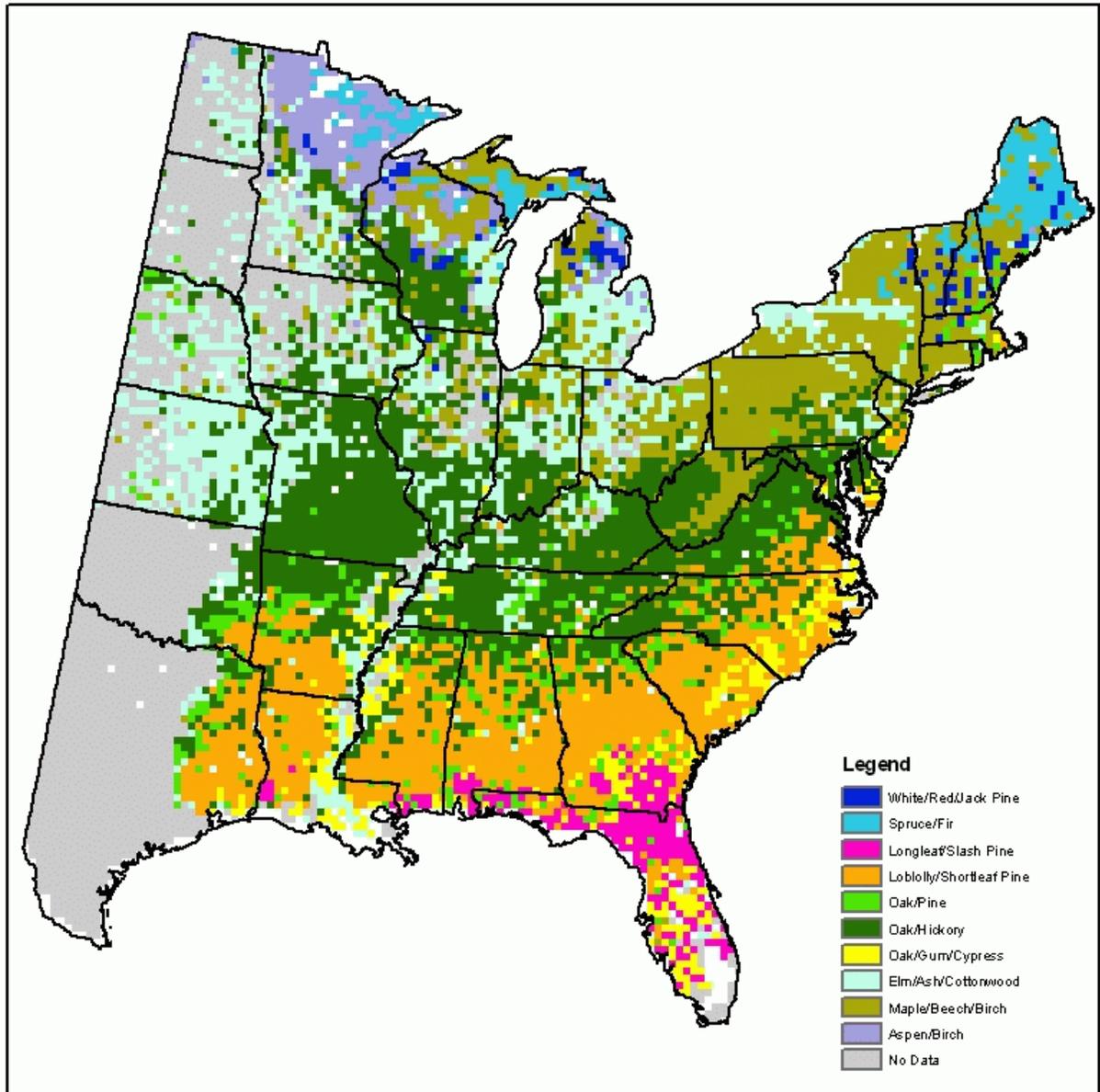


Figure 1.7. Forest types mapped by USDA Forest Service Tree Atlas.

Future distributions of tree species in the Appalachian Mountains have been predicted primarily through a variety of species distribution approaches, although some species-specific process-based models are being developed (Morin & Thuiller 2009). The niche approach extrapolates future species distributions based on current understandings of species' environmental requirements, but relies on the assumption that current distributions are in equilibrium with current climate, that

species' migration mechanisms will keep pace with changing environmental conditions, and that competition in any given place or time will not be substantially different than current competitive relationships (Morin, Augspurger, & Chuine 2007; Zurell et al. 2009; Elith, Kearney, & Phillips 2010). In contrast, the process-based approaches can include information about the species' adaptation strategies and competitive relationships in addition to their climatic requirements, if this detailed information is available.

One example of a niche-based or bioclimate envelope model is DISTRIB, a statistical approach that uses the predictive data mining tool Random Forests to train the model based on a species' preferred conditions today, and then maps those conditions in future climate scenarios to determine species assemblages in any given place (Prasad, Iverson, & Liaw 2006). The fact that species have not maintained compositional organization through changing climate in the past (Prentice et al. 1991; Williams et al. 2004) supports the niche model approach, that treats species individually, but the absence of competitive interactions or dispersal mechanisms in niche models is perhaps a significant limitation (Pearson & Dawson 2003). Range shifts predicted by DISTRIB for the forest types above include strong advancement of the oak-hickory forest type northward into New England replacing maple-beech-birch, and an expansion of oak-pine in the southern Appalachians (McKenney-Easterling et al. 2000; Iverson et al. 2008).

### **Study area – human geography**

The human geography of the Appalachians as it relates to its natural environment is a complex study in and of itself (Smethurst 2000; Nesbitt & Weiner 2001), but two human activities have had direct effects on Appalachian forests. While large scale biogeographical shifts may be largely driven by earth system processes, human land use (including timber production) and fire management (both setting and suppressing fires) have influenced forest structure and composition.

Logging was an extremely significant disturbance in many parts of the Appalachian forests, particularly during the 1800's and early 1900's. During the peak of timber harvest and land-clearing for agriculture in the mid 1800's, more than 80% of the landscape was open in central New England (Foster 1992). During the latter half of the 19<sup>th</sup> century, agricultural lands were abandoned and the process of natural reforestation saw species-specific recruitment advantages in former agricultural fields, logged forests, and standing forests. In part because of the longevity of trees, these successional dynamics closely tied to human land use patterns have long-term imprints on forest species composition and other characteristics (Christensen 1989). Historical geography is as important as paleoecology in the clues provided for understanding forest dynamics (Foster 2002).

While much is known about logging and other human influences on forests, fire regimes have been more difficult to reconstruct because fire scars in tree rings provide the only record of annually-resolved fire-history and they are only available back to the 17<sup>th</sup> century (Clark 1997b; McEwan, Dyer, & Pederson 2011). Charcoal in sediment cores, which are more widely available, is representative of large areas, not individual burns, so it has been difficult to discern causal relationships between fire frequency or severity and species abundance (Clark et al. 1997). Nonetheless, much is known about historical ignition sources, seasonality, and climatic variability, and associations with species have been vigorously debated.

The role of fire in pre-European and post-European settlement has been considerably explored and debated (Abrams 1992; Foster et al. 2002; Abrams 2003) with discussions focused at understanding the anthropogenic and climatic drivers of vegetative changes and subsequent consequences for fire regimes. Most studies have shown that historical and present-day fire regimes in the Appalachians are strongly influenced by humans through accidental and intentional ignition and fire suppression as opposed to natural ignition sources. Evidence of prescribed fire by Native Americans has been reported (Cronon 1983; Denevan 1992; Delcourt & Delcourt 1997; Brose et al.

2001) but others have downplayed these fires as being merely accidental (Russell 1981). Euro-American settlers continued to introduce an ignition source during land conversion and logging practices in the 1800's often involved fire to reduce slash residue and these fires often spread (Foster 1988). About 1930 the dominant human influence on fire became suppression (Nowacki & Abrams 2008).

The historical frequency of the human-set fires is difficult to determine, for reasons mentioned above, but a strong correlation with climatic conditions hints that fire frequency may have been governed by climate trends at long time scales (Neil Pederson, pers. comm.). Based on lake charcoal records in New England, fire frequency appears to have been strongly controlled by climate over the past 3500 years (Foster et al. 2002) resulting in variation in fire-dependent vegetation, e.g. pitch-pine or white pine in areas where climate was conducive for fire, and northern hardwood species where conditions were less suitable (Parshall & Foster 2002).

Fires are strongly seasonal, burning in the early spring before leaf-out when dry winter air has caused low fuel moisture or in the fall when deciduous leaves drop, increasing fuel loads and allowing sunlight to reach the forest floor, further drying fuels (Lafon, Hoss, & Grissino-Mayer 2005). Fire severity is typically limited to consumption of litter and fine fuels, resulting in seedling and sapling mortality but mature trees are rarely killed and canopy fires are limited to xeric ridges with forests that provide ladder fuels. The topographic complexity of the Appalachian Mountains introduces a finer scale spatial imprint on fire frequency and severity, however, as shallow soil depths, south-facing solar aspects, and wind exposure can lower fuel moisture levels and consequently increase fire risk.

While fire regimes in the eastern United States are less frequent and severe than other parts of the country (Finney et al. 2010) (due to higher average annual precipitation and higher

decomposition rates of fuel), fire has nonetheless been an important factor in determining the tree species composition of forests. It has been suggested that the higher fire frequencies of historical anthropogenic fire ignitions have been associated with the dominance of oak historically and that subsequent fire suppression has resulted in current observations of mesophication (Abrams 1992, 1998; Delcourt 1998; Brose et al. 2001; Abrams 2003). However, others have noted that climate has also played an important role in governing fire and species composition (Foster et al. 2002; McEwan et al. 2011) particularly temporal variability in precipitation (as opposed to total annual precipitation) (Lafon & Quiring 2012). Alternative explanations for the oak-maple transition, including forest clearing and successional dynamic responses, species composition shifts after American chestnut (*Castanea dentata*) decline, and herbivory and frugivory pressures on oak seedlings and acorns are also plausible (McEwan et al. 2011).

Despite the paucity of evidence over long time periods and large areas fuel models have associated the eastern U.S. with low to moderate spread rates and low flame lengths yielding low severity fires with very low risk of crown fire (Scott & Burgan 2005). Fire regimes vary across the mountain range. The northern Appalachians are estimated to have very long fire return intervals, on the order of 200 years, while southern Appalachian forests have shorter fire return intervals, perhaps 35 years (Rollins & Frame 2006) and in some places as short as 10 years (Shumway, Abrams, & Ruffner 2001). Fire suppression has not increased fire risk in the eastern U.S. as much as it has in the western U.S., but shrubby species like rhododendron (*Kalmia latifolia* L.) and mountain laurel (*Rhododendron maximum* L.) have increased in abundance as a result of canopy and fire disturbances and may support higher fire severity in the future as a result (Nowacki & Abrams 2008). Additionally, some tree species (like pitch pine *Pinus rigida* Mill. and table mountain pine *Pinus pungens* Lam.) are strongly associated with higher fire severity (Waldrop & Brose 1999; Brose & Waldrop 2006).

Overall a strong association of fire in oak and chestnut forests of New England and central Pennsylvania has been supported (Fuller et al. 1998; Foster et al. 2002; Abrams 2003). Maps of fire return intervals are consistent with these estimates (Fig. 1.8). The northern Appalachians are mapped in Fire Regime Groups V and III, corresponding to fire return intervals greater than 200 years and between 35 and 200 years respectively with moderate severity. Within an approximate 250-year window, 10 fires were detected in a 2000 ha area in southwestern New Hampshire with almost no spatial overlap pointing to long fire return intervals of at least 100 years and for the most part exceeding 250 years (Foster 1988). In the southern Appalachians Fire Regime Groups III and I have shorter return intervals, on the order of 35 years with low to moderate severity (Rollins & Frame 2006). Others have estimated more frequent fires (on the order of 10 year return intervals) in central Appalachians (Shumway et al. 2001). Fuel models in the Appalachians are mapped primarily as TL6 (moderate load, less compact, with moderate spread rate and low flame length) and TL2 (low load, compact, with very low spread rate and very low flame length), with other fuel models with similar fire behavior characteristics (Scott & Burgan 2005) (Fig. 1.9). Fires associated with these fuels can influence species composition by favoring species that can survive low-intensity fire in the sapling stage. Unlike logging, these fires are less likely to introduce successional opportunities by creating large clearings.

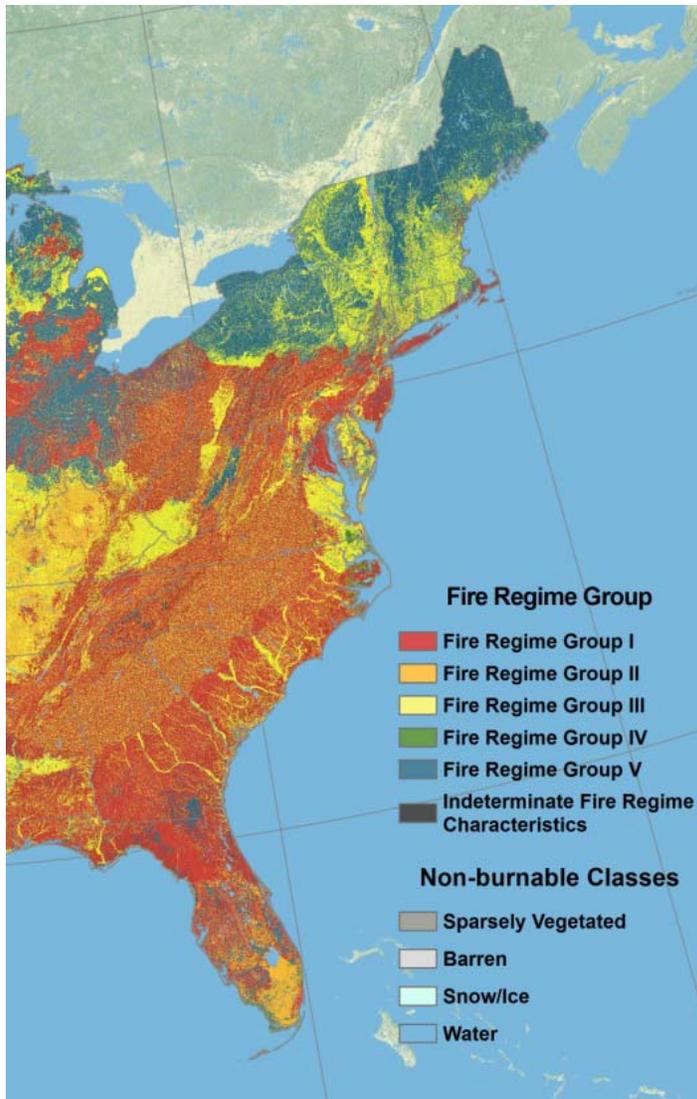


Figure 1.8. Fire Regime Groups mapped for the conterminous U.S. specifying expected fire return intervals and fire severity.

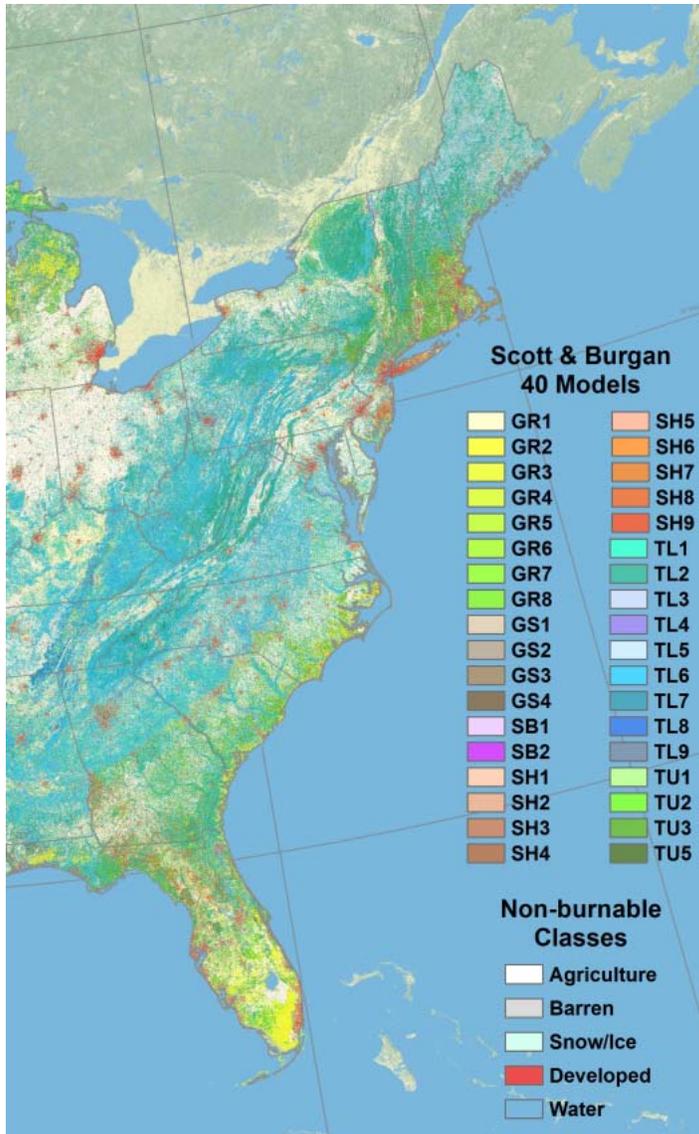


Figure 1.9. Scott and Burgan fuel models mapped for the conterminous U.S. (Scott & Burgan 2005)

## **Dissertation Motivation**

I am interested in the influence of terrain on species' distributions in the context of global climate change because of its potential to provide microclimate refugia. Much work on diversity gradients across latitudes and elevations has been done over the last two centuries, but most has taken a static view toward the relationship. I am interested in the role of terrain as species' distributions *change*. This perspective is motivated by the anticipated rapid climate change and paleoecological studies in the eastern US that have resulted in conflicting hypotheses of species range shifts since the last glacial maximum. A study of chloroplast DNA in red maple (*Acer rubrum*) and American beech (*Fagus grandifolia*) (McLachlan et al. 2005) found that these two species could not have migrated as fast as previously estimated and could not have originated in the deep south as deduced from fossil pollen records (e.g. (Davis 1983; Delcourt, Delcourt, & Webb 1983). McLachlan et al. (2005) suggests that Appalachian terrain might have provided refugia much further north than previously assumed possible for small populations that became the source populations for post-glacial northward migration. Other researchers have also found evidence for climate refugia in the Appalachians (Delcourt & Delcourt 1998; Williams et al. 2004; McKenney et al. 2007). This suggestion, combined with the very different trajectories of migration resulting from the two research approaches, in part led to current research questions that make up Chapters 2 and 3 of this dissertation.

**Does topographic complexity correlate with biodiversity patterns in the Appalachians?**

**Can graph theory (network theory), applied to geospatial variables affecting plant migration, reveal routes of least resistance for northward migration in response to climate change?**

These questions are focused on the role of terrain in supporting species persistence and in influencing seed dispersal mechanisms. But changes in forest composition in the Appalachians will not be dictated by dispersal processes alone, but also by disturbances that effect regeneration, like fire.

**In what ways will fire regimes be different under future climate scenarios?**

**How do forest types respond to changes in fire regimes and/or climate?**

**Are there implications for the role of Appalachian forests in global carbon cycling?**

These research questions also address important land management questions in the Appalachian region. For example, three of five risks and vulnerabilities identified by the Natural Resources Working Group in the Pennsylvania Climate Adaptation Working Group include shifts in species composition, interaction of stresses and disturbances, and barriers to connectivity (*Pennsylvania Climate Change Action Plan 2009*). Literature reviews here and in following chapters reveal considerable knowledge about current conditions including tree species distributions and composition, land cover and other barriers to connectivity, and predictions of change that are well informed by past and present biogeophysical relationships. Nonetheless, improved forecasts of biological response to climate change can significantly improve probabilities of successful natural resource management during a period of rapid climatic change.

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## **CHAPTER 2:**

**Topographic complexity explains tree diversity**

**with implications for climate adaptation**

## Introduction

As climate changes, plant species' survival has historically been contingent upon genetic and/or migratory adaptation (Davis & Shaw 2001; Walther et al. 2002). Topography is important in determining species' distributions and migratory responses to climate change because, over a wide range of spatial scales, climate gradients are generated by elevation, slope, aspect, and surface shape (Loarie et al. 2009). More specifically, topographic heterogeneity is linked to species richness (Rahbek & Graves 2001; Kreft & Jetz 2007) through microclimate diversity (Rahbek & Graves 2001; Loarie et al. 2009; Anderson & Ferree 2010). However, few studies have investigated the linkage between terrain complexity and species richness at regional or continental scales (but see (Rahbek & Graves 2001; Coblenz & Riitters 2004; Anderson & Ferree 2010)) – and none have attempted to map the adaptive capacity of landscapes based on topography. We analyzed topographic metrics in the Appalachian Mountains (eastern U.S.) and found that measures of topographic roughness correlated with tree species diversity. Furthermore, places known for biological rarity or endemism were associated with terrain that minimizes habitat area loss corresponding to increasing elevation. These metrics combined with the increasing availability of topographic datasets present a potentially powerful and accessible tool for conservation planning worldwide. The metrics developed and applied in this study can be used to identify places where the physical setting is inherently supportive of migratory adaptation especially considering projected climatic shifts. Understanding how biodiversity is generated and sustained is increasingly critical to inform conservation strategies that strive to meet global biodiversity targets (2010 Biodiversity Indicators Partnership 2010) and optimize landscape connectivity (Loss, Terwilliger, & Peterson 2011), such as assisted migration (Loss et al. 2011) and site prioritization (Brooks et al. 2006; Anderson & Ferree 2010).

Extending from Georgia to Maine (U.S.), the Appalachian Mountains provide latitudinal and elevational gradients along which to investigate the relationship between topography and biodiversity. We calculated the following measures of topographic pattern that may be uniquely related to species migration as a climate adaptation: 1) roughness metrics that indicate microclimate and habitat diversity and the potential to provide refugia under changing climate conditions, 2) area loss with elevation as a consequence of mountain shape (also known as hypsography) that constrains upslope migration in response to climate warming, and 3) distance between mountains to indicate the degree to which topography may impede northward migration for species with limited dispersal distances. Each metric was compared to a tree species diversity index based on the Forest Inventory and Analysis dataset (Iverson et al. 2008). We found that measures of topographic roughness were correlated with tree species diversity in the Appalachian Mountains, while area loss with elevation and mountain-to-mountain distance were not correlated.

Linkages between topography and species distributions have long been hypothesized. Early biogeographers noted that mountainous topography was associated with higher species richness (Willdenow 1811). This relationship between topography and biodiversity may be explained by the fact that topography is a strong determinant of a number of important physical habitat features, including weather patterns (windward versus leeward sites, decreasing temperature with elevation, precipitation), solar insolation, soil depth and type, and hydrology. Consequently, complex topographies provide a high density and diversity of climate and soil conditions as a result of the close proximities of land surfaces with differing aspect, exposure, altitude, and slope (Peterson, Schreiner, & Buckingham 1997; Anderson & Ferree 2010). Over geologic time, areas with complex topographies may allow more species to survive by providing microclimate refugia (Willis & Bhagwat 2009; Dobrowski 2011) into which species can disperse to find suitable conditions under changing climate (Guisan & Zimmermann 2000). The complex topographies of the deeply incised

valleys and dense drainage patterns of the weathered Appalachian Mountains may provide evidence of this topographic role. Chloroplast DNA evidence suggests that mountains provided refugia for tree species during glacial periods facilitating post-glacial northward migration (McLachlan, Clark, & Manos 2005).

Under climate change, the altitude-for-latitude temperature model ( $1^{\circ}\text{C}/167\text{ m}$  altitude compared to  $1^{\circ}\text{C}/145\text{ km}$  latitude) and the climatic sensitivity of vegetation along altitudinal gradients make upslope migration an important early indicator of migratory response to warming (Jump, Mátyás, & Peñuelas 2009) as species find suitable temperature regimes at higher and higher elevations. However, habitable area decreases with elevation resulting in increased competition for resources and consequently smaller populations – with the potential for extirpation or extinction (Peters & Darling 1985; Lomolino 2001; Peterson 2003). The weaker latitudinal temperature gradients require long-distance migrations (Loarie et al. 2009), but northward migration may be facilitated by linear landscape features or fine-scale terrain patterns with short distances between mountains. The southwest-northeast orientation of the Appalachian Mountains may also have facilitated migration over geologic time unlike east-west mountain ranges like the Swiss Alps (Hewitt 2000).

Because topography can be seen as an integrator of important habitat determinants and digital elevation models are available in North America (Bolstad, Swank, & Vose 1998), and increasingly globally (e.g. ASTER GDEM(METI-NASA 2009)), topographic metrics may provide a convenient indicator of biodiversity and ecological adaptation to climate change, contributing to conservation management worldwide. Previous studies of topographic metrics have focused on mean elevation, elevation range (relief), slope, aspect, or solar insolation (Bolstad et al. 1998; Odom & McNab 2000; Rahbek & Graves 2001; Hofer et al. 2008) and some have extended the analysis to include topographic complexity or roughness (Coblentz & Riitters 2004). Another approach has been to use

species-area relationships to explore whether or not species richness declines with elevation, finding instead that maximum species richness is likely at an intermediate elevation and that species density (after accounting for losses of habitat area with elevation) may be nearly constant across an elevational transect (Lomolino 2001). Connectedness of topographic features has also been investigated but associations with species richness are mixed (White & Miller 1988; Coblenz & Rütters 2004).

## **Methods**

We evaluated 24 topographic metrics that we considered to be related to climate change adaptation (Table 1) and explored correlations with measures of biodiversity (Shannon Index, richness, and dominance). These topographic metrics were calculated for 662 50 km x 50 km (250,000 ha) samples of elevation from the National Elevation Dataset, enveloping the Appalachian Mountains. The sample points were selected from a grid with 25 km spacing between central nodes (Appendix Fig. A.2). The 250,000 hectare extent was chosen to include more than one mountain in almost every topographic sample. Metrics describing topographic roughness, area loss with elevation, and nearest neighbor distances were calculated using ArcMap 10.0, FRAGSTATS 3.3 (McGarigal et al. 2002), R, and Python (see Appendix A). Sensitivity analyses were performed to test the effect of NED resolution, sample location (Appendix Fig. A.3) (see Appendix A), and elevation sample spatial extent (Appendix Fig. A.4). In general, these sensitivity analyses demonstrate that the results reported here are robust – variability of terrain metrics associated with sample size, location, and resolution is small compared to the variability among regions (see Appendix A).

Datasets representing biodiversity over large geographic areas, such as the Appalachian Mountains, are difficult to generate and present a challenge for correlating physical and biological characteristics (Rahbek & Graves 2001). Here we used the Forest Inventory Analysis Dataset (FIA),

which provided a consistent sampling methodology over the entire study area (Iverson et al. 2008). The Shannon Diversity Index was calculated as the sum of  $(IV * \ln(IV))$  for all species present in a plot, where IV is the importance value of the species based on basal area and number of stems (Fig. 2.1). Species richness (total number of species) (Fig. 2.2) and species dominance (maximum importance value) (Fig. 2.3) were also considered as alternate measures of biodiversity. Spearman's rho was used to measure correlation between topographic metrics and tree species diversity measures (Appendix Fig. A.7a-c).

Table 2.1. Descriptions of topographic metrics including methods, tools, relevance, and literature.

<b>Metric</b>	<b>Definition</b>	<b>Tools<sup>1</sup></b>	<b>Ecological Relevance</b>	<b>References</b>
<b>Elevation Range</b>	Maximum Elevation – Minimum Elevation within a sample area	ArcGIS 10.0, Raster Statistics	A greater elevation range (sometimes called relief) provides a wider range of climate spaces for temperature and precipitation.	(Lu 2008, Pérez et al. 2008)
<b>Standard Deviation of Elevation</b>	Standard deviation of elevations within a sample area	ArcGIS 10.0, Raster Statistics	Similar to Elevation range, but indicating the degree of variability across the sample area	(Coblentz and Riitters 2004, Hoehstetter et al. 2008, Hofer et al. 2008, Lu 2008)
<b>Rugosity</b>	3-dimensional surface area / 2-dimensional surface area	ArcGIS 10.0, 3D Analyst, Surface Volume Tool	Higher values are found in areas with greater altitudinal variation and gentler slopes, which may provide a wider range of climate spaces.	(Lu 2008)
<b>Density of Topographic Contours</b>		FRAGSTATS 3.3, (Area/Density/Edge Metrics), Patch Density	This metric provides an indication of slope and elevation range. Higher densities represent areas with a higher diversity of climate niches.	(Dinesh 2009, Lu 2008)
<b>Fractal Dimension</b>	$2 * \ln(0.25 * \text{Patch Perimeter}) / \ln(\text{Patch Area})$	FRAGSTATS 3.3 (Shape Metrics), Fractal Dimension Index	Fractal dimension has been evaluated for topography (Gilbert 1989, Mark and Aronson 1984) but not using contour lines which should provide an integrated index of aspect variability (Coblentz and Riitters 2004, Pérez et al. 2008) and landform variability (coves and noses) (Odom and McNab 2000). These topographic characteristics govern sun and wind exposure, and effect hydrology and soil depth, so the variability therein should represent the density of diverse habitats.	(O'Neill et al. 1988)
<b>Perimeter to</b>	Patch Perimeter (m) /	FRAGSTATS 3.3 (Shape Metrics),	Ecological relevance is similar to fractal	(Dinesh 2009)

<b>Area Ratio</b>	Patch Area (m <sup>2</sup> )	Perimeter to Area Ratio	dimension	
<b>Shape</b>	Patch perimeter / minimum possible patch perimeter for the same area	FRAGSTATS 3.3 (Shape Metrics), Shape Index	Ecological relevance is similar to fractal dimension	(Dinesh 2009)
<b>Nearest Neighbor</b>	Distance between patches of the same elevation	FRAGSTATS 3.3, (Isolation/Proximity Metrics), Euclidean Nearest Neighbor Distance	If species are adapted to a temperature at a given elevation, northward migration may require wind-dispersed seed to cross valleys to sites at the same elevation (Ware 1999). Rare long distance seed dispersal events on the order of 100-300 m may result from uplifting wind conditions (R. Nathan et al. 2002), but more common maximum distances are approximately 50 m (R Nathan and Muller-Landau 2000).	(Hochstetter et al. 2008)
<b>Hypsography<sup>3</sup></b>	Rate of change of 3-dimensional surface area with increasing elevation	ArcGIS 10.0, 3D Analyst, Surface Volume Tool	Habitat area contracts at higher and higher elevations (R. L. Peters and Darling 1985). Species migrating upslope may experience greater competition for resources.	(Hurtrez, et al. 1999, Ohmori 1993, Strahler 1952, H. D. Thompson 1941)

1. ArcGIS 10.0 produced by ESRI. FRAGSTATS 3.3 produced by Kevin McGarigal and others (McGarigal et al. 2002). Additional tools and processes were written in Python (2.6 and 2.7) using arcpy and rpy with R (R Development Core Team 2011).

