SPATIAL DYNAMICS OF BIODIVERSITY-BASED ECOSYSTEM SERVICES IN THE SOUTHERN APPALACHIAN MOUNTAINS

By

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Contents

Abstract

SPATIAL DYNAMICS OF BIODIVERSITY-BASED ECOSYSTEM SERVICES IN THE SOUTHERN APPALACHIAN MOUNTAINS

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Under the supervision of Professor Monica G. Turner

at the University of Wisconsin – Madison

Ecosystem services – the contributions from nature to human well-being – have received increasing emphasis in ecological research and conservation planning. Decision-makers need to know where and how ecosystem services are produced to evaluate tradeoffs among different ecological, economic, and societal goals, such as the maintenance of biodiversity or increasing development. Yet, major questions remain regarding how spatial patterns of ecosystem services change over time, cultural ecosystem services remain relatively understudied, and the relationship between biodiversity and ecosystem services remains unresolved. This dissertation addresses knowledge gaps in ecosystem service science by using a combination of empirical field data, social and ecological datasets, process-based biophysical models, and statistical models to study spatial dynamics of ecosystem services in the Southern Appalachian Mountains, a rural, amenity-based region in the United States. Chapter 1 investigates spatial patterns of bioenergy production and land-use competition under future climate scenarios. The remaining three chapters focus on landscape patterns of cultural ecosystem services, advance our understanding of the role of biodiversity in providing cultural ecosystem services, and highlight the importance of underlying ecology and phenology of biotic communities in the provision of cultural ecosystem services.

Using estimates of bioenergy production through 2100 under moderate and very high emissions scenarios, simulation results demonstrated that the spatial locations of high bioenergy supply (i.e., hotspots) shifted as climate changed and were often co-located with areas currently in food production or at high risk of development conversion. Tradeoffs among bioenergy production, crop production, and exurban expansion varied spatially with climate change over time, suggesting the importance of considering future conditions when managing current landscapes to sustain ecosystem services. Using empirical data on wildflower blooms and bird communities, I developed spatial-temporal models of biodiversity-based cultural ecosystem services (i.e., wildflower viewing and birdwatching). Spatial patterns of cultural ecosystem services changed from spring through summer, and these spatial dynamics of cultural ecosystem services affected accessibility of ecosystem services to the public. Results also indicated that beneficiaries of cultural ecosystem services (i.e., birdwatchers) altered use patterns during the same time period, revealing that social preferences play an important role in transfer of cultural ecosystem services. Social preferences also revealed that flower abundance was the most important component of wildflower biodiversity (including species richness, evenness, abundance, number of colors, and presence of key species) to predict people's aesthetic preference for wildflower communities. Further, this research empirically tested the hypothesis that increased species richness leads to increased cultural ecosystem service value. Collectively, this research provides insights into the spatial patterns and dynamics of ecosystem services in amenity-based landscapes, and emphasizes the importance of considering temporal dynamics and social preferences to inform conservation and management efforts directed at sustaining ecosystem services.

Introduction

Ecosystem services–the contributions from nature to human well-being–have received increasing emphasis in ecological research and conservation planning. The idea of ecosystem services, however, is not new (Mooney and Ehrlich 1997) and can be traced from George Perkins Marsh's Man and Nature in 1864 through Vogt's work on natural capital (1948) and Aldo Leopold's land ethic (1949). The concept of ecosystem services can be observed in the multiple-use paradigm of forestry (Seymour and Hunter 1999) and ecosystem management (Grumbine 1994, Christensen et al. 1996), and the ecological underpinnings for ecosystem services benefited from a rich intellectual history on ecosystem ecology (Tansley 1935, Lindeman 1942, Odum 1953, Golley 1993) and current research on biodiversity and ecosystem function (Cardinale et al. 2012).

The term 'ecosystem services', attributed to Ehrlich and Ehrlich (1981), became widely used in research following publication of Gretchen Daily's (1997) book and completion of the Millennium Ecosystem Assessment (MA 2005) which highlighted that globally 15 of 24 investigated ecosystem services are declining, and future human well-being will likely decline as a result. A major emphasis from the MA was the need to increase research on measuring, modeling and mapping ecosystem services to better assess changes and allow societies to make informed decisions (Bennett et al. 2005, MA 2005, Carpenter et al. 2006). While research on ecosystem services has increased and theory related to assessing ecosystem services continues to develop (Carpenter et al. 2006, Daily and Matson 2008, Daily et al. 2009, Kareiva et al. 2011), understanding how spatial patterns of ecosystem services change over time remains limited, cultural ecosystem services remain relatively understudied, and the relationship between biodiversity and ecosystem services remains unresolved (Carpenter et al. 2009, Bennett et al.

2009, 2015, Chan et al. 2012a, Tallis et al. 2012, Balvanera et al. 2014). Decision-makers need to know where and how ecosystem services are produced to evaluate tradeoffs among different ecological, economic, and societal goals, such as the maintenance of biodiversity or increasing development.

Recent studies have revealed spatially explicit tradeoffs and synergies among ecosystem services (e.g., Raudsepp-Hearne et al. 2010, Qiu and Turner 2013), but many studies have emphasized production landscapes dominated by agricultural or urban land use. Fewer studies have considered ecosystem services in rural landscapes, such as the Southern Appalachians, that are characterized by exurban development and dependent on nature-based economies (but see Peterson et al. 2003, Turner et al. 2012, Bateman et al. 2013). Furthermore, little attention has been paid to the temporal dynamics of ecosystem service and biodiversity patterns and interactions (Kremen et al. 2007, Koch et al. 2009, Holland et al. 2011). Integrating biodiversity and ecosystem services research at a scale relevant to decision makers is a key research priority in ecology (e.g., Reyers et al. 2012, Mace et al. 2012, Wu 2013).

Ecosystem service studies have evolved over time to use empirically derived and process-based models that consider more detailed spatial and temporal data (e.g. soil, climate, management within land-use types) (e.g., Sharp et al. 2016). However, over half of ecosystem service studies still use relatively simple approaches, such as lookup tables which attribute fixed values of ecosystem services to given land-use/land-cover types (Lautenbach et al. 2015), despite concern that simple proxies obscure heterogeneity in ecosystem service supply and simplify relationships between landscape gradients, biodiversity and ecosystem services (Eigenbrod et al. 2010). For many ecosystem services, ecosystem service supply is related to the presence, abundance, diversity and functional characteristics of service-providing organisms (Luck et al.

2009), and thus the ecology of these organisms is likely to affect where, when, and how ecosystem services are produced (Kremen 2005, Luck et al., 2009). For these biodiversity-dependent ecosystem services, the use of these simple spatial patterns has been referred to as a lack of biophysical realism (Seppelt et al. 2011, Cardinale et al. 2012) and limits the ability of researchers to provide decision-makers with reliable estimates of ecosystem service capacity (Bennett et al. 2015).

While tremendous progress has been made in modeling the supply of regulating and provisioning services ecosystem services (Seppelt et al. 2011, 2012, Martínez-Harms and Balvanera 2012, Maes et al. 2012, Lautenbach et al. 2015), cultural ecosystem services are relatively understudied. Cultural ecosystem services have proven challenging to model due to their dependence on both biophysical attributes and the experiences of users or beneficiaries (Chan et al. 2012a, 2012b), and, though consistently recognized as important, are seldom quantified (Feld et al. 2009, Daniel et al. 2012). Furthermore, cultural ecosystem service models remain limited in scope with only 17% including multi-temporal assessments and less than 25% incorporating spatially explicit information (Hernández-Morcillo et al. 2013). Thus, understanding of the supply and dynamics of cultural ecosystem services lags behind that of other ecosystem services.

To manage ecosystem services sustainably, decision-makers need first to understand what is the capacity of the landscape to produce an ecosystem service. Increasingly researchers recognize that measuring supply alone is not sufficient to understand landscape patterns of ecosystem service delivery (Fisher et al. 2009, Johnson et al. 2012, Tallis et al. 2012, Villamagna et al. 2013, Mitchell et al. 2015). However, few studies have distinguished among the capacity of a landscape to produce an ecosystem service, the ability for people to use or access that ecosystem service, the societal demand for that service, and future pressure from environmental and anthropogenic change on that service (Tallis et al. 2012, van Oudenhoven and de Groot 2013, Villamagna et al. 2013, Burkhard et al. 2014). For cultural ecosystem services, understanding both the biophysical capacity and social capacity is particularly important (Villmagna et al. 2013). For example, freshwater fishing depends not only on the presence and abundance of fish species, but also on the human, social, and built inputs that allow access to the streams (Boyd and Banzhaf 2007, Villamagna et al. 2014). By including analysis that goes beyond the supply of an ecosystem service, research can provide better information to decision-makers about where ecosystem service benefits can be enhanced through additional effort such as increasing access for potential beneficiaries.

This dissertation addresses the effects of climate change, landscape patterns, and biodiversity on the spatial and temporal patterns of provisioning and cultural ecosystem services in the French Broad River Basin – as semi-rural, amenity-based landscape in the Southern Appalachian Mountains. I quantified and mapped the projected provision of 3 bioenergy crops under current and future (to 2100) climate conditions, and assessed how spatial patterns of this provisioning service and tradeoffs among the service and other land uses changed over time (Chapter 1). Chapters 2 through 4 address biodiversity-based cultural ecosystem services and advance our understanding of the role biodiversity plays in the supply of these services. I conducted repeat-surveys of bird and wildflower communities to develop statistical models used to map wildflower viewing (Chapter 2) and birdwatching (Chapter 4) supply, and assessed changes in biotic communities affected the supply of these services over time and how those changes affected public access to the service. In Chapter 3, I conducted a discrete-choice experiment aimed at determining the relative effect of species richness versus other biodiversity components on cultural ecosystem service value, and addressed the hypothesis that increased species richness leads to increased cultural ecosystem service value.

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Chapter 1 – Landscape patterns of bioenergy in a changing climate: implications for crop allocation and land-use competition

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Abstract

Rural landscapes face changing climate, shifting development pressure, and loss of agricultural land. Perennial bioenergy crops grown on existing agricultural land may provide an opportunity to conserve rural landscapes while addressing increased demand for biofuels. However, increased bioenergy production and changing land use raise concerns for tradeoffs within the food-energy-environment trilemma. Heterogeneity of climate, soils, and land use complicate assessment of bioenergy potential in complex landscapes creating challenges to evaluating future tradeoffs. The hypothesis addressed herein is that perennial bioenergy production can provide an opportunity to avoid agricultural land conversion to development. Using a process-based crop model, we assessed potential bioenergy crop growth through 2100 in a southern Appalachian Mountain region and asked: (1) how mean annual yield differed among three crops (switchgrass, giant miscanthus, and hybrid poplar) under current climate and climate change scenarios resulting from moderate and very-high greenhouse gas emissions; (2) how maximum landscape yield, spatial allocation of crops, and bioenergy hotspots (areas with highest potential yield) varied among climate scenarios; and (3) how bioenergy hotspots overlapped with current crop production or lands with high development pressure. Under both climate change scenarios, mean annual yield of perennial grasses decreased (-4% to -39%), but yield of hybrid poplar increased (+8% to +20%) which suggests that a switch to woody crops would maximize bioenergy crop production. In total, maximum landscape yield increased by up to 90,000 Mg yr^{-1} (6%) in the 21st Century due to increased poplar production. Bioenergy hotspots (>18 Mg $ha^{-1}yr^{-1}$) consistently overlapped with high suburban/exurban development likelihood and existing row crop production. If bioenergy production is constrained to marginal (non-crop) lands, landscape yield decreased by 27%. The removal of lands with high development probability from crop production resulted in losses of up to 670,000 Mg yr^{-1} (40%). This study demonstrated that tradeoffs among bioenergy production, crop production, and exurban expansion in a mountainous changing rural landscape vary spatially with climate change over time. If markets develop, bioenergy crops could potentially counter losses of agricultural land to development.

Keywords: biomass, climate change, land use, *Panicum virgatum, Miscanthus giganteus, Populus*

Introduction

Human population growth has placed increased demands for food, fiber, and fuel production on rural and semi-rural landscapes throughout the United States and Europe while simultaneously contributing to the conversion of agricultural lands to exurban development (Francis et al. 2012). The ability of rural and semi-rural landscapes to provide food, fiber, and fuel as well as conservation of natural and social heritage may be altered as climate warms and suburban and exurban development expand (Theobald and Romme 2007, Brown et al. 2010, IPCC 2013, Hatfield et al. 2014). Perennial biomass crops have emerged as an alternative agricultural land use to meet increased demand for non-fossil fuel based energy (Powlson et al. 2005, Gopalakrishnan et al. 2009, Chen et al. 2011, U.S. Department of Energy 2011). Perennial biomass crops have received considerable support from governments at local, state, and country-levels and are expected to play a large role in future energy production (Dale et al. 2014). Bioenergy, in the form of biomass crops, crop residues, and municipal wastes, currently provides 10% of the global primary energy supply (IEA 2014). Demand for bioenergy is expected to increase three- to ten-fold by 2050 in order to achieve reduced emissions goals in energy and transport sectors (IEA 2011, 2012). In semi-rural landscapes, bioenergy crop production may provide an opportunity to maintain agricultural landscapes and social heritage; however, it is difficult to assess this potential in landscapes with steep environmental gradients and complex land-use patterns.

Most assessments of bioenergy potential have focused on global and national scales (Cook and Beyea 2000, Campbell et al. 2008, Nair et al. 2012, Kang et al. 2014) or large industrial agriculture landscapes (Jain et al. 2010); few studies assess bioenergy production at a regionally relevant scale or consider local variation in soils, climate, topography, and land use (Field et al. 2008, Kukk et al. 2010, US Department of Energy 2011). Changing climate conditions pose additional challenges on agricultural lands because current crops may have altered productivity in the future, and the viability of new options – such as bioenergy crops – is uncertain. Crop production will be affected by climate change in complex ways, depending on how individual crops respond to changes in atmospheric carbon dioxide concentrations, temperature, and precipitation (Hatfield et al. 2011). Elevated carbon dioxide concentrations contribute to increased plant growth and water use efficiency (WUE) (e.g. “carbon fertilization effect”), but these gains may be offset by greater temperature or moisture stress (Hatfield et al. 2011). Global mean annual temperature is projected to increase by up to 4°C by 2100 and be accompanied by increased frequency of extreme events and greater climate variability (IPCC 2014). Across landscapes, crop responses will be complicated by heterogeneity in soils (e.g. increased soil respiration or texture-specific changes in soil moisture) (Jasper et al. 2006, Whitby and Madritch 2013).

Crop models have been combined with climate scenarios to examine the vulnerability of agricultural production to changing climate patterns (e.g., Lobell and Field 2007, Challinor et al. 2010, Lobell and Gourdji 2012), but few studies have also considered changing land use and land-use competition (Hoogwijk et al. 2005, Schröter et al. 2005). In North America, increased development pressure threatens the persistence of rural landscapes and farmers can often realize substantial economic gains by selling their land (Olson and Lyson 1999). Removing farmland through development may alter a region's ability to adapt agricultural production to climate change (Fraser et al. 2011, IPCC 2014). In addition, exurban or urban development has wide-ranging impacts such as decreased water quality, increased invasive species presence, and biodiversity loss (Gavier-Pizarro et al. 2010, Radeloff et al. 2010, Lumpkin et al. 2012, Webster et al. 2012).

Increased demand for bioenergy can provide an additional commodity for farmers and thereby may aid in farmland protection (Campbell et al. 2008, Fargione et al. 2009). Moreover, bioenergy crops provide additional benefits, including climate change mitigation and habitat for wildlife, and offer alternatives to row-crop agriculture (U.S. Department of Energy 2011, Robertson et al. 2011, Dale et al. 2011a, Blank et al. 2014). Bioenergy crop production that sustains rural landscapes may confer environmental benefits but is most likely to be successful if producers can harvest at levels that are able to maintain their livelihood (Dale et al. 2010). Increased bioenergy production may also increase competition for land (e.g. the 'food, energy, and environment trilemma' (Tilman et al. 2009)). Conflicts between food and fuel production may be alleviated by planting bioenergy crops on marginal lands, defined herein as land not currently used for food production (Campbell et al. 2008, Valentine et al. 2012, Gelfand et al. 2013, Gopalakrishnan et al. 2006).

The semi-rural landscapes of the Southern Appalachian Mountains are identified as suitable for cultivating perennial bioenergy crops (Dale et al. 2011, Nair et al. 2012, Behrman et al. 2013) and, typical of semi-rural landscapes in the eastern U.S., have a long history of agriculture and timber harvest beginning in the late 1700s (Gragson and Bolstad 2006). Widespread agricultural abandonment began in the mid-1900s (Ramankutty and Foley 1999, Gragson and Bolstad 2006). and was followed by an increase in forest cover and expansion of exurban and suburban housing development (Wear and Bolstad 1998). Continued urbanization is expected to lead to declines in crop, pasture, and forested land within the region throughout the 21st century (Wear 2011). In contrast to the large industrial agricultural landscapes of the Midwest, biophysical complexity leads to steep gradients in soil and climate conditions, creating substantial environmental heterogeneity (e.g., Whittaker 1956, Turner et al. 2003) that influences land-use patterns and agricultural productivity. The extent to which perennial bioenergy crops may be agriculturally feasible across these complex and changing landscapes is unknown. Regional crop models that incorporate both climate scenarios and potential land-use competition provide a means for exploring potential bioenergy supply given alternate futures in biophysically complex regions with diverse land use patterns and drivers of environmental change.

Here, we assess potential bioenergy crop yield of switchgrass (*Panicum virginatum*), giant miscanthus (*Miscanthus x giganteus*), and hybrid poplar (*Populus* x sp) in western North Carolina under current climate and future climate scenarios resulting from medium and high-emissions (e.g., IPCC Representative Concentration Pathway (RCP) 4.5 and RCP 8.5). The three crops are suitable for biomass energy under current technologies, and are under research and development as biofuel energy sources. Under projected market expansion, the three crops are likely candidates for biomass production in the Southern Appalachian Mountains and globally (Walsh et al. 2003, McLaughlin and Kszos 2005, Heaton et al. 2008). Other sources of biomass energy such as residues from annual crops and urban waste as well as forest biomass are possible in this region (U.S. Department of Energy 2011). We focus on the effects of biophysical complexity and climate change on perennial bioenergy crops to explore whether these crops have potential to augment the current crop portfolio in a diverse agricultural landscape. We used a process-based crop model and asked:

(1) How does potential mean annual yield differ among three perennial bioenergy crops under current and projected future climate in a complex, heterogeneous landscape?

(2) How do maximum landscape yield, crop allocation, and the extent of bioenergy hotspots (areas with highest potential yields) vary among climate scenarios?

(3) To what extent do bioenergy hotspots overlap with agricultural land at high risk of conversion to development?