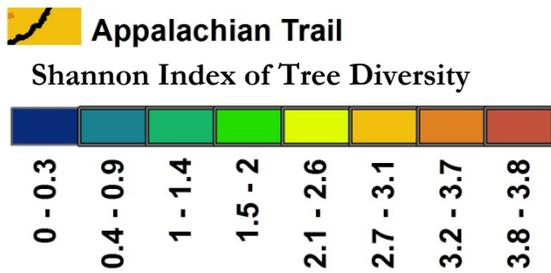
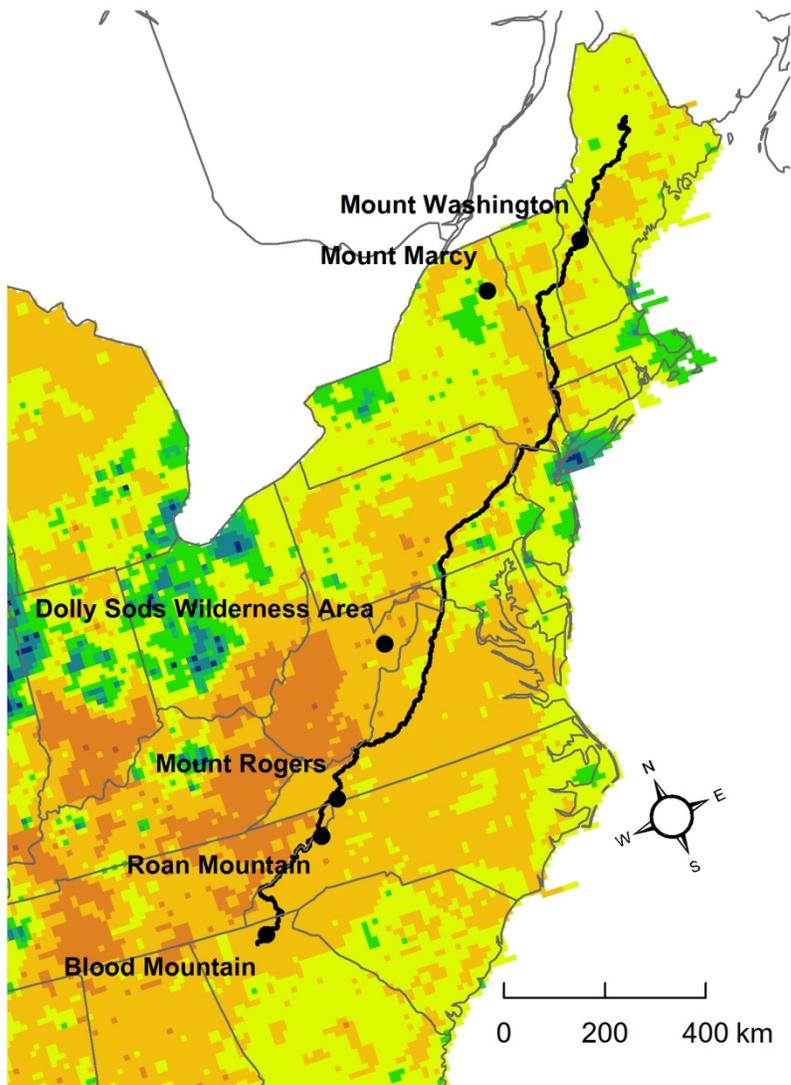


Figure 2.1. Map of tree species diversity. This map of the Shannon Diversity Index is based on Forest Inventory Analysis Data courtesy of Louis Iverson et al. (Iverson et al. 2008).

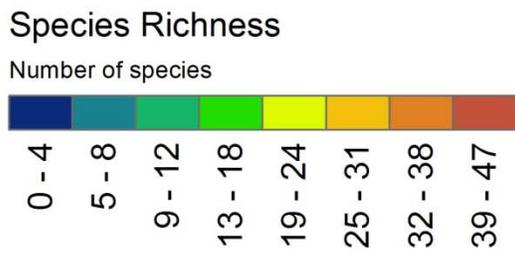
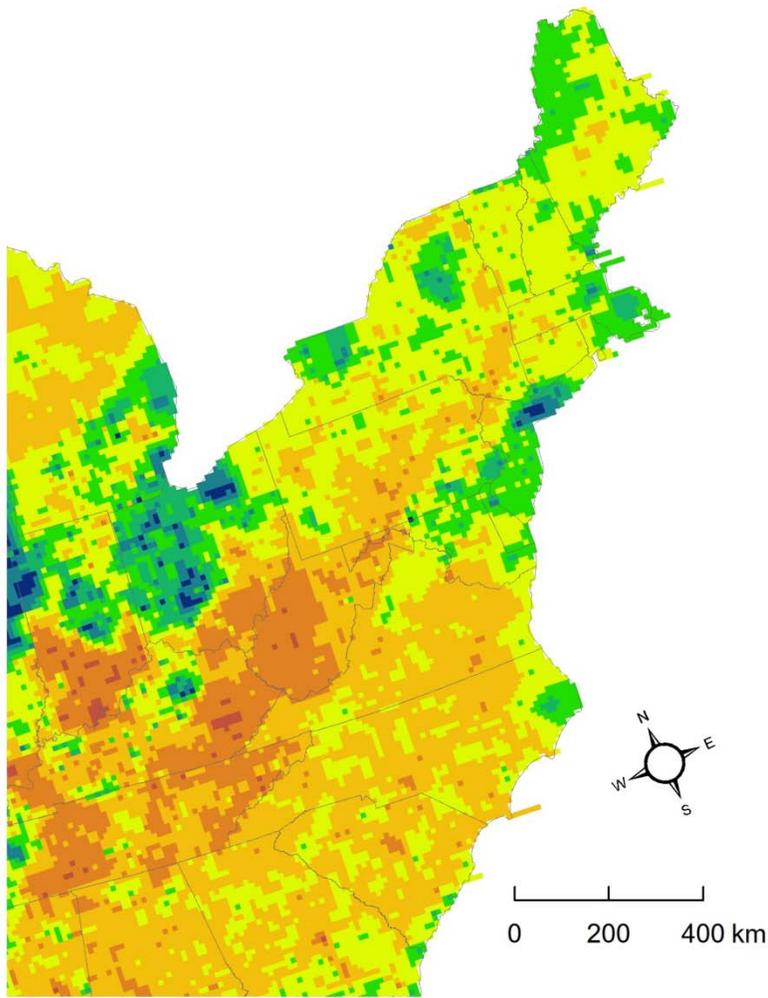


Figure 2.2. Map of species richness based on Forest Inventory Analysis Data courtesy of Louis Iverson et al. (Iverson et al. 2008).

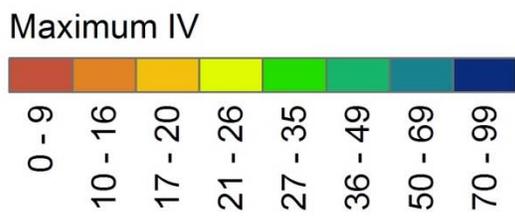
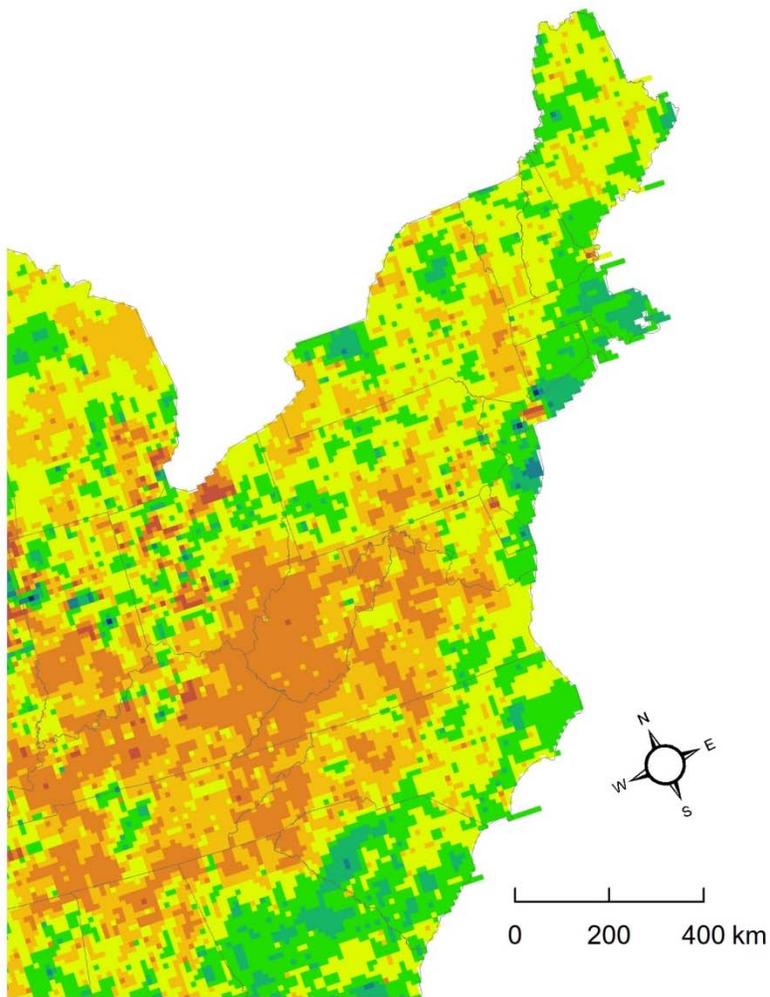


Figure 2.3. Map of species dominance (maximum IV) based on Forest Inventory Analysis Data courtesy of Louis Iverson et al. (Iverson et al. 2008).

## Results

Topographic roughness was correlated positively with tree species biodiversity. The density of contour lines defining topographic elevation gradients (indicative of average slope) showed the strongest correlation with tree species diversity (Fig. 2.4a) (Spearman's  $\rho$  0.69,  $p < 0.0001$ ; Appendix Fig. A.7a). Within the study area, the roughest terrain was found in western West Virginia and the Tennessee-North Carolina border (including Great Smoky Mountains National Park) (Fig. 2.4a) where Shannon diversity indices and species richness were high (in the top 10% and 20% respectively) (Fig. 2.1 and 2.2), and species dominance was low (in the bottom 33%) (Fig. 2.3). The smoothest terrain was found in the mid-Atlantic and northeastern regions, as well as at the eastern edges of the study area where the mountains transition to foothills. These areas had higher individual species dominance, lower species counts, and lower Shannon diversity indices.

Change in area with elevation was not correlated with tree species diversity (Spearman's  $\rho$  -0.128,  $p < 0.0005$ ; Appendix Fig. A.7a) across the study area. However, it may still be a useful topographic metric for identifying biologically important places. Roan Mountain, Tennessee, Great Smoky Mountains National Park on the North Carolina/Tennessee border, Mount Rogers, Virginia, and the White Mountains, Vermont, are known for their high biodiversity, rarity, or endemism and are located in places with low losses of area with increasing elevation (Fig. 2.1 and Fig. 2.4b). Loss of habitat area with increasing elevation is related to elevation range (or relief), but not linearly (Appendix Fig. A.8). Distances between mountain features are closest in the southern Appalachians where mountains have smaller extents than in the northern Appalachians (Fig. 2.4c), but across the entire Appalachian region, nearest neighbor distances between mountains were not correlated with tree species richness (Spearman's  $\rho$  -0.28,  $p < 0.0001$ ; Appendix Fig. A.7a). We expected that mountains that were close together would facilitate intermountain migration through wind-dispersal and thus increase biodiversity, but our results do not support this.

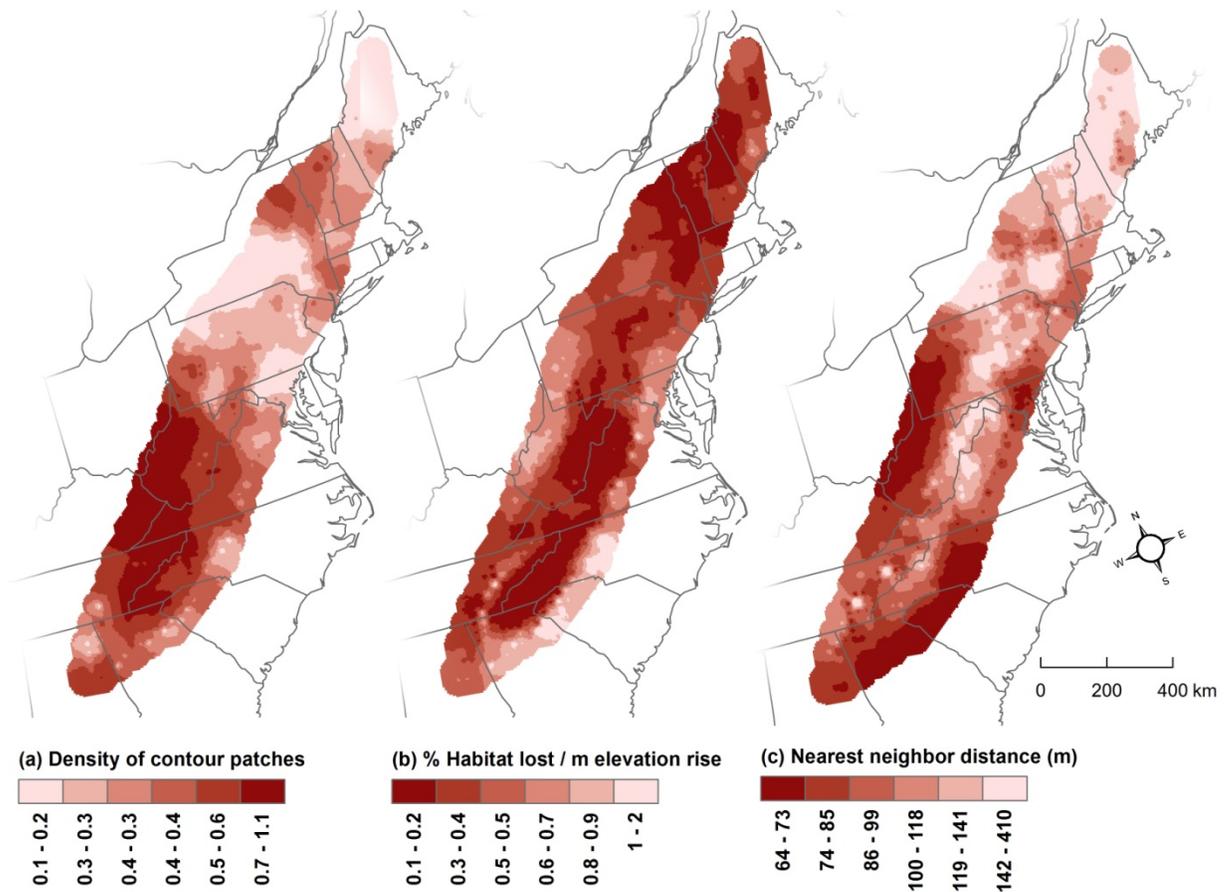


Figure 2.4. Maps of terrain metrics representative of each of the three classes of metrics, roughness, loss of habitat. Higher saturation represents areas that are hypothesized to be relatively more supportive of ecological adaptation to climate change as opposed to the lighter areas where species may be more vulnerable to climate change. a) topographic roughness (density of contour patches shown here) show higher degrees of roughness in the southern Appalachians indicating higher densities of microclimate and diverse habitats. b) hypsography – the lower losses of habitat with increasing elevation fall along the spine of the Appalachians where upslope migration will provide opportunities for climate adaptation. c) nearest neighbor distance – distances between similar elevations are shortest in the foothills or plateaus around the mountains potentially providing greater opportunities for latitudinal migration.

## Discussion

Topography is only one of a number of very important factors (e.g. geology, soils, land use, and disturbance history) influencing biodiversity (Anderson & Ferree 2010), and thus it cannot be the only indicator of a land unit's conservation value. For example, human impacts are weakest where terrain inhibits access and this may explain why topographic roughness was positively correlated with tree species richness while other topographic metrics were not. However, because other important factors in biodiversity are strongly correlated with topography, topography may integrate these patterns in a way that can simplify predictive forecasts of potential biodiversity patterns.

Biodiversity datasets at large spatial extents are limited (Rahbek & Graves 2001). The FIA data used in this study is invaluable because it is generated using uniform protocols at a continental scale. However, FIA data is not a surrogate for potential biodiversity because it only includes tree species, may not adequately represent the range of elevations in the Appalachians, has a coarse sampling rate (1/5000 acres). Biodiversity datasets that better represent high elevations or broader taxa would be necessary to further evaluate the role of habitat contraction with elevation in upslope migration.

Topographic metrics offer a promising geographic index of climate vulnerability that could serve as a baseline for conservation site prioritization, planning for managed relocations between protected areas, and identification of important migration corridors. For example, the mid-Atlantic region of the study area had low relief and large average inter-mountain distances, indicating that topography may introduce a barrier to northward dispersal. Furthermore, a high degree of forest fragmentation due to agriculture and recent increases in energy extraction (coal, natural gas, and wind) in this region continue to threaten habitat connectivity, potentially interfering with migratory adaptive responses to climate change (McDonald et al. 2009). A network approach can incorporate

these confounding factors to build on topographic analyses and reveal preferential pathways for migration (Chapter 3 of this Dissertation).

The positive species-area relationship is a foundation of biogeographical understanding of species diversity. Despite having standardized the data by 2-dimensional area, our results still show evidence of this tenet as cells with greater surface area (3-dimensional area, measured here as rugosity) were correlated with cells with high species richness (Spearman's rho 0.56,  $p < 0.0001$ ; log-transformed data had an  $r^2$  of 0.27; Appendix Fig. A.7b and A.9). In fact, all measures of terrain complexity, or roughness, were strongly correlated with tree species diversity, supporting Loarie et al.'s expectation (2009) that mountainous landscapes may shelter species under changing climate and McLachlan's suggestion (McLachlan et al. 2005) that the Appalachian Mountains specifically provided refugia for tree species during the last glacial maximum. The results are also consistent with the work of Anderson and Ferree (Anderson & Ferree 2010) who argue that geophysical conditions that currently support high biodiversity are likely to continue to be home to a high diversity of species regardless of climatic change. In addition, our results showing that intermountain distance is not related to species diversity seem to agree with White and Miller's (1988) conclusion that intermountain distance has not caused ecological isolation.

The magnitude of anthropogenic climate change may not be as great a threat as the pace, which is often determined to exceed the natural adaptation capacity of many species, potentially resulting in a sharp loss of biodiversity (Davis & Shaw 2001). The approach described here is a step toward an era of conservation planning informed by the static snapshots that species inventories provide, but also incorporating information about landscape features that support or suppress species dispersal, establishment, and successful regeneration.

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## **CHAPTER 3:**

### **Dispersal vectors and site suitability influence migration networks**

## **Abstract**

Over geologic time, climatic change has driven biogeographical shifts of plants, but determining historical migration routes or rates has been challenging. Predicting migratory responses to modern climate change has additional complexity because the change is expected to be rapid compared to historical climate change and habitats are more fragmented. Here, we provide an alternative assessment of migration potential that relies on geospatial data describing site suitability for species' establishment and mechanisms of species' dispersal – defining the pattern and process of successful migration. Analyzing the migration potential of species through the Appalachian mountains, we considered key mechanisms that govern establishment (e.g., pH, elevation, and forest cover) and dispersal (e.g., wind speed). We used a network analysis approach to map alternative networks based on each permeability factor. Results indicated that the southern Appalachians are broadly supportive of migration for wind-dispersed, high elevation plant communities. However, wind-dispersal and site suitability constrain migration through the mid-Atlantic along the Allegheny front and the Allegheny plateau. Network analyses such as this can be used to develop effective and efficient conservation for any focal species or community because results integrate a variety of migration preferences and highlight critical habitats.

## **Introduction**

Current plant species' distributions reflect the cumulative effect of multiple long-distance migration events over geologic time (Prentice, Bartlein, & Webb 1991; Nathan & Muller-Landau 2000; Schurr et al. 2009), and future species' ranges are predicted to shift rapidly poleward in response to anthropogenic warming over the next century (e.g., Lawler et al. 2009, Thomas et al. 2004, Walther et al. 2002). Yet biogeography and ecology have not deconstructed the mechanisms and processes that determine spatial distributions making it difficult to predict future migratory

responses (Wiens & Donoghue 2004). Furthermore, habitat fragmentation and loss as a result of human land use may inhibit species' resilience to these changes through migration (Johnson & Webb 1989; Malcolm et al. 2002; Higgins, Lavorel, & Revilla 2003; Svenning & Skov 2007) and concerns for biodiversity preservation have been raised if migration rates are slower than the velocity of climate change (Pitelka 1997; Malcolm et al. 2002; Scheller & Mladenoff 2005; Svenning & Skov 2007; Nathan et al. 2011). Therefore, attention has been focused on facilitating natural migration by enhancing landscape connectivity (Loss, Terwilliger, & Peterson 2011; Renton, Shackelford, & Standish 2012).

Facilitating natural migration requires an improved understanding of how plants migrate, (by what vectors, e.g. wind, water flow, gravity, and animal dispersal), and where plants regenerate, (for example, where conditions are suitable for germination, establishment, maturity, and reproduction). Dispersal and establishment are typically species-specific, and this has led researchers to choose focal or "surrogate" species for connectivity studies (Baldwin et al. 2010; Theobald et al. 2012). Yet, to date, there are no regional approaches to conservation and ecosystem management that can be used to generalize species' ability to adapt to climate change including aspects of both habitat condition that may influence establishment together with species movement and dispersal potential.

In general, landscape-level connectivity assessments use land use classifications to determine habitat patches and/or movement probabilities because nearly all species are affected by habitat fragmentation or loss associated with human development (Goetz, Jantz, & Jantz 2009; Baldwin et al. 2010; Anderson, Clark, & Olivero Sheldon 2012) and there is a strong theoretical basis for predicting the effects of fragmentation on species' persistence (King & With 2002; Fahrig 2003). However, this simplification to patch-level analysis of fragmentation blurs the distinction between how plants migrate and where they establish, each of which may need to be represented by distinct variables or different data forms. For example, spatially heterogeneous patterns of site suitability

may be represented by geospatial “vector” data (polygons) while dispersal vectors may be best represented by raster data (meshes or grids). A single focus on habitat patches to describe the permeability of the landscape limits the exploration of migration pathways to site suitability rather than including movement vectors. This likely oversimplifies natural migratory adaptation to climate change that requires successful dispersal, establishment, reproduction, and regeneration in new places with suitable conditions. In cases where mechanistic dispersal vectors are known, connectivity models can reflect more specific migration requirements and preferences. Thus, an approach is needed recognizing that relatively static physical conditions (like topography and soils) will continue to support biological diversity or rare species (Anderson & Ferree 2010), but that also embraces the idea that movement through these landscapes depends on dispersal vectors. Unlike other indices of landscape connectivity (Saura & Pascual-Hortal 2007) our approach integrates unlimited numbers of geospatial variables, including mechanistic data layers.

A practical approach for analyzing landscape connectivity employs graph (or network) theory (Cantwell & Forman 1993; Urban & Keitt 2001) to assess the degree of connectivity between habitats, the relative cost of moving from one habitat to another, or the spatial patterns of preferential pathways through a landscape. Most simply, graphs (networks) are comprised of nodes connected by edges (Harary 1969) which can be used to represent habitats (nodes) and movement probabilities (edges), thus merging pattern (patch size and shape) with process (dispersal) (Urban & Keitt 2001; Baldwin et al. 2010). This general framework has been applied to a wide range of connectivity questions across multiple spatial scales and community levels (Goetz et al. 2009; Baldwin et al. 2010; Anderson et al. 2012; Theobald et al. 2012). With the increasing availability of geospatial data and the development of computational tools (see (Kupfer 2012) for a review) it has become practical to model migration pathways using network theory.

While most seed dispersal distances are shorter than a few dozen meters, rare long-distance dispersal has a disproportionate effect on the dynamics of plant distributions, so the concerns described above have driven seed dispersal investigations to focus on long-distance-dispersal mechanisms (Schurr et al. 2009). In fact, Nathan et al. (2011) determined that mean horizontal wind speed was the only important geographically variable parameter in determining the spread rate of wind-dispersed species.

From the standpoint of seedling establishment, geologic substrate has been hypothesized as being an important determinant of broad-scale biodiversity patterns due to associated soil chemical processes including pH (Anderson & Ferree 2010). Land cover determines many site characteristics that are relevant to regeneration including soil chemistry, soil moisture, and light availability (Härdtle, von Oheimb, & Westphal 2003). Topography is an important factor in determining site suitability since it influences temperature and precipitation that govern microclimatic conditions (Rahbek & Graves 2001; Loarie et al. 2009).

Considering wind-dispersal and acidic habitat preferences as key factors influencing migration potential, we used Fraser fir (*Abies fraseri*), intermediate balsam fir (bracted or Canaan fir) (*A. balsamea* var. *phanerolepis* Fern.), and Carolina hemlock (*Tsuga caroliniana*) as the basis for our network analysis. These species are currently found in high elevation habitats in the southern Appalachian Mountains (U.S.A.), and are at risk of extinction as a result of climate change (Delcourt & Delcourt 1998; Potter, Hargrove, & Koch 2010). Fraser fir and Carolina hemlock are found on highly acidic sites and all three species have lightweight seeds that are dispersed in the fall primarily by wind (See Appendix A). Both of the high elevation habitats chosen as network endpoints are largely within federally owned lands. The southern patch is within Great Smoky Mountains National Park, the Nantahala National Forest and the Pisgah National Forest and smaller embedded wilderness areas. The northern patch is almost completely within the White Mountain National Forest and associated

embedded wilderness areas. A network approach is used to identify the most advantageous migration pathways between these endpoints considering both dispersal vectors and regeneration potential, demonstrating that the approach is capable of integrating pattern (where) and process (how). Specifically, we ask: how do migration networks differ in spatial pattern and resistance distance when based on dispersal vectors, establishment conditions, and their interaction?

Factors affecting migration of high-elevation, wind-dispersed plants have different spatial patterns (datasets are listed in Table 3.1). The southern Appalachians have higher elevations (up to 1862 m based on the GTOPO30 GDEM dataset used in this study) than the rest of the study area, although the northern Appalachians have almost equal relief as a result of lower base elevations. The Allegheny Front, a prominent topographic feature that stretches from West Virginia through northeastern Pennsylvania marks the eastern edge of the Allegheny plateau and the parallel ridges of the Ridge and Valley province from Virginia through Pennsylvania have high average annual wind speeds (estimated to be greater than 7.5 m/s (16.8 mph) at 50 m above land surface). Mapped wind speed magnitudes are most accurate in grassy areas with low slope, because vegetative and topographic roughness can decrease estimated wind speed by one or more power classes, but relatively high wind speeds on ridges in the mid-Atlantic have been verified (Elliott et al. 1987). Forest cover is common, especially at high elevations and in areas with less urban or agricultural land use such as the southern Appalachians. Soil pH ranges from 3.2 to 7.8 throughout the study area with acidic conditions (pH of 4-5) found at high elevations and pockets in southern New York State.

## **Methods**

We used Circuitscape (v. 3.5) to generate maps of movement probabilities (current densities) and calculate resistance distance (an indication of the relative ease of movement) (McRae & Shah 2009) (See Appendix B). Circuitscape creates an electrical circuit analog in which network nodes

represent landscape locations and conductance between nodes represents the ease of movement (permeability). Analysis of the circuit is performed by introducing 1 Amp (A) of current at a cluster of cells over 1000 m elevation in the southern Appalachians while another high elevation cluster of cells in the northern Appalachians is set to ground (0 Volt (V)). Effective resistance between these endpoints (source and sink nodes) is calculated by Circuitscape according to Ohm's Law (Voltage=Current \* Resistance ( $V=IR$ )). For all analyses, an 8-neighbor rule was used to create "edges" between adjacent raster cells in the permeability datasets (circuit nodes) and average conductance of adjacent nodes in the landscape permeability datasets was assigned to the edges between adjacent raster cells.

Dispersal vectors and regeneration potential were considered separately and in combination to determine potential migration pathways between places with similar habitat conditions. Landscape permeability (based on single variables or averages of multiple variables) was provided to Circuitscape as a raster of conductivity values and was prepared from publicly available geospatial data (Table 3.1). To minimize edge effects, the network domain was extended beyond the Appalachian Mountains from -85.5 degrees longitude to the east coast of the U.S. and north to 32.3 degrees latitude (Fig 3.1). Datasets were cropped to this domain before resampling to 5 km resolution, and standardizing the scale (data processing is explained in Table 3.2).

Table 3.1. Network Permeability Datasets

	Role	Magnitude	Source
Wind	Dispersal vector. High wind speeds can disperse seed further and support natural migration of wind-dispersed seeds	0 – 11.9 m/s mean wind speed 50 m above the land surface	National Renewable Energy Lab (NREL) Wind Class (Elliott et al. 1987) at 200 m resolution.
Forest Cover	Regeneration Suitability. NLCD values 41, 42, and 43 are forested land covers and support natural migration of forest species	22.7% of the study area is in forested land cover	National Land Cover Dataset 2006 (NLCD) (Fry et al. 2011) at 30 m resolution.
Elevation	Regeneration Suitability. High elevations are more supportive of natural migration of high elevation species.	0 – 1862 m	GTOP30 GDEM (30 arc second resolution)
Soil pH	Regeneration Suitability. Low pH soils are more supportive of natural migration of acid-loving species	3.2-7.8	SSURGO (prepared at 4 km resolution by Mathew Peters et al, unpublished.)

Table 3.2. Data preparation steps

Step 1	Crop to domain	20 U.S. States north of 32.3 degrees latitude to the Canadian border and east of -85.5 degrees longitude to the Atlantic coast.
Step 2	Resample (up or downscaling to 5 km)	<ul style="list-style-type: none"> <li>– Elevation data native resolution was 1 km. (Block Statistics using maximum value.)</li> <li>– pH data native resolution was 4 km. (Resampled using cell center.)</li> <li>– wind data, native resolution was 200 m. (Block Statistics using average.)</li> <li>– NLCD data native resolution was 30 m. Forested cover reclassified to 10, all other cover reclassified to 1, Block Statistics using average.</li> </ul>
Step 3	Rescale (1 – 10)	Rescaled value = $1 + (\text{raw value} - \text{min. raw value}) / \text{scale factor}$ Scale factor = range of raw values / range of rescaled values(9) (Rescaling facilitates comparison between permeability analyses.)
Step 4	Combined layers	Layers were combined by averaging conductance values

Maps of current (Amps) reveal different critical migration pathways based on different dispersal vectors and establishment conditions. High currents, and thus high migration potential, are found if 1) the cells are marginally conductive, but the adjacent cells (alternative pathways) are completely

inhospitable leaving the marginal pathway critically important or 2) the cells are very conductive, and even though the surrounding area is also suitable, migration is more likely to take place in the highly conductive area. Along with the current map, Circuitscape provides the effective resistance of the network (a single resistance value equal to the combination of all edge resistances) allowing comparisons of permeability among network analyses.

## **Results**

In general, lower currents (0.009 to 0.016 Amps) were mapped in the southern Appalachians where conditions are broadly supportive of migration, no advantageous pathway emerges, and flow is diffuse (Fig. 3.1). In contrast, the Allegheny Front in the Mid-Atlantic region concentrates current (0.017 to 0.022 Amps) because high wind speeds, high elevations, forested land cover, and low pH provide more suitable conditions for the focal species than the plateau to the west or the valleys to the east.

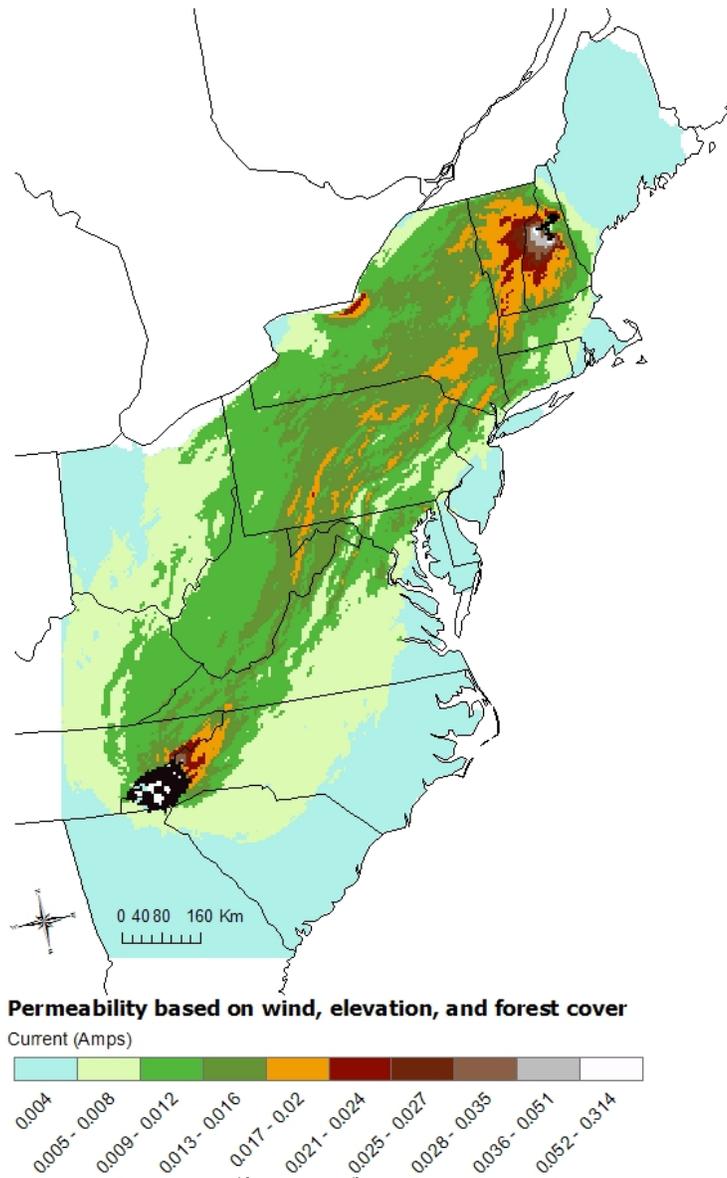


Fig. 3.1. Map showing relative importance of habitats for tree migration based on wind speed, elevation, and forest cover. Orange, red, and brown show places where higher currents indicate a concentration of migration (higher probabilities of flow).

Results suggest that on average, dispersal vectors and establishment suitability result in comparable network structures across the region as a whole. Network simulations using elevation, forest cover, and wind to define permeability (separately and in combination) show very small differences in mean current ( $\sim 0.014$  Amps), a partial consequence of the normalization of the permeability datasets (maximum conductance was set to 10) (Table 3.2 and 3.3, Fig. 3.2). Somewhat surprisingly, comparisons between permeability factors showed almost no difference in the standard deviation of the current. However, effective resistance better discriminates among networks. High wind speeds are isolated throughout the mountain range resulting in a high resistance distance of  $0.941 \Omega$ , but the mountain range is more continuously forested, resulting in a low resistance distance of  $0.216 \Omega$ . The relatively high elevational difference between the peaks and valleys compensates in some part for the lower elevations of the mid-Atlantic and this spatial pattern results in an intermediate resistance distance of  $0.442 \Omega$ . As in the combined permeability circuit map, maximum currents (other than around the endpoints) indicate concentrated migration potential and potentially critical landscape characteristics for migration based on each permeability factor (Fig. 3.2 and Table 3.3).

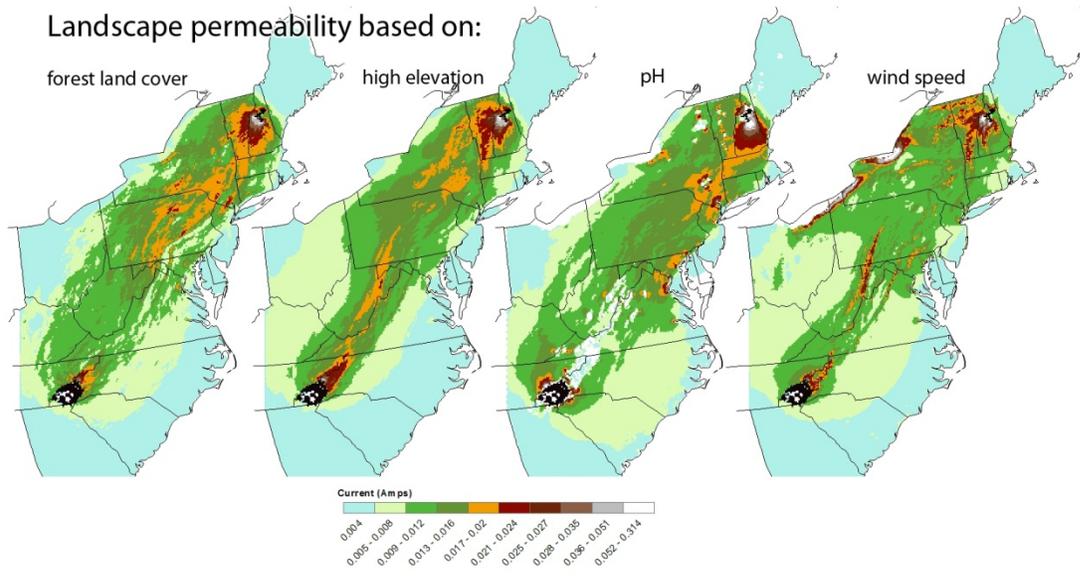


Fig. 3.2. Maps showing results for permeability datasets (forest land cover, high elevation, pH, and wind speed) evaluated independently.

Table 3.3 Current and resistance results for individual and combined permeability datasets.

	Mean Current (Amps)	Maximum Concentrated Current (Amps)	Standard Deviation	Resistance Distance <sup>1</sup> ( $\Omega$ )
Forest Cover (Fig. 3.2a)	0.0140	0.0230 Vicinity of the Hudson River in southern NY where the Sterling Forest Corporation and Harriman, Bear Mountain, Palisades, and Clarence Fahnestock Mem. State Parks protect forest cover in an otherwise heavily developed area.	0.0832	0.216
High Elevation (Fig. 3.2b)	0.0139	0.0203 Vicinity of Dolly Sods Wilderness, Monongahela N.F. (part of the Allegheny front)	0.0832	0.442
pH (Fig. 3.2c)	0.0125	0.0353 On the Hudson River in southern NY	0.0677	0.373
Wind (Fig. 3.2d)	0.0143	0.3155 On the Allegheny Front east of the Canaan Valley National Wildlife Refuge and the Dolly Sods Wilderness, but not within public ownership.	0.0835	0.941
Wind, Forest Cover	0.0142	0.0209 Southern portion of Green Mountain National Forest, VT	0.0835	0.342
High Elevation, Forest Cover	0.0140	0.0208 Southern portion of Green Mountain National Forest, VT	0.0832	0.287
Wind, High Elevation, Forest Cover (Fig. 1)	0.0141	0.0197 Allegheny Front in Pennsylvania mostly in state lands, (Gallitzin State Forest and Game Lands)	0.0835	0.368
Wind, High Elevation, Forest Cover, pH	0.0125	0.0298 Vicinity of the Hudson River in southern NY	0.0677	0.479

1. Resistance distance is the effective resistance between the two endpoint nodes (the southern and northern ends of the Appalachian network). Effective resistance is the value of a single resistor that could be equivalently substituted for the configuration of resistances in the network of many nodes.

## Discussion

Many of the areas of maximum migration potential identified are located within or at least near existing protected areas – but this association is the result of an auto-correlation since protected areas are more likely to be forested than adjacent lands, and forest cover was one of the determinants of permeability. Still, the network simulations identify a few landscapes that may be important for migration but are not already protected, particularly the Allegheny Front in West Virginia and Pennsylvania, and parts of southern New York.

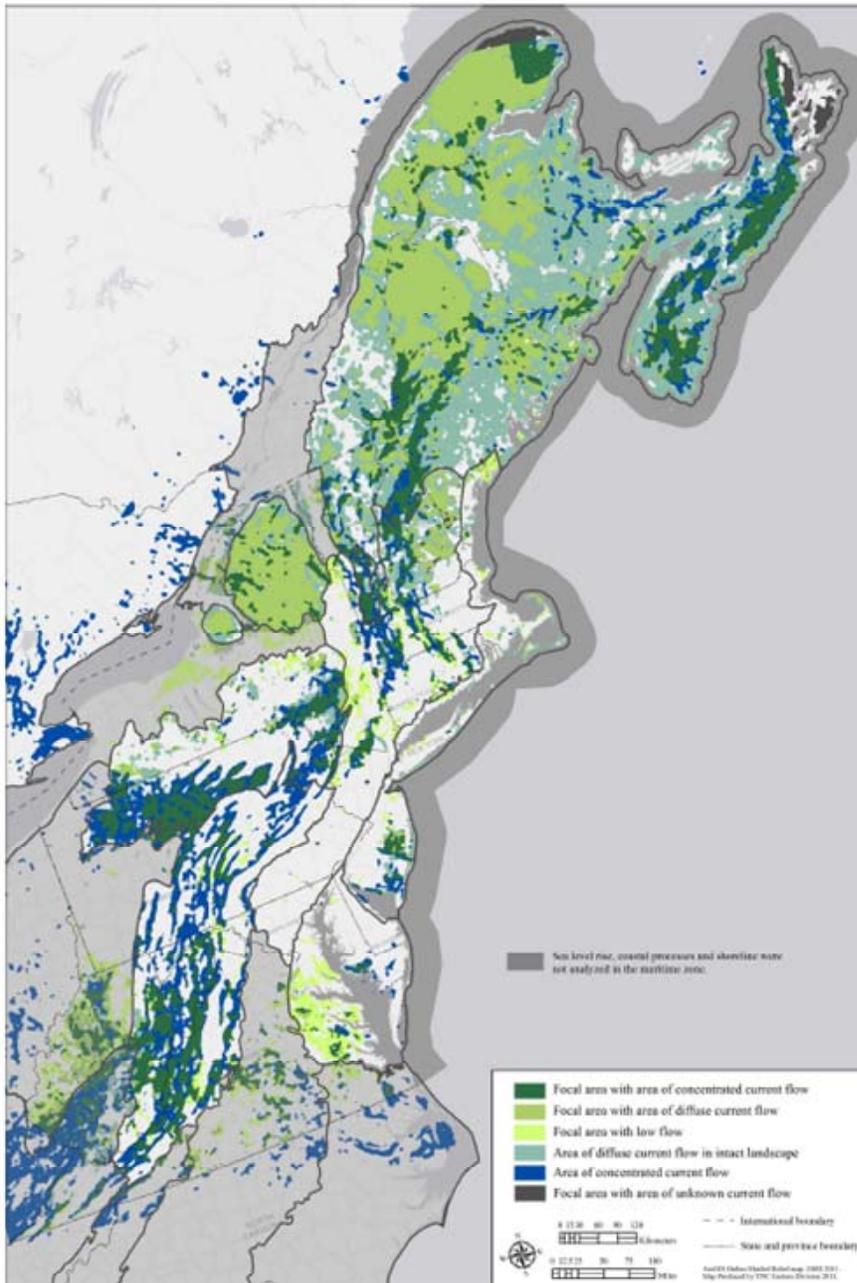
A number of factors must be considered when preparing a network model of landscape connectivity. First, many physical conditions are auto-correlated (soil characteristics and topography for example) and some conditions can arguably be considered more important than others. When justified, it is possible to weight conductance layers in the combined network conductance layer to promote the importance of some variables over others. To the extent that trends in dispersal mechanisms are known, migration networks under future conditions may also be predicted. For example, wind speeds are expected to decline by ~10% in the Northern Hemisphere with increases in forest cover and climate change (Breslow & Sailor 2002; Vautard et al. 2010). As we have shown, variables affecting regeneration may be incorporated either as determinants of suitable habitat (patches between which current flows) or as continuous measures of permeability (the conductance surface that determines the ease of flow).

To characterize migration potential for other species complexes of interest, spatial datasets documenting patterns of dispersal vectors or suitability will need to be prepared. For example, blue jays are known dispersers of fagaceous seeds, selecting viable seed and caching seed in the ground in places that are suitable for germination and establishment (Johnson & Webb 1989). A permeability layer based on blue jay abundance could be combined with regeneration condition layers for these trees to map migration pathways. The study reported here has specific application for wind-

dispersed high-elevation plant species, but perhaps more importantly it demonstrates an approach for analyzing migration potential at large spatial scales for a wide range of species if dispersal vectors and regeneration conditions are known.

Results of simulations based on different permeability layers have different implications for conservation management. Of the four permeability factors investigated here, only forest cover can be actively managed, unlike wind, elevation and soil pH. Reforestation programs could enhance migration potential by expanding the area of suitable sites for regeneration but are unlikely to have any influence on the physical template at broad scales. Yet, accounting for the fixed nature of the geophysical template can help prioritize landscape protection resources to align with the migration potentials. For example, energy development (coal, natural gas, and wind) in the region is likely to accelerate habitat fragmentation, which could interfere with climate-driven migration (McDonald et al. 2009). Prioritization of energy extraction activities that minimizes impact in regions that have narrow and concentrated migration pathways may reduce ecological impacts.

Habitat prioritization is a critical goal of conservation agencies, but is rarely performed at landscape or regional scales and often neglects the need to consider both dispersal and habitat suitability metrics together. Given the availability of land use and land cover datasets, fragmentation is often considered as a surrogate for dispersal (Iverson, Schwartz, & Prasad 2004). Indeed, independent analyses of least resistive migration pathways based on land use and land cover in the mid-Atlantic and northern Appalachians confirmed the importance of the Allegheny front, the Allegheny plateau in Pennsylvania, areas in southern New York State, and western Massachusetts and southern Vermont as critically important habitat for migration potential (Anderson et al. 2012; Theobald et al. 2012) (Fig. 3.3). While the study described here included landscape layers that represented a mechanistic dispersal process, the results coincidentally showed similar spatial patterns.



Map 6.36: Networks of resilient sites based on linkages and focal areas. This map integrates the focal areas with the regional flow concentrations. In the map, focal areas located in areas of high flow concentrations are shown in olive green. Focal areas that are large and highly intact have diffuse flow and are shown in pale green. Key linkages are shown in areas with no focal area but high amounts of concentrated flow, and these are shown in dark blue. Blue-green areas are fairly intact regions with diffuse flow but no identified focal area.

Figure 3.3. Results of Circuitscape analysis by Anderson, Clark and Sheldon showing areas with high current flow. Mapped focal areas have been identified by the Nature Conservancy as priorities for conservation for reasons other than probability of migratory advantage.

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## **CHAPTER 4:**

**Influence of fire and climate on vegetation and carbon storage in the Appalachians**

## Introduction

For 20,000 years, when not glaciated, the Appalachians have been forested (Davis 1981). As glaciers retreated, plant species migrated northward through species-specific dispersal processes and rates (Prentice, Bartlein, & Webb 1991) resulting in new community compositions. Paleoecological studies have mapped species range shifts over this time period (Delcourt, Delcourt, & Webb 1983; Davis & Shaw 2001; McLachlan, Clark, & Manos 2005). At all temporal scales, climate also influences successional dynamics by triggering episodic disturbances like wildfire (Jackson et al. 2009). At the same time, climatic changes affect fire regimes by changing fuel moisture among other factors, and fire is known to affect vegetation distributions (Foster et al., 1997).

Understanding these changes in climate, vegetation, and fire are particularly important because forests play a significant role in the global carbon cycle, storing ~45% of terrestrial carbon, contributing ~50% of terrestrial net primary production, and sequestering large amounts of carbon annually equivalent to ~33% of anthropogenic carbon emission (Bonan 2008). Temperate forests account for 6.9% of the forest area in the world and store 6.4% of the forest carbon (Watson et al. 2000). Forest fires can abruptly change the carbon status of a forest (Running 2008) and interactions between fire and climate represent a key unknown in climate change predictions (Bonan 2008). Much work has focused on developing management prescriptions to maximize net carbon sequestration in forests, but within the U.S. this work has been focused in the western states where some areas experience severe fires that release carbon abruptly through combustion of dead and live woody biomass and over a period of time as trees killed by the fire decompose (Kashian et al. 2006; Hurteau & North 2009). Forest ecosystems with long fire return intervals can be carbon neutral because even though fires are often severe and release much of the carbon in the system, regrowth is rapid and uninterrupted by disturbance and carbon is quickly re-absorbed (Smithwick et al. 2009; Hurteau & North 2009). In the context of anthropogenic climate change, it is important to improve

the capability of models to predict forest carbon storage, and the accuracy of such predictions requires the incorporation of disturbances like wildfire, and their effects on stored carbon.

Carbon storage in forests is linked to vegetation. Biogeographical descriptions of the Appalachian forests describe vegetation that aligns with temperature gradients from south to north and low elevations to high elevations (Bailey 1976; Eyre 1980; McNab & Avers 1994; Prasad et al. 2007). The southern Appalachians are characterized by oak (*Quercus sp.*) and hickory (*Carya sp.*) dominated forests while hardwoods (*Acer sp.*, *Fagus sp.*, *Betula sp.*) are found in the northern Appalachians. Based on well-established relationships constructed by correlating species' distributions with climate regime patterns, warming climates are projected to result in potential range shifts or extinctions (Iverson & Prasad 1998; Williams & Jackson 2007; Iverson et al. 2008) and some of these changes have already been observed (Parmesan & Yohe 2003; Parmesan 2006; Beckage et al. 2008; Woodall et al. 2009).

However, while much is known about biogeographical responses to climate change in the eastern U.S., the relationship with fire has been more difficult to reconstruct because fire scars in tree rings provide the only record of annually-resolved fire-history and they are only available back to the 17<sup>th</sup> century (Clark 1997b; McEwan, Dyer, & Pederson 2011). Charcoal in sediment cores, which are more widely available, is representative of large areas, not individual burns, so it has been difficult to discern causal relationships between fire frequency or severity and species abundance (Clark 1997a). Nonetheless, much is known about historical ignition sources, seasonality, and climatic variability, and associations with species have been vigorously debated.

Most studies have shown that historical and present-day fire regimes in the Appalachians are strongly influenced by humans through accidental and intentional ignition and fire suppression as opposed to natural ignition sources. Evidence of prescribed fire by Native Americans has been reported (Cronon 1983; Denevan 1992; Delcourt & Delcourt 1997; Brose et al. 2001) but others

have downplayed these fires as being merely accidental (Russell 1981). Euro-American settlers continued to introduce an ignition source during land conversion and logging practices in the 1800's often involved fire to reduce slash residue and these fires often spread (Foster 1988). About 1930 the dominant human influence on fire became suppression (Nowacki & Abrams 2008).

The historical frequency of the human set fires is difficult to determine, for reasons mentioned above, but a strong correlation with climatic conditions hints that fire frequency may have been governed by climate trends at long time scales (Neil Pederson, pers. comm.). Fires are strongly seasonal, burning in the early spring before leaf-out when dry winter air has caused low fuel moisture or in the fall when deciduous leaves drop, increasing fuel loads and allowing sunlight to reach the forest floor, further drying fuels (Lafon, Hoss, & Grissino-Mayer 2005). Fire severity is typically limited to consumption of litter and fine fuels, resulting in seedling and sapling mortality but mature trees are rarely killed and flames almost never transition to the canopy. The topographic complexity of the Appalachian Mountains introduces a finer scale spatial imprint on fire frequency and severity, however, as shallow soil depths, south-facing solar aspects, and wind exposure can lower fuel moisture levels and consequently increase fire risk.

Despite the paucity of evidence over long time periods and large areas fuel models have associated the eastern U.S. with low to moderate spread rates and low flame lengths yielding low severity fires with very low risk of crown fire (Scott & Burgan 2005). Fire regimes vary across the mountain range. The northern Appalachians are estimated to have very long fire return intervals, on the order of 200 years, while southern Appalachian forests have shorter fire return intervals, perhaps 35 years (Rollins & Frame 2006) and in some places as short as 10 years (Shumway, Abrams, & Ruffner 2001). Fire suppression has not increased fire risk in the eastern U.S. as much as it has in the western U.S., but shrubby species like rhododendron (*Kalmia latifolia* L.) and mountain laurel (*Rhododendron maximum* L.) have increased in abundance as a result of canopy and fire disturbances

and may support higher fire severity in the future as a result (Nowacki & Abrams 2008).

Additionally, some tree species (like pitch pine *Pinus rigida Mill.* and table mountain pine *Pinus pungens Lam.*) are strongly associated with higher fire severity (Waldrop & Brose 1999; Brose & Waldrop 2006).

The humid temperate climate of the Appalachian Mountains is expected to become warmer in the future, with greater changes in the northeastern U.S. than the southeastern U.S. Based on the results of 16 general circulation models accessed through the Nature Conservancy's Climate Wizard, under a low emission scenario (B1), temperatures are expected to increase by 1.5-2° C, with some models predicting just 1° C of warming and some predicting more than 3° C of warming. Under a high emissions scenario (A2), predicted increases in temperature range from 3° C warmer in the south to 4° C warmer in the north, by the 2080s, with some models predicting as little as 1.5° C warming in the south or as much as 5° C warming in the north. In the low emissions scenario, in the same time frame, precipitation is expected to increase slightly throughout the region, by roughly 5%, although some models (INM-CM3.0, IPSL-CM4, and MIROC3.2 (medres)) predict up to 10% less precipitation in the south. Predictions for the high emissions scenario show the same trends, increases in precipitation of roughly 10% throughout the region although the same three models predict less precipitation in the southern U.S. by up to 25% (MIROC3.2 (medres)). More extreme droughts will result from either a reduction in precipitation or an increase in temperature (and consequent evapotranspiration) or both (Barber, Juday, & Finney 2000).

A major challenge in modeling interactions between climate, fire regimes, and vegetation lies in matching spatial, temporal, and biotic scales between landscape and modeling realms to accurately represent the future. For example, the topographic diversity and absence of homogeneous forest stands results in intricate spatial patterns of fire susceptibility and fire sizes which can not easily be

represented by the coarse spatial grain of a dynamic global vegetation model (DGVM). Furthermore, feedbacks generated by species-specific fire effects can not be investigated using DGVM's that model at plant functional group levels. Response lags that occur in reality are difficult to model despite the long temporal record of the dynamics of response because doing so requires codifying more response mechanisms and increasing either the temporal grain or extent. Computational limitations of DGVMs simply prohibit fine scale incorporation of spatial, temporal, and biotic patterns and processes – yet forecasting climate-fire-vegetation dynamics in places like the Appalachians at large enough spatial extents to improve models of global carbon cycling remains an important goal.

Given the importance of forest carbon under anthropogenic climate change and the lack of understanding of interactions between climate, forests, and fire, we simulated future climate scenarios using a DGVM (MC1) to answer the following questions:

**In what ways will fire regimes be different under future climate scenarios?**

**How do forest types respond to changes in fire regimes and/or climate?**

**Do changes in fire regimes or climate have implications for the role of Appalachian forests in global carbon cycling?**

## **Methods**

Dynamic global vegetation models (DGVMs) integrate models that forecast potential biogeographic distributions of vegetation (based on plant functional types (PFTs) or biomes) with ecosystem process models that simulate ecosystem biogeochemistry (Cramer et al. 2001). Fire has previously been incorporated into these models to simulate postfire succession and subsequent changes to PFT distributions at relatively broad scales (Thonicke et al. 2001; Lenihan et al. 2003; Bachelet et al. 2005; Lenihan et al. 2008). MC1 is a deterministic physiologically-based

biogeographical model (MAPPS) with an emergent fire module (MCFire) and a modified biogeochemical module based on CENTURY that predicts vegetation lifeform (but not species) and fire regimes (Bachelet et al. 2001). Fire incidence and behavior is influenced by the fuel load generated by the vegetation type and by the fuel moisture, which is effected by the climate. Climate also influences the vegetation type through specific biogeographical rules related to temperature and precipitation thresholds, and fire influences vegetation type by changing the carbon balances in live, dead, and soil pools.

Although it is possible to run MC1 at 4 km resolution for the entire Appalachian range, computational limitations favored the selection of four 120 km by 120 km domains in the following locations: the highlands of Georgia just southwest of the Great Smoky Mountains, central Pennsylvania including the ridge and valley province, central New York, and northeastern Maine (Fig. 4.1). These domains encompass the full range of forest types, topographic and soil variability, and climate conditions present in the Appalachians and thus provided a tractable arena in which to test model sensitivity. For the remainder of the chapter, these domains are referred to by their state names.

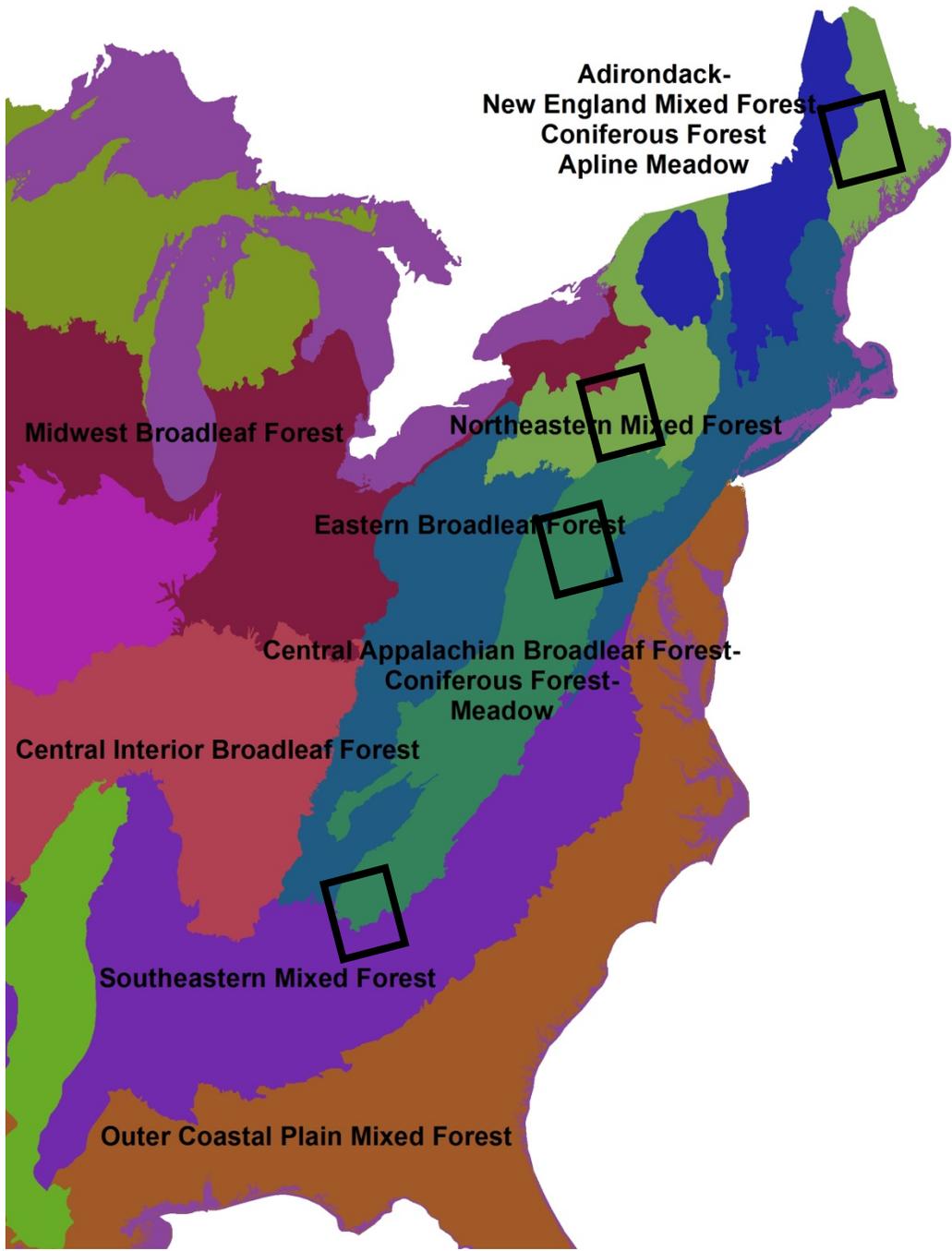


Figure 4.1. Locations of domains with forest biogeography from Ecomap.