Study Area Description

We used a ten-county area in western North Carolina (WNC), comprising 11,440 km^2 and including parts of the southern Blue Ridge and Great Smoky Mountains (Figure 1) to explore patterns of potential bioenergy crop productivity in a diverse landscape. Elevation ranges from 300 to 2040 m with steep topographic gradients leading to considerable variation in soil and climate conditions over short distances (Bolstad et al. 1998). Climate varies seasonally with warm, humid summers and cool winters. Annual mean precipitation is 1397 mm and occurs year round. Mean daily temperatures are 3.1, 11.7, 21.1, and 12.7 ˚C for winter, spring, summer, and fall respectively. Soils are broadly classified as Ultisols or Inceptisols. At finer classification, over 1000 soil types, designated as map units by the USDA Soil Survey, are represented on current agricultural land in WNC (Soil Survey Staff 2013).

Land cover is dominated by forest (81%); agricultural lands make up approximately 10% of the land base and are typically located at low to mid-elevations (USDA CDL 2012). The remaining 9% of land cover is classified as developed, water, or barren. Agriculture, while occupying a smaller portion of the land base, generated nine times the 2011 annual cash receipts than all forest-based products combined in the WNC region (NCDAS 2013). Approximately 20% of the agricultural land in WNC is harvested cropland; the remaining agricultural land is primarily pasture or small woodlots (NCDAS 2013). Crop production represented 70% of farm cash receipts in the region in 2011, 40% of those receipts were generated from the sale of vegetables, fruits, nuts and berries (NCDAS 2013).

Because of its scenic beauty, the region is popular for tourism and retirement living, with populations increasing by 48% between 1976 and 2006 (Vogler et al. 2010). If current land conversion trends continue, projections suggest that an additional 5% of the land not currently protected will be converted to development by 2030 and human populations will increase by an additional 40% by 2050 (Vogler et al. 2010, GroWNC 2013). Stakeholders in the Southern Appalachians are interested in identifying alternatives to exurban development that maintain the ecological and aesthetic character of these landscapes and sustain multiple ecosystem services (GroWNC 2013) and visitors to WNC express strong preferences for the scenic quality of farmland (Kask et al. 2002, Mathews 2009). In recent years, multiple farmland conservation initiatives have established in the region (Gragson et al. 2008).

Materials and methods

Bioenergy crop yield in current and projected future climate

We simulated annual yield of three bioenergy crops using a process-based crop growth model, ALMANAC (Kiniry et al. 1992). ALMANAC has been parameterized for over 120 crops and used widely across multiple regions (Kiniry et al. 2005; see Kiniry et al. 1992 for full explanation of model inputs). We calibrated ALMANAC using mean biomass yields for switchgrass (a native warm-season grass), giant miscanthus (a non-native warm-season grass) and hybrid poplar (a hybridized fast-growing native tree) grown in Fletcher, North Carolina during 2008 – 2012 (Palmer et al. 2014, Stout et al. 2014). The default parameters for switchgrass “Southern lowland ecotype”, giant miscanthus, and hybrid poplar were used, with a few modifications based on literature, expert knowledge, and calibration to observed data (J. Kiniry pers comm) (see Appendix A1). For all scenarios, management parameters assumed a planting date of April 10 during the first year of simulation and no irrigation. Fertilizer was applied as necessary to eliminate nitrogen limitation during model runs. For the two perennial grasses, simulations ran for 10 years with annual harvest on October 15. For poplar, simulations followed a 12-year, short-rotation coppice cycle with harvesting occurring on October 15 in year 4, 8, and 12. Variation in local management will affect potential bioenergy crop productivity (McLaughlin and Kszos 2005, Djomo et al. 2015), but we chose to hold management constant to isolate effects of climate change and environmental heterogeneity on bioenergy crop production. Sensitivity of ALMANAC to changes in climate, soil, and management parameters is well understood (Xie et al. 2003), but we performed a sensitivity analysis to understand its behavior in our landscape. Results of the sensitivity analysis revealed differences in crop growth responses between the grasses and hybrid poplar to changes in precipitation and soil texture and demonstrated that grass yields were more sensitive to changes in precipitation on finer textured soils while hybrid poplar yields tended to increase with increasing precipitation, across all soil types (Appendix A2).

ALMANAC simulates field-scale crop production. We used existing gridded climate and soil datasets to delineate unique soil-climate combinations representing all possible field conditions across agricultural land in the study area. Daily Surface Weather and Climatological Summary (DayMet) (http://www.daymet.org/) data (1 km^2 grid cells) were overlaid with Soil

Survey Geographic (SSURGO) data (map scale 1:20,000) to generate a soil-climate layer, resulting in 69,645 unique soil-climate combinations. We simulated bioenergy crop growth by running ALMANAC under current and future climate conditions for each of the three crops for each soil-climate combination. Soil parameters for all scenarios were assembled from the USGS SSURGO dataset (Soil Survey Staff 2013).

Current climate scenario

Input parameters for the current climate scenario were obtained from existing data sources. ALMANAC contains a weather generator subroutine, which generates daily weather based on climate drivers (Kiniry et al. 1997). Daily climate drivers included monthly minimum and maximum temperature, mean monthly precipitation and the standard deviation of precipitation within each month, mean solar radiation, wind speed, and relative humidity and were assembled from a 30-yr (1981-2001) DayMet dataset (Thornton et al. 2012). The Daymet database is available at daily time steps at a 1-km resolution and was developed from data measured at a large number of weather stations. The monthly climate variables were mapped at a 1-km resolution to create a Baseline Climate surface and were used as input into the ALMANAC model to simulate bioenergy yields under current conditions.

Future climate scenarios

Future climate scenarios used downscaled daily climate drivers and carbon dioxide concentrations assembled from global circulation model (GCM) model-averaged climate projections from the CMIP-5 multi-model ensemble (Appendix A2) for the mid-century (2040-2050) and late-century (2090-2100) under medium and high-emissions scenarios: representative concentration pathway (RCP) 4.5 and RCP 8.5 (Maurer et al. 2007, Brekke et al. 2013). We created “future climate” scenarios by combining model-averaged global circulation model

(GCM) climate predictions with the finer scale baseline climate data using the “delta method” (Hamlet et al. 2010). This approach is limited in that it assumes that relationships between variables in the baseline climate at high resolution are likely to be maintained under future conditions.

We downloaded data from a subset of the available CMIP-5 GCMs (see Table A4 for complete list) corresponding to three time series: historical observed (1980 – 2000), mid-21st century (2040 – 2050), and late-21st century (2090 – 2100), at daily time-steps, for three variables (minimum and maximum temperature, and precipitation) for RCPs 4.5 and 8.5. For each time period and each of GCM, we calculated the same nine monthly statistics as calculated for the “Baseline Climate” inputs (Table A3). We averaged the monthly statistics across the GCMs to create a multi-model ensemble dataset describing the average monthly climate conditions for each time period. We calculated the anomaly (or delta) with respect to the average observed climate (1980 – 2000) for each the variables and months. Anomaly values were used to create raster Climate Change surfaces for each of the nine variables at 1/8° latitude-longitude (~12 km) resolution. Finally, Future Climate surfaces were created by “adding” the anomalies to Baseline Climate surface for each variable and each month. For temperature, anomalies were added to observational baselines. Rainfall anomalies were added as absolute changes relative to the baselines (Ramirez-Villegas and Jarvis 2010). The resulting Future Climate surfaces (1-km resolution) were used as input into the ALMANAC model to simulate bioenergy yields under moderate (RCP 4.5) and extreme (RCP 8.5) climate change during to future time periods (2040 – 2050 and 2090 – 2100).

The magnitude of climate change depends on the emissions scenario with RCP 4.5 resulting in likely increases in global surface temperature of 1.1 to 2.6°C and RCP 8.5 leading to likely increases of 2.6 to 4.8°C by the end of the 21st century (IPCC 2014). Precipitation changes are not expected to be uniform, but precipitation is expected to increase under both RCP 4.5 and RCP 8.5. The southeastern United States is located in a transition zone between projected wetter and projected drier conditions, therefore future precipitation projections for the region are uncertain (Carter et al. 2014). Our model-average climate scenarios resulted in spatially varied precipitation, with some locations experience increases in precipitation and others experiencing decreases. ALMANAC uses the average monthly precipitation, standard deviation of precipitation, as well as the probability and number of wet days per month to generate daily rainfall values allowing us to account for both spatial and temporal variation in projected precipitation (Kiniry et al. 1997).

Crop yield

We calculated mean annual yield (Mg ha^{-1} yr^{-1}) of each crop for each soil-climate combination. For statistical analysis, we randomly sampled 6000 soil-climate combinations (~10% of the entire dataset) to reduce the likelihood of spurious results due to the high sample size of our simulated data (White et al. 2014). Differences among bioenergy crops under current climate were analyzed using repeated measures ANOVA with crop type as the main effect. Change in mean annual yield (relative to yield under current climate) under climate change scenarios was analyzed separately by crop type for the mid and late 21st century. Change in mean annual yield was analyzed using repeated measures ANOVA with climate scenario (RCP pathway) as the main effect.

Maximum landscape yield, crop allocation, and bioenergy hotspots

For each climate scenario, mean annual yield (Mg yr^{-1}) from bioenergy crop simulations was mapped back to the landscape using 1-ha grid cells. If a grid cell included more than one soil-climate combination, the mean of all the combinations was used. All scenarios were conducted on land currently in agricultural land use (defined as row crop, pasture, or fallow) or recently abandoned (USDA CDL 2012); the remainder of the landscape was considered unavailable for bioenergy crop production.

Maximum landscape yield and crop allocation. To determine the maximum landscape yield, we assigned each cell to the bioenergy crop with the highest yield for each scenario. The proportion of the agricultural landscape assigned to each crop type to maximize landscape yield under each climate scenario was recorded. Maximum landscape yield (Mg yr^{-1}) for the resulting mixed-crop landscape was calculated by summing across grid cells. Individual crop yield (Mg yr^{-1}) for the resulting mixed-crop landscape is reported for each scenario. Differences in proportional crop allocation among current climate and future climate scenarios were assessed using Chi-square test for significance.

Bioenergy hotspots. Lands capable of producing high yields (> 10 Mg ha^{-1} yr^{-1}, considered an economically viable level of production) and very high yields (> 18 Mg ha^{-1} yr^{-1}, which represented the top 20% of the baseline yield distribution and we considered bioenergy hotspots), were identified for each climate scenario, and their total area (ha) and total yield (Mg yr^{-1}) were calculated by summing across these map cells.

Bioenergy hotspots and land-use competition

Food vs. Fuel. Potential conflict between food production (defined here as row crop or fruit tree production) and bioenergy production was determined by calculating the percent overlap of bioenergy hotspots with the distribution of current food crops. We then created a marginal-land-only scenario by removing land used for current food crop production from potential bioenergy production. Maximum landscape yield (Mg yr^{-1}), bioenergy hotspot area (ha) and total hotspot yield (Mg yr^{-1}) were calculated for the marginal-land-only scenario under each climate condition, and changes in these response variables were calculated to represent the potential bioenergy production “lost” to competition with food production in each climate scenario. We did not account for potential changes in the distribution of food production with climate change, assuming that the areas currently under cultivation represent the highest value agricultural land within the region.

Development vs. Fuel. Potential conflict between suburban/exurban development and bioenergy production was determined by calculating the percent overlap of bioenergy hotspots with areas having a high probability (> 80%) of land use conversion to non-agricultural uses such as residential housing (Vogler et al. 2010). We removed these high risk lands from potential bioenergy production, retaining all other agricultural lands. Maximum landscape yield (Mg yr^{-1}), bioenergy hotspot area (ha) and total hotspot yield (Mg yr^{-1}) were calculated for high development scenarios under each climate condition. Percent change in maximum landscape yield, bioenergy hotspot area, and total bioenergy hotspot yield represent the bioenergy production “lost” to competition with development.

Results

ALMANAC estimated biomass productivity well for switchgrass, giant miscanthus, and hybrid poplar in the Southern Appalachian Mountains (Table 1). The simulated 3-yr average (2009 – 2012) was within 3% of harvest data for switchgrass and 2% for miscanthus. Harvest data were only available for two years (2009 and 2012) for hybrid poplar; the difference between simulated and observed yields for those years was within 10%. These results suggest that ALMANAC is a satisfactory model for projecting biomass productivity potential in western North Carolina.

Bioenergy crop yield under current and future climate

Under current climate, mean annual yield of miscanthus, switchgrass, and hybrid poplar on agricultural land was high and varied among crops (F(2,5998) = 481.72, $p < 0.0001$), with simulated harvests of 15.8, 15.6, and 14.1 Mg ha^{-1} yr^{-1} respectively (Table 2). Mean annual yield varied across soil-climate combinations (range: 0 to 28 Mg ha^{-1} yr^{-1}). Mean annual yield of all three crops increased for the period of 2040-2050 under the medium emissions scenario (RCP 4.5) but decreased under the very-high emissions scenario (RCP 8.5) (Table 2). Mean annual yields for the period of 2090-2100 varied among crops. Under the RCP 4.5 scenario, mean annual yield predicted for switchgrass changed little relative to current conditions (<0.5%), but mean annual yield of miscanthus decreased (- 4%), and hybrid poplar yield increased (+ 8%) (Table 2). The RCP 8.5 scenario led to further decreases in the mean annual yield of miscanthus (-39%) and switchgrass (-14%) and substantial increases in hybrid poplar mean annual yield (+21%).

Maximum landscape yield, crop allocation, and bioenergy hotspots

Maximum landscape yield and crop allocation. Under current climate, maximum landscape yield of bioenergy on agricultural land in the study area was 1.5 million Mg yr^{-1} (Table 3). Under projected future climate, maximum landscape yield increased by 2.1% by 2050 but declined slightly (<1%) by 2100 under the RCP 4.5 scenario. Maximum landscape yield varied little (<1%) under RCP 8.5 by 2050. However, the RCP 8.5 scenario led to large decreases (-14 to -39%) in yield of grasses and large increases (20%) in poplar yield by 2100. Maximum landscape yield increased in the late-century by 90,000 Mg yr^{-1} (6%) under the RCP 8.5 scenario, primarily due to increased poplar production.

The allocation of bioenergy crops required to maximize landscape yield in all future climate scenarios differed substantially from that in current climate (Figure 2). Under current climate conditions, maximum yield crop required most of the agricultural landscape allocated to miscanthus (70%), followed by switchgrass (17%) and hybrid poplar (13%). Maximizing bioenergy production under both climate scenarios required allocating more land to switchgrass and poplar and less land to miscanthus by 2050. Land area allocated to miscanthus continued to decrease, reaching nearly zero under the RCP 8.5 scenarios, while the allocation of land to poplar increased to over 90% by 2100 (Figure 2).

Bioenergy hotspots. Under current climate, over 97% of the study area was predicted to have high annual yields (> 10 Mg ha^{-1} yr^{-1}) of at least one bioenergy crop, and bioenergy hotspots (> 18 Mg ha^{-1} yr^{-1}) occupied 22% of the study area (Figure 3). Climate change scenarios led to increases in bioenergy hotspot area. By 2100, bioenergy hotspots occupied 29% and 61% of the study area under RCP 4.5 and RCP 8.5 scenarios, respectively (Figure 4). Bioenergy hotspot yield increased in all climate change scenarios (Table 4). Under the RCP 4.5 scenarios, bioenergy hotspot yield was predicted to be highest in the mid-century (580,000 Mg yr^{-1}) while under the RCP 8.5 scenario the highest bioenergy hotspot yield (1,100,000 Mg yr^{-1}) was predicted at the end of the 21st century.

Bioenergy hotspots and land use competition

Food vs. Fuel. Across all climate scenarios, 28 to 30% of bioenergy hotspots were co-located with current row crop or fruit production. The area of overlap was largest in the late-century under RCP 8.5, due to large increases in bioenergy hotspot area (Table 4). Marginal-land-only scenarios led to 27% reductions of maximum landscape yield in all climate conditions. Bioenergy hotspot area (ha) and total bioenergy hotspot yield (Mg yr^{-1}) were reduced by 28 to

30% in each climate scenario, suggesting that the proportion of bioenergy production "lost" to competition with food production remains constant across all climate scenarios.

Development vs. Fuel. Overall 60% of the agricultural land in the study area, or 570 km^2, was at high-risk of development (>80% probability of conversion). In all scenarios, bioenergy hotspots overlapped 46 to 53% with high development probability (Figure 4). High development scenarios led to consistent declines of 37 to 39% in maximum landscape yield across all climate scenarios as compared to baseline development and current climate scenario (Table 4). In high-development scenarios, bioenergy hotspot yield (Mg yr^{-1}) declined by 32 to 38% under RCP 4.5 scenarios but increased under RCP 8.5 scenarios due to large increases in hybrid poplar productivity expanding the area of bioenergy hotspots by late 21st century (Table 4).

Discussion and conclusions

Our study identified spatial allocations of bioenergy crop types that could maximize bioenergy production in the landscape as well as locations that are likely to be hotspots of bioenergy production under current and projected climate change. Using a mechanistic plant growth model to simulate bioenergy crop yield, we showed that giant miscanthus, switchgrass, and hybrid poplar have substantial yield potential in the complex landscapes of the Southern Appalachians. Under climate change, maximum landscape yield of bioenergy increased by up to 90,000 Mg yr^{-1} in the 21st Century. However, the type and extent of crops that maximize bioenergy yield will shift from grasses to woody species as climate warms during the 21st century, and tradeoffs among competing demands for multiple land uses – food, housing and fuel – are likely. While the potential tradeoffs between bioenergy production, food production, and exurban expansion are not surprising, our study shows that the geographic locations of these tradeoffs vary substantially under changing climate. Further, there were striking differences in potential tradeoffs in the short-term versus long-term. Additionally, our study highlights the potential for bioenergy crops to mediate tradeoffs between development and the cultural heritage and landscape aesthetics that comprise the character of this region.

Bioenergy production has been suggested as a means for improving rural land-tenure and mediating increased urbanization, particularly in conjunction with rural development programs (Dale et al. 2011). In our study, areas of high bioenergy production potential consistently overlapped with areas at high risk of conversion to development under both current and future climate scenarios. Thus, bioenergy crop production, in conjunction with active farmland protection programs and incentives, could provide a mechanism to maintain farmland in heterogeneous landscapes.

Projected climate change led to increases in estimated landscape-level yields due to increased growth of hybrid poplar. These results are consistent with studies showing increases in productivity of poplar and other C3 species under CO_2 fertilization but limited increases or declines in productivity of C4 plants (Liberloo et al. 2006). Our study evaluated changes in potential bioenergy crop productivity across steep biophysical gradients and in response to changed CO_2 levels, temperature and precipitation predicted under RCP 4.5 and RCP 8.5 scenarios. Long-term climate change may result in increased winter storms, flooding events or drought in this region (Walsh et al. 2014) and further studies should address the vulnerability of crop productivity to these disturbance events. It is possible that new hybrids, developed to grow under changed climate conditions, could alter short- and long-term biomass production potential and provide options for farmers to adapt to weather-related disturbances (Ghirme and Craven 2011, Saibi et al. 2013).