Two parameters influence the incidence of emergent fire. The ‘fine fuel moisture code’ (FFMC) and the ‘buildup index’ (BUI) are used by the Canadian Wildland Fire Information System to account for the effects of fuel moisture on fire behavior (Stocks et al. 1989). The fine fuel moisture code is a numeric rating of the moisture content of litter (typically in the range of 80-90), the higher the number the lower the moisture content and the higher the flammability, and influences the seasonality of fire events. The buildup index, a drought index, is a numeric rating of the total amount of fuel available for combustion (typically in the range 20-70). In MC1, when daily FFMC or BUI rise above the user-defined threshold parameters, fire events are triggered. These parameters were used to manipulate fire regimes under historical climate conditions to investigate the role of fire in vegetation and carbon dynamics independent of climate change. Under future scenarios both indices increase and are therefore responsible for the increased incidence of fire in future simulations.

Elevation and soil datasets for the eastern U.S were produced at 4 km resolution and used for all MC1 simulations. MC1 simulations were prepared with equilibrium and spinup phases that are run for 3000 and 1000 years respectively using detrended historical data to develop potential vegetation and all other biogeochemical conditions. Climate variables including monthly precipitation, and maximum, minimum, and mean temperature were provided as input datasets. Historical simulations used PRISM climate data (1895-2005 (114 years)) at 4km resolution (Daly et al. 2000, 2002). To predict changes in fire regimes for the 21<sup>st</sup> century we used a range of future climate scenarios that provided the necessary input variables and bracketed the expected change: CSIRO (mk3.5), Hadley (CM3), and MIROC (3.2) under the SRES A2 scenario (100 years) including maximum temperature, minimum temperature, precipitation, and vapor pressure. Other simulation options are specified in Appendix D. Parameter values that were customized for the Appalachians including fire module reference trees and CENTURY parameters are provided in Appendix E.

To understand fire regimes under historical and future conditions, and the combined effect of shifts in fire regimes and warming on vegetation types and carbon storage, we ran MC1 under a range of fire and climate conditions (Fig. 4.2). We tested a wide range of FFMC and BUI threshold parameters (74-90 and 40-75 respectively) to determine which values generated fire regimes that best matched historical fire regimes in each of the domains (parameterization). This sensitivity analysis also permitted us to isolate the effect of fire from the effect of climate in the future by selecting the threshold parameter level with historical climate that provided an analogous fire regime to that generated under future climate conditions (Fig. 4.2 upper left). Finally, we simulated historical and future climates with fire suppression (no emergent fire) to test the effect of climate alone on vegetation types and carbon pools (Fig. 4.2 bottom).

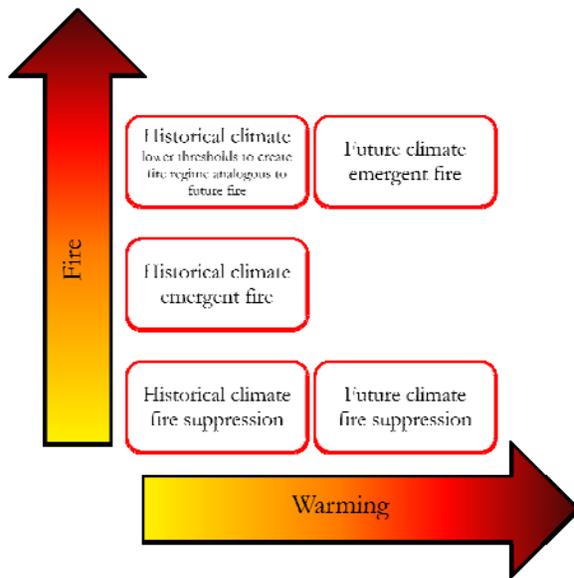


Figure 4.2. Fire and climate relationships between simulations.

To summarize fire regimes, vegetation distributions, and carbon storage, we produced the following annual output variables for all cells.

- Burn\_year, flag indicating the occurrence of fire
- PART\_BURN<sub>yr</sub>, % area of the cell that burned during a fire event

- Ffmc\_ann\_max, maximum ffmc value during the year
- Bui\_ann\_max, maximum bui value during the year
- Bio\_consume\_live, carbon in live biomass consumed by fire
- Bio\_consume\_dead, carbon in dead biomass consumed by fire
- FIRE\_KILLEDyr, carbon in live biomass killed by fire
- C\_SOMyr, soil carbon
- C\_ECOSYSyr, total ecosystem carbon
- C\_NONVEGyr, soil and litter carbon
- C\_FORESTyr, live tree carbon
- NPPyr, net primary production
- VTYPEyr, potential vegetation type

A fire severity index reflecting the role fire plays in successional dynamics was also developed (Eq. 4.1).

$$FireIndex_{cell} = \sum_{fires} \%CellAreaBurned * \frac{(Carbon_{LiveKilled} + Carbon_{LiveConsumed})}{Carbon_{Forest}} \quad Eq. 4.1$$

The fire index increases as fire size increases and as the portion of live biomass killed or consumed increases. This index and all other reported statistics were produced using custom python scripts (Appendix F-H).

## Results

Threshold parameter sensitivity. In general, as fine fuel moisture code (FFMC) and build up index (BUI) threshold parameters are lowered, more cells meet the fire criteria and larger areas of the domains burn at least once during the simulation period (Table 4.1). Fire size (the area within a cell that burns) decreases as the number of fires per cell increases, and fire severity, as judged by tree biomass killed by fire, also decreases but our fire severity index response is moderated by

compensating responses of fire size and total forest carbon. Carbon in live trees increases with fewer fires across the domain.

Table 4.1 Fire regime results for threshold parameter sensitivity analysis under historical climate and future climate with the selected base threshold parameter setting (FFMC=88, BUI=73).

Simulation (FFMC / BUI) <sup>1</sup>	Fire Extent (%) <sup>2</sup>	Number of fires <sup>3</sup>	Fire size <sup>4</sup> (portion)	Live trees killed by fire <sup>5</sup> (gC*m <sup>-2</sup> )	Forest carbon <sup>6</sup> (gC*m <sup>-2</sup> )	Fire Severity Index <sup>7</sup>
<b>Maine</b>						
90 / 75	15	5	0.57	1340	8837	0.44
<b>88 / 73</b>	<b>15</b>	<b>5</b>	<b>0.57</b>	<b>1340</b>	<b>8837</b>	<b>0.44</b>
86 / 70	55	2	0.78	1937	7989	0.40
82 / 65	78	3	0.70	1651	7162	0.43
78 / 60	90	4	0.56	1238	6526	0.42
74 / 55	92	9	0.34	695	6194	0.33
74 / 40	92	48	0.05	102	6224	0.06
<b>CSIRO A2</b>	<b>96</b>	<b>3</b>	<b>0.54</b>	<b>1543</b>	<b>8539</b>	<b>0.36</b>
<b>Hadley A2</b>	<b>69</b>	<b>1</b>	<b>0.77</b>	<b>2304</b>	<b>9798</b>	<b>0.35</b>
<b>MIROC A2</b>	<b>0</b>	<b>1</b>	<b>0.14</b>	<b>268</b>	<b>10029</b>	<b>0.006</b>
<b>New York</b>						
90 / 75	0	0	0	0		0
<b>88 / 73</b>	<b>0</b>	<b>1</b>	<b>1</b>	<b>1815</b>	<b>6832</b>	<b>0.33</b>
86 / 70	40	5	0.37	703	6460	0.15
82 / 65	64	7	0.35	665	6233	0.14
78 / 60	76	10	0.3	588	6141	0.13
74 / 55	82	14	0.21	429	6084	0.10
74 / 40	92	44	0.05	103	6011	0.03
<b>CSIRO A2</b>	<b>93</b>	<b>17</b>	<b>0.15</b>	<b>301</b>	<b>6101</b>	<b>0.38</b>
<b>Hadley A2</b>	<b>90</b>	<b>10</b>	<b>0.30</b>	<b>646</b>	<b>6288</b>	<b>0.43</b>
<b>MIROC A2</b>	<b>80</b>	<b>6</b>	<b>0.46</b>	<b>897</b>	<b>5915</b>	<b>0.39</b>
<b>Pennsylvania</b>						
90 / 75	0	0	0	0		0
<b>88 / 73</b>	<b>0</b>	<b>1</b>	<b>0.91</b>	<b>1706</b>	<b>5459</b>	<b>0.32</b>
86 / 70	31	3	0.52	981	4222	0.19
82 / 65	38	6	0.31	554	3882	0.12
78 / 60	40	10	0.18	323	3861	0.08
74 / 55	41	17	0.09	158	3893	0.04
74 / 40	44	52	0.02	33	3949	0.01
<b>CSIRO A2</b>	<b>67</b>	<b>11</b>	<b>0.15</b>	<b>280</b>	<b>5030</b>	<b>0.30</b>
<b>Hadley A2</b>	<b>50</b>	<b>4</b>	<b>0.19</b>	<b>944</b>	<b>4979</b>	<b>0.35</b>
<b>MIROC A2</b>	<b>24</b>	<b>1</b>	<b>0.95</b>	<b>1965</b>	<b>5968</b>	<b>0.37</b>
<b>Georgia</b>						
90 / 75	14	2	0.81	1575	7677	0.46
<b>88 / 73</b>	<b>14</b>	<b>2</b>	<b>0.78</b>	<b>1504</b>	<b>7676</b>	<b>0.44</b>
86 / 70	46	7	0.35	743	7428	0.18
82 / 65	74	9	0.33	734	7173	0.16
78 / 60	82	12	0.16	575	7100	0.13
74 / 55	90	16	0.19	426	7033	0.10
74 / 40	97	43	0.04	93	6989	0.03
<b>CSIRO A2</b>	<b>98</b>	<b>22</b>	<b>0.15</b>	<b>363</b>	<b>7617</b>	<b>0.43</b>
<b>Hadley A2</b>	<b>97</b>	<b>24</b>	<b>0.13</b>	<b>385</b>	<b>7474</b>	<b>0.44</b>
<b>MIROC A2</b>	<b>94</b>	<b>7</b>	<b>0.35</b>	<b>871</b>	<b>7650</b>	<b>0.47</b>

1. In each domain, the first 7 rows labeled with the threshold pairings are the historical simulations and the three future simulations were all run with the 88 / 73 threshold pair.
2. Fire extent is the number of cells in the domain that had at least one fire, divided by the total number of cells in the domain.
3. The number of fires is the average number of fire events in cells that had fires during the 114 year historical period or the 100 year future simulation period.
4. Fire size is the average fraction of a cell burned by a fire during a given event. One cell is 4km x 4km (1600 ha or 3954 acres)
5. Live trees killed by fire is the average (across fires and cells) carbon in live biomass killed by fire.
6. Forest carbon is the average carbon in live trees in all cells whether they burned or not.
7. As calculated by the algorithm provided in Equation 4.1.

Threshold parameterization. Across the domains, some interesting results emerge (Table 4.1).

Based on other estimates of fire return intervals and fire severities explored above, setting the FFMC threshold parameter to 88 and the BUI threshold parameter to 73 yields 5 fires in 114 years in Maine, 1 in 114 years in New York and Pennsylvania, and 2 fires in 114 years fires in Georgia. Based on the fire return intervals and severities predicted by the LandFire model results and the Scott and Burgan fuel models (Scott & Burgan 2005; Rollins & Frame 2006), these predictions may be too frequent in Maine, about right in New York and Pennsylvania, and too infrequent in Georgia.

Table 4.2 Fire regime results for the benchmark threshold pair in four domains.

Historic al (88 / 73)	Fire Extent (%) <sup>2</sup>	Number of fires <sup>3</sup>	Fire size <sup>4</sup> (portion)	Live trees killed by fire <sup>5</sup> (gC*m <sup>-2</sup> )	Forest carbon <sup>6</sup> (gC*m <sup>-2</sup> )	Fire Severity Index <sup>7</sup>
Maine	15	5	0.57	1340	8837	0.44
New York	0	1	1	1815	6832	0.33
Pennsylv ania	0	1	0.91	1706	5459	0.32
Georgia	14	2	0.78	1504	7676	0.44

1. Fire extent is the number of cells in the domain that had at least one fire, divided by the total number of cells in the domain.
2. The number of fires is the average number of fire events in cells that had fires over the 114 year historical period.
3. Fire size is the average fraction of a cell burned by a fire during a given event. One cell is 4km x 4km (1600 ha or 3954 acres)
4. This is measured by the average (across fires (over time) and cells) carbon in live biomass killed by fire.
5. This is the average carbon in live trees in all cells whether they burned or not.
6. As calculated by the algorithm provided in Equation 4.1.

Question 1. In what ways will fire regimes be different under future climate scenarios?

Predictions of future fire regimes based on future climate are mixed (See Table 4.1 for detailed results). Fire frequency decreases in Maine (from 5 fires in 114 years to 3 fires under CSIRO and 1 fire under Hadley and MIROC in 100 years). In New York, Pennsylvania, and Georgia, the fire frequency increases from 1 fire in 114 years to 6-17 in 100 years, 1-11 in 100 years, and 7-24 in 100 years, respectively. In all states MIROC predicts the lowest frequencies (no change in Pennsylvania), and with the exception of Georgia, CSIRO predicts the highest frequency.

Linked with these changes in future fire frequencies, fire severity is predicted to go down when fire frequency increases, and vice versa. In New York 1815 gC m<sup>-2</sup> live trees killed by fire under historical conditions dropped to 300-900 gC m<sup>-2</sup> trees killed. In Pennsylvania live trees killed by fire fell from 1706 gC m<sup>-2</sup> to 280-944 gC m<sup>-2</sup> for CSIRO and Hadley, but increased to 1965 gC m<sup>-2</sup> for MIROC. In Georgia, live trees killed fell from 1504 gC m<sup>-2</sup> to 363-871 gC m<sup>-2</sup>. Maine, where fire frequencies rose, had an increase in trees killed by fire from 1340 gC m<sup>-2</sup> to 1543-2304 gC m<sup>-2</sup> for CSIRO and Hadley, but a unique decline in trees killed by fire under the MIROC scenario to 268 gC m<sup>-2</sup>.

Where future simulations predict changes in fire regimes they usually indicate an increase in the total area within the domain that experiences burns (this is not the same as fire size.) CSIRO and Hadley predict and increase in the percent of the domain in Maine from 54-81%. These two models predict an increase of 90-93% in New York, 60-67% in Pennsylvania, and 83-84% in Georgia. MIROC predicts and increase in the domain burned in New York (80%) and Georgia (80%), but weaker effects in Pennsylvania (24%) and a decline in burned area in Maine (-15%)

Question 2: How do forest types respond to changes in fire regimes and/or climate?

Fire suppression and choice of FFMC and BUI threshold parameters had no effect on the dominant vegetation type (indicating that fire has little or no effect on forest type) but decreased forest cover from 97 to 87 % under CSIRO and 93 to 77 % under Hadley in Pennsylvania (no changes in other states). However, future warming can cause shifts in different dominant vegetation type (Table 4.3). In Maine, predicted forest type changes from temperate evergreen needleleaf forest to temperate cool mixed forest, in New York the historical forest is a temperate deciduous broadleaf forest and only the MIROC future climate causes a shift to temperate warm mixed forest, in Pennsylvania the temperate deciduous broadleaf forest becomes more dominant under future scenarios, and in Georgia the historical dominance of temperate deciduous broadleaf forest shifts to a temperate warm mixed forest. All four domains were dominantly forested (as opposed to woodland, shrubland, or grassland) in every cell averaged over time. There was a shift toward a uniformly temperate climate in Maine and in Georgia a shift toward subtropical with the warmer future scenarios.

Table 4.3. Vegetation type for each domain under historical and future climate conditions. In cases where the fire suppression simulation showed different results they are reported in parentheses.

	Dominant Vegetation Type <sup>1</sup>	Percent area of dominant type <sup>2</sup>	Percent classified as Temperate <sup>3</sup>	Percent classified as Forest <sup>4</sup>
Maine				
Historical	Temperate Evergreen Needleleaf Forest	96	79	100
CSIRO A2	Temperate Cool Mixed Forest	69	95	99 (100)
Hadley A2	Temperate Cool Mixed Forest	62	94	99 (100)
MIROC A2	Temperate Cool Mixed Forest	78	98	100
New York				
Historical	Temperate Deciduous Broadleaf Forest	100	100	100
CSIRO A2	Temperate Deciduous Broadleaf Forest	78	98	100
Hadley A2	Temperate Deciduous Broadleaf Forest	86	81	99 (100)
MIROC A2	Temperate Warm Mixed Forest	43	54	95 (100)
Pennsylvania <sup>5</sup>				
Historical	Temperate Deciduous Broadleaf Forest	83	100	92
CSIRO A2	Temperate Deciduous Broadleaf Forest	93 (99)	93 (100)	87 (97)
Hadley A2	Temperate Deciduous Broadleaf Forest	88 (95)	90 (93)	77 (93)
MIROC A2	Temperate Deciduous Broadleaf Forest	76	100	95
Georgia				
Historical	Temperate Deciduous Broadleaf Forest	99	100	100
CSIRO A2	Temperate Warm Mixed Forest	75	89	100
Hadley A2	Temperate Warm Mixed Forest	67	64	99 (100)
MIROC A2	Temperate Warm Mixed Forest	74	34	100

1. Dominance was determined by finding the average dominant vegetation classification for each cell over the simulation time period, and then finding the most common average dominant vegetation classification among domain cells.
2. Percent area is the number of cells with the same average dominant vegetation classification divided by the total number of cells.
3. Percent classified as temperate is the average over domain cells of the percent of time the cell spent in a temperate vegetation classification. (Vegetation classes 8 – 18)
4. Percent classified as forest is the average over domain cells of the percent of time the cell spent in a forest vegetation classification. (Vegetation classes 4, 7 – 11, 19 – 22, and 36)
5. In Pennsylvania, some ridges are classified as Coniferous xeromorphic woodland. The percent woodland in this domain is 3% (historical), and 1.8, 3.3, and 0 % (CSIRO, Hadley, and MIROC, respectively).

Question 3: Do changes in fire regimes or climate have implications for the role of Appalachian forests in global carbon cycling? Across all domains and simulations, and for all carbon pools, fires decreased total ecosystem carbon storage (below ground (live and dead), soil, above ground (live and dead)) (Fig. 4.3a-d). However, the fire effect was minor under historical climate and fire regimes, and more significant in future scenarios, especially in New York and Georgia where all three future climate predictions resulted in roughly 35% less carbon due to increased future fire than would be stored in the absence of fire.

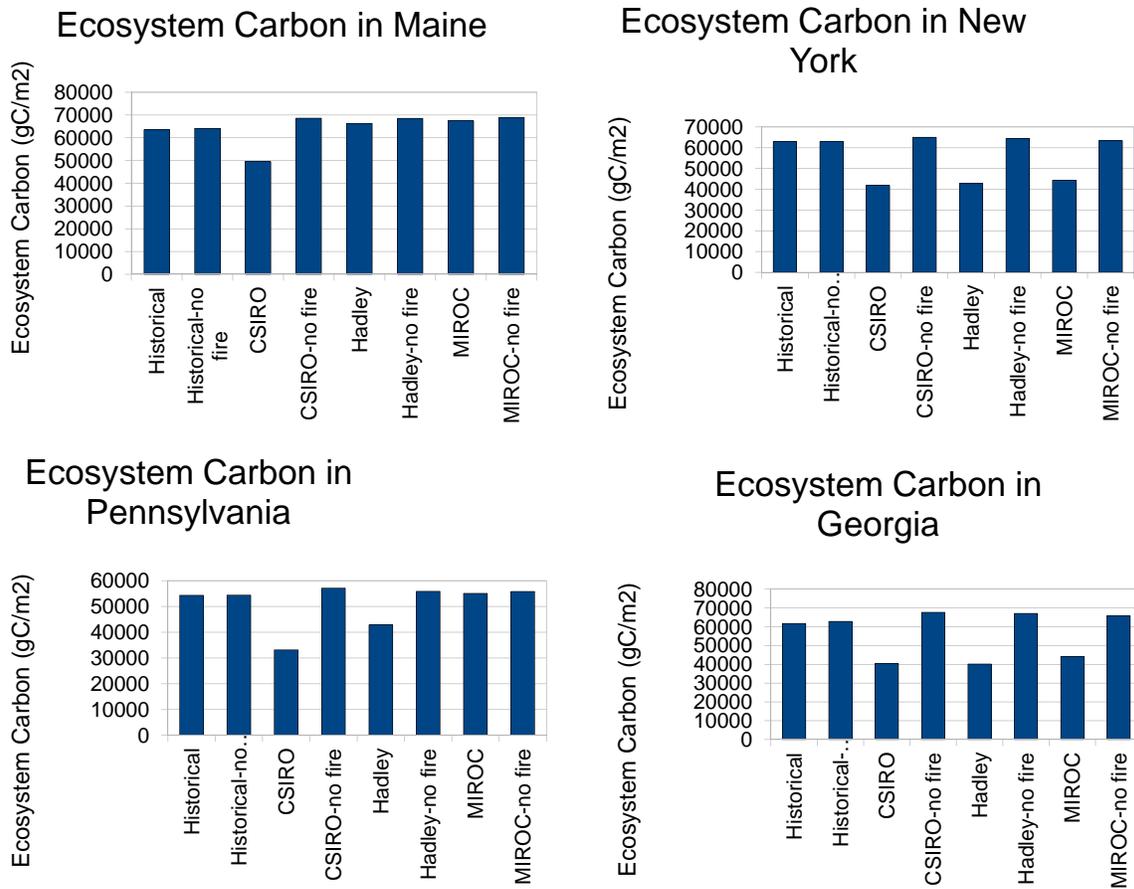


Figure 4.3. Ecosystem carbon under historical and future climate scenarios with and without fire for each of the test domains. a) Maine, b) New York, c) Pennsylvania, d) Georgia.

## Discussion

Parameterizing a fire model in the east presents a number of challenges. First, records on which to base estimates of fire frequency and severity are sparse. Secondly, many areas have fire return intervals greater than the historical climate data used in these simulations. Because of this, considerable uncertainty remains in the choice of a fine fuel moisture code threshold parameter of 88 and a build-up index threshold parameter of 73. Furthermore, because these threshold parameters are set at the command line when the simulation is executed, they cannot be customized on the basis of forest type, one pair must be set for the entire domain. The short simulation times relative to “natural” fire return intervals make it difficult to parameterize the model, but our results showing fires are too frequent in Maine and not frequent enough in Georgia imply that defining thresholds based in some way on forest type or species composition may generate more accurate fire regimes throughout the region.

These simulations clearly point to a greater effect from warming temperatures than from fire effects on forest type. Historical climate with no fire, historical fire, and inflated fire (by lowering FFMC and BUI threshold parameters) show strong increases in fire frequency as expected, but almost no differences in dominant vegetation type (although the higher fire regimes can in some cases result in lower forest cover.) Future climate showed almost no effect of fire regimes on vegetation classification. We show that fire regime shifts in these forests, such as a decrease in fire severity with increasing fire frequency, seem to represent negative feedbacks that limit the fire effects on vegetation.

Fire does appear to reduce potential carbon storage in Appalachian forests under future scenarios due to the increase in fire frequency. This presents a potential positive feedback with global climate change as the warming promotes fires and fires release carbon, which could promote

more warming. On the other hand, it may present an opportunity for forest management to mitigate carbon releases from forest fire. Fire suppression can result in unintended increases in fire severity in many forests due to fuel build-up, but this is less of a problem in eastern forests where production and decay rates are balanced and this leads to lower fuel loads (Graham & McCarthy 2006). If this fuel decay continues under future climate conditions, these results suggest that fire suppression and thus carbon storage may be a viable management action in the interest of terrestrial carbon storage, since fire suppression did not result in more severe fires within the study areas.

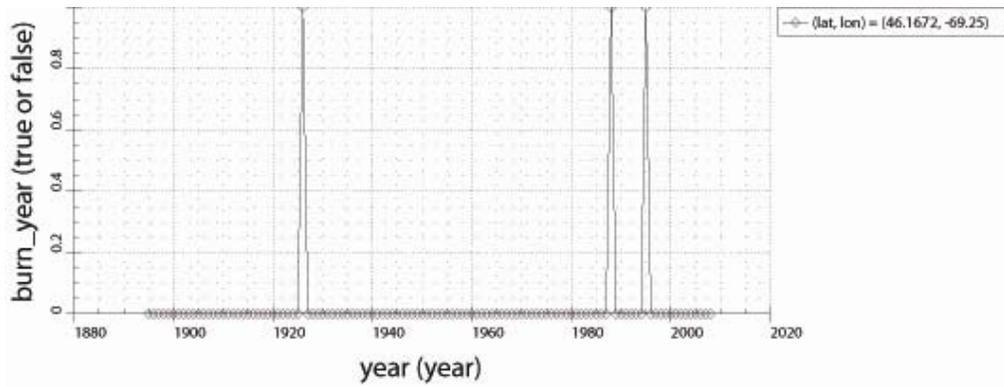
There remain a number of uncertainties. Fire regimes in the southern Appalachians are the combined result of climate and vegetation. As these fire-adapted and fire-promoted species migrate northward, fire frequencies may increase in the mid-Atlantic thus enhancing the selection of fire-adapted species and accelerating the forest compositional shift. However, if fires are driven more by climate than vegetation and fuels, this interaction will be minimized. In this case the greater impact on Appalachian forests would be an increased risk of severe and or widespread drought – the effects of which may not be captured by the future climate models and scenarios driving this study.

Dynamic interactions are complex, and correlation between variables does not imply causation. Nonetheless, exploring these temporal correlations (Fig. 4.4 a-c) may provide some insight into the question of whether or not fires are more influenced by climate or vegetation in this region. In the 1925 fire (north-central Maine) (Fig. 4.4a), vegetation type switched from temperate evergreen needleleaf forest to boreal evergreen needleleaf forest roughly concurrently (Fig. 4.4b). In this case, vegetation shift could not have triggered a fire, at least not in any real sense. More likely, low precipitation in 1921, 1924, and 1925 triggered the fire in 1925 (Fig. 4.4c). The fires in 1987 also followed drought years in 1985-1987, but in this case the shift to boreal evergreen needleleaf preceded the fire event and was persistent from 1982-1989. Although this location reverted to

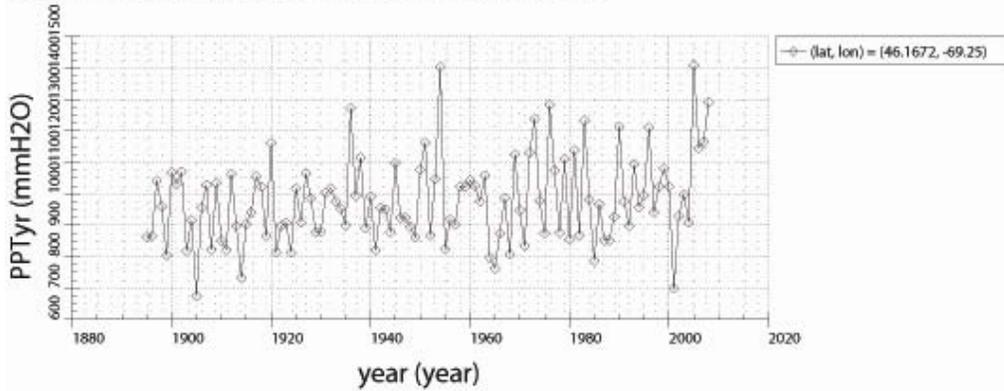
temperate evergreen needleleaf forest briefly, it returned to the boreal forest type from 1993-1997, during which the 1995 fire took place.

This very limited evidence leaves open the question of whether or not fire events are more influenced by climate or vegetation – a question that is certainly not new in the field of fire science. Answers to this question would help shed light on potential feedbacks between climate, species composition, and fire regimes and would improve the prediction of future forest condition in the Appalachians.

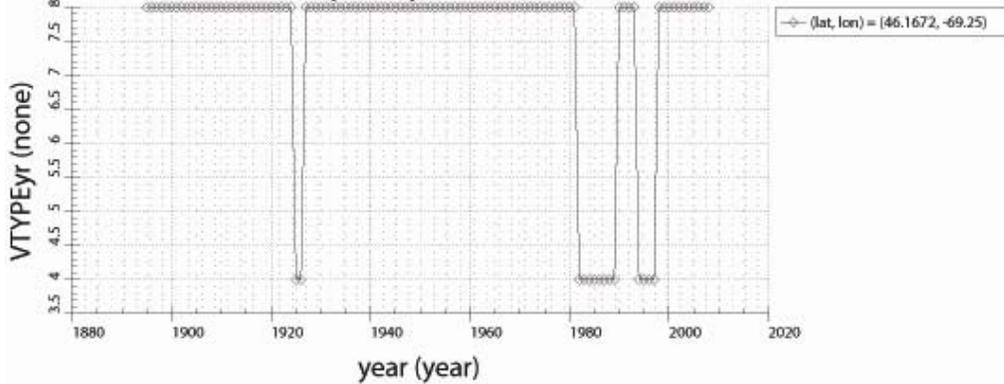
The results described here demonstrate the importance of regional-scale studies. While much finer grained topographic patterns strongly affect fire behavior and fire extent in ways that can not be captured in a DGVM, the coarser spatial scale employed here facilitates an exploration of climate, fire, and vegetation relevant to predicting trends in earth systems over the next century. Heterogeneity of climate and fire effects on vegetation exists at all scales. In this research the MIROC climate scenario in particular predicted different magnitude and direction of change in fire regimes across the four locations in the eastern U.S. The importance of the predictions of a small shift in from forest to woodland in Pennsylvania and dramatic losses of carbon in most areas under future climate depends on the scalar perspective (over long time periods and large areas, and viewed at biotic levels above the species level). The absence of abrupt shifts in vegetation type is a promising indicator of a resilient forest system, but the strong predicted increase in fire frequency will require adjustments in forest fire management in the near term.



flag indicating burn occurred this year



unsmoothed annual precipitation



potential vegetation type

Figure 4.4. Time series of results from MC1 for north-central Maine showing a) vegetation type (temperate evergreen needleleaf forest (VTYPE=8) and boreal evergreen needleleaf forest (VTYPE=4)), b) precipitation, and c) incidence of fire during the historical period.

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**CHAPTER 5:**

**Resilience of Appalachian Forests**

Given the anticipated rapid climate change, there is a great urgency to understand the dynamics of complex natural systems and apply theory to the practice of natural resource stewardship with more accuracy and efficiency than ever before (Heller & Zavaleta 2009). Goals for natural resource management have often been based on static snapshots of resource conditions because it is impossible to “manage” nature while “allowing” the state transitions associated with vegetative succession or disturbances like fire. Resilience theory has helped provide a framework for understanding change in ecosystems, but practical application has remained challenging.

The notion of resilience, introduced by C.S. Holling in 1973, provides an important theoretical framework for these investigations because it shows how interactions between biota and physical drivers can lead to seemingly abrupt transitions between states. (Holling 1973) defined resilience as a property of the system that “determines the persistence of relationships within a system and is a measure of the ability of the system to absorb changes of state variables, driving variables, and parameters, and still persist”; by contrast, stability was defined as “the ability of a system to return to an equilibrium state after a temporary disturbance.” In an exploration of possible behavior Holling (1973) identified domains of attraction containing locally stable states.

Since 1973, numerous explorations of these ideas have contributed conceptual developments. Engineering resilience (recovery time) has been distinguished from ecological resilience (amount of disturbance necessary to cause a state change) (Gunderson 2000). Within ecological resilience, numerous papers have explored the idea of thresholds (tipping points) separating alternative stable states with the goal of understanding how, why, and when ecosystems may be driven into new states (Muradian 2001; Scheffer et al. 2001; Peters et al. 2004; Burkett et al. 2005; Groffman et al. 2006; Dakos et al. 2008) and whether or not such state changes represent a shift in variables (e.g. community composition or functional relationships) or a shift in parameters (the underlying basis that defines state stability) (Beisner, Haydon, & Cuddington 2003).

Holling's (1973) definition of resilience requires an ecosystem to *persist* – but what constitutes *persistence*? In the context of a single species, *persistence* means survival over extinction or extirpation. But in the context of a forest community, *persistence* depends on what is valued. A forest products company may consider any future state in which forest growth rates meet logging goals to represent a resilient forest, regardless of the species composition, while an organization working to preserve biodiversity would consider minimal losses of species richness to represent a resilient forest. Hunters might consider the forest resilient if it can continue to provide adequate habitat for game species, and hikers and other outdoor enthusiasts might see the forest as relatively unchanged if the foundation species remained dominant. Truly, to see a forest as resilient is to judge that the past and future states are equivalent by some metric and through some lens (Carpenter et al. 2001).

A more modern definition, “Resilience is the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks” (Walker et al. 2004) permits change with a judgment of whether or not “essentially” the same functions are maintained. For eastern forests, this kind of definition has been reinterpreted. “Ecosystem health and sustainability... can be defined and measured in terms of carbon, nutrient, and water cycling rates and pool sizes, resistance and resilience to catastrophic disturbances.” (Vose 2000) The additional specificity of this definition helps bridge from theory to practice, but judgments of the sensitivity of the system to changes in measurement remain.

Considering the rapid anthropogenic climate change confronting ecosystems over the next 100 years, feared catastrophic ecosystem shifts (Breshears, López-Hoffman, & Graumlich 2011), and potential feedbacks within the global carbon cycle (Cox et al. 2000; Kurz et al. 2008), shifts between ecosystem states with vastly different carbon storage capacity are a top concern for the planet (Watson et al. 2000). Carbon storage varies in forests worldwide (Table 5.1).

Table 5.1. Carbon storage by biome type globally. Adapted from Watson et al. (2000).

Biome	Area	Carbon			Total per Area (Gt C per 10 <sup>6</sup> km <sup>2</sup> )
		Vegetation (Gt C)	Soils (Gt C)	Total (Gt C)	
<b>Temperate Forests</b>	<b>10.4</b>	<b>59</b>	<b>100</b>	<b>159</b>	<b>15.3</b>
Tropical forests	17.6	212	216	428	24.3
Boreal forests	13.7	88	471	559	40.8
Tropical savannas	22.5	66	264	330	14.6
Temperate grasslands	12.5	9	295	304	24.3
Deserts and semideserts	45.5	8	191	199	4.4
Tundra	9.5	6	121	127	13.3
Wetlands	3.5	15	225	240	68.6
Croplands	16.0	3	128	131	8.2
Total	151.2	466	2011	2477	16.4
<b>Temperate Forest by percentage</b>	<b>6.9 %</b>	<b>12.7 %</b>	<b>5.0 %</b>	<b>6.4 %</b>	

Temperate forests have relatively low soil carbon but relatively high vegetative carbon. When compared with other forest types, temperate forests have roughly average carbon storage on a per area basis. Dynamic Global Vegetation Models focus predictions on state changes at the level of plant functional types because shifts between forest and grassland (for example) have strong effects on the carbon cycle, but also because prediction of species-level state changes continues to be computationally limited. While carbon releases from current fire regimes in the Appalachians seem to be limited, future carbon storage under more frequent fire intervals may be lower than at present (see Chapter 4).

Our actions today (land development, forest harvest, fire suppression or prescription, air pollution and atmospheric deposition, greenhouse gas emissions, forest management, natural resources stewardship etc.) all play a role in determining what these future forests will look like and what services they provide (Folke et al. 2004). At the present time, however, we lack the ability to

generate a synthetic and comprehensive understanding of the interactions between these human actions and ecosystem responses. Without this understanding, and an open debate regarding which forest characteristics are most valued, determining management goals and plans to reach them is nearly impossible. First assessing, and then building Appalachian forest resilience is fundamental to successfully managing these forests through a century of potentially rapid climate change (Scheffer et al. 2001).

While the concept of resilience has become a standard approach for thinking about the sensitivity of systems to perturbations, regime shifts have been easier to demonstrate with theoretical models than empirical observation (Scheffer et al. 2001). This is due, in part, to interactions of phenomena across scales of space, time, and ecological organization that disguise underlying mechanisms with layers of complexity (Scheffer et al. 2001; Peters et al. 2004). While shifts in species composition as a result of climate, fire, disease, or pests might be seen by some as a sign of non-resilient responses at short time scales, these shifts may be seen by others as the adaptive responses of a resilient forest to external stresses on long time scales (Peterson, Allen, & Holling 1998; Carpenter et al. 2001; Smithwick 2011). In fact, high diversity has been seen as a stabilizing characteristic because it can provide functional redundancy that permits species to substitute for each other and satisfy the requirement that the system maintain functional processes (MacArthur 1955; Peterson et al. 1998). To the extent that functional redundancy can be provided by species interacting with the ecosystem at different scales, the redundancy offers a greater degree of stability and/or resilience (Tilman 1997; Peterson et al. 1998).

Despite the recognized difficulties in applying concepts of resilience to specific systems, progress has been made in bridging theory and real-world ecological dynamics. Carpenter et al. (2001) used two case studies to demonstrate that when resilience is defined in terms of a disturbance and a

response, model and field measures can be used to predict thresholds. (Lenton et al. 2008) identify eight “policy-relevant tipping points” (e.g. arctic summer sea ice) for which critical values for single control parameters can be used to assess transition timescales and the degree of reversibility of the key impacts. Importantly, the crossing of one threshold can immediately trigger other thresholds, especially at other scales, to be crossed in a cascading fashion (Kinzig et al. 2006).

Despite complexity inherent in multi-scalar resilience assessments, Scheffer et al. demonstrate that the strongest cases for “alternative stable states” involve observations of repeated shifts, studies of feedback mechanisms, and models showing that these mechanisms can explain the repeated shifts. Similar to the framework of Carpenter et al. (2001), I investigate historical examples of disturbances affecting Appalachian forests, to understand resilience in the context of global climate change. For each example resilience is determined in the context of the spatial and temporal scales, a disturbance and the ecological response.

**Quaternary Forest Regrowth** - Glaciation displaced temperate species to refugia in the southern U.S. and migration (among other ecosystem dynamics) has generated the forest distributions we are familiar with today.

Spatial Scale:	Global
Temporal Scale:	1.5 Ma to present
Disturbance:	Global Climate Change
Ecological Response:	Forest Regrowth

Paleoecological approaches have provided much detailed description of forests in the eastern U.S. over the last 1.5 Ma (the Quaternary Period) (Davis & Shaw 2001) and these long-term records are better sources of data on which to base a description of “natural” conditions and inform planning for long-term management of resources (Willis & Birks 2006). While climatic change is

clearly an important driver of species' range shifts, forest composition at any given time represents the combined effect of climate with species-specific diseases, migration rates, accommodation to stages of soil formation, and anthropogenic impacts (Graham 1999). During the quaternary period, deciduous forests in eastern North America and east Asia survived significant climate changes while similar forests in Europe did not. The resilience of the North American and Asian deciduous forests has been attributed to topography that facilitated migration and the absence of competing anthropogenic land uses (Graham 1999; Hewitt 2000). European deciduous forests had neither advantage, and it may be argued that climate change coupled with land use change drove ecosystems from one domain of attraction to another.

**Southern Appalachian Multi-Year Dustbowl Drought** – The dustbowl drought was spatially extensive and multi-year. In this example, forest impacts were documented in great detail near Asheville, NC, where species-specific tree mortality occurred on specific landforms, but impacts were restricted to the scale of a forest stand.

Spatial Scale:	Experimental Forest
Temporal Scale:	1925-1929
Disturbance:	Regional Drought
Ecological Response:	Tree Mortality

The dust-bowl drought with below average precipitation from 1921 to 1927, and with 1925 annual precipitation just 32 % of the 27-year average in Asheville, NC, caused leaves to brown and even fall on ridges and upper slopes in Bent Creek Experimental Forest; about half of the drought-affected trees died within 4 years of drought or secondary causes (Hursh & Haasis 1931). Species showed very different responses to the drought. For example, black oak (*Quercus velutina*), red oak (*Quercus rubra*), and scarlet oak (*Quercus coccinea*) had severe leaf damage during the drought and almost 100% mortality 4 years later, while chestnut oak (*Quercus prinus*), pine species (*Pinus sp.*), and

hickory species (*Carya sp.*) showed less evidence of injury and almost 100% survived. The strongest drought effect was in shallow soils with bedrock outcrops, and the high clay content presumably made the 5% oven-dry soil moisture completely unavailable to the trees. Hursh and Haasis (1931) also implicated disease, noting that the climatic conditions may have disturbed natural resistance of scarlet oak to the shoestring fungus associated with the roots. Because these significant shifts in species composition were confined to specific landforms, the long-term and broader-extent effect of the drought does not constitute a shift from one state to another, and it can be argued the ecosystem is seen as resilient to this level of drought. But if instead, the value of the ecosystem is focused on non-tree species with shorter lifespans and/or small territories, the drought-induced mortality may demonstrate a lack of resilience to drought.

**Land-clearing for timber and/or agriculture** – European settlement was associated with widespread clearing for agriculture, timber-production, and fuel. After abandonment, most of these lands have regrown forests, although legacy effects continue.

Spatial Scale:	Nested, local - regional
Temporal Scale:	1850 – present
Disturbance:	Land-clearing
Ecological Response:	Forest Regrowth

Clearing of temperate forests has occurred world-wide for timber harvest or land conversion to agriculture, amounting to a reduction in forest cover of about  $600 \times 10^6$  ha (Houghton 1995). In the eastern U.S., forests were cleared for agricultural land conversion, timber harvest, and fuel (Williams 1982). Land cover typically reverts to a forested condition when abandoned (Compton & Boone 2000), but a number of legacy effects remain. Severe and abrupt disturbances, like clear-cutting, can accelerate background successional processes resulting in abrupt changes in species composition (Abrams & Scott 1989). Natural reforestation of abandoned lands has, in fact, resulted in

demonstrable shifts in species composition including homogenization (Foster, Motzkin, & Slater 1998).

Understory communities appear to have long-term reductions in cover and diversity (Duffy & Meier 1992; Wyatt & Silman 2010) but others have concluded the effects are strongly determined by disturbance intensity and colonizing species (Belote, Jones, & Wieboldt 2011). In the Great Smoky Mountains, regeneration forests of at least 80 years of age in areas with histories of concentrated settlement have significantly less down deadwood coarse debris, while logging histories did not leave such strong legacy effects in the coarse woody debris (Webster & Jenkins 2005). Forest clearing also has long-term (80-110 yr) effects on above-ground biomass (192 Mg/ha in forests with disturbance history vs. 261 Mg/ha in old-growth forests), forest floor organic matter (more in burned and logged sites than under old-growth stands), and nitrogen cycling (nitrification rates were lower in forests with disturbance history than old-growth stands) (Goodale & Aber 2001). Logging also leaves a legacy in the spatial patterning of nutrient distributions (Likens et al. 1970; Fraterrigo et al. 2005; McLaughlan et al. 2007). The combined effects of changes in overstory and understory species composition and soil conditions including soil chemistry following agricultural abandonment have been associated with increased invasion of non-native plants (Kuhman, Pearson, & Turner 2011).

**American chestnut canker, eastern hemlock wooly adelgid** – The Appalachian forests experienced a significant decline in a dominant species when American chestnuts were devastated by canker. Today, the hemlock wooly adelgid could inflict a similar impact if eastern hemlock does not survive the spread of this non-native insect pest.

Spatial Scale:	Regional
Temporal Scale:	1900 – present
Disturbance:	Species-specific disease and pest
Ecological Response:	Tree Mortality

American chestnut (*Castanea dentata*) was co-dominant with oak for at least 1400 years until chestnut blight, a wind-dispersed canker pathogen (*Cryphonectria parasitica*), was noticed in 1904 in New York. Within 50 years, chestnut trees were reduced to an understory tree across its range (Ellison et al. 2005). Following the decline of American chestnut, eastern hemlock (*Tsuga canadensis*) expanded (Ellison et al. 2005). But in 1951 the hemlock wooly adelgid (*Adelges tsugae*), originally from southern Japan, was reported near Richmond, VA and has now spread south to Georgia, north to Maine, and west to Kentucky and Tennessee. Given current rates of mortality and lack of effective control, hemlock may be eliminated from much of its range within a few decades (Ford et al. 2012). The consequences of this loss of a dominant species are functional, and arguably represent a system that is not resilient, at least on a short-time scale. Infested stands are less productive, have stronger seasonal hydrology, and accelerated rates of decomposition and nutrient cycling (Martin 2012). Because the species has a wide geographic range encompassing a wide range of conditions, successional trajectories do not appear to be directed toward a single replacement species (Ellison et al. 2005). Other examples of species-level threats include the emerald ash-borer on ash trees and the gypsy moth that attacks oaks preferentially.

### **Does the past demonstrate resilience in the future?**

In each of the examples above, species composition was affected by disturbance but the site returned to forested cover. Furthermore, forest types remained within the range of oak-hickory, hardwood, and mixed deciduous-evergreen. Translated to the ball and cup heuristic (Gunderson 2000), species composition or forest types are nearby shallow cups with weak stability, while the entire basin of forest types is separated from a basin of savannah or grasslands by a high, well-defined ridge and stronger stability. Reductions in the adaptive capacity of an ecosystem (Gunderson

2000) can be seen as making the cups shallower and transitions between cups easier (Martin 2012). Thresholds may be approached abruptly through disturbances (especially concurrent with extreme conditions) or slowly as conditions trend continuously.

The Appalachians have a number of intrinsic characteristics that enhance resilience – a high species diversity means that general plant functional types can remain constant even when one or another species succumbs to a stress (e.g. the impact of chestnut and now hemlock decline) (e.g. Tilman 1997); a high degree of topographic complexity over small spatial extents provides a density of microclimates that support this high diversity of species even under changing climatic conditions (demonstrated in Chapter 2 of this dissertation); and the orientation of the mountain range along the vector of climate change (past, present, and future) facilitates migration (demonstrated by paleoecological research and expanded in Chapter 3). From the perspective of the global carbon cycle, if there is an alternative ‘stable’ state to the current forested state for the Appalachians, none of the diverse historical disturbances described above have caused the ecosystem to cross a threshold.

In general, it would appear that ecosystems are more resilient when assessed at large scales. A given stressor may eliminate a species (low biotic level) but leave a forest (high biotic level) with otherwise similar leaf area, litter, or soil conditions. In just a year (short time scale), people can clear large patches of forest, but after 100 years of abandonment (long time scales) the forest (high biotic level) has grown back, although soil and nutrient processes may lag still. Finally, while disturbances with small spatial extents may be severe and ecosystems in these locations will be radically altered, when the ecosystem is viewed at a large spatial extent, the overall function of the forest seems to be maintained.

The historical examples presented above can help us predict the degree to which forest responses will be resilient to given changes – but the interactions are complex, and in some cases unprecedented (O'Brien, Sygna, & Haugen 2004). If ecosystem stressors of the past did not drive the Appalachian forests permanently toward a non-forested state, this may not be an assurance that future conditions will not (Foster et al. 1997). Compounded perturbations and the ecological surprises they generate will become more common as more pervasive anthropogenic impacts overlay rapid global climate change (Paine, Tegner, & Johnson 1998). In particular, even if the magnitude of climate change is unremarkable, a fast pace of change could cause regime shifts that would not take place if thresholds were approached more slowly (e.g. equilibria can develop if vegetation responses are short relative to the period of climate change (Webb 1986)). Conversely, extremely rapid climate change (in terms of trends or frequency of disturbance) could kill individuals and interfere with genetic or migratory adaptation processes if these responses require comparatively long time periods. The comparison of time scales of climate change and response processes highlights the vulnerability of trees which typically require 20-30 years to reach reproductive age and conversely the advantage of insects, some of which can have multiple generations in one year.

In the eastern U.S. we can anticipate 3-4 °C warming over the next 100 years, with more warming in the northeastern U.S. than the southeastern U.S. and smaller changes in precipitation of up to 10% increase, although there is a possibility the southeastern U.S. might receive less rainfall. Tree species are expected to migrate northward, uniquely, in response to warming temperatures. While there is considerable concern that historical migration rates are slower than the velocity of climate change (Malcolm et al. 2002; Svenning & Skov 2007), temperature increases of 3-4 C, alone, may threaten only the species inhabiting small spatial extents, particularly those on mountain tops.

But temperature does not act alone. Warmer temperatures increase evapotranspiration rates, thereby decreasing soil moisture and causing drought stress in trees (Barber, Juday, & Finney 2000). While there is a predicted increase in precipitation in the Appalachians, it is unclear if this will be sufficient to compensate for the potential water deficit associated with increased temperature and evapotranspiration. Even if the net hydrologic effect is neutral in average years, extreme events will undoubtedly expose the forests to infrequent severe droughts. This effect may be gradual or abrupt and no forest type or climate zone is invulnerable (Allen et al. 2010). Even in humid forests, drought can cause tree mortality as seen historically in the dust bowl example described above (Hursh & Haasis 1931) and more recently in the Amazon during the 2005 and 2010 droughts (Lewis et al. 2011). The prospect of a change in drought severity or frequency presents a potential challenge to historic Appalachian resilience.

There are at least three explanations for drought-induced forest-mortality: 1) extreme drought and heat cause cavitation of water columns in the xylem, 2) water stress weakens trees by limiting metabolism resulting in carbon deficits, and 3) warm periods support population growth of pests and diseases allowing them to overwhelm weakened host trees (Adams et al. 2010; Allen et al. 2010). One such example is the increase in red maple (*Acer rubrum*) over oak species (*Quercus* sp.) that may represent a decline in forest resilience because while red maple may survive predicted climate change, it is susceptible to Asian longhorned beetle (Dodds & Orwig 2011; Martin 2012). Direct tree mortality is another concern. Trees that reach maturation under historical conditions with infrequent drought may be particularly poorly adapted to survive extreme droughts because below-ground architecture has not been optimized for water extraction. Furthermore, drought-stressed trees consume carbohydrate reserves more quickly but cannot photosynthesize due to closed stomata making trees more and more vulnerable to pest outbreaks or diseases (Williams et al. 2012). Obviously, wildfire becomes more frequent and/or more severe under drought conditions when all fuels have lower moisture content.

In this dissertation I have developed and applied tools that contribute to an improved understanding of Appalachian forests and can be used to develop management strategies across this region:

- 1) Describing the role of topography in supporting species survival of global climate change over geologic time, both quantitatively and qualitatively. These results are broadly applicable to montane geographies world-wide, and can be used locally to prioritize conservation activities and maximize biodiversity conservation.
- 2) Offering a network theory approach to integrate spatially heterogeneous factors describing migration potential. This method is applicable in any geographic setting where

relevant data can be used to predict migration pathways. In the Appalachians it has highlighted the potential importance of the Allegheny Front for northward migration of plants with wind-dispersed seeds.

3) Exploring fire regimes and future climates in the Appalachians with the conclusion that these forests are unlikely to undergo abrupt transitions over the next 100 years when considered at large spatial extents, long temporal scales, and high biotic levels. Localized abrupt transitions are possible where soil and climate conditions increase likelihood of severe storms or fires or other disturbances or where single species are strongly dominant and potentially limit functional redundancy. Predicted increases in fire frequency can slowly change dominant forest species by suppressing saplings that are vulnerable to fire.

There is no question that Appalachian forests will change – in species composition, disturbance regimes, habitat quality, species diversity, timber production, and many other ways. All of these characteristics are ecosystem services that are valued to differing degrees by different stakeholders. Whether or not the forests of the future are “desirable” is a human judgment, and it can be based either on our needs and desires or on what we understand to be best for all species. In general, most species will be able to adapt to slow changes, regardless of the direction or magnitude. My research and the examples explored in this chapter demonstrate that the Appalachians have intrinsic properties (high legacy biodiversity, high topographic complexity, and others) that damp responses to climate change – improving persistence for all species.

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## Appendix A: Supplementary Figures, Methods, and Results

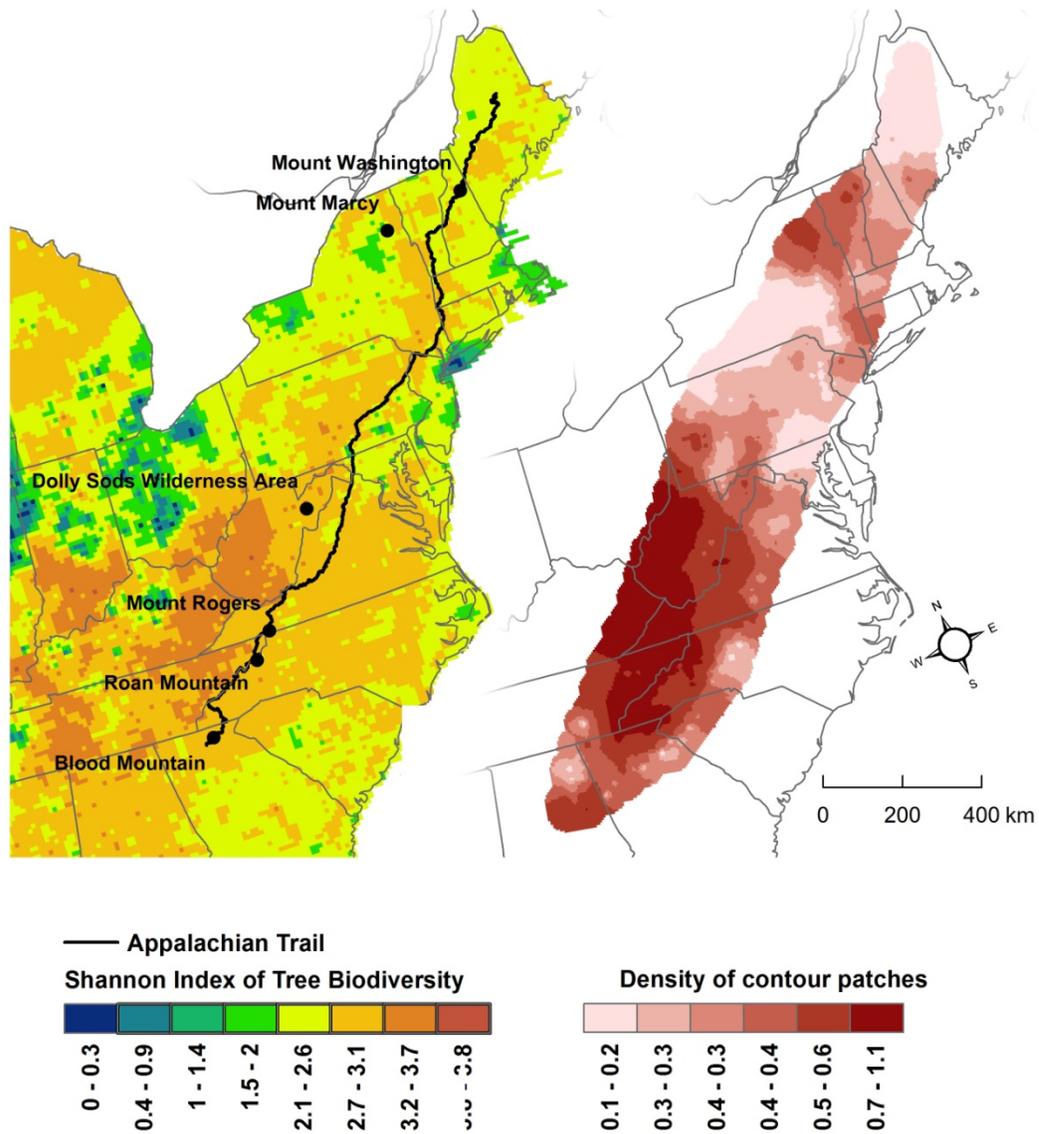


Figure A1. Summary of Results. Shannon Diversity Index is mapped on the left, and the best topographic predictor of diversity, density of contour lines is mapped on the right.

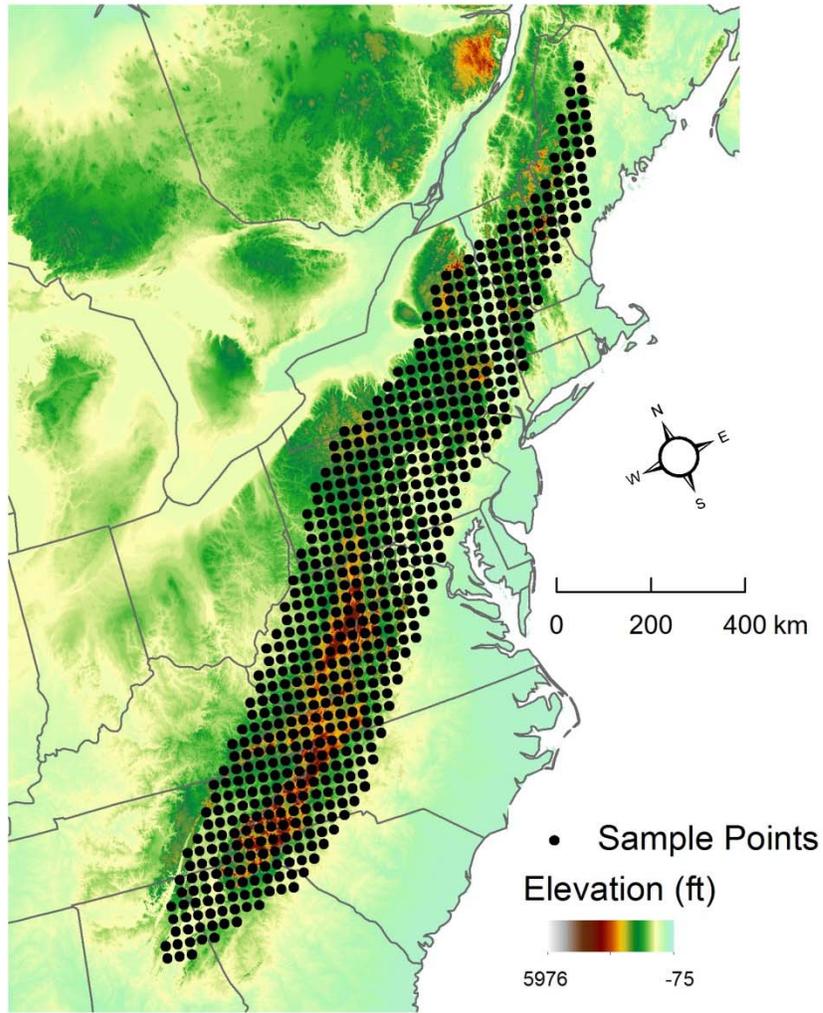


Figure A2. Map of study area with locations of 50 km x 50 km elevation samples.