Tradeoffs between provisioning services, such as the production of bioenergy, and regulating, cultural and supporting services, such as water quality, aesthetic views and biodiversity, are common in the ecosystem services literature (Raudsepp-Hearne et al. 2010, Qiu and Turner 2013). A shift from grasses to woody crops to maximize bioenergy production would increase afforestation, leading to potential tradeoffs with other ecosystem services such as water availability (Perry et al. 2001), aesthetics, and species diversity (Li et al. 2014). Afforestation reduces overall streamflow and low flows in a watershed suggesting future tradeoffs between bioenergy production and water provisioning; however, afforestation can also lead to gains in water quality by reducing pollutant loads (van Dijk and Keenan 2007). Conversion of grassland or cropland to forest-based biomass can also lead to decreases in greenhouse gas emissions (Daystar et al. 2014). Afforestation would reduce grassland habitat in this forest-dominated landscape (Drummond and Loveland 2010), leading to possible declines in grassland nesting birds and other species reliant on open habitats (Brennan and Kuvlesky 2005). However, in landscapes such as the study area where natural land cover is forest, afforestation could more closely resemble prior conditions (Navarro and Pereira 2012) and bioenergy tree plantings could provide a low-contrast matrix and increase forest connectivity (Brockerhoff et al. 2008). Afforestation due to production of hybrid poplar would also lead to decreased landscape heterogeneity and change the aesthetics of the region, which has potential to affect stakeholders' perceptions of the landscape (Lindborg et al. 2009, Ruskule et al. 2013).

Bioenergy productivity hotspots were often co-located with areas currently in food production or at high risk of conversion to development, suggesting that competition with food production or exurban development may impact the future capacity to produce bioenergy in this landscape. Increasing development (e.g. high-development scenario) led to greater declines in bioenergy hotspot compared to eliminating competition with current food production (e.g. marginal land only). Across all climate scenarios, high bioenergy yields were possible on nearly half the agricultural land predicted to have high development pressure (>80% probability of conversion). Loss of agricultural land to development could greatly decrease the region's ability to produce bioenergy, suggesting that there are unrealized opportunity costs associated with landowners' decisions that should be incorporated into regional energy and agricultural planning, particularly with regard to human adaptation to climate change.

Our study suggests that high-yielding bioenergy crops offer farmers an additional commodity and an opportunity to offset agricultural land conservation costs. However, a number of environmental, economic, and socio-political constraints currently limit bioenergy crop production by farmers (Atwell et al. 2010, Skevas et al. 2014). The current lack of a strong market for perennial bioenergy crops and the uncertainties related to small landowners' market access, including the ability to transport crops across existing or improved infrastructure, will affect the opportunities for bioenergy crop production to contribute to farmland conservation in the United States. Our study, in accordance with others, suggests that farmers will be able to grow bioenergy crops on agricultural land not suitable for high-value food crops (Valentine et al. 2012, Werling et al. 2014). This additional income could tip the balance of economic forces in favor of keeping a farm in business and prevent conversion of farmland to more economically attractive land uses, like development (Dale et al. 2011b). Agricultural policies such as the availability of subsidies and incentives for growing bioenergy crops or setting aside land in return for compensation will influence the real potential for bioenergy production to supplant development in rural areas (Lovett et al. 2009, Barney and DiTomaso 2010, Bryngelsson and Lindgren 2013, Myhre and Barford 2013). Our results suggest that the bioenergy potential of marginal lands should not be ignored and bioenergy provides an additional alternative for farmers planning in the uncertainty of a changing climate (Dale et al. 2010).

Rural landscapes produce multiple goods and ecosystem services; this study highlighted potential tradeoffs among bioenergy production, crop production, and exurban expansion given projected climate change. Impacts of increased bioenergy production have been explored as part of "food, energy, environment trilemma" (Tilman et al. 2009). In rural landscapes at risk of exurban expansion, we suggest that bioenergy production may result in a win-win solution in the "trilemma" by avoiding potential environmental impacts of exurban development. Where bioenergy hotspots overlap with high-risk of exurban development, bioenergy crop production may lead to benefits by increasing energy production while also conferring environmental benefits through land conservation. When compared to exurban encroachment on agricultural land, perennial bioenergy crops (e.g. warm-season grasses or fast-growing trees) enhance climate regulation, nutrient and water cycling (Dale et al. 2014) and have either positive or neutral effects on biodiversity conservation (Immerzeel et al. 2014, Werling et al. 2014).

While bioenergy crop yields are projected to be high enough to provide opportunities to sustain rural farmlands facing competing demands on the land base, actual landscape change may take multiple pathways depending on individual farmers' land-use decisions. Individual decision making is complex and influenced by multiple factors such as personality, cultural context, and life events as well as perceived land suitability for a particular crop at the farm and regional scale (Atwell et al. 2010, Cope et al. 2011). Private land owner decisions and their future behaviors are key uncertainties in assessing future land use patterns and competition. Future research would benefit from considering heterogeneous behavior of decision makers

(Pattanayak et al. 2004) and accounting for the fact that yield optimization is only one of many landowner goals (Sengupta et al. 2005, Greiner et al. 2009).

Our study estimates bioenergy crop generation potential and uses bioenergy crop yield to evaluate potential tradeoffs between bioenergy production, food production, and development. We evaluate tradeoffs with food production by analyzing the co-location of high bioenergy potential with current crop production. Considering that food crop yields will also be impacted by climate change (Challinor et al. 2009), future research should include projected yield and spatial variation of possible food crops under climate scenarios (Lehmann et al. 2013). In diverse agricultural landscapes with relatively small farms, farmers' crop choices are likely to be flexible and may be particularly adaptable to climate change (Howden et al. 2007, Veteto 2008, Crane et al. 2011). More research is needed to identify whether shifts in food crop production leads to greater or lesser tradeoffs with bioenergy crop production in heterogeneous landscapes.

Results from our study indicate that there is high potential for heterogeneous landscapes to produce bioenergy both currently and in changing climates, but spatial and temporal variation in potential yield will result in multiple, shifting landscape-level tradeoffs. Our findings illustrate the importance of incorporating realistic yield estimates, environmental heterogeneity, and socio-economic forces in studies aimed at understanding the role of new crop production in future landscapes. Our study highlights regional and temporal contrasts in spatial patterns of bioenergy production and identifies important opportunities for bioenergy crop production to offset land conversion to development.

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ECOLOGICAL ARCHIVES

The Appendix for this paper includes a description of model parameters used for ALMANAC simulation of bioenergy crops, a sensitivity analysis to changes in parameters, and future climate scenario descriptions. The Appendix is available online.

Tables

Table 1. Simulated and observed yields for 2009 - 2012 in Fletcher, NC. Observed yields reported by Palmer *et al*. 2014 and Stout *et al*. 2014.

Switchgrass Yield (Mg ha^{-1} yr^{-1})			
	Observed	Simulated	% Difference
3-year mean (2009 – 2012)	19.03	19.63	+ 3%
Miscanthus Yield (Mg ha^{-1} yr^{-1})			
	Observed	Simulated	% Difference
3-year mean (2009 – 2012)	18.3	17.97	- 2%
Poplar Yield (Mg ha^{-1} yr^{-1})			
	Observed	Simulated	% Difference
2009 Harvest	9.4	8.5	- 10%
2012 Harvest	14.7	15.4	+ 5%

Table 2. Mean simulated yield (Mg ha^{-1} yr^{-1}) of three bioenergy crops on agricultural land in western North Carolina under current and future climate scenarios resulting from medium (RCP4.5) and very-high (RCP8.5) emissions. Mean and CV are the spatial mean and variation within the study area. Simulations were run on unique soil-climate combinations representing all possible field conditions.

		Crop Yield (Mg ha^{-1} yr^{-1}) Mean (CV)		
		Miscanthus	Switchgrass	Poplar
1981 – 2011	Average Current Climate	15.82 (0.24)	15.56 (0.21)	14.12 (0.18)
2040 - 2050	RCP 4.5	16.11 (0.24)	15.99 (0.24)	14.66 (0.22)
	RCP 8.5	15.2 (0.26)	15.47 (0.28)	13.96 (0.34)
2090 - 2100	RCP 4.5	15.15 (0.27)	15.59 (0.28)	15.22 (0.25)
	RCP 8.5	9.65 (0.40)	13.32 (0.38)	17.12 (0.24)

Table 3. Maximum landscape yield of bioenergy crops on agricultural land in western North Carolina under current and future climate scenarios resulting from medium (RCP4.5) and very-high (RCP8.5) emissions. Individual yield of each crop is reported for each scenario.

		Maximum Landscape Yield (Mg yr^{-1})	Individual crop yield (Mg yr^{-1})		
			Miscanthus	Switchgrass	Poplar
Current Climate		1,552,519	1,089,115	261,599	201,806
2040 - 2050	RCP 4.5	1,585,169	588,442	599,557	364,519
	RCP 8.5	1,563,495	339,361	544,972	668,285
2090 - 2100	RCP 4.5	1,549,758	375,830	564,616	612,073
	RCP 8.5	1,642,808	5,631	93,269	1,453,618

Table 4. Bioenergy hotspot area and yield under multiple scenarios of climate and land-use competition on agricultural land in western North Carolina

		Bioenergy hotspot (>18 Mg ha^{-1}yr^{-1}) % of landscape	Bioenergy hotspot yield (Mg yr^{-1})	High-development scenario: bioenergy hotspot yield (Mg yr^{-1})	Marginal-land scenario: bioenergy hotspot yield (Mg yr^{-1})
1981 – 2011	Current Climate	22.1%	409,095		
2040 - 2050	RCP 4.5	31.5%	589,735	279,342	414,572
	RCP 8.5	26.8%	490,913	253,335	349,767
2090 - 2100	RCP 4.5	28.8%	527,552	267,393	376,026
	RCP 8.5	61.0%	1,095,182	590,112	787,056

Figure captions

Figure 1. Map of the ten county region in western North Carolina considered for bioenergy production. Shaded areas indicate current or fallow agricultural land.

Figure 2. Percent of the agricultural landscape in western North Carolina potentially allocated to each bioenergy crop, based on simulated maximum yields under current climate (baseline) and future climate scenarios.

Figure 3. Projected shifts in the distribution of bioenergy crop productivity on agricultural land in western North Carolina from current climate conditions to future climate scenarios resulting from medium (RCP4.5) and very-high (RCP8.5) emissions during the mid- and late-21st century. Blue regions represent "bioenergy productivity hotspots" and produce > 18 Mg $ha^{-1}yr^{-1}$.

Figure 4. Overlap of bioenergy productivity hotspots with high development probability under current climate conditions and future climate scenarios resulting from medium (RCP4.5) and very-high (RCP8.5) emissions scenarios.

Figure 1

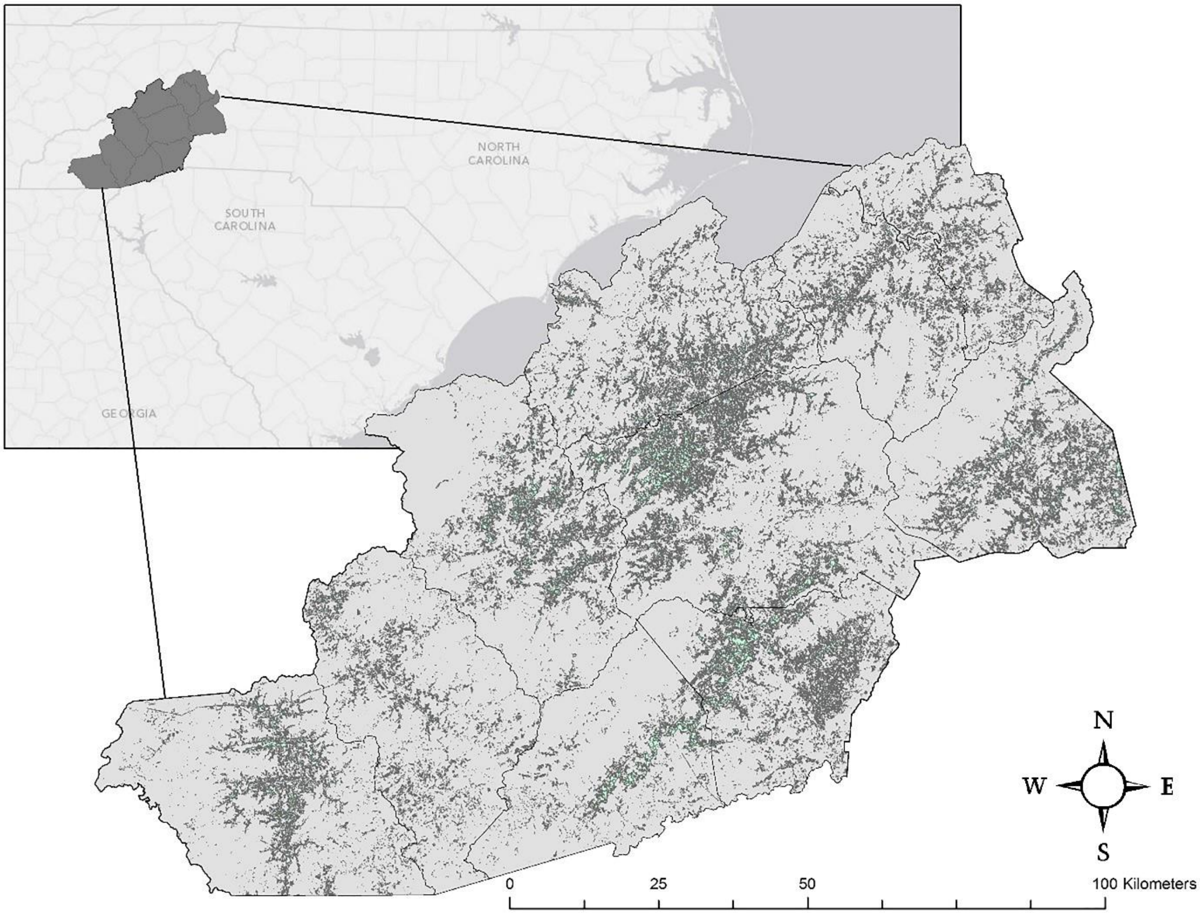

NORTH
CAROLINA
SOUTH
CAROLINA
GEORGIA
N
W
E
S
0
25
50
100 Kilometers

Figure 2

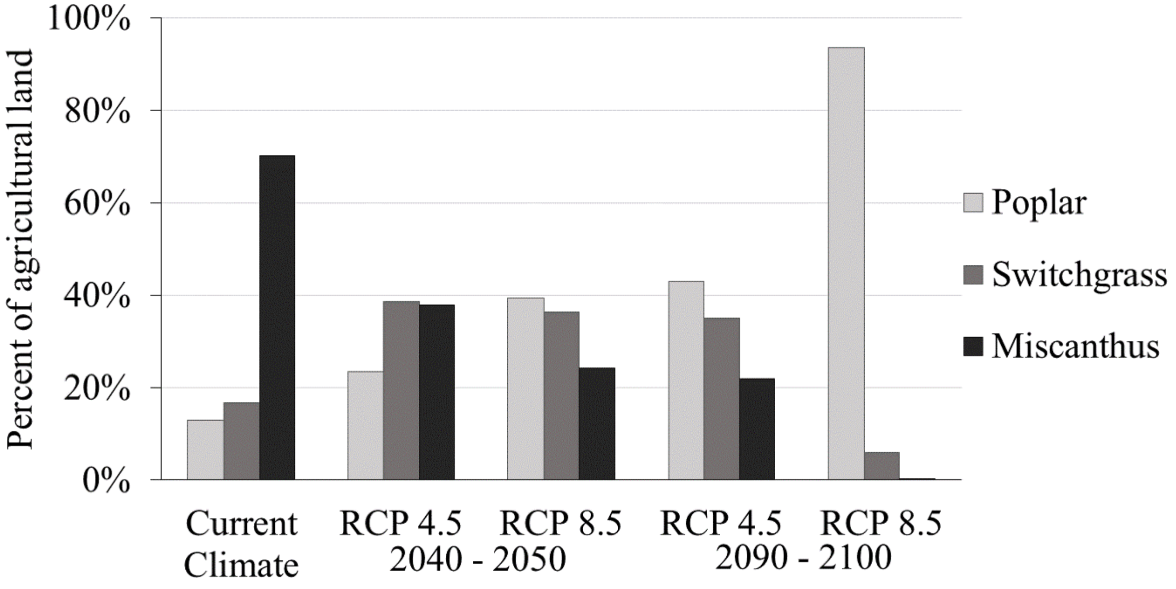

100%
80%
60%
40%
20%
0%
Percent of agricultural land
Poplar
Switchgrass
Miscanthus
Current Climate
RCP 4.5
RCP 8.5
2040 - 2050
RCP 4.5
RCP 8.5
2090 - 2100

Figure 3

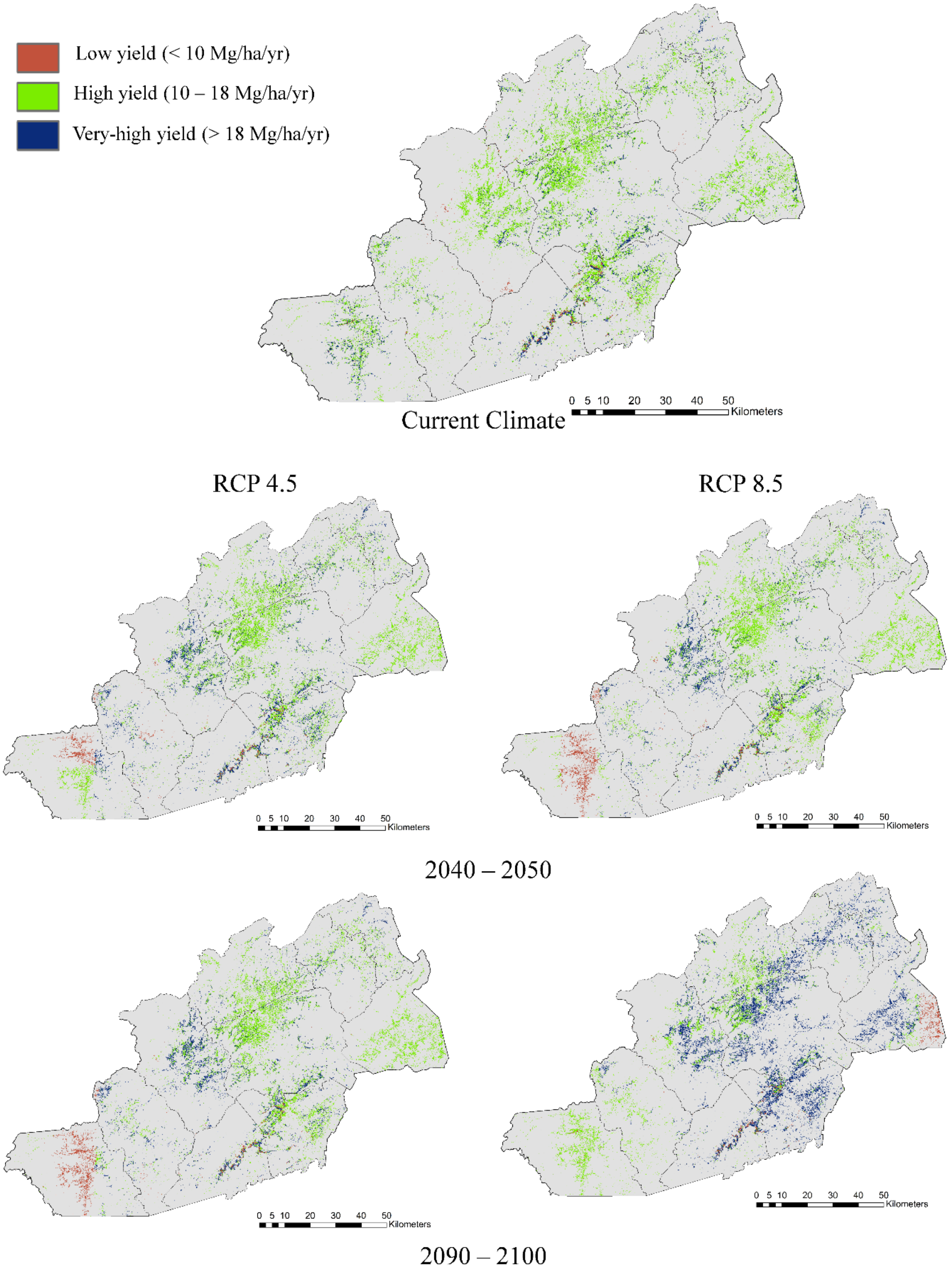
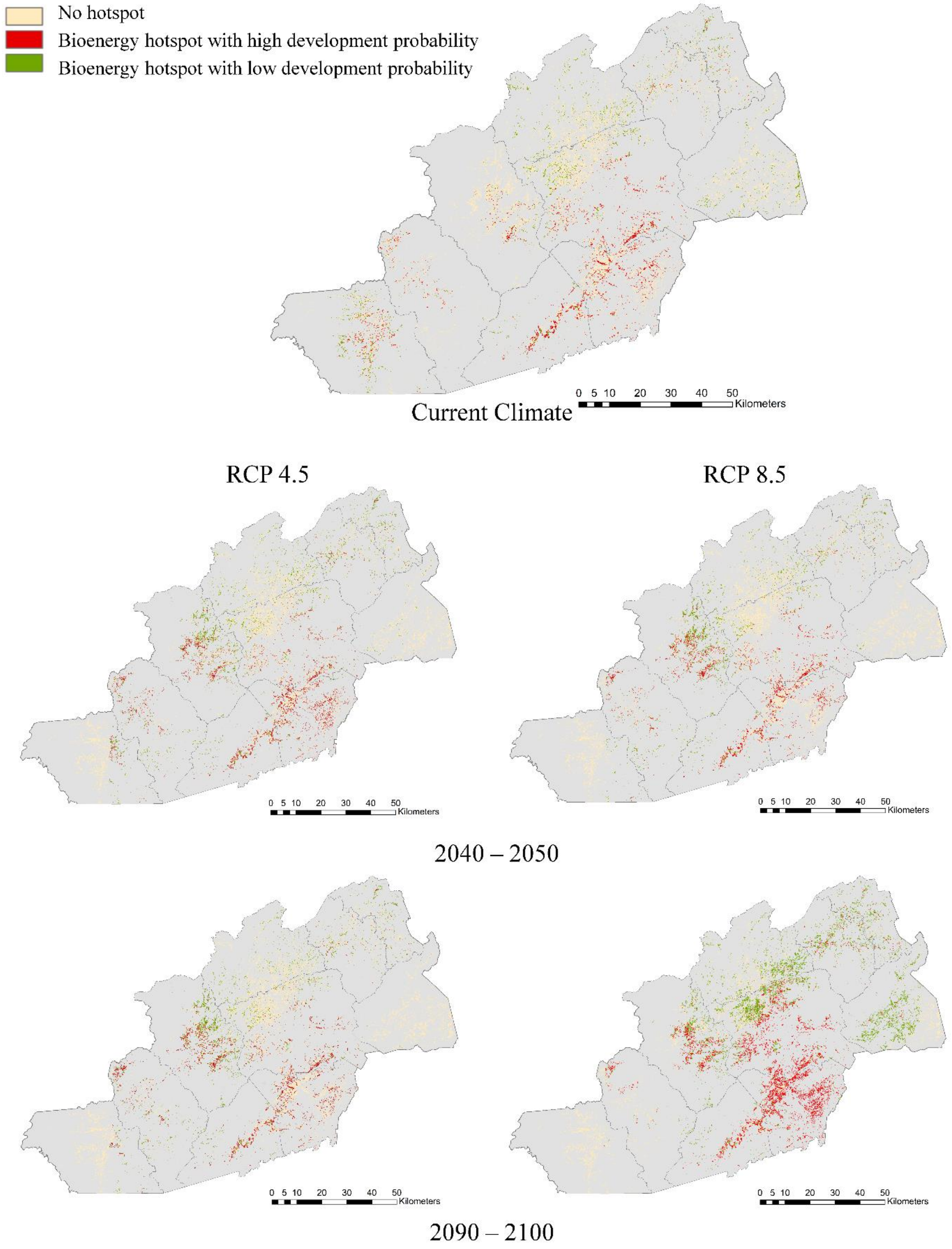

Low yield (< 10 Mg/ha/yr)
High yield (10 – 18 Mg/ha/yr)
Very-high yield (> 18 Mg/ha/yr)
Current Climate
0 5 10 20 30 40 50 Kilometers
RCP 4.5
RCP 8.5
2040 – 2050
2090 – 2100

Figure 4


No hotspot
Bioenergy hotspot with high development probability
Bioenergy hotspot with low development probability
0 5 10 20 30 40 50 Kilometers
Current Climate
RCP 4.5
RCP 8.5
0 5 10 20 30 40 50 Kilometers
0 5 10 20 30 40 50 Kilometers
2040 – 2050
0 5 10 20 30 40 50 Kilometers
0 5 10 20 30 40 50 Kilometers
2090 – 2100

Supplemental Material

Appendix

Appendix for "Landscape patterns of bioenergy in a changing climate: implications for crop allocation and land-use competition"

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Appendix Contents

A1 Description of model parameters used for ALMANAC simulation of bioenergy crops

This section provides a detailed description of the crop parameters used for the simulation of production of switchgrass, giant miscanthus, and hybrid poplar using ALMANAC, calibrated to western North Carolina. The default parameters for switchgrass "Southern lowland ecotype", giant miscanthus, and hybrid poplar were used, with a few modifications based on literature, expert knowledge, and calibration to observed data. In this study, radiation use efficiency (RUE), maximum leaf area index (DMLA), and degree-days to maturity (PHU) parameters were adjusted (Kiniry *et al.* 2012; J. Kiniry pers. comm.). PHU values are crop specific and were calculated using long-term maximum and minimum temperature data, the base temperature required by the plant to grow, and the average number of days for the plant to reach maturity (Phillips 1950, Kiniry et al. 2008). For poplar, DMLA was increased to 10.0, PHU was decreased to 1100, and RUE was set at 42. All other parameters remained the same as those presented in Macdonald *et al*. (2008). For switchgrass, DMLA was set at 6.0 and PHU was adjusted to 1500. All other parameters are reported in Kiniry *et al.* (1996). For miscanthus, DMLA was increased to 10.0 and PHU was adjusted to 1400. Other parameters remained as reported in Kiniry *et al.* (2011, 2012).

A2 Sensitivity analysis of crop growth to changes in soil type and climate

We explored crop yield sensitivity to variation in soil and climate using a basic sensitivity analysis. We simulated 10-year mean crop yields for hybrid poplar, miscanthus, and switchgrass for a baseline scenario and investigated crop yield sensitivity by changing the input variables of soil texture, rainfall, maximum and minimum temperature. Crop yield sensitivity was defines as the change in yield relative to the baseline scenario. Data sets for sensitivity analysis are referred to as scenario data sets. In each scenario data set, only one variable was changed; all other variables were kept the same as the “baseline” data set. Each variable investigated was chosen due to expected effects on crop growth and relation to the environmental heterogeneity in the study area. Under projected climate change and over the region, rainfall and maximum temperature show a wide range among years and locations. Soil texture relates to plant available water (PAW) and the ability of soils to sustain crops during drought. In each scenario, the amount of change in each variable was determined by the range found in the measured values.

In the baseline scenario, soil parameters were set to match Bradson loam (BaB), a soil type found within the region with soil texture (% clay) and soil available water storage (AWS) approximating the mean of all soil types found in the region. Climate parameters included monthly precipitation (mm), monthly maximum and minimum temperature (degrees C) and were set to the mean for the study region.

Soil texture scenarios. The soil texture scenarios included simulations run using 1000 soil types, representing a range of soil textures from <5% to 90%. For all crops, yield declined with increasing percent clay in the soil (Figure A1). The sensitivity ratios, defined as the change in yield divided by the change in soil texture, was highest for miscanthus (-0.55) as compared to switchgrass (-0.32) and hybrid poplar (-0.22) suggesting that miscanthus crop yield would be constrained to well-drained, coarse soils.

Precipitation scenarios. Baseline simulations used the mean monthly precipitation. Six scenarios were created by increasing/decreasing precipitation by a single standard deviation, setting precipitation to the minimum and maximum found in the study region, and setting precipitation to 10% above the maximum and 10% below the minimum (Figure A2). Grasses declined with changes in precipitation, with the largest declines (-10%) due to increasing precipitation (Figure A3). Conversely, hybrid poplar yield increased with increasing precipitation.

Temperature scenarios. Crop yield sensitivity to changes in both minimum (Tmin) and maximum (Tmax) monthly temperatures was examined by creating six scenarios for each temperature variable. The scenarios were similar to precipitation scenarios with the baseline using the mean monthly Tmin or Tmax and the other scenarios representing a change of one standard deviation, the minimum or maximum, and 10% above the maximum and 10% below the minimum for each variable. The direction of crop response was consistent across all three crops, with yield decreases when temperatures were decreased and yield increases when temperatures increased. Hybrid poplar yield sensitivity was stronger to changes in maximum temperature, while the grasses had stronger sensitivity to changes in minimum temperature (Table A1).

Combined Climate and Soil Scenarios. A final set of sensitivity analysis scenarios varied one climate parameter as well as soil texture parameters. Yield sensitivity to changes in precipitation was highest in finer texture soils: increased precipitation resulted in increased yield on coarser soil and decreased yields on fine soils. Yield sensitivity to changes in temperature was consistent across all soil types, with increases in temperature tending to increase crop yield (Figure A4).

A3 Future climate scenario description

We created future climate scenarios by combining downscaled global circulation model (GCM) climate predictions with finer scale historical climate data using the so called "delta method" (Hamlet et al. 2010). In addition, atmospheric carbon dioxide concentrations were adjusted to match the time period (2040 – 2050 and 2090 – 2100) and representative concentration pathway (RCP 4.5 and 8.5), respectively (Table A2). We acknowledge that this approach relies on the assumption that relationships between variables in the baseline climate at high resolution are likely to be maintained under future conditions.

Baseline Climate. We used the Daymet database for the United States (http://www.daymet.org/; Thorton *et al.*, 1997) to calculate the "Baseline Climate" conditions for western North Carolina. The Daymet database is available at daily time steps at a 1-km resolution and was developed from data measured at a large number of weather stations. We downloaded daily climate data for the period of 1980 to 2011 and calculated 30-year averages of multiple monthly variables to serve as a baseline (Table A3). The monthly climate variables were mapped at a 1-km resolution to create a Baseline Climate surface and were used as input into the ALMANAC model to simulate bioenergy yields under current conditions.

Future GCM predictions and anomalies. Multiple GCMs have been used in the Fifth Assessment Report (IPCC 2013), with outputs produced for different emission scenarios or representative concentration pathways (RCPs). Different GCMs have been evaluated on a global scale by the Coupled Models Intercomparison Project (CMIP), the latest of which (CMIP5) comprises 29 different modeling groups (Taylor et al. 2012). We downloaded downscaled CMIP5 climate projections from a subset of the available CMIP5 GCMs (Table A4) corresponding to three time series: historical observed (1980 – 2000), mid-21st century (2040 – 2050), and late-21st century (2090 – 2100), at daily time-steps, for three variables (minimum and maximum temperature, and precipitation) for RCPs 4.5 and 8.5. Data were downloaded from the US Bureau of Reclamation "Downscaled CMIP3 and CMIP5 Climate and Hydrology Projections" archive (http://gdo-dcp.ucllnl.org/downscaled_cmip_projections).

Tables and Figures

Table A1. Crop yield sensitivity to changes in soil and climate parameters using the crop model ALMANAC.

	Parameter			
	Soil Texture (% Clay)	Precipitation	Maximum Temperature	Minimum Temperature
Hybrid Poplar	0.169	0.039	0.246	0.191
Miscanthus	0.253	0.036	0.209	0.328
Switchgrass	0.128	0.081	0.232	0.346

Table A2. Emissions concentration scenarios from CMIP5 including projected carbon dioxide concentration for ALMANAC modeling time steps.

	RCP4.5	RCP8.5
Scenario Description	Stabilization without overshoot to 4.5 W/m^2 (~650 ppm CO_2 eq); stabilization after 2100.	Rising forcing pathway leading to 8.5 W/m^2 (~1370 ppm CO_2 eq) by 2100.
Future CO2 ppm* 2040 - 2050	474	515
Future CO2 ppm 2089 - 2099	536	890
Temperature anomaly (°C)	2.4	4.9
SRES equivalent	SRES B1	SRES A1F1

* RCP Database V2.0.5 http://tntcat.iiasa.ac.at:8787/RcpDb/dsd?Action=htmlpage&page=compare; *Median temperature anomaly over pre-industrial levels and SRES comparisons based on nearest temperature anomaly, from Rogelj et al. 2012*

Table A3. Monthly climate variables required for input into ALMANAC model, calculated from Daymet baseline climate data and future climate scenarios.

Temperature variables (4)	Average monthly maximum and minimum temperature, Monthly standard deviation of maximum and minimum daily temperature
Precipitation variables (5)	Average monthly precipitation, Monthly standard deviation of daily precipitation, Monthly probabilities of wet day after dry day and wet day after wet day, Average number days of rain per month

Table A4. The CMIP5 multi-model ensemble used in this study used 11 models, listed with the institutions providing the model output.

Modeling Center (or Group)	**Institute ID**	**Model Name**
Beijing Climate Center, China Meteorological Administration	BCC	BCC-CSM1.1
Canadian Centre for Climate Modelling and Analysis	CCCMA	CanESM2
National Center for Atmospheric Research	NCAR	CCSM4
Commonwealth Scientific and Industrial Research Organization in collaboration with Queensland Climate Change Centre of Excellence	CSIRO-QCCCE	CSIRO-Mk3.6.0
NOAA Geophysical Fluid Dynamics Laboratory NASA Goddard Institute for Space Studies	NOAA GFDL NASA GISS	GFDL-ESM2M
Institut Pierre-Simon Laplace, Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies	MIROC	MIROC-ESM MIROC-ESM-CHEM
Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for Environmental Studies, and Japan Agency for Marine-Earth Science and Technology	MIROC	MIROC5
Meteorological Research Institute	MRI	MRI-CGCM3
Norwegian Climate Centre	NCC	NorESM1-M

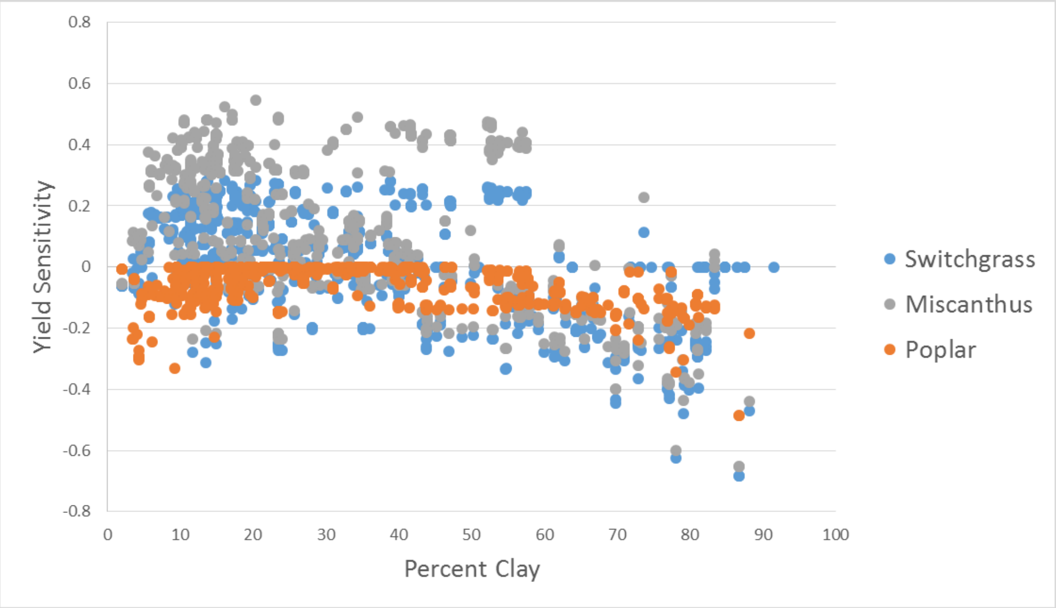

Figure A1. Yield sensitivity of three bioenergy crops to changes in soil texture.