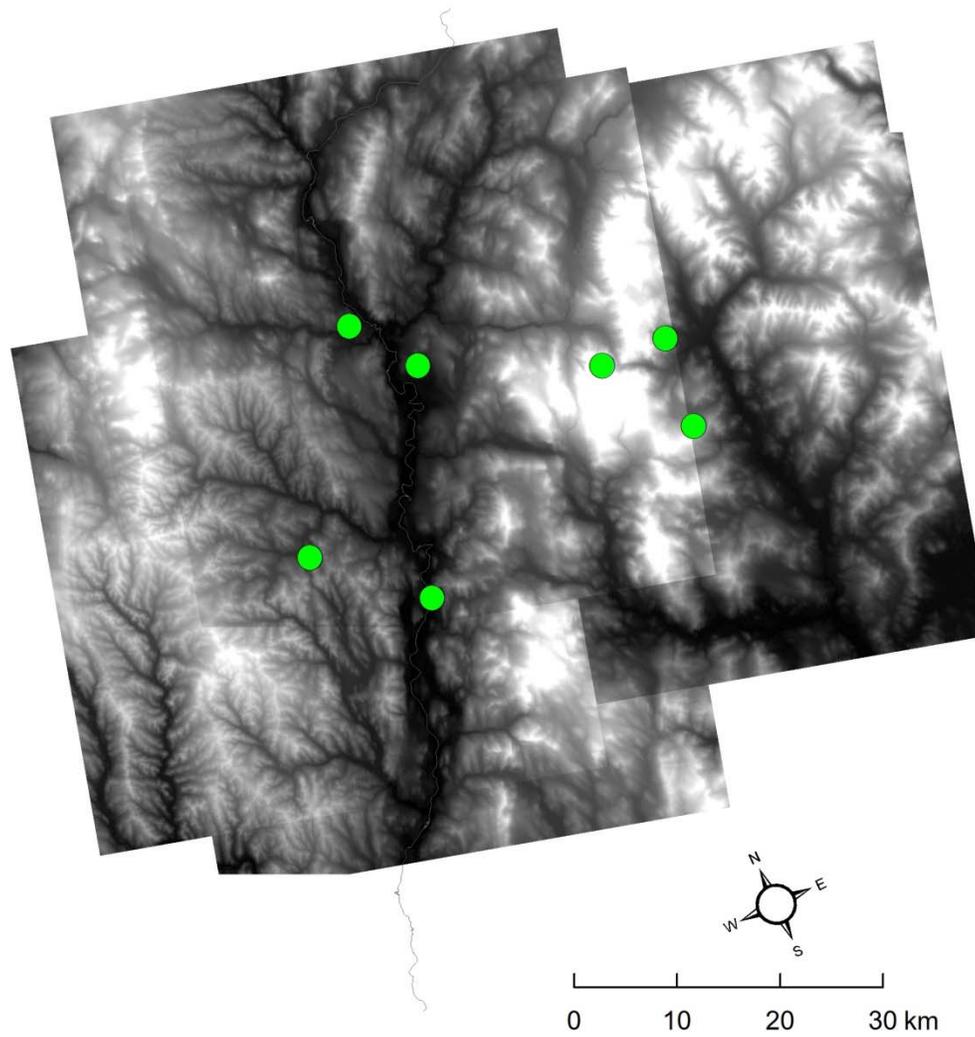


Figure A3. Example of sensitivity analysis using 7 randomly generated locations for elevation sampling in New Hampshire.

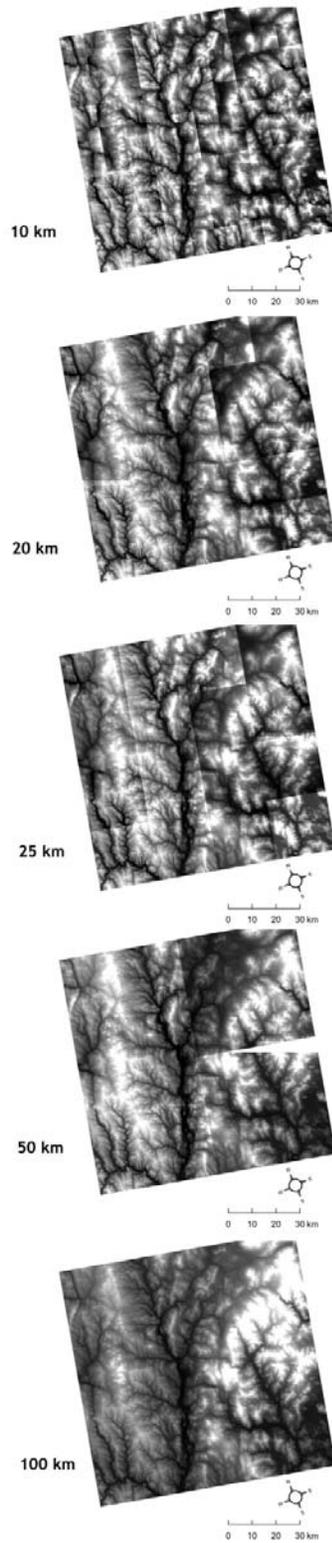
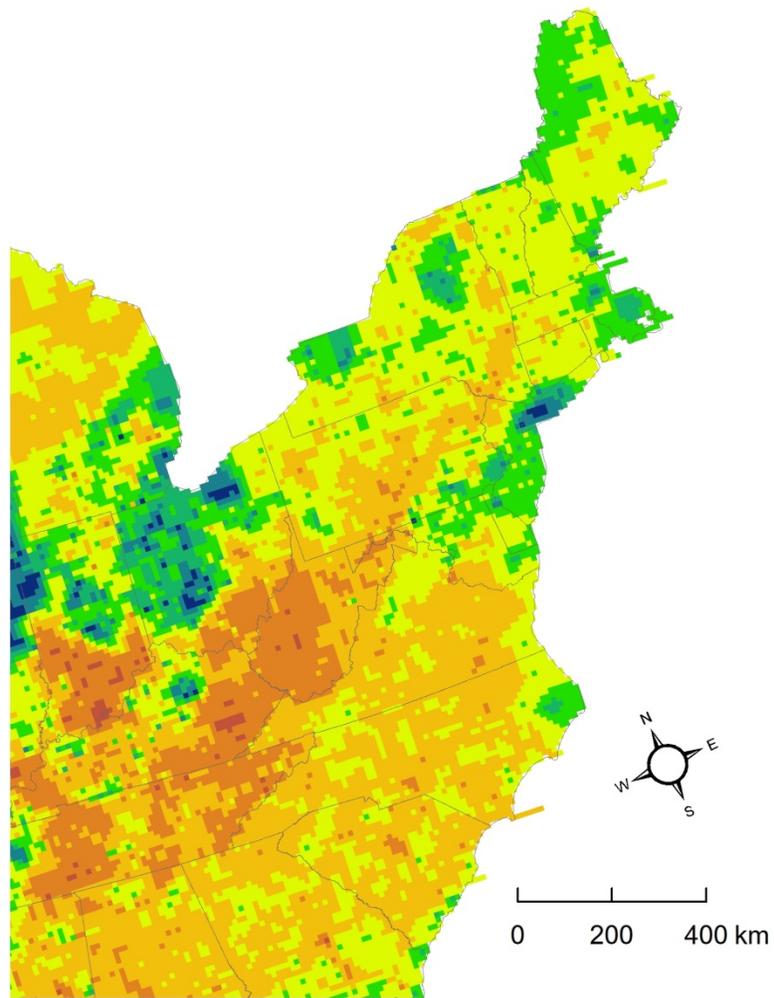


Figure A4. Example of sensitivity analysis using 5 elevation sample sizes ranging from 10 km x 10 km to 100 km x 100 km.



### Species Richness

Number of species

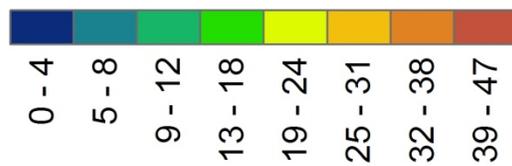


Figure A5. Species Richness. This is the number of tree species based on FIA data, higher numbers (red) represent greater diversity.

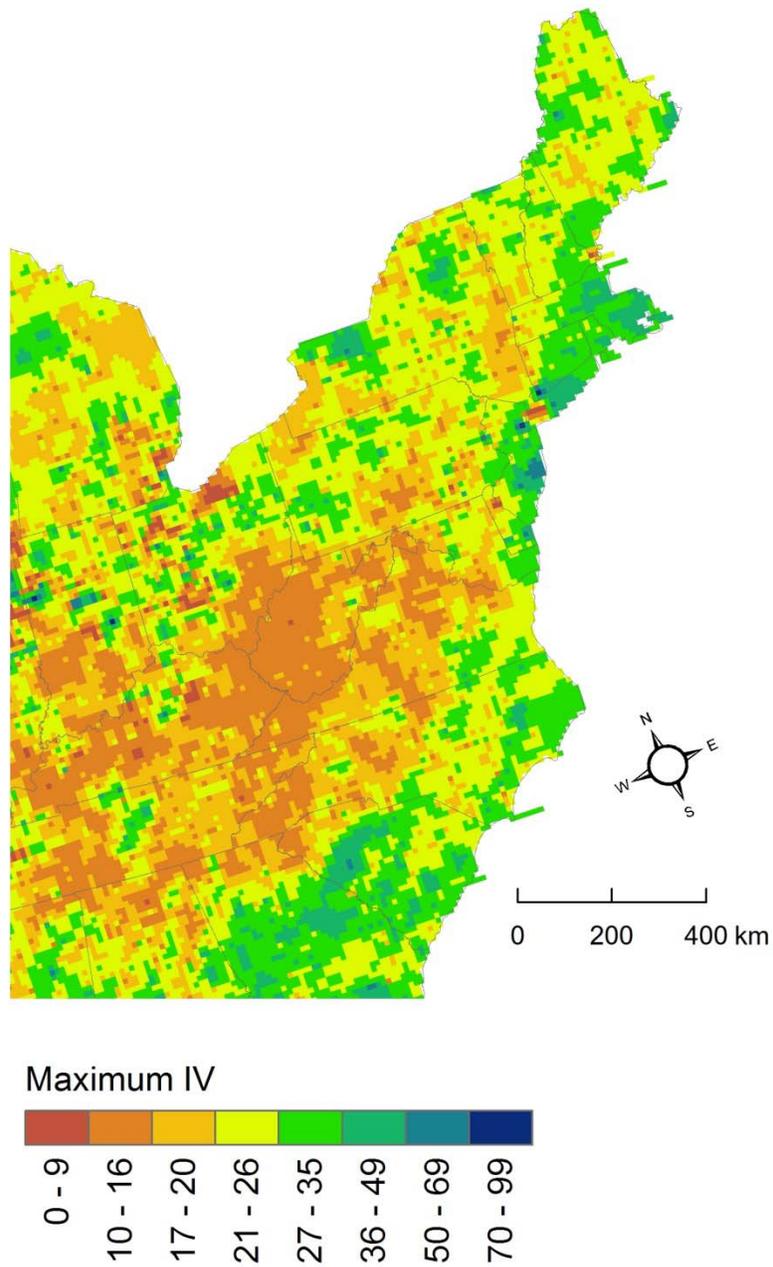


Figure A6. Maximum Importance Value. This is the highest importance value for a species in each cell based on FIA data. Lower numbers (red) represent cells that are not dominated by any species and are therefore more diverse.

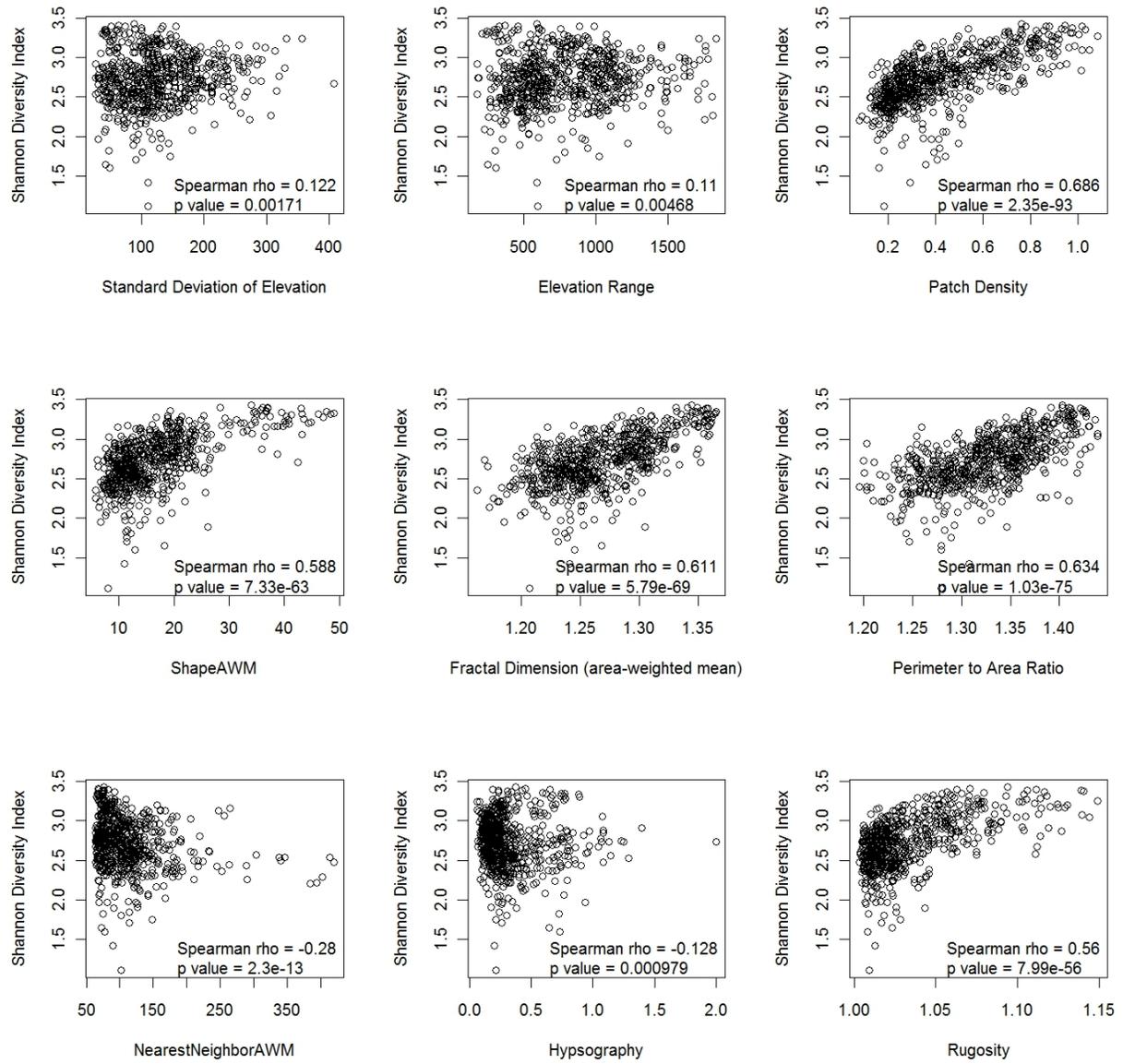


Figure A7a Correlations (spearman Rho) between terrain metrics and Shannon Diversity Index.

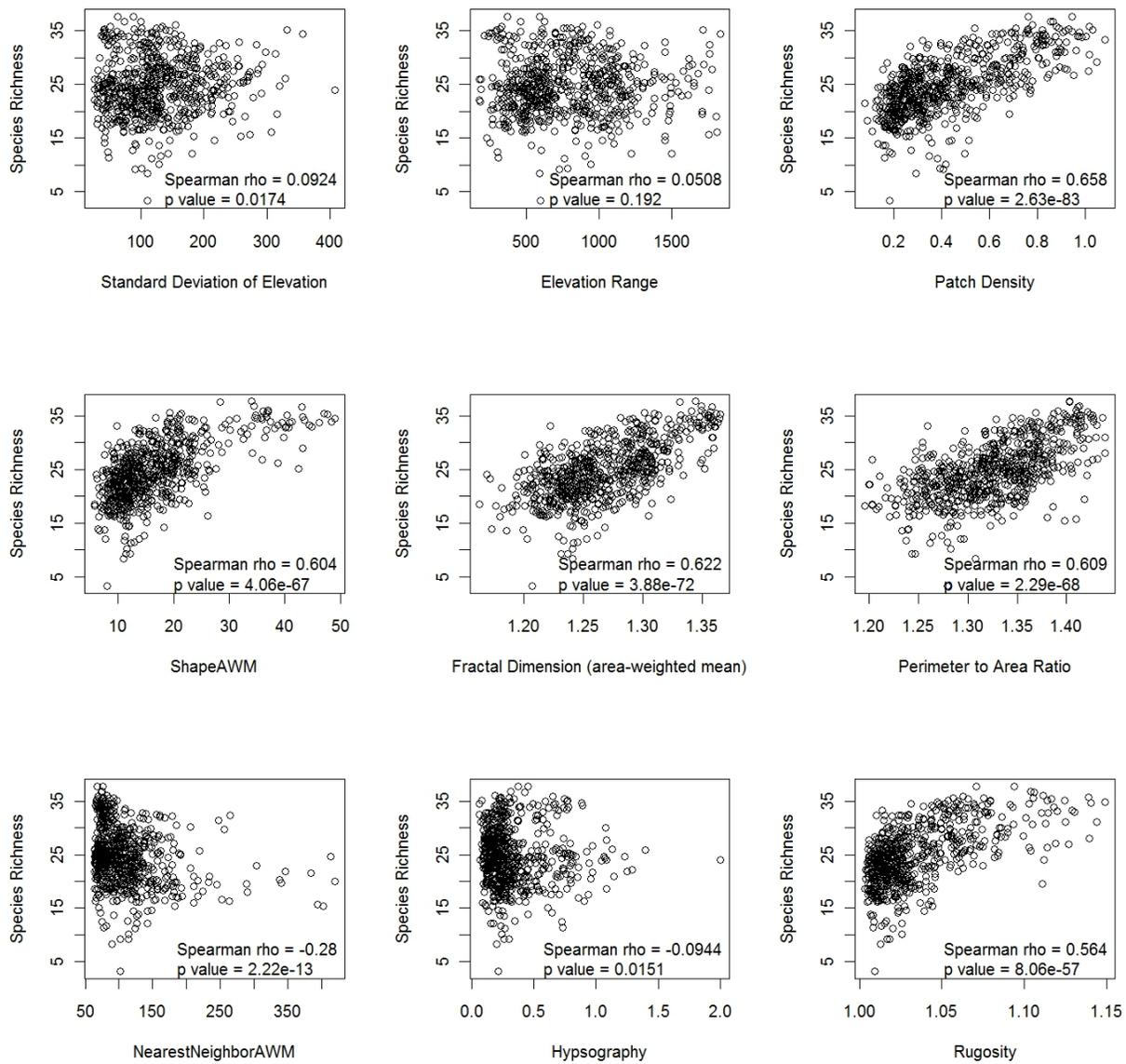


Figure A7b. Correlations (spearman Rho) between terrain metrics and Species Richness.

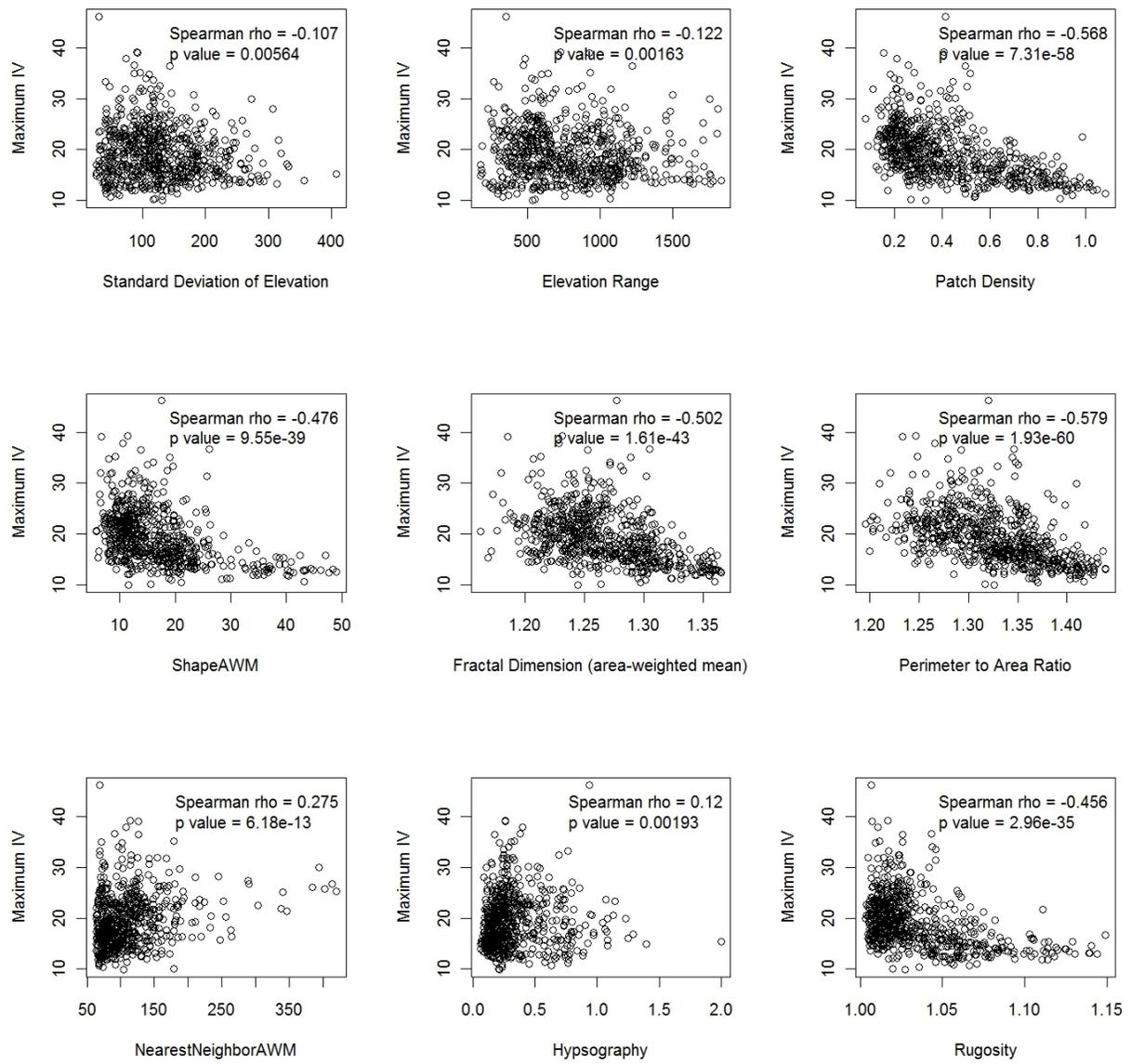


Figure A7c. Correlations (spearman Rho) between terrain metrics and Maximum IV.

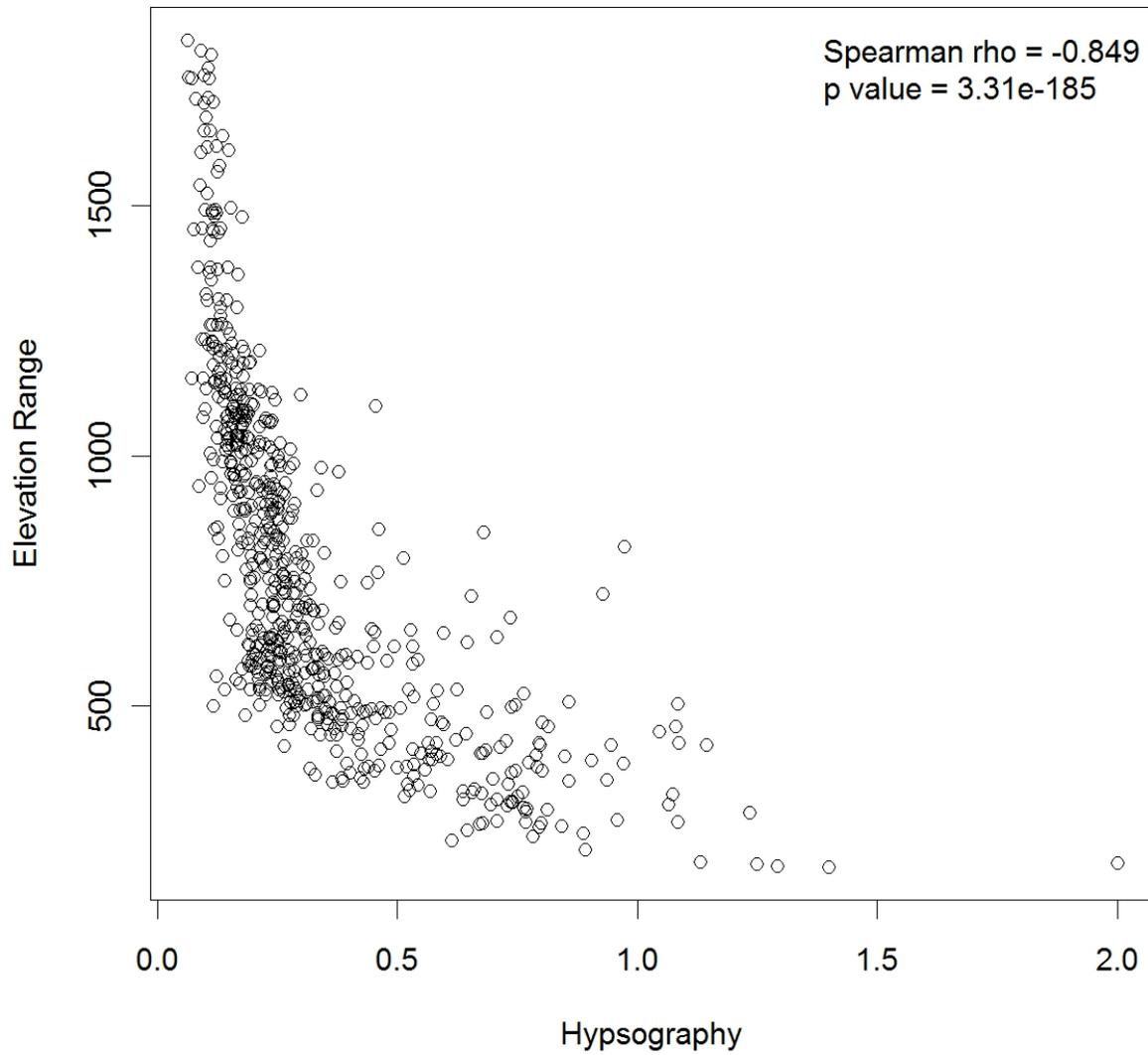


Figure A8. The relationship between elevation range and change in habitat area with elevation (hypsography).

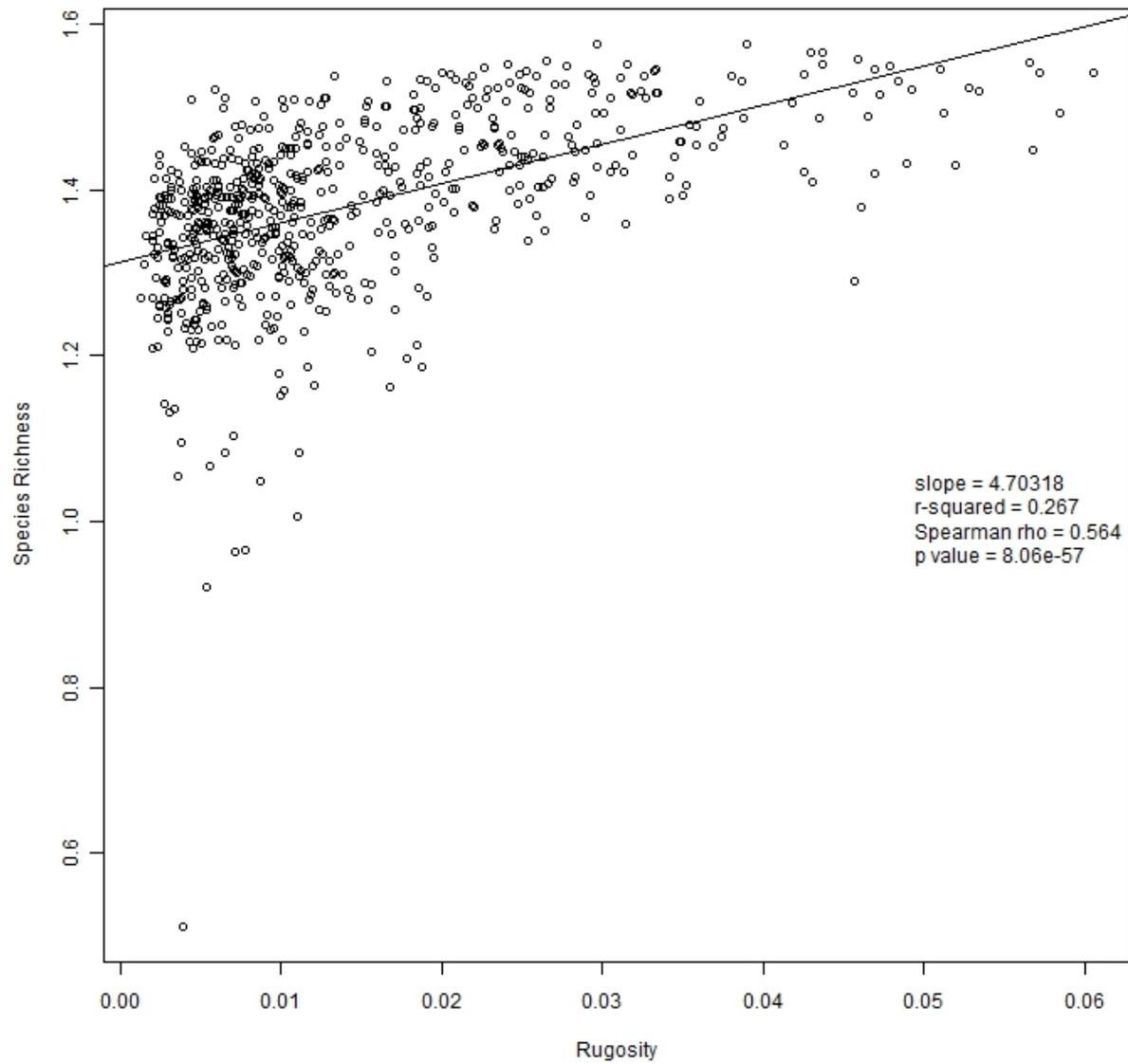


Figure A9. Species Richness as a function of rugosity (3-dimensional area divided by 2-dimensional area) in log-log scale. This is similar to a species-area relationship showing an increase in species richness in cells with larger 3-dimensional surface area.