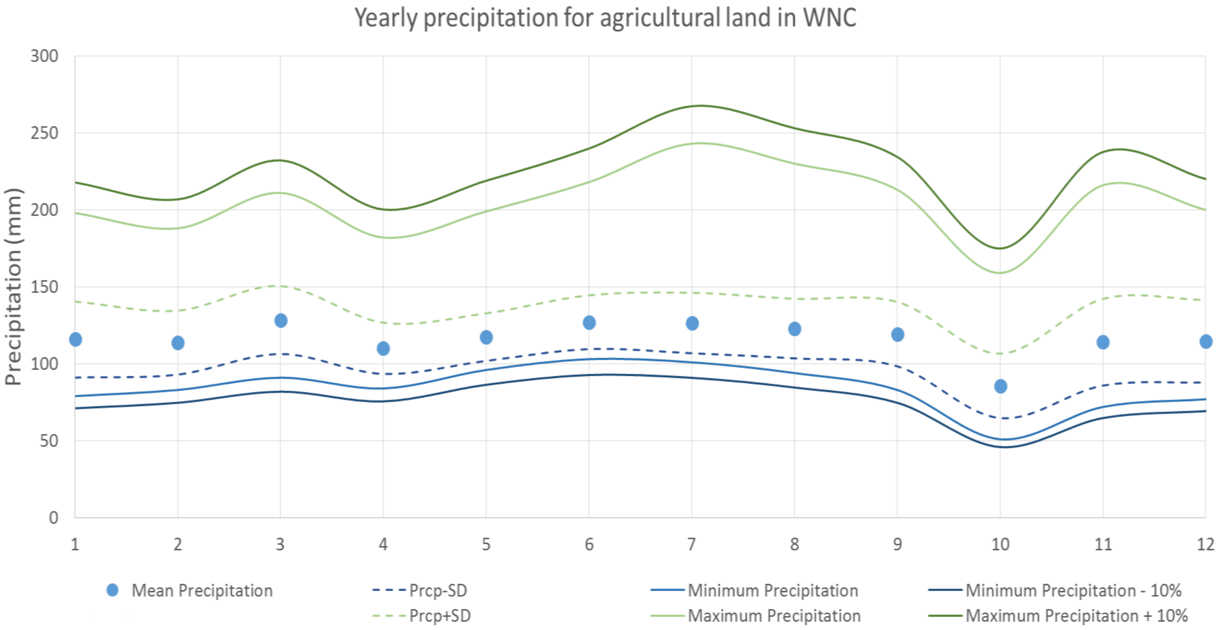

Figure A2. Monthly precipitation (cm) used to evaluate crop yield sensitivity to changes in precipitation using the ALMANAC model. Baseline simulations used the mean monthly precipitation.

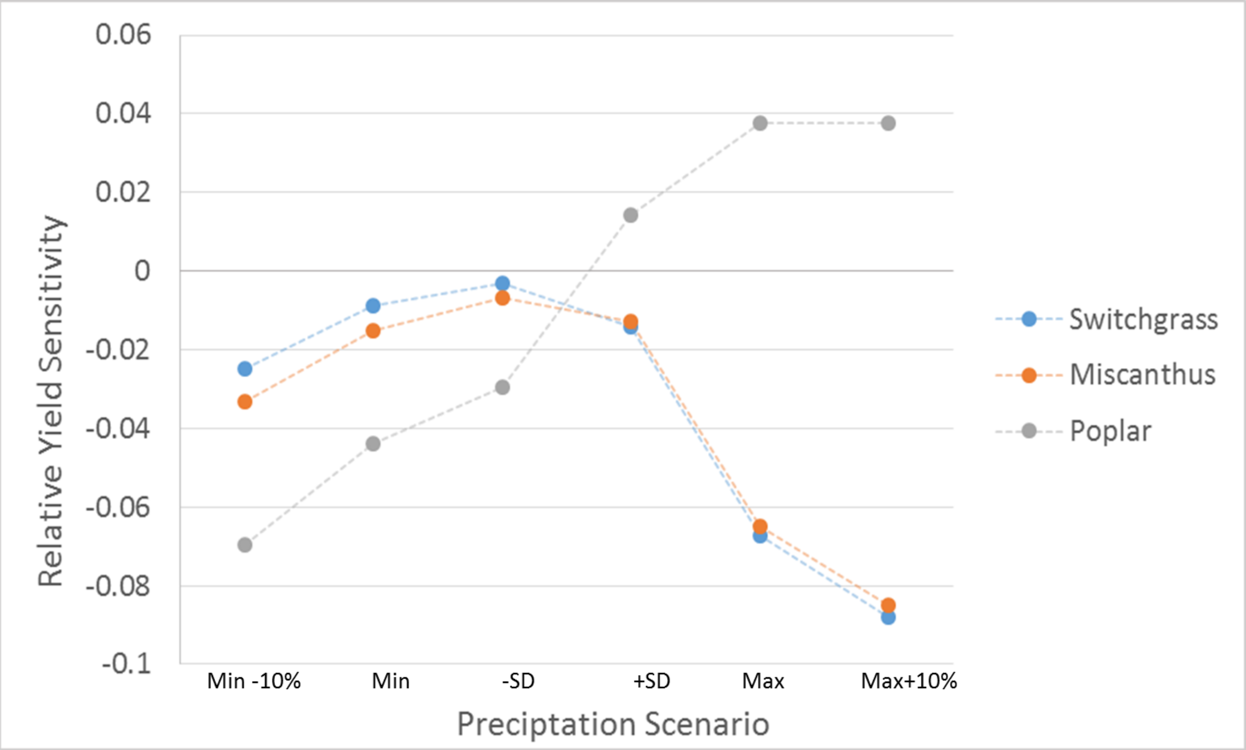

Figure A3. Crop yield sensitivity to changes in monthly precipitation (mm) parameters.

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Chapter 2 – Landscape dynamics of floral resources affect the supply of a biodiversity-dependent cultural ecosystem service

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Abstract

Context. Cultural ecosystem services, many of which depend on biodiversity, are recognized as important but seldom quantified biophysically across landscapes. Furthermore, many ecosystem service models are static, and the supply of cultural ecosystem services may be misrepresented if seasonal shifts in biotic communities are ignored.

Objectives. We modeled landscape dynamics of wildflower blooms in a temperate montane landscape to determine (1) how floral resources (wildflower species richness, abundance, timing, and presence of charismatic species) changed over the growing season, (2) how projected wildflower viewing hotspots varied over space and time, and (3) how spatial shifts in floral resources affected potential public access to wildflower viewing.

Methods. Data were collected at 63 sites across a rural-to-urban gradient in the Southern Appalachian Mountains (USA). Generalized linear models were used to identify factors affecting floral resources at two temporal scales. Floral resources were projected across the landscape and hotspots of wildflower viewing were quantified using overlay analysis.

Results. Floral resources were affected by topoedaphic conditions, climate, and surrounding building density and changed seasonally. Seasonal models revealed locational shifts in ecosystem service hotspots, which changed the proportion of hotspots accessible to the public and identified wildflower-viewing opportunities unnoticed by static models.

Conclusion. Relationships between landscape gradients, biodiversity, and ecosystem service supply varied seasonally, and our models identified cultural ecosystem service hotspots otherwise obscured by simple proxies. Landscape models of biodiversity-based cultural ecosystem services should include seasonal dynamics of biotic communities to avoid under- or over-emphasizing the importance of particular locations in ecosystem service assessments.

Keywords

Cultural services, ecosystem service capacity, temporal pattern, wildflowers, nature-based recreation

Introduction

Sustaining the supply of ecosystem services has become a primary goal of landscape management worldwide. Ecosystem services are integral to policies at local, regional and national levels (Millennium Ecosystem Assessment 2005; TEEB 2009), and sustainable management of the supply of ecosystem services depends on understanding their ecology (Kremen 2005). Substantial progress has been made in understanding regulating and provisioning services, including the development of production functions that link biophysical processes to ecosystem service supply and allow ecosystem services to be mapped and evaluated at multiple spatial and temporal scales (Daily and Matson 2008; Kareiva et al. 2011). Cultural ecosystem services (the non-material benefits received from nature) are consistently recognized as important, but are often considered difficult to measure and are seldom quantified (Feld et al. 2009; Daniel et al. 2012). Thus, understanding of the supply and dynamics of cultural ecosystem services lags behind that of other ecosystem services.

Cultural ecosystem services, such as ecotourism, nature observation and human well-being, often depend directly upon biodiversity (Naidoo and Adamowicz 2005; Fuller et al. 2007; Mace et al. 2012), but are largely absent from biodiversity-ecosystem service studies (Cardinale et al. 2012, with notable exceptions, see: Quetier et al. 2007; Villamagna et al. 2014). Many cultural ecosystem services rely on seasonally dynamic species. For example, appreciation of fall foliage color depends on seasonal variation in the biotic community (Wood et al. 2013); wildflower viewing depends on flower phenology (Turpie and Joubert 2004), which can vary by species and environmental setting; and wildlife watching varies with seasonal differences in species presence, abundance and behavior (Lambert et al. 2010). Thus, supply of many biodiversity-based ecosystem services is likely shift seasonally. However, ecosystem service studies have tended to use simple indicators and static data sources that ignore the ecology and temporal dynamics of biotic communities (Kremen 2005; Luck et al. 2009). Early studies of ecosystem services used simple models based on land-use proxies to describe the spatial pattern of service provision (Chan et al. 2006; Troy and Wilson 2006). Few ecosystem service studies addressed the contribution of biodiversity to ecosystem services (Kremen 2005). Ecosystem service studies have evolved over time to use empirically-derived and process-based models that consider more detailed spatial and temporal data (e.g. soil, climate, management within land-use types) (e.g., Sharp et al. 2016) but cultural ecosystem service models remain limited with only 17% including multi-temporal assessments and less than 25% incorporating spatially explicit information (Hernández-Morcillo et al. 2013). Models of ecosystem services that represent static spatial distributions (Anderson et al. 2009; Raudsepp-Hearne et al. 2010; Holland et al. 2011a) may obscure heterogeneity in ecosystem service supply and simplify relationships between landscape gradients, biodiversity and ecosystem services (Eigenbrod et al. 2010).

Viewing and photographing wildflowers is among the fastest growing forest-based recreation activities in the United States, with over 40% of adults participating (Cordell 2012), and an exemplar of a cultural ecosystem service that depends directly on biodiversity. Wildflower viewing depends on the presence of wildflower blooms, which are heterogeneous in time and space. Spatial-temporal dynamics of floral resources have strong effects on plant-pollinator interactions (Kremen et al. 2007; Williams and Winfree 2013; Matteson et al. 2013) but consequences of landscape-scale variation in floral resources for cultural ecosystem services are unknown (Lavorel et al. 2011; Quijas et al. 2012). Variation in floral resources may have important impacts for management of nature-based economies (Turpie and Joubert 2004; Sakurai et al. 2011).

Few studies assess spatial-temporal variation in floral resources at the community level and seldom examine flower communities from an anthropogenic perspective. Spatial variation in floral resources can result from distribution patterns of particular species or functional groups responding to climate conditions or local environmental factors such as topography, soils, and disturbance history (Hermy and Verheyen 2007; Jackson et al. 2012; Gornish and Tylianakis 2013) as well as temporal variation in flowering due to climate and seasonality (Fitter and Fitter 2002; Cleland et al. 2007; Crimmins et al. 2008; Holden et al. 2011; Aldridge et al. 2011; Crimmins et al. 2013). Spatial and temporal patterns of floral resources are affected by human modification of the surrounding landscape (Ford et al. 2000; Tscharntke et al. 2005; Foley et al. 2005; Knapp et al. 2012). Increased anthropogenic influence is associated with increases in non-native flora (Kuhman et al. 2010), declines in phylogenetic diversity (Knapp et al. 2012), and advanced onset of flowering (Neil et al. 2010) while changes in forest cover and structure are associated with shifts in understory plant communities including reduced species richness, cover and abundance of native herbs and increased cover of non-native species (Bellemare et al. 2002; Vellend 2005; Kuhman et al. 2011).

We sampled wildflower communities across topoedaphic, climatic, and land use gradients in the southern Appalachian Mountains and asked: (1) How do floral resources (wildflower species richness, abundance, timing, and presence of charismatic species) change over the growing season, and what factors explain this variation? (2) How do projected hotspots of floral resources vary over space and time? (3) How do spatial shifts in floral resource affect potential public access to cultural ecosystem service supply? We hypothesized that topoedaphic conditions would have strong effects on all floral resources and that flower species richness would decline with increased anthropogenic influence.

Methods

Study Area

The French Broad River Basin (FBRB), located within the Southern Blue Ridge physiographic region in the southern Appalachian Mountains, covers an area of 7330 km^2. Elevation ranges from 300 m to 2100 m, and the climate is characterized by mild winters (-2°C), warm summers (23°C) and abundant precipitation (1020 – 2440 mm annually) (Thornton et al. 2012). Soils are generally Incepticols, with some Ultisols (Soil Survey Staff 2013). The region is characterized by high biodiversity and ecotourism is popular (SAMAB 1996). The regional economy changed in the last century from resource extraction (e.g., timber) and agricultural production to a nature-based, amenity-driven economy, leading to altered patterns of land use and land cover (Wear and Bolstad 1998; Turner et al. 2003; Gragson and Bolstad 2006). North Carolina tourism office estimates that tourism’s impact increased from $269 million in 1991 to $901 million in 2013 in one urban center in the region, with combined visitor expenditures for 2014 over $1330 million for the FBRB (Strom and Kerstein 2015, VisitNC 2016). While no data specifically report dollars generated by ecotourism, overnight visitors to the North Carolina Mountain Region reported participating in rural sightseeing (26%), visiting state/national parks (23%), wildlife viewing (14%), hiking/backpacking (10%), nature/ecotouring (9%), other nature

(8%), and birdwatching (4%) during 2014 (VisitNC 2016). From 1976 to 2006, human population increased by 48% (Vogler et al. 2010), accompanied by increased exurban, low-density housing development and increased forest land cover. The FBRB is dominated by forest (75%), mainly secondary growth. Forest types consist of spruce-fir (*Picea-Abies*) and northern hardwoods at high elevations, mixed hardwood species at lower elevations, and mixed mesophytic forests on lower slopes and coves (SAMAB 1996). Agriculture comprises 12% of the landscape, over 70% of which is managed as meadow or pasture. Urban areas constitute 12% of the landscape and the remainder consists of shrubland, water, or barren land (all <1%) (Homer et al. 2012). Recent stakeholder interviews indicate that area residents strongly value biodiversity and are concerned for the futures of ecosystem services, particularly cultural ecosystem services (GroWNC 2013).

Wildflower surveys

Site selection

Wildflower communities were surveyed at 63 sites located on public and private property (SM Figure S1). We stratified the study area by elevation, building density, and land use. Sites were located in forested areas (n=51) or open fields (e.g., pastures or low-intensity hay fields, n=12) and within 150 m of trails or roads to characterize floral resources likely to be visible to people. Sites on public property were randomly located using the Sampling Design tool for ArcGIS 10.0. Private property site selection followed an iterative process. First, we invited property owners to participate through messages to area landowner networks as well as personal and professional networks. Second, each property was evaluated relative to our stratification scheme and visited to determine site-suitability (e.g. accessibility, areas without active cultivation). Study sites were randomly located on the selected properties using digitized maps of the property boundaries and the Sampling Design tool for ArcGIS 10.0.

Survey methods

A 50 x 2 m belt transect was established at each site. We avoided areas of active cultivation or horticulture. Sites were visited at least once every three weeks from April 1 to August 8, 2014. During each visit, we tallied the number of flowering individuals, identified each flowering individual to species, and estimated percent cover of flowers along the transect. We classified each species using charismatic species status. Charismatic species were determined by conducting a search of tourism websites using the terms “western North Carolina”, “southern Appalachian Mountains”, or “Asheville, North Carolina” and listing all flowering species mentioned by name or appearing in photographs on those websites; species that appeared on ≥ 40% of tourism websites were considered charismatic (SM Table S1). Data post-processing included grouping some of the flower species to genus based on similarity in appearance and potential misidentification. See Supplemental Materials for a complete list of species observed in bloom and grouped species (SM Table S2). All analyses used the grouped list.

Covariate Data

Each site was assigned a site type (i.e., forest=1 or open=2). Environmental variables were extracted from GIS data. Elevation, slope, aspect, and topographic position index (TPI) were calculated from the National Elevation Dataset 30-meter digital elevation model (DEM) (Gesch et al. 2002). The TPI describes the relative position of a site given nearby terrain; negative values indicate that a site is below the average elevation of its neighborhood (e.g., valleys and coves) whereas positive values indicate it is above the average elevation of its neighborhood (e.g., ridges and hilltops). We converted aspect to a relative moisture index ranging from 1 to 16, with SSW (1) as the driest aspect and NNE (16) as the wettest (Day and Monk 1974). Soil percent organic matter was extracted from the SSURGO soil database (Soil Survey Staff 2013).

Climate data for 2014 were calculated from the Daymet dataset (Thornton et al. 2012) which provides 1-km gridded estimates of daily weather for North America, including daily minimum and maximum temperature, precipitation occurrence and amount. We used cumulative growing degree days (GDD) and precipitation accumulated to the end of our sampling season to characterize climate for the full sampling period.

Building density (building units per hectare) was quantified by tallying all buildings located within 100 m of each study site. We used centroids of digitized building footprints obtained from county government GIS offices to locate buildings. We quantified vegetation structure and forest canopy cover from LIDAR (light detection and ranging) data. See Supplementary Methods for more details.

Data analysis

Analysis of observed floral resources

Nine response variables were calculated and represented three components of floral resources (i.e., flower species richness, flower abundance, and charismatic species richness). Flower species richness and flower abundance were analyzed at two temporal scales (i.e., full growing season and subseason).

(i) *Flower species richness:* To account for differences in observed species richness due to survey effort (e.g., weekly sampling versus tri-weekly sampling), we calculated flower species richness using species accumulation curves and the *vegan* package in R (Oksanen et al. 2015). We calculated flower species richness for the full 18-week season and for early spring, late spring, and summer (three 6-week subseasons).

(ii) *Flower abundance:* Peak bloom abundance, i.e., the maximum abundance during the full season, and subseason flower abundance, i.e., mean abundance within early spring, late spring, and summer, were calculated for each site.

(iii) *Charismatic species:* We calculated the proportional presence of charismatic species at each site as the number of charismatic species observed at that site divided by the total number of species observed at that site.

Factors influencing species richness, flower abundance, and flower timing were analyzed using Poisson regression and AICc model selection (*glm* function in package *lme4* for R; Bates et al. 2015). Binomial regression and AICc model selection were used to analyze the proportional presence of charismatic species. All covariates were standardized to mean = 0 and variance = 1, to directly compare regression coefficients as a measure of effect size. Candidate models included quadratic terms for building density, soil organic matter, and precipitation as well as interaction terms (growing degree days x building density; growing degree days x percent tree cover). For each response variable, the candidate suite of models included a full model with all covariates, single models for each predictor, and step-wise combinations of multi-variable models from the full model. Models were ranked according to second-order Akaike's information criterion (AICc) (Burnham and Anderson 2002). We inspected all models within ΔAICc < 2 of the top-ranked model. Results and coefficient estimates from all competing models within ΔAICc < 2 of the top model are presented in the Supplemental Information (SM Tables S4-S7). Below, we report covariate relationships with respect to the relative strength and direction of each covariate on the response variable across all competing models. See Supplementary Materials for more details on data analysis.