## Supplementary Methods

The National Elevation Dataset provides a continuous topographic surface to study linkages between terrain and species diversity. National Elevation Datasets (NED) tiles for the Appalachian region were downloaded from the USGS Seamless DataServer and merged in ArcGIS 10.0 (using the MosaicToNewRaster tool). NED resolution of 1 arc second, or approximately 30 m, was used throughout the domain, with a reported vertical accuracy of +/- 2.44 m (root mean square error)<sup>31</sup>. A grid with 25 km spacing (Fig. A2) was used as center points for 250,000 ha (50 km x 50 km) extracted samples of the NED (using the ArcGIS 10.0 clip tool). With 25 km spacing and 50 km edge dimensions, each sample overlaps its neighbors by 50%. The 25 km grid spacing provides an adequate spatial resolution to characterize the study area, while the 250,000 ha sample area is large enough to capture whole mountain features. Sensitivity analysis, described below, was performed to assess the effect of the elevation data resolution, sample size, and location on the metrics.

Several authors have reviewed techniques for quantitative description of topographic surfaces including shape irregularity metrics that link habitat patch shape irregularity to forest biodiversity<sup>32</sup>. Others have specifically identified terrain complexity (surface roughness) as important in analyses of landscape structure and have reviewed available metrics<sup>33,34</sup>. Previous studies of topographic metrics have focused on mean elevation, elevation range (relief), slope, aspect, or solar insolation<sup>5, 23, 25, 26</sup> and some have extended the analysis to include topographic complexity or roughness<sup>7</sup>. Another approach has been to use species-area relationships to understand declining richness with elevation<sup>20</sup>. Connectedness of features has also been investigated<sup>7, 27</sup>. Of the metrics reviewed in the literature, those that quantify an aspect of terrain that is related to species' adaptive responses to climate change, or to biodiversity in general were

selected for this study. Table S1 defines these selected metrics, describes the tools or methods used to measure them, explains the hypothetical ecological implications of the measured topographic characteristics, and provides references documenting prior applications of the metrics.

<b>Metric</b>	<b>Definition</b>	<b>Tools<sup>1</sup></b>	<b>Ecological Relevance</b>	<b>References</b>
<b>Elevation Range</b>	Maximum Elevation – Minimum Elevation within a sample area	ArcGIS 10.0, Raster Statistics	A greater elevation range (sometimes called relief) provides a wider range of climate spaces for temperature and precipitation.	34, 35
<b>Standard Deviation of Elevation</b>	Standard deviation of elevations within a sample area	ArcGIS 10.0, Raster Statistics	Similar to Elevation range, but indicating the degree of variability across the sample area	7, 25, 33, 34
<b>Rugosity</b>	3-dimensional surface area / 2-dimensional surface area	ArcGIS 10.0, 3D Analyst, Surface Volume Tool	Higher values are found in areas with greater altitudinal variation and gentler slopes, which may provide a wider range of climate spaces.	34
<b>Density of Topographic Contours</b>		FRAGSTATS 3.3, (Area/Density/Edge Metrics), Patch Density	This metric provides an indication of slope and elevation range. Higher densities represent areas with a higher diversity of climate niches.	34,36
<b>Fractal Dimension</b>	$2 * \ln(0.25 * \text{Patch Perimeter}) / \ln(\text{Patch Area})$	FRAGSTATS 3.3 (Shape Metrics), Fractal Dimension Index	Fractal dimension has been evaluated for topography <sup>37,38</sup> but not using contour lines which should provide an integrated index of aspect variability <sup>5,7</sup> and landform variability (coves and noses) <sup>26</sup> . These topographic characteristics govern sun and wind exposure, and effect hydrology and soil depth, so the variability therein should represent the density of diverse habitats.	39

<b>Perimeter to Area Ratio</b>	Patch Perimeter (m) / Patch Area (m <sup>2</sup> )	FRAGSTATS 3.3 (Shape Metrics), Perimeter to Area Ratio	Ecological relevance is similar to fractal dimension	<sup>36</sup>
<b>Shape</b>	Patch perimeter / minimum possible patch perimeter for the same area	FRAGSTATS 3.3 (Shape Metrics), Shape Index	Ecological relevance is similar to fractal dimension	<sup>36</sup>
<b>Nearest Neighbor</b>	Distance between patches of the same elevation	FRAGSTATS 3.3, (Isolation/Proximity Metrics), Euclidean Nearest Neighbor Distance	If species are adapted to a temperature at a given elevation, northward migration may require wind-dispersed seed to cross valleys to sites at the same elevation <sup>40</sup> . Rare long distance seed dispersal events on the order of 100-300 m may result from uplifting wind conditions <sup>41</sup> , but more common maximum distances are approximately 50 m <sup>42</sup> .	<sup>33</sup>
<b>Hypsography</b> <sup>45</sup>	Rate of change of 3-dimensional surface area with increasing elevation	ArcGIS 10.0, 3D Analyst, Surface Volume Tool	Habitat area contracts at higher and higher elevations <sup>50</sup> . Species migrating upslope may experience greater competition for resources.	<sup>43-46</sup>

2. ArcGIS 10.0 produced by ESRI. FRAGSTATS 3.3 produced by Kevin McGarigal and others<sup>29</sup>. Additional tools and processes were written in Python (2.6 and 2.7) using arcpy and rpy with R <sup>47</sup>.

As some have pointed out<sup>33,48</sup> the patch mosaic paradigm has not been well-suited to analyses of continuous data, like topography. In this study, topographic contours are used to create patches and patch shape is analyzed to quantify and compare topographic complexity. “Patches” are areas between contour lines, generated by classifying sample areas (Reclassify\_3D in Arc GIS 10.0). Instead of mean values, area-weighted mean values for Fractal Dimension, Shape, and Nearest Neighbor metrics were used to prevent the numerous small topographic contour patches from overwhelming the average and masking the characteristics of the largest contours which are more representative of the area<sup>49</sup>.

Hypsography has previously been used most by geomorphologists to compare the erosional state of mountains and indicate their age<sup>46,50</sup>. ArcGIS was used to calculate the 3-dimensional area below elevations from 0 to 2200 m in 50 m increments. Traditionally, a hypsography curve is a plot of area (on the x axis (often normalized)) and elevation (on the y-axis, also normalized). Here, the slope of a graph of area vs. elevation, calculated using R’s linear model ignoring the tails (between 5% and 95% of the cumulative surface area), represents the rate of change of 3-dimensional area per 100 m elevation gain. Only one grid point had a total elevation change of less than 50 m and its slope was assigned the maximum value (to indicate a loss of 100% of the area in 50 m).

Several tests were used to understand the effect of sample location, size, and NED resolution on fractal dimension and change in area with elevation. To test the effect of elevation sample location, a cluster of 7 points was randomly generated inside a circle of radius 25 km, in each of five test landscapes in North Carolina, West Virginia, Pennsylvania, New York, and New Hampshire (example Fig. A3). 50 km x 50 km NED sample areas were based on these random points and terrain metrics were generated for each elevation sample. The purpose of this test was

to determine whether or not there could have been a bias in the results related to the placement of the grid. In these same five test landscapes, 10000 km<sup>2</sup> (100 km x 100 km) sample areas, and four nested 50 km x 50 km sample areas, 16 25 km x 25 km sample areas, 25 20 km x 20 km sample areas, and 100 10 km x 10 km sample areas were analyzed to determine the effect of sample size on terrain metrics (Fig. A4). These different sized elevation samples were used to determine the scaling properties of the metrics. In North Carolina and Pennsylvania, in addition to the 1 arc-second NED, resolutions of 1/3<sup>rd</sup> arc second and 1/9<sup>th</sup> arc second were used to understand the effect of grain size on terrain metrics.

Tree species diversity was derived from the Forest Inventory Analysis Data and processed to provide importance values for each of 134 species in a 20 km x 20 km grid covering the eastern U.S.<sup>11</sup> For each 20 km x 20 km cell in the raw data, the Shannon Diversity index ( $IV \cdot \log(IV)$ ) (Fig. A1), the number of species (simple measure of richness) (Fig. A5), and the maximum importance value (measure of homogeneity) (Fig. A6), were calculated and interpolated to 10.9 km resolution using the inverse distance weighting tool in ArcGIS 10.0, and then values were extracted for each terrain analysis grid point. Some grid points have very low Shannon Diversity Indices and might be considered outliers because the low diversity is probably an indication of land use or land use history that reduced the number of tree species found in these places. (Several are near major urban areas like Atlanta, GA, Hagerstown, MD, and Pittsburgh, York, and Lancaster, PA.) Nonetheless, the reported results include all grid points. Most of the terrain metric datasets were non-normal so the relationship between terrain variables and diversity indices was determined using spearman correlation coefficients calculated between each topographic metric and the Shannon Diversity Index. P-values were low, on the order of  $1 \times 10^{-3}$  and lower (Fig. A7a-c).

## Supplementary Notes

The three measures of diversity, Shannon diversity index, species richness, and maximum importance value are related. The Shannon diversity index increases as the number of species in a cell increases but as the maximum importance value goes down. This explains why species richness and the Shannon Diversity index had opposite relationships with terrain metrics (Figs. A7a-c). Relationships between measures of topographic roughness and biodiversity can be fit by a linear model. For example, the relationship between Shannon index and density of contour patches has a slope of 0.98 ( $r^2 = 0.43$ ), demonstrating a very close relationship between tree species diversity and topographic complexity. The intercept of 2.3 may indicate a base level of biodiversity that exists independent of topographic complexity.

The main paper highlights the relationship between the density of contour patches and the Shannon index because this represents the most strongly correlated result. However, other measures of topographic roughness (rugosity, shape, fractal dimension, and perimeter to area ratio) were also positively correlated with tree species diversity, with Spearman's rho of 0.56, 0.59, 0.61, and 0.63 respectively ( $p < 0.0001$ ) (Fig. A7a), and these roughness metrics also correlated well with species richness (Fig. A7b). By contrast, measures of area loss with elevation and the nearest neighbor distances are not correlated with species diversity (Fig. A7a).

Despite the weak relationship between area loss with elevation and tree species diversity, relationships with other indications of diversity, rarity, or endemism were evident. For example, a cluster of four nodes on the northwestern side of Great Smoky Mountains National Park accounted for five out of the six lowest losses of area with elevation in the entire Appalachian region losing only 6% of the land surface per 100 m elevation gain. In contrast, flatter areas, like the foothills or the mid-Atlantic, have much higher losses of area with elevation (as much as 100

% per 100 m). Interestingly, although absolute elevation range is related to loss of area with elevation gain (Spearman's rho -0.85,  $p < 0.0000$ ) the relationship is non-linear (Supplementary Fig. A8).

Sensitivity of metrics to choices of sample area location, sample area size, and elevation data resolution were tested. Results indicated greater differences among regions than within regions. For example, the rate of change of habitat area with increasing elevation had a coefficient of variation (CV) (of the 7 randomly placed elevation samples within each test landscape) ranging from 6.5 in the New York test landscape to 32.6 in the North Carolina test landscape, (the average CV across the test landscapes was 21.2). By contrast, the variability in the rate of change of habitat area with increasing elevation between test landscapes had a coefficient of variation of 41.4 (North Carolina had an average loss of habitat area with elevation of 14.4 while New York's was 40.5). Thus while the exact location of an elevation sample in a given region affects the terrain metrics values, this effect is minor compared to the differences among the regions. Other metrics were similar. For example, fractal dimension had generally much lower variability within a test landscape, with CV ranging from 0.37 to 0.40, while the CV between the test landscapes was 2.54.

When investigating the effect of elevation sample size (10, 20, 25, 50, and 100 km samples), we found relatively small differences between 50 km and 100 km samples in all but the West Virginia test area, but losses of habitat area with elevation were greater the smaller the sample size for 10, 20, and 25 km samples in all landscapes, In New York, Pennsylvania, and North Carolina, coefficient of variation increased with the smaller sample sizes (NY: 0.09-0.27; PA: 0.15-0.71; NC: 0.31-0.81), while in New Hampshire it decreased (0.18-0.04) and in West Virginia it was relatively constant (~0.40-0.43). By contrast, larger elevation sample sizes tended

to have higher fractal dimensions (9.0-10.6 %) although standard error was quite low within the sets of sample elevation sizes (0.004).

Tests of elevation data resolution (1 arc-second, 1/3<sup>rd</sup> arc-second, and 1/9<sup>th</sup> arc-second) were incomplete because computational limitations prevented FRAGSTATS runs on the 1/9<sup>th</sup> arc-second dataset. Comparisons of the three resolution datasets yielded higher losses of area with increasing elevation in higher resolution samples in North Carolina (12.6 for the 1/9<sup>th</sup> arc second sample vs. 10.0 for the 1 arc second sample) but the opposite trend in Pennsylvania (26.7 for the 1/9<sup>th</sup> arc second sample vs. 28.2 for the 1 arc second sample). These limited results suggest that elevation data resolution does not appear to introduce a bias in terrain metrics. These results are consistent with Hurtrez (1999)<sup>43</sup> who found that hypsography was resolution independent and scale dependent.

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## Appendix B: High Elevation Species Information

	Scientific name	Age of reproduction	Season of seed release	Dispersal vector	Dispersal distance	Soil pH	Soil type	Elevation	Notes
Fraser fir	<i>Abies fraseri</i>	15 years	September-October	wind	274 m (50%) 1.6 km (maximum)	3.5-4.2	Inceptisol	1372 m min, 1676 m common, 2037 m max	Greatest threat is balsam wooly adelgid
Balsam fir	<i>Abies balsamea</i>	20-30 years	August - November	Wind and rodents	25 – 60 m (common), 160 m (maximum)	Wide range, but soil types are all typically acidic	Spodosol, Inceptisol, and Histosol		
Carolina hemlock	<i>Tsuga caroliniana</i>	~25 years	September - Winter	wind		3.5-4.5	Podzolization	400-1220 m	Threatened by hemlock wooly adelgid

Data for fraser and balsam fir are from Silvics of North America, data for Carolina hemlock is from [www.conifers.org](http://www.conifers.org) “The Gymnosperm Database” and the Forest Service Fire Effects Information System.

Coladonato, Milo 1993. *Tsuga caroliniana*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/> [2012, June 19].

## **Appendix C: Description of Circuitscape**

Circuitscape is a free open-source software program that reads raster data characterizing the ease of movement through a landscape and interprets the raster cells as nodes in a circuit with the cell values representing electric conductance or resistance between nodes. Modeling connectivity using electrical circuit theory has a number of advantages, particularly for the study described here. First, models of permeability that range continuously between complete barriers and perfectly connected places are best represented by raster fields of continually varying values. This raster grid translates readily into an electrical circuit where nodes are not discreet habitat patches, but data points in a surface. Second, effective electrical resistance goes down as more alternative pathways are provided (McRae et al. 2008). This is important for an ecological network modeling seed dispersal and regeneration because migration potential (conductance) is greatly enhanced when pathways are wider or more numerous. Third, it assumes the movement through the network proceeds according to a random walk rather than showing preference for least-cost paths as if “knowing” the network strengths and weaknesses at the outset (McRae et al. 2008). Finally, measures of landscape connectivity are relevant and intuitive. A very good measure of connectivity is the resistance distance defined as the effective resistance between a pair of nodes (McRae et al. 2008). Current at a node within a circuit model is proportional to the probability of movement through the node. Nodes with high current are pinch points – critical nodes for network connectivity (McRae et al. 2008).

## Appendix D: MC1 command line options

Command line options for each of the simulation phases:

### Equilibrium

```
./mc1 -Y 3000 -r $lv_row_range -c $lv_col_range -P Input/USeast4km -G WWETAC --  
set_code_flag ALT_TREE_ALLOMETRY --set_code_flag ALT_FUEL_LOAD --ffmc_EN  
$lv_ffmc_EN --ffmc_EN_DB $lv_ffmc_EN_DB --bui_EN $lv_bui_EN --bui_EN_DB  
$lv_bui_EN_DB --mask_file mask_east.nc -B Input/ModelParameters_63 -J co2ramp_3000 -N 1 -0  
0.041666667 -1 47.56304169 -2 -86.97917175 -Cm -m 2 -E 10. -g 0.67 -f spinupVars.txt -o  
../../Output/FS/Manuscript/EQ_NEA_08282012 -t -2
```

### Spinup

```
./mc1 -Y 1000 -r $lv_row_range -c $lv_col_range -P Input/USeast4km -G WWETAC --  
set_code_flag ALT_TREE_ALLOMETRY --set_code_flag ALT_FUEL_LOAD --ffmc_EN  
$lv_ffmc_EN --ffmc_EN_DB $lv_ffmc_EN_DB --bui_EN $lv_bui_EN --bui_EN_DB  
$lv_bui_EN_DB --mask_file mask_east.nc -B Input/ModelParameters_63 -J co2ramp_3000 -N 1 -0  
0.041666667 -1 47.56304169 -2 -86.97917175 -Cm -m 3 -E 10 -F 1 -f spinupVars.txt -o  
../../Output/FS/Manuscript/SU_NEA_08282012 -b  
../../Output/FS/Manuscript/EQ_NEA_08282012_bgc.nc -t -4 -i 1 -d 13456
```

### Historical

```
./mc1 -Y 114 -A 1895 -r $lv_row_range -c $lv_col_range -P Input/USeast4km -G WWETAC --  
set_code_flag ALT_TREE_ALLOMETRY --set_code_flag ALT_FUEL_LOAD --ffmc_EN  
$lv_ffmc_EN --ffmc_EN_DB $lv_ffmc_EN_DB --bui_EN $lv_bui_EN --bui_EN_DB  
$lv_bui_EN_DB --mask_file mask_east.nc -B Input/ModelParameters_63 -J  
co2ramp_SRESa2_200 -N 1 -0 0.041666667 -1 47.56304169 -2 -86.97917175 -Cm -m 4 -F 1 -E 10 -  
f OutputVars_bareminimum.txt -o  
../../Output/FS/Manuscript/Hist_NEA_09092012_withSpeciesFD -b  
../../Output/FS/Manuscript/SU_NEA_08282012_bgc.nc -t 12 -i 12 -d 13456 --depth-ratio-input
```

### Specifics:

-Y: duration of the simulation, years

-A: The first calendar year of the simulation

-r: restrict the simulation to a range of rows

-c: restrict the simulation to a range of columns

-P: path to the input files

-G: biogeography rule system (VEMAP, LYNX, NA8km, CA08, YOSE, WWETAC, VINCERA, US50km) I am using the WWETAC rules

--set\_code\_flag: A new tree allometry system was developed by Dave King and offers significant improvements for deciduous forests.

--set\_code\_flag: A new fuel local calculation developed by Dave King changes the calculation of dead wood. The standard MC1 calculation allocates dead wood to the 1, 10, 100, and 1000 hr fuel classes by %, and the new algorithm sets 1-hr fuel equal to litter + standing grasses, 10-hr and 100-hr fuel equals 50% of the dead fine wood and 100-hr fuel = dead coarse wood.

--ffmc\_EN and EN\_DB: fine fuel moisture code threshold settings for Evergreen Needleleaf and Deciduous Broadleaf

--bui\_EN and EN\_DB: buildup index threshold settings for Evergreen Needleleaf and Deciduous Broadleaf

--mask\_file: reduce computational time by restricting the model domain to a focal area.

-B: path to CENTURY parameter files

-J: CO2 ramp filename

-N: nitrogen limitation; 0=limited, 1=unlimited. (MC1 has never been parameterized for limited N conditions (Dominique Bachelet, pers. comm.)

-0: cell spacing in decimal degrees

-1: latitude of northwest corner (reference datum) in decimal degrees (row 0)

-2: longitude of northwest corner (reference datum) in decimal degrees (column 0)

-C: Calculate PET (m = Marks, p = Penman-Monteith)

-m: mode (1=MAPSS EQ; 2=CENTURY EQ; 3=MC transient seeded by mode 2; 4= MC transient seeded by mode 3)

-F: Fire mode (0=scheduled; 1=fire model)

-E: max Efold value

-f: file containing list of variables to include in output file. Careful, the more you choose, the slower this will run!

-o: output filename

-b: netcdf file to initialize one-step runs (like starting spinup, and using EQ to initialize it)

-t: Month start for bgc output

-i: Month interval for bgc output

-d: size (bytes) of the data\_point structure saved for warmstart

--depth-ratio-input: including this flag tells MC1 to read depth\_ratio data from a netcdf file with a specific value for each cell. This option is specific to the MC1 version used in this study.

## Appendix E: MC1 parameterization

MC1 is a hybrid model which employs the biogeochemical model CENTURY, the biogeographical model MAPSS, and the fire module MCFire. Each of these models relies on parameter sets that define rates, relationships, and characteristics of variables that interact through the functions at the heart of each of the models.

**CENTURY** calls external parameter files with a specific MC1 format. We updated tree.100 values based on parameterization for eastern forests provided by Cindy Keough (Natural Resource Ecology Laboratory, Colorado State University) (personal communication). Of importance were changes in the decomposition rate of dead fine wood which was increased by more than 50% from 0.9 to 1.5 while decomposition of dead large wood and dead coarse roots were decreased from 0.4 to 0.2 and 0.1 respectively.

SUPRT	-DN-	-EN-	-DB-	-EB-	
1.0					'DECID'
10000.	10000.	10000.	10000.	10000.	'PRDX(3)'
250. 250.	250.	250.	250.		'PRDX(4)'
26.0 15.	26.	30.	30.		'PPDF(1)'
45.0 30.	45.	45.	45.		'PPDF(2)'
1.5 0.5	1.50	1.0	1.0		'PPDF(3)'
2.5 5.0	2.5	2.5	3		'PPDF(4)'
30.0 100.0	100.0	20.0	20.0		'CERFOR(1,1,1)'
396.0	396.0	396.0	396.0	396.0	'CERFOR(1,1,2)'
40.0 40.0	40.0	40.0	40.0		'CERFOR(1,1,3)'
45.0 50.0	50.0	35.0	35.0		'CERFOR(1,2,1)'
500.0	500.0	500.0	500.0	500.0	'CERFOR(1,2,2)'
83. 83.	83.	83.	83.		'CERFOR(1,2,3)'
204. 310.	310.	120.0	120.0		'CERFOR(1,3,1)'
500.0	500.0	500.0	500.0	500.0	'CERFOR(1,3,2)'
70. 70.	70.	70.	70.		'CERFOR(1,3,3)'
250.0	900.0	600.0	200.0	150.0	'CERFOR(1,4,1)'
479. 479.	479.	479.	479.		'CERFOR(1,4,2)'
131. 131.	131.	131.	131.		'CERFOR(1,4,3)'
150. 600.	600.	150.	150.		'CERFOR(1,5,1)'
833. 833.	833.	833.	833.		'CERFOR(1,5,2)'
100. 100.	100.	100.	100.		'CERFOR(1,5,3)'
70.0 100.0	100.0	30.0	30.0		'CERFOR(2,1,1)'
396.0	396.0	396.0	396.0	396.0	'CERFOR(2,1,2)'
40.0 40.0	40.0	40.0	40.0		'CERFOR(2,1,3)'
70.0 81.0	81.0	60.0	60.0		'CERFOR(2,2,1)'
500.0	500.0	500.0	500.0	500.0	'CERFOR(2,2,2)'
83. 83.	83.	83.	83.		'CERFOR(2,2,3)'
250. 310.	310.	250.	180.		'CERFOR(2,3,1)'
500.0	500.0	500.0	500.0	500.0	'CERFOR(2,3,2)'
70. 70.	70.	70.	70.		'CERFOR(2,3,3)'
500.0	800.0	800.0	500.0	300.0	'CERFOR(2,4,1)'
479. 479.	479.	479.	479.		'CERFOR(2,4,2)'
131. 131.	131.	131.	131.		'CERFOR(2,4,3)'
400. 80.	80.	400.	300.		'CERFOR(2,5,1)'
833. 833.	833.	833.	833.		'CERFOR(2,5,2)'

100.	100.	100.	100.	100.	'CERFOR(2,5,3)'
59.0	90.0	90.0	59.0	40.0	'CERFOR(3,1,1)'
396.0		396.0	396.0	396.0	'CERFOR(3,1,2)'
40.	40.	40.	40.	40.	'CERFOR(3,1,3)'
50.0	80.0	80.0	50.0	76.0	'CERFOR(3,2,1)'
500.0		500.0	500.0	500.0	'CERFOR(3,2,2)'
83.	83.	83.	83.	83.	'CERFOR(3,2,3)'
99.	300.	300.	99.	84.	'CERFOR(3,3,1)'
500.0		500.0	500.0	500.0	'CERFOR(3,3,2)'
70.	70.	70.	70.	70.	'CERFOR(3,3,3)'
140.0		900.0	900.0	140.0	155.0 'CERFOR(3,4,1)'
479.	479.	479.	479.	479.	'CERFOR(3,4,2)'
40.0	40.0	40.0	40.0	40.0	'CERFOR(3,4,3)'
83.	550.	550.	83.0	155.0	'CERFOR(3,5,1)'
833.	833.	833.	833.	833.	'CERFOR(3,5,2)'
100.	100.	100.	100.	100.	'CERFOR(3,5,3)'
1.5					'DECW1'
0.02					'DECW2'
0.1					'DECW3'
0.28	0.37	0.37	0.28	0.25	'FCFRAC(1,1)'
0.21	0.34	0.34	0.21	0.25	'FCFRAC(2,1)'
0.1	0.10	0.10	0.1	0.10	'FCFRAC(3,1)'
0.33	0.18	0.18	0.33	0.30	'FCFRAC(4,1)'
0.08	0.01	0.01	0.08	0.10	'FCFRAC(5,1)'
0.28	0.37	0.37	0.28	0.34	'FCFRAC(1,2)'
0.21	0.34	0.34	0.21	0.25	'FCFRAC(2,2)'
0.1	0.10	0.10	0.1	0.11	'FCFRAC(3,2)'
0.33	0.18	0.18	0.33	0.22	'FCFRAC(4,2)'
0.08	0.01	0.01	0.08	0.08	'FCFRAC(5,2)'
0.02	0.00	0.03	0.00	0.07	'LEAFDR(1)'
0.02	0.00	0.03	0.00	0.07	'LEAFDR(2)'
0.02	0.00	0.03	0.00	0.07	'LEAFDR(3)'
0.02	0.00	0.03	0.00	0.07	'LEAFDR(4)'
0.02	0.00	0.03	0.00	0.07	'LEAFDR(5)'
0.02	0.00	0.03	0.00	0.07	'LEAFDR(6)'
0.02	0.00	0.03	0.06	0.07	'LEAFDR(7)'
0.02	0.00	0.03	0.06	0.07	'LEAFDR(8)'
0.02	0.00	0.03	0.06	0.07	'LEAFDR(9)'
0.02	0.00	0.03	0.06	0.07	'LEAFDR(10)'
0.02	0.00	0.03	0.00	0.07	'LEAFDR(11)'
0.02	0.00	0.10	0.00	0.07	'LEAFDR(12)'
0.008		0.012	0.004	0.01	0.007 'BTOLAI'
1500.0		2000.0	2000.0	1500.0	1000.0 'KLAI'
-0.47000					'LAI TOP'
6.	10.	10.	6.	6.	'MAXLAI'
1.0					'MAXLDR'
0.8000					'FORRTF(1)'
0.0					'FORRTF(2)'
0.0					'FORRTF(3)'
1500.00					'SAPK'
0.0					'SWOLD'
0.20300					'WDLIG(1)'
0.08000					'WDLIG(2)'
0.25000					'WDLIG(3)'

0.25000						'WDLIG(4)'
0.25000						'WDLIG(5)'
1.0	1.0	0.0	1.0	0.0		'WOODDR(1)'
0.032		0.05	0.05	0.04	0.03	'WOODDR(2)'
0.040		0.01	0.01	0.01	0.01	'WOODDR(3)'
0.0012		0.0008	0.0008	0.002	0.002	'WOODDR(4)'
0.0021		0.001	0.001	0.004	0.004	'WOODDR(5)'
0.000						'SNFXMX(2)'
-26						'DEL13C'
1.25						'CO2IPR'
0.75						'CO2ITR'
1.25						'CO2ICE(1,1,1)'
1.0						'CO2ICE(1,1,2)'
1.0						'CO2ICE(1,1,3)'
1.25						'CO2ICE(1,2,1)'
1.0						'CO2ICE(1,2,2)'
1.0						'CO2ICE(1,2,3)'
1.0						'CO2IRS'
1.0						'BASFC2'
400.0						'BASFC1'
2400.0		4800.0	4800.0	2400.0	2400.0	'SITPOT'

## MCFire

MC1 was developed in western forests and most users keep the black oak and Douglas fir parameters to characterize deciduous broadleaf and evergreen needleleaf trees respectively. We reduced the tree sizes by substituting chestnut oak for black oak - diameter at breast height (dbh) changed from 349 to 100 cm and maximum height changed from 3960 to 2400 cm. We also reduced tree size for evergreen needleleaf trees by substituting white pine for Douglas fir – dbh changed from 220 to 100 cm and maximum height changed from 8000 to 4000 cm.