Analysis of projected landscape patterns of wildflower resources

We created maps of projected wildflower resources using the *predict* function in the *raster* package for R (Hijmans and van Etten 2015) and predicted values from best-fitting models identified in the analysis above. For response variables with competing top models, we first mapped the predicted value from each of the competing top models. Final maps were created by calculating the weighted-average of the mapped top model predictions, using the corresponding AICc model weights, rather than using model-averaged coefficients (Grueber et al. 2011; Cade 2015). All input layers were standardized to z-scores based on the mean and variance of the sampled dataset (n=63) and referenced to the same UTM projection (NAD 1983 UTM 17N) and 30-m grid cell. For more detail on preparation of input data layers, see Supplemental Material. For maps of the standard error of each predicted response, see supplemental material (SM Figure S2).

Hotspots of individual floral resources were identified for each response variable by calculating the upper 20th percentile of projected values for 30-m grid cells (SM Figure 3). Hotspots for multiple floral resources were identified by overlaying maps of the upper 20th percentile of each response variable (*sensu* Qiu and Turner 2013). We identified hotspots at two temporal scales: full season and subseason (early spring, late spring, and summer) and analyzed temporal consistency of hotspots by assessing spatial concordance of hotspots among subseasons.

Analysis of wildflower viewing accessibility

We compared maps of projected floral resources to maps of public access to examine how access to floral resources changed over time. We identified public access as any publicly owned lands (e.g. federal and state-owned forests and parks) as well as locations within 30-m of public-use trails such as greenways and bike trails (Table S3). For each time period and each floral resource, we calculated the area overlap between hotspots and public access.

Results

Observed floral resources

(i) *Flower species richness:* Two hundred thirty flower species were recorded in bloom across all study sites from April 1– August 8, 2014 (see Table S2 for full list); this list was reduced to 173 flower species for analysis. Sites varied in the number of species recorded in flower throughout the season (April – August) with total flower species richness ranging from 2 to 34 species ($\bar{x}$=12 ± 0.88) per site. Mean flower species richness among all sites was similar through the growing season, but flower species richness at each site varied by subseason (Figure 1).

Total flower species richness was higher at sites with lower precipitation, tree cover and building densities (Table S4). There were strong non-linear effects of soil organic matter (positive quadratic effect) on flower species richness; richness declined at intermediate soil organic matter levels and increased at higher levels of organic matter. Flower species richness was also influenced by the interaction of growing degree days (GDD) with percent cover of trees and building density; at warmer sites, where GDD were higher, the negative effects of tree cover were dampened whereas the conditional effect of building density was more negative as GDD increased.

The relative effect of topoedaphic variables, climate, local vegetation, and building density on flower species richness varied among subseasons (Table S5). Climate, soil organic matter and building density were most important for flower species richness during early spring, with cumulative precipitation exerting the most influence on species richness. The effect of GDD on subseason flower species richness was positive in early spring as days warmed and species began to bloom before leaf out, but changed to negative in late spring as higher elevation sites had more species in bloom and the forest canopy closed. Building density was important for flower species richness with strong nonlinear effects in early spring, wherein the highest richness occurred at intermediate levels of building density, and strong negative effects in late spring and summer. Soil organic matter affected flower species richness in all seasons.

(ii) *Flower abundance:* Observed peak bloom abundance ranged from 8 to 1828 flowers per site ($\bar{x}$=194 ± 44.1). Peak bloom abundances at open sites ($\bar{x}$= 659 ± 170) were substantially higher than in forested sites ($\bar{x}$= 84 ± 14.7) and site type was most important for explaining peak bloom abundance. Topoedaphic conditions had significant effects on peak bloom abundance, with positive effects of soil organic matter, topographic moisture index, and slope (Table S6). The negative effects of topographic position index indicated that higher peak bloom abundances were found at lower topographic positions relative to the surrounding terrain. Climate affected peak bloom abundance with strong non-linear effects of precipitation. Building density had a small positive effect on peak bloom abundance.

Mean flower abundance changed through the season and differed between open and forested sites (Figure 2). Factors affecting flower abundance varied in their relative importance and direction of effect across subseasons. Site type was the most important factor during all subseasons, with higher flower abundances occurring at open sites. Climate and topoedaphic conditions had the greatest effects in early and late spring while GDD and building density had the strongest (negative) effects on summer flower abundance.

Topoedaphic factors varied in their effects on flower abundance over the season. Topographic wetness index had strong positive effects in early spring, but lower relative and negative effects on late spring and summer flower abundance. Slope had positive effects in early and late spring but negative effects in summer. Topographic position index had negative effects in early and late spring, but no effect on summer flower abundance. Soil organic matter was negatively related to flower abundance, with strong nonlinear (positive quadratic) effects, in all subseasons.

Growing degree days had a strong negative effect on flower abundance in all subseasons, but had the strongest relative effect during the late spring where it was the second most important factor explaining flower abundance. The effect of precipitation on flower abundance changed over the season, with negative quadratic effects in early and late spring and positive quadratic effects during summer.

Building density had strong negative effects on summer flower abundance and was among the most important factors explaining flower abundance during summer. The effect of building density on early spring flower abundance was positive and was of lower relative importance than climate and topoedaphic variables. In all subseasons, significant interactions indicate that surrounding building density effects were modulated by the effect of GDD.

(iii) *Charismatic species:* Charismatic species were present at all sites, representing 5 to 100% of the total flower species richness per site ($\bar{x}$= 35%). Competing top models predicting the proportion of total flower species richness comprised of charismatic species all included strong effects of topography and precipitation (Table S7). Greater proportions of charismatic species were found at moister sites (higher topographic wetness index) in valley or cove locations (lower topographic position index) with higher precipitation. However, these models explained a relatively small proportion (pseudo-R^2=0.25 to 0.30) of variance in the data.

Projected landscape patterns of wildflower resources

Projected floral resources varied substantially across the landscape and through the season and were spatially autocorrelated (all Moran's $I > 0.72$, $p < 0.001$). Hotspots of floral resources (the top 20th percentile of each component of floral resources), were not often spatially co-located or temporally consistent through the season (Figure 3). Hotspots of overall flower species richness were few in number and relatively small in size (patch density = 2.8 km^{-1}; area-weighted mean patch size = 0.15 ha). Hotspots of flower species richness varied in number and size across subseasons and were largest during early spring and most numerous during late spring (Table 1). Hotspots of peak bloom abundance were more numerous than overall flower species richness hotspots but smaller in size (patch density = 13.6 km^{-1}; area-weighted mean patch size = 0.04 ha). Hotspots of flower abundance were largest during summer and most numerous during the early spring (Table 1). Spatial concordance of hot spots of flower species richness and flower abundance covered 5% of the landscape in early spring, 10% in late spring and 7% in summer, and areas of concordance shifted with subseason (Figure 4a – 4c).

Four percent of the landscape was designated to be flower richness coldspots; locations that consistently had low values of flower species richness (e.g., bottom 20th percentile) across all three time periods. Conversely, 6% of the landscape consistently was in the top 20th percentile of flower species richness in early spring, late spring, and summer, e.g. wildflower richness hotspots (Figure 4d). Coldspots of wildflower abundance occupied 2% of the landscape while consistent wildflower abundance hotspots comprised 10% of the landscape (Figure 4e).

Accessibility of wildflower viewing

Up to 30% of the landscape within the study area is publicly accessible for wildflower viewing. The accessibility of wildflower richness hotspots fluctuated through the seasons, with the highest proportion (37%) accessible during the late spring (Figure 5). Wildflower abundance hotspots in late spring and summer were often located on privately-owned land, in pastures or fields. However, increases in blooming during July and early August led to an increase in the accessibility of abundance hotspots throughout the early spring to summer season: 25% accessible in early spring, 30% during the late spring, and 32% in the summer. Finally, publicly accessible land tended to have a larger proportion of charismatic species (e.g., > 45% of the total flower species richness at those locations) than private lands.

Discussion

Cultural ecosystem services, important but less well-studied than other ecosystem services, often depend on biotic communities that shift in response to changing environmental conditions and resources. However, temporal dynamics of biotic communities are rarely included in ecosystem service models. Wildflower viewing, an important cultural ecosystem service that contributes to the ecotourism economy in the Southern Appalachians (Watson et al. 1992), depends on the presence and abundance of seasonally-dynamic floral resources. We analyzed factors affecting the richness, abundance, and timing of flowers, mapped the projected supply of floral resources, and identified hotspots of cultural ecosystem service supply. Incorporating temporal dynamics of wildflower blooms identified complex seasonal relationships with environmental variables and uncovered seasonal variation in the supply and accessibility of potential ecosystem services.

Ecosystem services provided by wildflower communities are known to vary with land use/land cover and management intensity (Quetier et al. 2007; Fontana et al. 2014). Floral resources in the Southern Appalachians varied with land use, climate and topoedaphic conditions, and seasonal change in floral resources influenced projected landscape patterns of ecosystem services. The effect of climate on wildflower blooms varied throughout the season, reflecting shifts from lower to higher elevations. Peak bloom abundances tended to occur earliest on drier, warmer forested sites, which likely reflects understory plant community response to aspect-driven microclimate and light availability prior to canopy closure (Gilliam 2007).

Open sites were associated with increased flower abundances and longer flowering seasons than forested sites, while forested sites were associated with a higher proportion of charismatic species. Increased development on agricultural lands, consistent with projected land-use changes in the Southern Appalachians (Wear 2011) could decrease landscape capacity to provide wildflower viewing. Similarly, the strong negative effects of building density on flower species richness suggest that projected increases in residential development may lead to tradeoffs with floral resources. Maintaining a mixture of natural, semi-natural, and agricultural cover types in a pre-dominantly forested landscape may ensure a high diversity of floral resources across multiple seasons and provide increased opportunities to view wildflowers.

As expected, shifts in floral resources changed the locations of wildflower viewing opportunities throughout the season. Many of the open, private lands are considered visible and accessible from roads and trails throughout the region. Publicly accessible lands provide access to floral resources hotspots (e.g. the top 20th percentile of flower species richness or flower abundance), but only 37% of the area projected to be flower species richness hotspots were publicly accessible. Public access to flower abundance hotspots was highest during the summer, increasing over the season despite a strong shift to open, private lands in late spring and summer. This pattern is a consequence of many public lands, such as national forests, occurring at higher elevations. As wildflower bloom expands upward in elevation, hotspots in public lands also expand. These shifts, coupled with the high proportion of hotspots on private lands, highlight the potential for both public and private lands to have high cultural ecosystem service value and emphasizes the importance of private lands in maintaining ecosystem services (Schaich and Plieninger 2013).

Interannual variation in wildflower community phenology may also contribute to shifts in cultural ecosystem service supply (Forrest et al. 2010). Our study used data collected within one year and focused on identifying shifts in cultural ecosystem service supply resulting from seasonal shifts in wildflowers at a finer temporal resolution. Despite the potential for interannual variation, seasonal shifts in floral resources would still alter wildflower viewing supply and access to cultural ecosystem services. Our study adds to the expanding literature recognizing the need to incorporate temporal variation in ecosystem service assessments to fully describe patterns of ecosystem service supply (Nicholson et al. 2009; Holland et al. 2011b; Blumstein and Thompson 2015).

We provide one of the first examples incorporating temporal variability in biotic communities into a spatial assessment of cultural ecosystem service supply. The models presented in this study focus specifically on wildflower richness and abundance in a montane region of the Southern Appalachians. The study area is dominated by forests, with exurban development occurring under the forest canopy (Turner et al. 2003). Our sampling scheme reflected this forest dominance, with only 10 of our 63 sites located in open fields, which may have limited our power to detect variability among open fields. As with all statistical models, caution should be used before transferring these models to other regions as relationships between covariates may differ.

People interested in wildflower viewing (e.g., users of the ecosystem service) may value different components of floral resources based on their individual preferences, beliefs and expertise (Satz et al. 2013), as has been shown for wildlife viewing (Martin 1997). It is often assumed that species-rich views improve the aesthetic value of landscapes (Marshall and Moonen 2002) and increased flower color diversity may provide high cultural ecosystem service value (Quétier et al. 2009; Lindemann-Matthies et al. 2010). Flower-rich views may also increase aesthetic values of landscapes for some viewers (Junge et al. 2009) whereas others may be primarily interested in seeing specific wildflowers of cultural significance or rare species (Martin 1997). Our approach attaches importance to both diversity and abundance of flowers without asserting that one floral component (e.g. richness, abundance, or charismatic species presence) provides a greater or lesser cultural service value. Such differentiation requires understanding stakeholder preferences for particular wildflower arrangements (Turpie and Joubert 2004) and would allow for more detailed evaluation of how the potential wildflower supply affects actual cultural ecosystem service use.

Cultural ecosystem services are not well understood and have been seldom quantified in ecosystem services literature (Daniel et al. 2012). Often, simple proxies based on land-cover or coarse indicators are used to map cultural ecosystem services, such as mapping the amount of green space (Barthel et al. 2005), trails and other recreational facilities (Raudsepp-Hearne et al. 2010; Lovell and Taylor 2013), or some combination of land cover, local features, and nearby population (Qiu and Turner 2013; van Berkel and Verburg 2014). These simple indicators provide little insight into the capacity of a landscape to supply cultural ecosystem services under varying environmental conditions. Further, cultural ecosystem services are often excluded from analysis thereby inhibiting assessments of cultural services in relation to other services or under alternate management scenarios (Hernández-Morcillo et al. 2013).

Our empirical models accounted for temporal dynamics of a biodiversity-based cultural ecosystem service and identified patterns of cultural ecosystem service supply hotspots otherwise obscured by using simple proxies. Such models that incorporate the underlying ecology of cultural ecosystem services have potential to inform policy makers and managers (Daily et al. 2009) and, especially for services that depend on mobile or seasonal biodiversity (Kremen et al. 2007), should be incorporated in future studies to avoid under- or over-emphasizing the importance of particular landscape elements.

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Table 1. Summary of the number and size of patches of projected hotspots of floral resources in the French Broad River Basin, North Carolina. Results are reported for the entire study period and by season.

Projected floral resource		Threshold used to define hotspot	Number of hotspot patches	Hotspot patch density (km^{-1})	Area-weighted mean patch size (ha)
Flower species richness	Total (overall)	> 13 species	12,187	2.76	0.15
	Early spring	> 6 species	15,501	3.49	1.60
	Late spring	> 5 species	27,432	6.20	0.21
	Summer	> 5 species	14,230	3.22	0.07
Flower abundance	Peak bloom	> 810 flowers	58,717	13.56	0.04
	Early spring	> 470 flowers	28,231	8.69	0.13
	Late spring	> 410 flowers	39,148	8.86	0.17
	Summer	> 330 flowers	31,888	7.23	0.37

Figures captions

Figure 1. Observed flower species richness at study sites in the French Broad River Basin during early spring, late spring, and summer 2014.

Figure 2. Observed flower abundance at study sites in the French Broad River Basin during three subseasons between April and August 2014.

Figure 3. Projected distribution of (a) total flower species richness, (b) early spring richness, (c) late spring richness, (d) summer richness, (e) peak bloom abundance, (f) early spring abundance, (g) late spring abundance, and (h) summer abundance for the French Broad River Basin. Projections based on AICc-selected models from sites (n=63) sampled during Apr - Aug 2014.

Figure 4. Spatial distribution of combined hotspots of flower species richness and abundance during (a) early spring, (b) late spring, and (c) summer as well as the location of consistent hotspots (red) and coldspots (blue) of (d) flower species richness and (e) flower abundance across three subseasons.

Figure 5. Projected seasonal change in the proportion of floral resource hotspots within publicly accessible areas in the French Broad River Basin.

Figure 1.

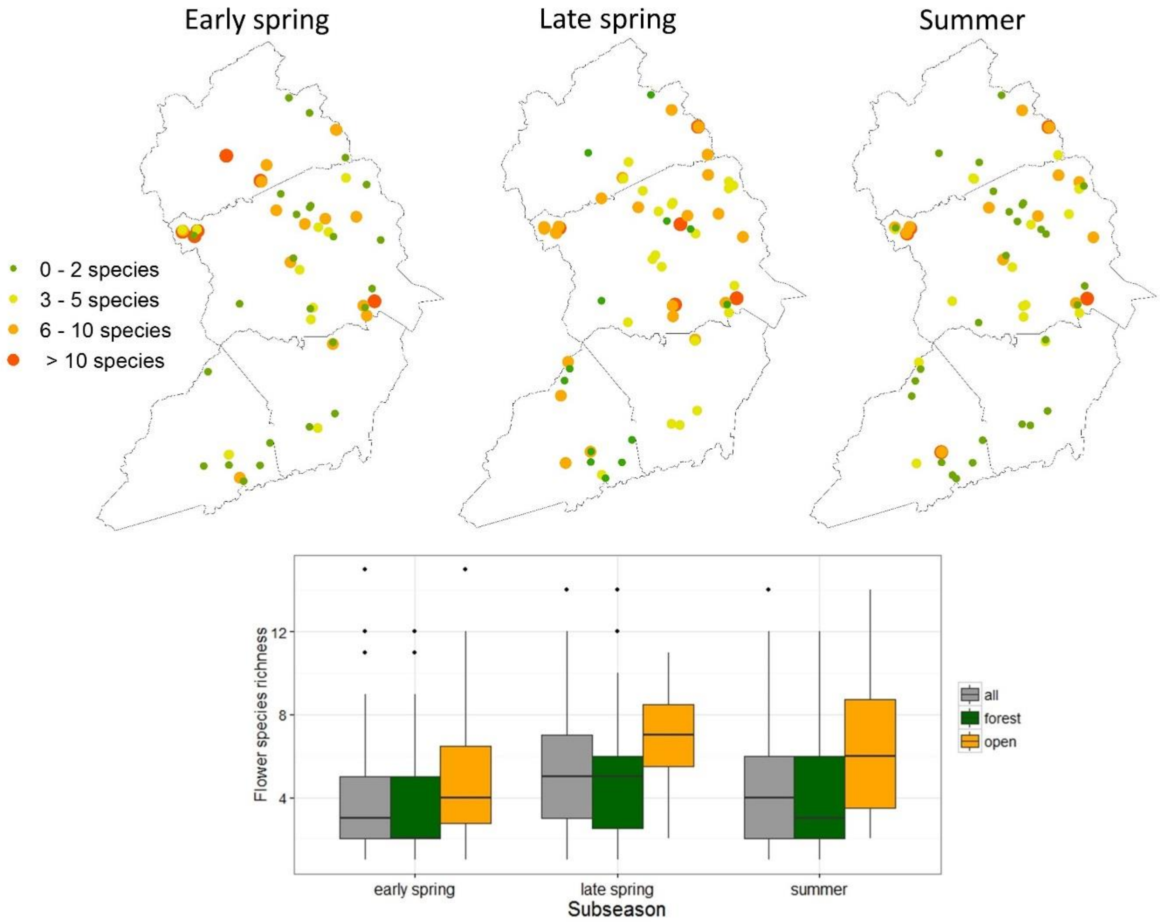

Early spring
Late spring
Summer
0 - 2 species
3 - 5 species
6 - 10 species
> 10 species
Flower species richness
12
8
4
all
forest
open
early spring
late spring
summer
Subseason

Figure 2.

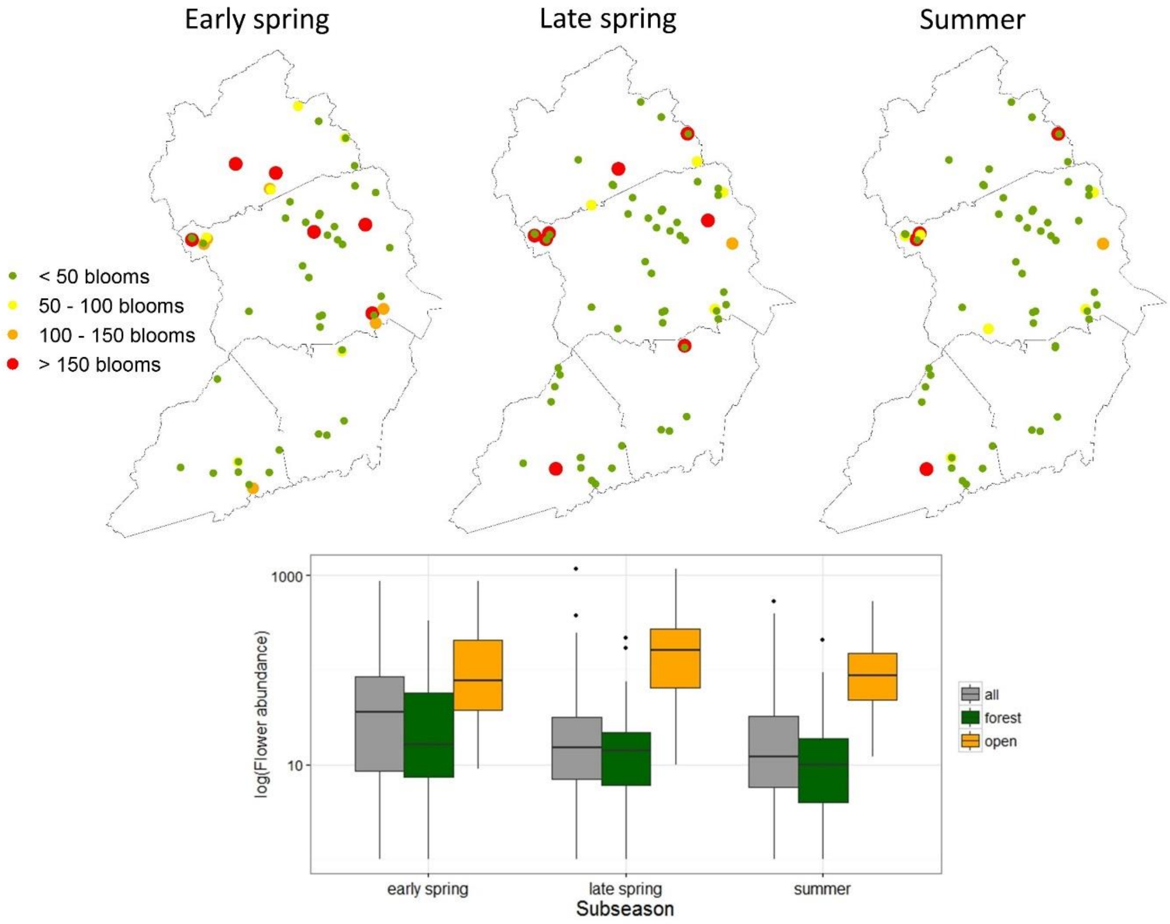
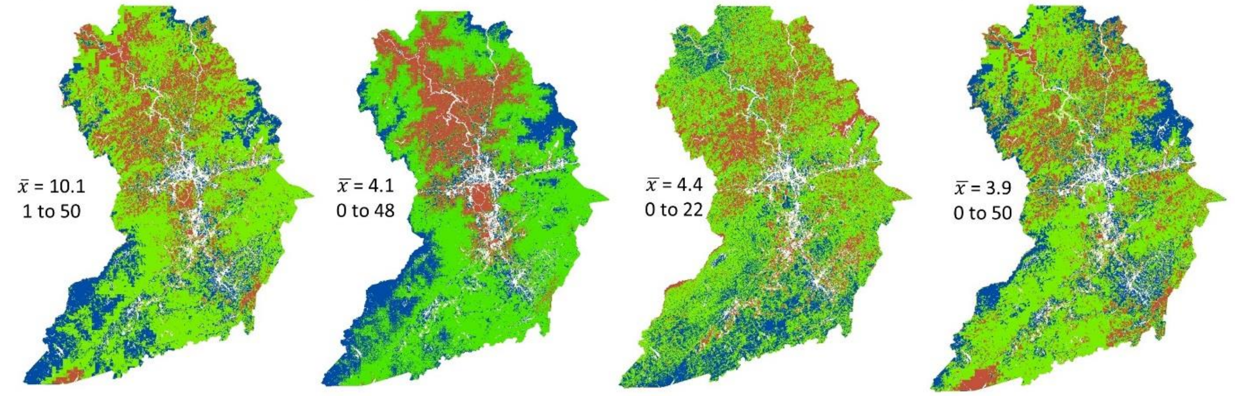

Early spring
Late spring
Summer
< 50 blooms
50 - 100 blooms
100 - 150 blooms
> 150 blooms
log(Flower abundance)
1000
10
early spring
late spring
summer
Subseason
all
forest
open

Figure 3.

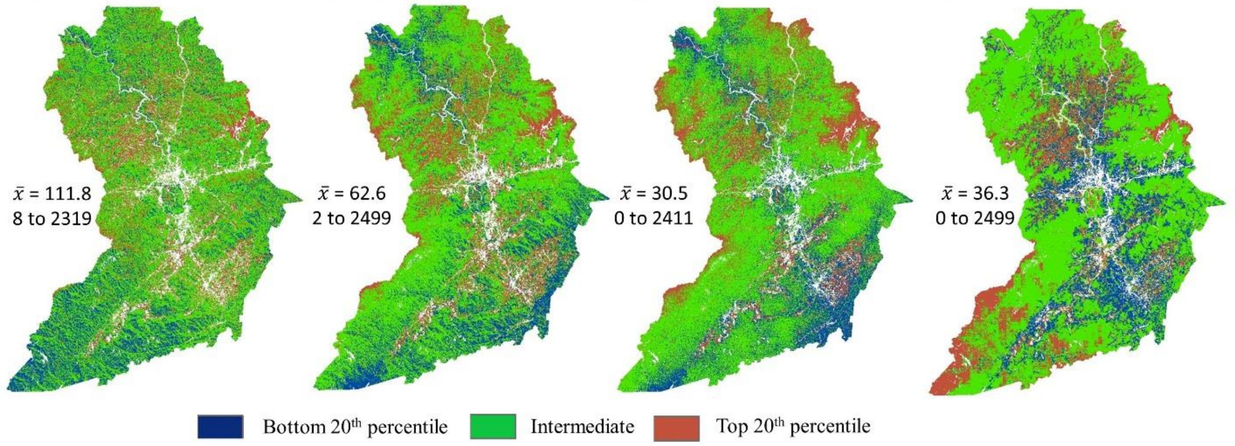


a) Overall flower richness

b) Early spring flower richness

c) Late spring flower richness

d) Summer flower species richness



e) Peak bloom abundance

f) Early spring flower abundance

g) Late spring flower abundance

h) Summer flower abundance

Figure 4.

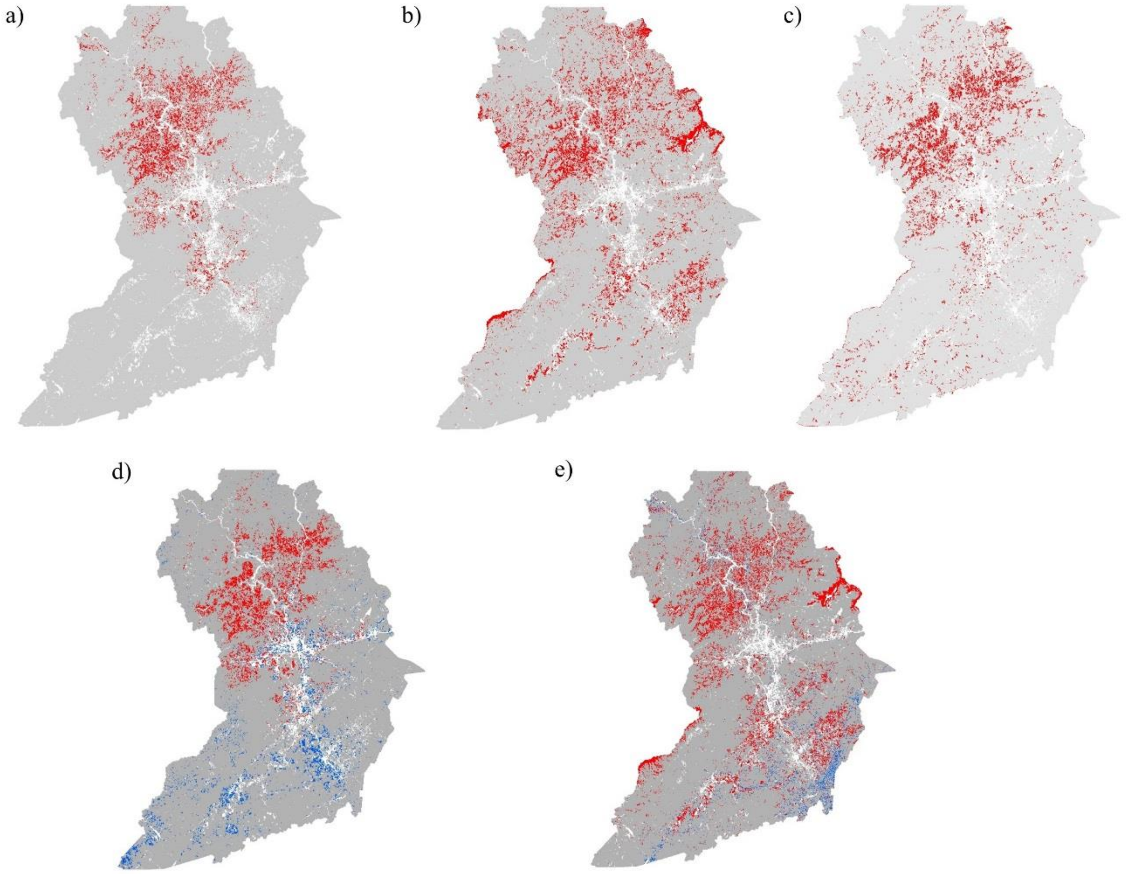
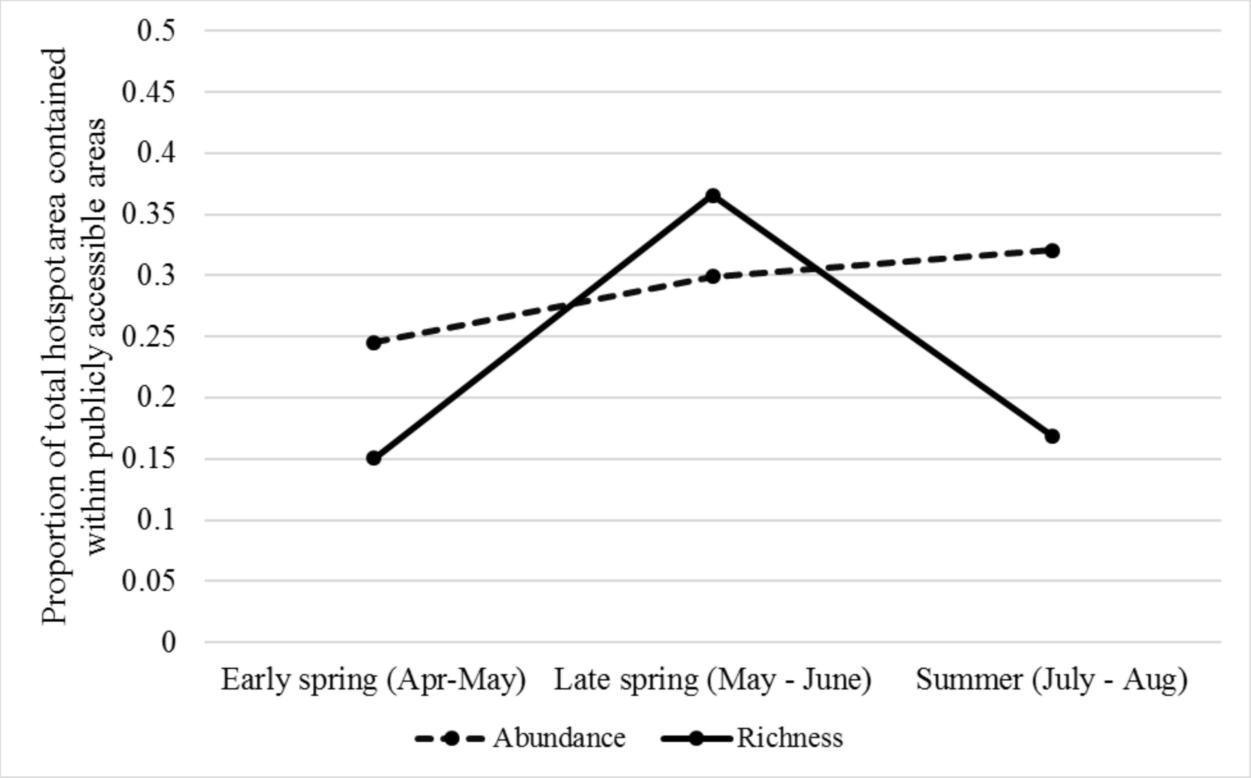


Figure 5.


Proportion of total hotspot area contained within publicly accessible areas
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Early spring (Apr-May)
Late spring (May - June)
Summer (July - Aug)
Abundance
Richness

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Supplemental Material

Electronic Supplementary Materials (Graves *et al*. – Landscape dynamics of floral resources affect the supply of a biodiversity-dependent cultural ecosystem service.)

1. **Supplementary Methods**
    a. Covariate Data
    b. Data analysis
    c. Maps of predictor variables
2. **Supplementary Tables**
3. **Supplementary Figures**

1. SUPPLEMENTARY METHODS

1a. Covariate data

Cumulative growing degree days (GDD) were calculated from January 1 to August 10, 2014 using a base temperature of 5° Celsius. Cumulative precipitation was calculated for the same time period. We used GDD and precipitation accumulated to the end of our sampling season in order to characterize the full sampling period. The end of season (i.e., January to August) cumulative GDD and precipitation were highly correlated (R^2=0.94 and R^2=0.79, respectively) with the start of season (i.e., January to April 1) values.

Vegetation structure and forest canopy cover were derived from LIDAR (light detection and ranging) data. Forest canopy cover was recorded as the proportion of LIDAR returns at each study site that were within the subcanopy or canopy layers (i.e., >2.0 m above ground). Discrete-return LIDAR data were collected in 2005 for the entirety of the study area during winter (NCDEM 2006). Vegetation height was measured from LIDAR first returns by subtracting the elevation of a bare-earth digital terrain model, derived from the same LIDAR data set, from the elevation of each return. Only first returns were used, and we excluded returns within digitized building footprints. Since the LIDAR data represent a time period prior to our field data collection, we verified the validity of these data by field validation and examining recent aerial photographs.

1b. Data analysis

For each response variable, we used generalized linear models (GLM) to assess the role of topoedaphic, climatic, and landscape variables in explaining spatial and temporal variation in floral resources (Table 1). After checking for collinearity among variables, we dropped elevation, which was strongly correlated with growing degree days ($\rho = -0.91$) and precipitation ($\rho = 0.51$). All environmental variables were standardized by subtracting the mean and dividing by the standard deviation, so that each variable had mean zero and variance = 1, allowing us to directly compare regression coefficients as a measure of effect size. Site type was included as a factor with two levels, forest (1) and open (2), and considered in models of flower abundance. Site type and percent forest canopy were never included in the same model. To account for possible non-linear relationships between flower species richness and urbanization, we included a quadratic form of building density in models of flower species richness. We also considered quadratic terms for soil organic matter and precipitation for each response variable. Finally, we included two interaction terms in the full model for each response variable to test for interactive effects between temperature and land use/land cover on floral resources, (growing degree days x building density; growing degree days x percent tree cover).

For each response variable, models included a full model with all the predictor variables, single models for each predictor, and step-wise combinations of multi-variable models from the full model. Models were ranked according to second-order Akaike's information criterion (AICc)

(Burnham and Anderson 2002). We inspected all models with respect to the top-ranked model (ΔAICc) and inspected all models within ΔAICc < 2. We report the results from all competing models within ΔAICc < 2 (Tables S1-S7) and report covariate relationships with respect to the relative strength and direction of its effect on the response variable across all competing models. Model residuals were checked for spatial autocorrelation and none was detected. For subseason models, we compared the rank-order of coefficient values for predictor variables at each time period to determine whether the relative importance of each variable changed during the season. For response variables with competing top models, we first mapped the predicted value from each of the competing top models. Final maps were created by calculating the weighted-average of the mapped top model predictions, using the corresponding AICc model weights, rather than using model-averaged coefficients (Grueber et al. 2011; Cade 2015)

Table 1. Summary of predictor variables for observed sites, presented as mean (min-max).

Category	Variable	Description	Study sites		Landscape	
			$\bar{x}$	min - max	$\bar{x}$	min - max
Topoedaphic	Elevation	Elevation a.s.l. (m)	809	537-1475	812	324 – 1934
	Aspect (TWI)	Degrees converted to topographic wetness index (Day and Monk 1974; 1 = driest, 16 = wettest)	8	2 – 15	8	1 – 16
	Slope	Slope gradient (%)	22.8	0.8 – 74.8	15.3	0 – 80.1
	Topographic position index	Local terrain position index	0.78	-5.44 – 8.44	0.01	-61.4 – 54.9
	Soil OM	Soil organic matter (%)	5.5	0 – 15	4.9	0.25 – 94

Climate	Growing degree days	Accumulated growing degree days from Jan – Aug 2014	2615.7	2136.5 – 2860.3	2638.7	1869.8 – 3116
	Precipitation	Cumulative precipitation (mm) during Jan – Aug 2014	801.8	597 – 1053	828	556 – 1297
Local Vegetation & Land use	Percent tree cover	Percent of lidar returns classified as subcanopy or canopy within 100 m	53	1 – 81	55	0 – 100
	Building density	Building density within 100m	0.36	0 – 2.58	0.43	0 – 23.9*
	Site type	Forest (1) or open (2) based on NLCD classification	NA	NA	NA	NA

* includes developed, urban areas not included in landscape projections.