## Appendix F: Program to calculate fire regime statistics from MC1 fire output variables.

```
# This program reads MC1 netcdf output files and calculates a fire index for all active cells.
# The file is in subversion repository under a project called MCD.

# Open code modules
import numpy
import scipy
from scipy.io import netcdf
import csv

# Set local directories and filename stubs
cellid_data_dir = '/Users/elizabethcrisfield/MC1/input/USeast4km/'
input_data_dir = '/Users/elizabethcrisfield/MCD/data_interaction/'
output_data_dir = '/Users/elizabethcrisfield/MCD/data_interaction/fire_index/'
#scenarios = 'Hist_', 'csiroa2_', 'hadleya2_'
scenarios = 'Hist_', 'fake'
#time_steps = '30_1', '30_2', '30_3', '10_4'
time_steps = '99y', 'fake'
hist_filename_stub = '09092012_year_original_discard'

hist_done = 'not_done_yet'
# INITIATE LOOP THROUGH SENARIOS
for scenario in scenarios:
    print scenario
    output_filename_stats = output_data_dir + scenario + "99y_annual_fire_stats.csv"
    output_file_stats_open = open(output_filename_stats, 'w')
    output_file_stats = csv.writer(output_file_stats_open, delimiter=',')
    output_file_stats.writerow("scenario, year, date, burn cell count, average forest carbon, average
part burn, average biomass consumed, average fire killed, average fire index, maximum fire index")
    # INITIATE LOOP THROUGH 30-YEAR TIME STEPS
    for ts in time_steps:
        if (scenario == 'Hist_' and hist_done == 'done'):
            print "Hist is done"
            continue
        else:
            # I/O
            if (scenario == 'Hist_'):
                input_file = input_data_dir + scenario + hist_filename_stub + ".nc"
            else:
                input_file = input_data_dir + scenario + ts + ".nc"
            #Read netcdf file
            raw_nc_file = netcdf.netcdf_file(input_file, 'r')
            mask_temp = raw_nc_file.variables['mask']
            mask = mask_temp[:]
```

```

nlat = raw_nc_file.dimensions['lat']-2
nlon = raw_nc_file.dimensions['lon']
rows = range(nlat)
cols = range(nlon)

year_temp = raw_nc_file.variables['year']
year_labels = year_temp[:]
no_years = len(year_labels)
print no_years
years = range(no_years)

burn_year_temp = raw_nc_file.variables['burn_year']
burn_year = burn_year_temp[:]

part_burn_temp = raw_nc_file.variables['PART_BURNyr']
part_burn = part_burn_temp[:]

bio_consume_live_temp = raw_nc_file.variables['bio_consume_live']
bio_consume_live = bio_consume_live_temp[:]

fire_killed_temp = raw_nc_file.variables['FIRE_KILLEDyr']
fire_killed = fire_killed_temp[:]

C_FOREST_temp = raw_nc_file.variables['C_FORESTyr']
C_FOREST = C_FOREST_temp[:]

raw_nc_file.close()
# MAIN
# Initialize variables
forest_carbon = {}
cumul_fire_index = {}
burns = {}
average_part_burn = {}
average_bio_consume_live = {}
average_fire_killed = {}
average_fire_index = {}
max_fire_index = {}
# INITIATE LOOP THROUGH YEARS
for y in years:
    if ts == "30_1":
        date = y
        first_years = no_years
    if ts == "30_2":
        date = y + first_years
    if ts == "30_3":
        date = y + first_years + 30
    if ts == "10_4":
        date = y + first_years + 60

```

```

if ts == "99y":
    date = y
    cell_count = 0
    active_cell_count = 0
    max_fire_index_temp = 0
    cumul_fire_index_year = 0
    burn_count = 0
    forest_carbon_list = []
    part_burn_list = []
    bio_consume_live_list = []
    fire_killed_list = []
    # INITIATE LOOP THROUGH ROWS
    for row in rows:
        # INITIATE LOOP THROUGH COLUMNS
        for col in cols:
            cell_count += 1
            # Screen for active cells
            if mask[row,col] == 1:
                active_cell_count += 1
                forest_carbon_list.append(C_FOREST[y,row,col])
                if C_FOREST[y,row,col] > 5000:
                    # Screen for burn years
                    if burn_year[y,row,col] == 1:
                        burn_count += 1
                        # # Calculate fire index
                        fire_index_cell = part_burn[y,row,col]*(bio_consume_live[y,row,col] + fire_killed[y,row,col]) /
C_FOREST[y,row,col]
                        #print fire_index_cell
                        if fire_index_cell > max_fire_index_temp:
                            max_fire_index_temp = fire_index_cell
                            cumul_fire_index_year += fire_index_cell
                            part_burn_list.append(part_burn[y,row,col])
                            bio_consume_live_list.append(bio_consume_live[y,row,col])
                            fire_killed_list.append(fire_killed[y,row,col])
                            forest_carbon[y] = numpy.mean(forest_carbon_list)
                            if burn_count > 0:
                                burns[y] = burn_count
                                average_part_burn[y] = numpy.mean(part_burn_list)
                                average_bio_consume_live[y] = numpy.mean(bio_consume_live_list)
                                average_fire_killed[y] = numpy.mean(fire_killed_list)
                                average_fire_index[y] = cumul_fire_index_year/active_cell_count
                                max_fire_index[y] = max_fire_index_temp
                            else:
                                burns[y] = 0
                                average_part_burn[y] = 0
                                average_bio_consume_live[y] = 0
                                average_fire_killed[y] = 0
                                average_fire_index[y] = 0

```

```
max_fire_index[y] = 0
# OUTPUT
domain_stats = scenario, y, date, burns[y], forest_carbon[y], average_part_burn[y],
average_bio_consume_live[y], average_fire_killed[y], average_fire_index[y], max_fire_index[y]
print domain_stats
output_file_stats.writerow([domain_stats])
if (scenario == 'Hist_' and hist_done == 'not_done_yet'):
    hist_done = 'done'
output_file_stats_open.close()
```

## Appendix G: Python script to summarize dominant vegetation classes.

```
# This program reads MC1 netcdf output files and calculates vegetation classification statistics
for all active cells.
# The file is in subversion repository under a project called MCD.

# Open code modules
import numpy
import scipy
from scipy.io import netcdf
from collections import Counter
import csv

# Set local directories and filename stubs
cellid_data_dir = '/Users/elizabethcrisfield/MC1/input/USeast4km/'
input_data_dir = '/Users/elizabethcrisfield/MC1/output/Manuscript_Sensitivity/Historical/'
#input_data_dir = '/Users/elizabethcrisfield/MC1/output/Manuscript_Sensitivity/Future/'
output_data_dir = '/Users/elizabethcrisfield/MCD/data_interaction/fire_index/sensitivity/'

scenarios = 'Hist_ME_8873_nofire', 'Hist_ME_9075_042', 'Hist_ME_8873_042',
'Hist_ME_8670_042', 'Hist_ME_8265_042', 'Hist_ME_7860_042', 'Hist_ME_7455_042',
'Hist_ME_7440_042', 'csiropa2_8873_ME', 'csiropa2_8873_ME_nofire', 'hadleya2_8873_ME',
'hadleya2_8873_ME_nofire', 'miroca2_8873_ME', 'miroca2_8873_ME_nofire',
'Hist_NY_8873_nofire', 'Hist_NY_8873_042', 'Hist_NY_8670_042', 'Hist_NY_8265_042',
'Hist_NY_7860_042', 'Hist_NY_7455_042', 'Hist_NY_7440_042', 'csiropa2_8873_NY',
'csiropa2_8873_NY_nofire', 'hadleya2_8873_NY', 'hadleya2_8873_NY_nofire', 'miroca2_8873_NY',
'miroca2_8873_NY_nofire', 'Hist_PA_8873_nofire', 'Hist_PA_8873_042', 'Hist_PA_8670_042',
'Hist_PA_8265_042', 'Hist_PA_7860_042', 'Hist_PA_7455_042', 'Hist_PA_7440_042',
'csiropa2_8873_PA', 'csiropa2_8873_PA_nofire', 'hadleya2_8873_PA', 'hadleya2_8873_PA_nofire',
'miroca2_8873_PA', 'miroca2_8873_PA_nofire', 'Hist_GAh_8873_nofire', 'Hist_GAh_9075_042',
'Hist_GAh_8873_042', 'Hist_GAh_8670_042', 'Hist_GAh_8265_042', 'Hist_GAh_7860_042',
'Hist_GAh_7455_042', 'Hist_GAh_7440_042', 'csiropa2_8873_GAh', 'csiropa2_8873_GAh_nofire',
'hadleya2_8873_GAh', 'hadleya2_8873_GAh_nofire', 'miroca2_8873_GAh',
'miroca2_8873_GAh_nofire', 'Hist_GAl_8873_nofire', 'Hist_GAl_9075_042',
'Hist_GAl_8873_042', 'Hist_GAl_8670_042', 'Hist_GAl_8265_042', 'Hist_GAl_7455_042',
'Hist_GAl_7440_042', 'csiropa2_8873_GAl', 'csiropa2_8873_GAl_nofire', 'hadleya2_8873_GAl',
'hadleya2_8873_GAl_nofire'

# INITIATE LOOP THROUGH SENARIOS
for scenario in scenarios:
# I/O
input_file = input_data_dir + scenario + "_year.nc"
# Read netcdf file
raw_nc_file = netcdf.netcdf_file(input_file,'r')
# print raw_nc_file.variables
mask_temp = raw_nc_file.variables['mask']
```

```

mask = mask_temp[:]
nlat = raw_nc_file.dimensions['lat']-2
# print nlat
nlon = raw_nc_file.dimensions['lon']
# print nlon
# row_max = mask_temp.shape[0]
# col_max = mask_temp.shape[1]
rows = range(nlat)
cols = range(nlon)

year_temp = raw_nc_file.variables['year']
year_labels = year_temp[:]
no_years = len(year_labels)
years = range(no_years)

burn_year_temp = raw_nc_file.variables['burn_year']
burn_year = burn_year_temp[:]

VTYPE_temp = raw_nc_file.variables['VTYPEyr']
VTYPE = VTYPE_temp[:]

raw_nc_file.close()

output_filename_main = output_data_dir + "fire_index_" + scenario + ".csv"
output_file_main_open = open(output_filename_main, 'w')
output_file_main = csv.writer(output_file_main_open, delimiter=',')
output_file_main.writerow("cell_id, fire_index")
# MAIN
# Initialize variables
percent_time_woodland = {}
dominant_vtype = {}
percent_time_forest = {}
percent_time_temperate = {}
cell_count = 0
active_cell_count = 0
burn_cell_count = 0
# INITIATE LOOP THROUGH ROWS
for row in rows:
# INITIATE LOOP THROUGH COLUMNS
for col in cols:
cell_count += 1
cell_id = cell_count
vtype_list = []
# Screen for active cells
if mask[row,col] == 1:
active_cell_count += 1
vtype4 = 0
vtype5 = 0

```

```
vtype6 = 0
vtype7 = 0
vtype8 = 0
vtype9 = 0
vtype10 = 0
vtype11 = 0
vtype12 = 0
vtype13 = 0
vtype14 = 0
vtype15 = 0
vtype16 = 0
vtype17 = 0
vtype18 = 0
vtype19 = 0
vtype20 = 0
vtype21 = 0
vtype22 = 0
vtype23 = 0
vtype24 = 0
vtype25 = 0
vtype26 = 0
vtype27 = 0
vtype28 = 0
vtype29 = 0
vtype36 = 0
vtype37 = 0
vtype38 = 0
```

```
# INITIATE LOOP THROUGH YEARS
```

```
for y in years:
vtype_list.append(VTYPE[y,row,col])
if VTYPE[y,row,col] == 4:
vtype4 +=1
elif VTYPE[y,row,col] == 5:
vtype5 += 1
elif VTYPE[y,row,col] == 7:
vtype7 += 1
elif VTYPE[y,row,col] == 8:
vtype8 += 1
elif VTYPE[y,row,col] == 9:
vtype9 += 1
elif VTYPE[y,row,col] == 10:
vtype10 += 1
elif VTYPE[y,row,col] == 11:
vtype11 += 1
elif VTYPE[y,row,col] == 12:
vtype12 += 1
elif VTYPE[y,row,col] == 13:
```

```

vtype13 += 1
elif VTYPE[y,row,col] == 14:
vtype14 += 1
elif VTYPE[y,row,col] == 15:
vtype15 += 1
elif VTYPE[y,row,col] == 16:
vtype16 += 1
elif VTYPE[y,row,col] == 17:
vtype17 += 1
elif VTYPE[y,row,col] == 18:
vtype18 += 1
elif VTYPE[y,row,col] == 19:
vtype19 += 1
elif VTYPE[y,row,col] == 20:
vtype20 += 1
elif VTYPE[y,row,col] == 21:
vtype21 += 1
elif VTYPE[y,row,col] == 22:
vtype22 += 1
elif VTYPE[y,row,col] == 23:
vtype23 += 1
elif VTYPE[y,row,col] == 24:
vtype24 += 1
elif VTYPE[y,row,col] == 25:
vtype25 += 1
elif VTYPE[y,row,col] == 26:
vtype26 += 1
elif VTYPE[y,row,col] == 27:
vtype27 += 1
elif VTYPE[y,row,col] == 28:
vtype28 += 1
elif VTYPE[y,row,col] == 29:
vtype29 += 1
elif VTYPE[y,row,col] == 36:
vtype36 += 1
elif VTYPE[y,row,col] == 37:
vtype37 += 1
elif VTYPE[y,row,col] == 38:
vtype38 += 1
else: print 'trouble - VTYPE wasnt defined'
dominant = 0
maximum_vtype = max(vtype4, vtype5, vtype7, vtype8, vtype9, vtype10, vtype11, vtype12,
vtype13, vtype14, vtype15, vtype16, vtype17, vtype18, vtype19, vtype20, vtype21, vtype22, vtype23,
vtype24, vtype25, vtype26, vtype27, vtype28, vtype29, vtype36, vtype37, vtype38)
if vtype4 == maximum_vtype: dominant = 4
elif vtype5 == maximum_vtype: dominant = 5
elif vtype7 == maximum_vtype: dominant = 7
elif vtype8 == maximum_vtype: dominant = 8

```

```

elif vtype9 == maximum_vtype: dominant = 9
elif vtype10 == maximum_vtype: dominant = 10
elif vtype11 == maximum_vtype: dominant = 11
elif vtype12 == maximum_vtype: dominant = 12
elif vtype13 == maximum_vtype: dominant = 13
elif vtype14 == maximum_vtype: dominant = 14
elif vtype15 == maximum_vtype: dominant = 15
elif vtype16 == maximum_vtype: dominant = 16
elif vtype17 == maximum_vtype: dominant = 17
elif vtype18 == maximum_vtype: dominant = 18
elif vtype19 == maximum_vtype: dominant = 19
elif vtype20 == maximum_vtype: dominant = 20
elif vtype21 == maximum_vtype: dominant = 21
elif vtype22 == maximum_vtype: dominant = 22
elif vtype23 == maximum_vtype: dominant = 23
elif vtype24 == maximum_vtype: dominant = 24
elif vtype25 == maximum_vtype: dominant = 25
elif vtype26 == maximum_vtype: dominant = 26
elif vtype27 == maximum_vtype: dominant = 27
elif vtype28 == maximum_vtype: dominant = 28
elif vtype28 == maximum_vtype: dominant = 29
elif vtype36 == maximum_vtype: dominant = 36
elif vtype37 == maximum_vtype: dominant = 37
elif vtype38 == maximum_vtype: dominant = 38

```

```

dominant_vtype[cell_id] = dominant
percent_time_temperate[cell_id] = (vtype8 + vtype9 + vtype10 + vtype11 + vtype12 + vtype13
+ vtype14 + vtype15 + vtype16 + vtype17 + vtype18)/len(years)
percent_time_forest[cell_id] = (vtype4 + vtype7 + vtype8 + vtype9 + vtype10 + vtype11 +
vtype19 + vtype20 + vtype21 + vtype22 + vtype36)/len(years)
percent_time_woodland[cell_id] = (vtype5 + vtype12 + vtype13 + vtype14 + vtype15 +
vtype23 + vtype24 + vtype25 + vtype26 + vtype37)/len(years)
else:
dominant_vtype[cell_id] = -9999
percent_time_temperate[cell_id] = -9999
percent_time_forest[cell_id] = -9999
percent_time_woodland[cell_id] = -9999
percent_temperate = 0
percent_woodland = 0
percent_forest = 0
domain_dominant_vtype_list = []
percent_temperate_list = []
percent_forest_list = []
percent_woodland_list = []
# STATS
cell_count = 0
active_cell_count = 0
for row in rows:

```

```

for col in cols:
    cell_count += 1
    cell_id = cell_count
    if mask[row,col] == 1:
        active_cell_count += 1
        domain_dominant_vtype_list.append(dominant_vtype[cell_id])
        percent_temperate_list.append(percent_time_temperate[cell_id])
        percent_forest_list.append(percent_time_forest[cell_id])
        percent_woodland_list.append(percent_time_woodland[cell_id])
        domain_dominant_vtype_counter = Counter(domain_dominant_vtype_list)
        domain_dominant_temp = domain_dominant_vtype_counter.most_common(1)
        domain_dominant_temp2 = domain_dominant_temp[0]
        domain_dominant_vtype = domain_dominant_temp2[0]
        domain_dominant_vtype_cells = domain_dominant_temp2[1]
        domain_dominant_vtype_percent = 100*domain_dominant_vtype_cells/active_cell_count
        # print domain_dominant_vtype, domain_dominant_vtype_percent
        percent_temperate = numpy.mean(percent_temperate_list)
        percent_forest = numpy.mean(percent_forest_list)
        percent_woodland = numpy.mean(percent_woodland_list)
        # OUTPUT
        domain_vtype_stats = scenario, domain_dominant_vtype, domain_dominant_vtype_percent,
percent_temperate, percent_forest, percent_woodland
        print domain_vtype_stats
        output_file_main_open.close()

```

## Appendix H: Python script to calculate carbon pool statistics.

```
# This program reads MC1 netcdf output files and calculates a fire index for all active cells.
# The file is in subversion repository under a project called MCD.

# Open code modules
import numpy
import scipy
from scipy.io import netcdf
import csv

# Set local directories and filename stubs
cellid_data_dir = '/Users/elizabethcrisfield/MC1/input/USeast4km/'
input_data_dir = '/Users/elizabethcrisfield/MC1/output/Manuscript_Sensitivity/Historical/'
#input_data_dir = '/Users/elizabethcrisfield/MC1/output/Manuscript_Sensitivity/Future/'
output_data_dir = '/Users/elizabethcrisfield/MCD/data_interaction/fire_index/sensitivity/'

#scenarios = 'Hist_ME_9075_042', 'Hist_ME_8873_042', 'Hist_ME_8670_042',
'Hist_ME_8265_042', 'Hist_ME_7860_042', 'Hist_ME_7455_042', 'Hist_ME_7440_042',
'csiropa2_8873_ME', 'hadleya2_8873_ME', 'miroca2_8873_ME', 'Hist_NY_8873_042',
'Hist_NY_8670_042', 'Hist_NY_8265_042', 'Hist_NY_7860_042', 'Hist_NY_7455_042',
'Hist_NY_7440_042', 'csiropa2_8873_NY', 'hadleya2_8873_NY', 'miroca2_8873_NY',
'Hist_PA_8873_042', 'Hist_PA_8670_042', 'Hist_PA_8265_042', 'Hist_PA_7860_042',
'Hist_PA_7455_042', 'Hist_PA_7440_042', 'csiropa2_8873_PA', 'hadleya2_8873_PA',
'miroca2_8873_PA', 'Hist_GAh_9075_042', 'Hist_GAh_8873_042', 'Hist_GAh_8670_042',
'Hist_GAh_8265_042', 'Hist_GAh_7860_042', 'Hist_GAh_7455_042', 'Hist_GAh_7440_042',
'csiropa2_8873_GAh', 'hadleya2_8873_GAh', 'miroca2_8873_GAh', 'Hist_GAl_9075_042',
'Hist_GAl_8873_042', 'Hist_GAl_8670_042', 'Hist_GAl_8265_042', 'Hist_GAl_7455_042',
'Hist_GAl_7440_042', 'csiropa2_8873_GAl', 'hadleya2_8873_GAl'
scenarios = 'Hist_ME_8873_nofire', 'Hist_ME_9075_042', 'Hist_ME_8873_042',
'Hist_ME_8670_042', 'Hist_ME_8265_042', 'Hist_ME_7860_042', 'Hist_ME_7455_042',
'Hist_ME_7440_042', 'csiropa2_8873_ME', 'csiropa2_8873_ME_nofire', 'hadleya2_8873_ME',
'hadleya2_8873_ME_nofire', 'miroca2_8873_ME', 'miroca2_8873_ME_nofire',
'Hist_NY_9075_042', 'Hist_NY_8873_nofire', 'Hist_NY_8873_042', 'Hist_NY_8670_042',
'Hist_NY_8265_042', 'Hist_NY_7860_042', 'Hist_NY_7455_042', 'Hist_NY_7440_042',
'csiropa2_8873_NY', 'csiropa2_8873_NY_nofire', 'hadleya2_8873_NY', 'hadleya2_8873_NY_nofire',
'miroca2_8873_NY', 'miroca2_8873_NY_nofire', 'Hist_PA_8873_nofire', 'Hist_PA_9075_042',
'Hist_PA_8873_042', 'Hist_PA_8670_042', 'Hist_PA_8265_042', 'Hist_PA_7860_042',
'Hist_PA_7455_042', 'Hist_PA_7440_042', 'csiropa2_8873_PA', 'csiropa2_8873_PA_nofire',
'hadleya2_8873_PA', 'hadleya2_8873_PA_nofire', 'miroca2_8873_PA', 'miroca2_8873_PA_nofire',
'Hist_GAh_8873_nofire', 'Hist_GAh_9075_042', 'Hist_GAh_8873_042', 'Hist_GAh_8670_042',
'Hist_GAh_8265_042', 'Hist_GAh_7860_042', 'Hist_GAh_7455_042', 'Hist_GAh_7440_042',
'csiropa2_8873_GAh', 'csiropa2_8873_GAh_nofire', 'hadleya2_8873_GAh',
'hadleya2_8873_GAh_nofire', 'miroca2_8873_GAh', 'miroca2_8873_GAh_nofire',
'Hist_GAl_8873_nofire', 'Hist_GAl_9075_042', 'Hist_GAl_8873_042', 'Hist_GAl_8670_042',
'Hist_GAl_8265_042', 'Hist_GAl_7455_042', 'Hist_GAl_7440_042', 'csiropa2_8873_GAl',
```

```
'csiroa2_8873_GAI_nofire', 'hadleya2_8873_GAI', 'hadleya2_8873_GAI_nofire',  
'miroca2_8873_GAI', 'miroca2_8873_GAI_nofire'
```

```
# INITIATE LOOP THROUGH SENARIOS  
for scenario in scenarios:  
    # I/O  
    input_file = input_data_dir + scenario + "_year.nc"  
    # Read netcdf file  
    raw_nc_file = netcdf.netcdf_file(input_file,'r')  
    # print raw_nc_file.variables  
    mask_temp = raw_nc_file.variables['mask']  
    mask = mask_temp[:]  
    nlat = raw_nc_file.dimensions['lat']-2  
    # print nlat  
    nlon = raw_nc_file.dimensions['lon']  
    # print nlon  
    # row_max = mask_temp.shape[0]  
    # col_max = mask_temp.shape[1]  
    rows = range(nlat)  
    cols = range(nlon)  
  
    year_temp = raw_nc_file.variables['year']  
    year_labels = year_temp[:]  
    no_years = len(year_labels)  
    years = range(no_years)  
  
    burn_year_temp = raw_nc_file.variables['burn_year']  
    burn_year = burn_year_temp[:]  
  
    part_burn_temp = raw_nc_file.variables['PART_BURNyr']  
    part_burn = part_burn_temp[:]  
  
    bio_consume_live_temp = raw_nc_file.variables['bio_consume_live']  
    bio_consume_live = bio_consume_live_temp[:]  
  
    bio_consume_dead_temp = raw_nc_file.variables['bio_consume_dead']  
    bio_consume_dead = bio_consume_dead_temp[:]  
  
    fire_killed_temp = raw_nc_file.variables['FIRE_KILLEDyr']  
    fire_killed = fire_killed_temp[:]  
  
    C_SOM_temp = raw_nc_file.variables['C_SOMyr']  
    C_SOM = C_SOM_temp[:]  
    C_NONVEG_temp = raw_nc_file.variables['C_NONVEGyr']  
    C_NONVEG = C_NONVEG_temp[:]  
  
    C_FOREST_temp = raw_nc_file.variables['C_FORESTyr']  
    C_FOREST = C_FOREST_temp[:]
```

```

C_ECOSYS_temp = raw_nc_file.variables['C_ECOSYSyr']
C_ECOSYS = C_ECOSYS_temp[:]
VTYPE_temp = raw_nc_file.variables['VTYPEyr']
VTYPE = VTYPE_temp[:]

raw_nc_file.close()

output_filename_main = output_data_dir + "fire_index_" + scenario + ".csv"
output_file_main_open = open(output_filename_main, 'w')
output_file_main = csv.writer(output_file_main_open, delimiter=',')
output_file_main.writerow("cell_id, fire_index")
# MAIN
# Initialize variables
soil_carbon = {}
nonveg_carbon = {}
forest_carbon = {}
ecosystem_carbon = {}
cumul_fire_index = {}
average_fire_index = {}
cumul_vtype = {}
burns = {}
average_vtype = {}
average_part_burn = {}
average_bio_consume_live = {}
average_fire_killed = {}
cell_count = 0
active_cell_count = 0
burn_cell_count = 0
# INITIATE LOOP THROUGH ROWS
for row in rows:
# INITIATE LOOP THROUGH COLUMNS
for col in cols:
cell_count += 1
cell_id = cell_count
cumul_fire_index_cell = 0
burn_count = 0
soil_carbon_list = []
nonveg_carbon_list = []
forest_carbon_list = []
ecosystem_carbon_list = []
vtype_list = []
part_burn_list = []
bio_consume_live_list = []
fire_killed_list = []
# Screen for active cells
if mask[row,col] == 1:
active_cell_count += 1
# INITIATE LOOP THROUGH YEARS

```

```

for y in years:
    soil_carbon_list.append(C_SOM[y,row,col])
    nonveg_carbon_list.append(C_NONVEG[y,row,col])
    forest_carbon_list.append(C_FOREST[y,row,col])
    ecosystem_carbon_list.append(C_ECOSYS[y,row,col])
    vtype_list.append(VTYPE[y,row,col])
    soil_carbon[cell_id] = numpy.mean(soil_carbon_list) #average soil carbon for the cell over the
entire period of record
    nonveg_carbon[cell_id] = numpy.mean(nonveg_carbon_list) #average nonveg carbon for the
cell over the entire period of record
    forest_carbon[cell_id] = numpy.mean(forest_carbon_list) #average forest carbon for the cell
over the entire period of record
    ecosystem_carbon[cell_id] = numpy.mean(ecosystem_carbon_list) #average ecosystem carbon
for the cell over the entire period of record
    else:
        soil_carbon[cell_id] = numpy.mean(soil_carbon_list) #average soil carbon for the cell over the
entire period of record
        nonveg_carbon[cell_id] = numpy.mean(nonveg_carbon_list) #average nonveg carbon for the
cell over the entire period of record
        forest_carbon[cell_id] = numpy.mean(forest_carbon_list) #average forest carbon for the cell
over the entire period of record
        ecosystem_carbon[cell_id] = numpy.mean(ecosystem_carbon_list) #average ecosystem carbon
for the cell over the entire period of record
    else:
        soil_carbon[cell_id] = -9999
        nonveg_carbon[cell_id] = -9999
        forest_carbon[cell_id] = -9999
        ecosystem_carbon[cell_id] = -9999
        total_vtype_temp = 0
        total_average_soil_carbon_temp = 0
        total_average_nonveg_carbon_temp = 0
        total_average_forest_carbon_temp = 0
        total_average_ecosystem_carbon_temp = 0
    # STATS
    cell_count = 0
    for row in rows:
        for col in cols:
            cell_count += 1
            cell_id = cell_count
            if mask[row,col] == 1:
                total_average_soil_carbon_temp += soil_carbon[cell_id]
                total_average_nonveg_carbon_temp += nonveg_carbon[cell_id]
                total_average_forest_carbon_temp += forest_carbon[cell_id]
                total_average_ecosystem_carbon_temp += ecosystem_carbon[cell_id]
            soilc = total_average_soil_carbon_temp / active_cell_count
            nonveg = total_average_nonveg_carbon_temp / active_cell_count
            forestc = total_average_forest_carbon_temp / active_cell_count
            ecosystemc = total_average_ecosystem_carbon_temp / active_cell_count

```

```
# OUTPUT
cell_count = 0
carbon_stats = scenario, soilc, nonveg, forestc, ecosystemc
print carbon_stats
output_file_main_open.close()
```

## VITA

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### ***Education***

Pennsylvania State University, PhD 2012, Geography (Biogeography and Landscape Ecology)  
Dissertation Title: Climate change impacts on forests: modeling relationships between static landscape patterns and dynamic vegetation responses  
University of Georgia, MS, 1999, Agronomy (Soil Physics) Thesis Title: Modeling the effect of precipitation, horizonation, and slope on lateral flow  
James Madison University, *Magna Cum laude*, BS, 1994, Physics

### ***Teaching and Research Positions***

2008-2012 Research Assistant, Pennsylvania State University (University Park, PA)  
2006-2007 Adjunct Physics Professor, Lord Fairfax Community College (Middletown, VA)  
2006-2007 Physics Teacher, Clarke County High School (Berryville, VA)  
2005-2006 Science Communications Specialist, Everglades National Park (Homestead, FL)  
2003-2005 Water Resources Liaison, Everglades National Park (Washington, DC)  
2000-2003 Hydrologist, Everglades National Park (Homestead, FL)  
1996-1999 Research Assistant, University of Georgia (Athens, GA)  
1995-1996 Math Teacher, Murray High School (Charlottesville, VA)

### ***Publications***

Crisfield, Elizabeth. Climate change impacts on forests: modeling relationships between static landscape patterns and dynamic vegetation responses. Doctoral Dissertation, The Pennsylvania State University, University Park, PA, 2012.  
Dufour, Caroline and Elizabeth Crisfield, Eds. The Appalachian Trail MEGA-Transect. Harpers Ferry, WV: Appalachian Trail Conservancy, 2008.  
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