1c. Maps of predictor variables

Input layers were created for each predictor variable in order to project landscape floral resources using the *predict* function in the *raster* package for R. All input layers were standardized to z-scores based on the mean and variance of the sampled dataset (n=63) and referenced to the same UTM projection (NAD 1983 UTM 17N) and 30-m grid cell. The 30-m grid cell was chosen to correspond with the common resolution of Landsat land use/land cover data as well as the National Elevation Dataset digital elevation model.

We used raster data with a 30-m pixel resolution from the 2014 National Crop Data Layer (CDL; USDA NASS 2014) to create maps of site type, where all forested land cover types were classified as forest and any pasture, hay, or grassland cover types were classified as open. Soil organic matter maps used the gridded soil survey geographic (gSSURGO) database for North Carolina (Soil Survey Staff 2015). Maps of elevation, slope, aspect, and topographic shape index (TSI) were calculated from the National Elevation Dataset 30-meter digital elevation model

(DEM) (Gesch et al. 2002). We converted aspect to a relative moisture index ranging from 1 to 16, with SSW (1) as the driest aspect and NNE (16) as the wettest (Day and Monk 1974).

We created maps of forest canopy cover and building density within 100 m of each 30-m pixel using a moving window analysis in GIS. Building density (building units per hectare) was quantified by counting the number of buildings located within 100 m of the center of each 30-m cell using digitized building footprints obtained from county government GIS offices and converting to buildings per hectare by dividing by the moving window area (3.142 ha). Forest canopy cover maps were created using the proportion of LIDAR returns within the analysis window (3.142 ha circle, centered on each 30-m cell) within the subcanopy or canopy layers (i.e., >2.0 m above ground). Discrete-return LIDAR data were collected in 2005 (NCDEM 2006) for the entirety of the study area during winter. Vegetation height was measured from LIDAR first returns by subtracting the elevation of a bare-earth digital terrain model, derived from the same LIDAR data set, from the elevation of each return. Only first returns were used, and we excluded returns within digitized building footprints.

Climate data for the 2014 survey year were extracted from the Daymet data set (Thornton et al. 2014) which provides gridded estimates of daily weather for North America at a 1-km resolution, including daily minimum and maximum temperature, precipitation occurrence and amount. We used these data to calculate the accumulated growing degree days (GDD) and total accumulated precipitation from January 1 to August 10 for each study site. Growing degree days were calculated using 5°C as a base temperature. Climate data were resampled to 30-m resolution using bilinear interpolation and projected to NAD 1983 UTM 17N.

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2. SUPPLEMENTARY TABLES

SM Table S1. List of wildflower species observed on tourism websites and the proportion of websites on which each was observed. Wildflower species observed on ≥40% of websites were classified as charismatic species.

Flowering Species Mentioned	**Scientific Name**	**# of website occurrences**	**% of websites**
Any trillium species	*Trillium spp.*	27	100%
Any violet species	*Viola spp.*	13	100%
Bloodroot	*Sanguinara candensis*	6	60%
Bluebead or Clintons lily	*Clintonia borealis or umbellulata*	5	50%
Bluets	*Houstonia spp.*	4	40%
Buttercups	*Ranunculus spp.*	5	50%
Butterfly weed	*Asclepias tuberosa*	5	50%
Catawba rhododendron	*Rhododendron catawbiesne*	5	50%
Catesby's Trillium	*Trillium catesbaei*	5	50%
Columbine	*Aquilegia canadensis*	6	60%
Crested dwarf iris	*Iris cristata*	6	60%
Dutchman's breeches	*Dicentra cucullaria*	7	70%
Fire Pink	*Silene virginica*	7	70%
Flame azalea	*Rhododendron calendulaceum*	7	70%
Foam flower	*Tiarella cordifolia*	5	50%
Galax	*Galax aphylla*	4	40%
Gray's lily	*Lilium grayi*	4	40%
Jack-in-the-Pulpit	*Arisaema triphyllum*	4	40%
Large-flowered trillium	*Trillium grandiflorum*	6	60%
Mayapple	*Podophyllum peltatum*	4	40%
Mountain laurel	*Kalmia latifolia*	7	70%
Painted trillium	*Trillium undulatum*	6	60%
Phlox	*Phlox carolina*	5	50%
Pink lady (orchid)	*Cyripedium pubescens*	6	60%
Pinkshell azalea	*Rhododendron vaseyi*	5	50%
Showy orchis	*Gelaris spectablis*	6	60%
Solomon's Seal	*Polygonatum biflorum or pubescens*	4	40%
Spring beauty	*Claytonia caroliniana*	6	60%
Squirrel corn	*Dicentra canadensis*	4	40%
Trout lily	*Erythronium umbilicatum*	5	50%
Turkscap lily	*Lilium superbum*	7	70%
Vaseys Trillium	*Trillium vaseyi*	4	40%
Wake robin	*Trillium erectum*	6	60%

Wild geranium	*Geranium maculatum*	8	80%
Yellow lady slipper	*Cyprepedium calceaolus*	5	50%

SM Table S2. List of all species observed in flower during the study, coded by final grouping for analysis.

Common Name	Scientific Name	Group
Yarrow	*Achillea millefolium*	
White baneberry	*Actaea pachypoda*	
Black cohosh	*Actaea racemosa*	
Red baneberry	*Actaea rubra*	
Small-flowered agrimony	*Agrimonia parviflora*	
Garlic mustard	*Allium tricoccum*	
Garlic mustard	*Alliaria petiolata*	
Amaranth	*Amaranthus spp.*	
Shadbush	*Amelanchier spp.*	
Fly poison	*Amianthium muscaetoxicum*	
Pearly everlasting	*Anaphalis margaritacea*	
Canada anemone	*Anemone canadensis*	
Wood anemone	*Anemone quinquefolia*	
Thimbleweed	*Antennaria virginica*	
Thimbleweed	*Anemone virginiana*	
Puttyroot orchid	*Aplectrum hyemale*	
Smooth rockcress	*Arabis laevigata*	
Goat's beard	*Aruncus dioicus*	
Large thyme-leaved sandwort	*Arenaria serpyllifolia*	
Jack-in-the-Pulpit	*Arisaema triphyllum*	
False goat's beard	*Astilbe biternata*	
Fourleaf milkweed	*Asclepias quadrifolia*	Asclepias
White milkweed	*Asclepias variegata*	Asclepias
Aster	*Aster spp.*	Aster
Virginia oak-leech	*Aureolaria virginica*	
Yellowrocket	*Barbarea vulgaris*	
Rattlesnake fern	*Botrychium virginianum*	
Mustard spp.	*Brassica spp.*	Brassica
Cut-leaved toothwort	*Cardamine concatenata*	
Wood crinkleroot	*Cardamine diphylla*	
Hairy bittercress	*Cardamine hirsuta*	
Sand bittercress	*Cardamine parviflora*	
New Jersey tea	*Ceanothus americanus*	
Chickweed spp.	*Cerastium spp.*	
Fairy wand	*Chamaelirium luteum*	
Spotted wintergreen	*Chimaphila maculata*	
Wild sensitive plant	*Chamaecrista nictitans*	
Green and gold	*Chrysogonum virginianum*	
Common chicory	*Cichorium intybus*	

Enchanter's nightshade	*Circaea lutetiana*	
Thistle spp.	*Cirsium spp.*	
Carolina springbeauty	*Claytonia caroliniana*	
Wild basil	*Clinopodium vulgare*	
Bear corn	*Conopholis americana*	
Asiatic dayflower	*Commelina communis*	
Flowering dogwood	*Cornus florida*	
Tickseed spp.	*Corydalis flavula*	
Coreopsis	*Coreopsis spp.*	
Rock harlequin	*Corydalis sempervirens*	
Hawthorn spp.	*Crataegus spp.*	
Canadian honewort	*Cryptotaenia canadensis*	
Moccasin flower	*Cypripedium acaule*	
Queen Anne's lace	*Daucus carota*	
Naked-flowered tick trefoil	*Desmodium nudiflorum*	
Wild yam	*Dioscorea villosa*	
Eastern shooting star	*Dodecatheon meadia*	
Eastern purple coneflower	*Echinacea purpurea*	
False rue anemone	*Isopyrum biternatum*	
Trout lily	*Erythronium americanum*	
Annual fleabane	*Erigeron annuus*	Erigeron
Fleabane	*Erigeron spp.*	Erigeron
Robin's plantain	*Erigeron pulchellus*	Erigeron
Flowering spurge	*Euphorbia corollata*	
White wood aster	*Eurybia divaricata*	
Rough boneset	*Eupatorium pilosum*	
Spotted joe pye weed	*Eutrochium maculatum*	Eutrochium
Sweetscented joe pye weed	*Eutrochium purpureum*	Eutrochium
Buckwheat	*Fagopyrum esculentum*	
Galax	*Galax aphylla*	
Bedstraw	*Galium aparine*	Galium
Northern bedstraw	*Galium boreale*	Galium
Licorice bedstraw	*Galium circaezans*	Galium
Lanceleaf wild licorice	*Galium lanceolatum*	Galium
Purple bedstraw	*Galium latifolium*	Galium
Fragrant bedstraw	*Galium triflorum*	Galium
Bedstraw spp.	*Galium spp.*	Galium
Showy orchid	*Galearis spectabilis*	
Bear huckleberry	*Gaylussacia ursina*	
Spotted geranium	*Geranium maculatum*	
White avens	*Geum canadense or other Geum spp.*	Geum
Ground ivy	*Glechoma hederacea*	

Rattlesnake plantain	*Goodyera pubescens*	
Alumroot	*Heuchera americana*	
Purplehead sneezeweed	*Helenium flexuosum*	
Sharp-lobed hepatica	*Hepatica acutiloba*	
Meadow hawkweed	*Hieracium pratense*	
Woodland bluet	*Houstonia purpurea*	
Wild hydrangea	*Hydrangea arborescens*	
Yellow star grass	*Hypoxis hirsuta*	
St. John's Wort	*Hypericum perforatum*	
Cat's ear	*Hypochaeris spp.*	
Jewelweed	*Impatiens capensis*	
Pale touch-me-not	*Impatiens pallida*	
Iris spp.	*Iris spp.*	
Mountain laurel	*Kalmia latifolia*	
Canada nettle	*Laportea canadensis*	
Daisy spp.	*Lapsana communis*	
Deadnettle	*Lamium spp.*	Lamium
Oxeye daisy	*Leucanthemum vulgare*	
Spicebush	*Lindera benzoin*	
Lovage	*Ligusticum canadense*	
Lily spp.	*Lilium spp.*	
Carolina lily	*Lilium michauxii*	
European privet	*Ligustrum vulgare*	
Indian-tobacco	*Lobelia inflata*	
Honeysuckle	*Lonicera spp.*	
Hairy woodrush	*Luzula acuminata*	
Lanceleaf loosestrife	*Lysimachia lanceolata*	Lysimachia
Whorled yellow loosestrife	*Lysimachia quadrifolia*	Lysimachia
False Solomon's seal	*Maianthemum racemosum*	
Field mint	*Mentha arvensis*	
Meehan's mint	*Meehania cordata*	
Narrowleaf cowwheat	*Melampyrum lineare*	
Black medick	*Medicago lupulina*	
Indian cucumber root	*Medeola virginiana*	
Partridgeberry	*Mitchella repens*	
White bergamot	*Monarda clinopodia*	
Wild bergamot	*Monarda fistulosa*	
Pinesap	*Monotropa hypopithys*	
Indianpipe	*Monotropa uniflora*	
Spring forget-me-not	*Myosotis verna*	
Common evening primrose	*Oenothera biennis*	
Clayton's sweetroot	*Osmorhiza claytoni*	Osmorhiza
Longstyle sweetroot	*Osmorhiza longistylis*	Osmorhiza

Woodsorrel	*Oxalis spp.*	Oxalis
Great yellow woodsorrel	*Oxalis grandis*	Oxalis
Common yellow woodsorrel	*Oxalis stricta*	Oxalis
Poppy	*Papaver spp.*	
Pokeweed	*Phytolacca americana*	
American lopseed	*Phryma leptostachya*	
Meadow phlox	*Phlox maculata*	Phlox
Creeping phlox	*Phlox stolonifera*	Phlox
Plantain	*Plantago spp.*	
Dwarf cinquefoil	*Potentilla canadensis*	
Smooth Solomon's seal	*Polygonatum biflorum*	Polygonatum
Hairy Solomon's seal	*Polygonatum pubescens*	Polygonatum
Mayapple	*Podophyllum peltatum*	
Common Cinquefoil	*Potentilla simplex*	
Yellow manadarin	*Prosartes lanuginosa*	
Common selfheal	*Prunella vulgaris*	
Mountainmint	*Pycnanthemum spp.*	
Buffalo nut	*Pyrularia pubera*	
Littleleaf buttercup	*Ranunculus abortivus*	Ranunculus
Tall buttercup	*Ranunculus acris*	Ranunculus
Bristly buttercup	*Ranunculus hispidus*	Ranunculus
Buttercup spp.	*Ranunculus spp.*	Ranunculus
Rosebay rhododendron	*Rhododendron maximum*	Rhododendron 1
Smooth azalea	*Rhododendron arborescens*	Rhododendron 2
Flame azalea	*Rhododendron calendulaceum*	Rhododendron 2
Virginia meadow-beauty	*Rhexia virginica*	
Multiflora rose	*Rosa multiflora*	
Black/raspberry spp.	*Rubus spp.*	Rubus
Curly dock	*Rumex crispus*	
Black-eyed susan	*Rudbeckia hirta*	
Bloodroot	*Sanguinaria canadensis*	
Lyreleaf sage	*Salvia lyrata*	
Canadian blacksnakeroot	*Sanicula canadensis*	Sanicula
Clustered blacksnakeroot	*Sanicula odorata*	Sanicula
Largefruit blacksnakeroot	*Sanicula trifoliata*	Sanicula
Saxifrage spp.	*Saxifraga spp.*	
Figwort	*Scrophularia marilandica*	
Ragwort spp.	*Scuttellaria spp.*	
Golden ragwort	*Senecio aureus*	
Woodland stonecrop	*Sedum ternatum*	
Narrowleaf blue-eyed grass	*Sisyrinchium angustifolium*	
Starry campion	*Silene stellata*	

Fire pink	*Silene virginica*	
Roundleaf greenbrier	*Smilax rotundifolia*	
Carolina horsenettle	*Solanum carolinense*	
Goldenrod	*Solidago spp.*	Solidago
Japanese meadowsweet	*Spiraea japonica*	
Star chickweed	*Stellaria pubera*	Stellaria
Grass-like starwort	*Stellaria graminea*	Stellaria
Common chickweed	*Stellaria media*	Stellaria
Star chickweed	*Stellaria pubera*	Stellaria
Betony	*Stachys officinalis*	
Rose twisted stalk	*Streptopus roseus*	
Dandelion	*Taraxacum officinale*	
Early meadow-rue	*Thalictrum dioicum*	Thalictrum
Rue anemone	*Thalictrum thalictroides*	Thalictrum
Hairy-jointed meadowparsnip	*Thaspium barbinode*	Thaspium
Purple meadowparsnip	*Thaspium trifoliatum*	Thaspium
Heartleaf foamflower	*Tiarella cordifolia*	
Crippled cranefly	*Tipularia discolor*	
Eastern poison ivy	*Toxicodendron radicans*	
Ohio spiderwort	*Tradescantia ohiensis*	Tradescantia
Zigzag spiderwort	*Tradescantia subaspera*	Tradescantia
Virginia spiderwort	*Tradescantia virginiana*	Tradescantia
Field clover	*Trifolium campestre*	Trifolium
Clover spp.	*Trifolium spp.*	Trifolium
Field clover	*Trifolium pratense*	Trifolium
Field clover	*Trifolium repens*	Trifolium
Nodding trillium	*Trillium cernuum*	Trillium
Red trillium	*Trillium erectum*	Trillium
Large-flowered trillium	*Trillium grandiflorum*	Trillium
Trillium spp.	*Trillium spp.*	Trillium
Southern nodding trillium	*Trillium rugelii*	Trillium
Toadshade trillium	*Trillium sessile*	Trillium
Painted trillium	*Trillium undulatum*	Trillium
Venus' looking-glass	*Triodanis perfoliata*	
Stinging nettle	*Urtica dioica*	
Largeflower bellwort	*Uvularia grandiflora*	Uvularia
Perfoliate bellwort	*Uvularia perfoliata*	Uvularia
Mountain bellwort	*Uvularia puberula*	Uvularia
Sessileleaf bellwort	*Uvularia sessilifolia*	Uvularia
Bellwort	*Uvularia spp.*	Uvularia
Blueberry spp.	*Vaccinium spp.*	Vaccinium
Highbush blueberry	*Vaccinium corymbosum*	Vaccinium

Deerberry	*Vaccinium stamineum*	Vaccinium
Mullein	*Verbascum spp.*	
Veronica	*Veronica spp.*	
White vervain	*Verbena urticifolia*	
Bunch flower	*Melanthium virginicum*	
Mapleleaf viburnum	*Viburnum acerifolium*	Viburnum
Viburnum spp.	*Viburnum spp.*	Viburnum
Vetch spp.	*Vicia spp.*	
White violet	*Viola blanda*	Violoa
Halberdleaf yellow violet	*Viola hastata*	Viola
Common blue violet	*Viola spp.*	Viola
Halberdleaf yellow violet	*Viola pedata*	Viola
Downy yellow violet	*Viola pubescens*	Viola
Wild pansy	*Viola rafinesquii*	Viola
Roundleaf yellow violet	*Viola rotundifolia*	Viola
Common blue violet	*Viola sororia*	Viola
Striped cream violet	*Viola striata*	Viola
Johnny jumpup	*Viola tricolor*	Viola
Golden alexander	*Zizia aurea*	Zizia
Meadow alexander	*Zizia trifoliata*	Zizia
Zizia spp.	*Zizia spp.*	Zizia

SM Table S3. GIS data and data sources used in this study.

Variable	**Dataset and source**
Elevation	National Elevation Dataset digital elevation model (DEM). Data available from the U.S. Geological Survey: http://viewer.nationalmap.gov/viewer/
Aspect (TWI)	Calculated using GIS from DEM layer
Slope	Calculated using GIS from DEM layer
TSI	Calculated using GIS from DEM layer
Soil OM	Soil Survey Geographic (SSURGO) dataset. Credit: Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Available online at http://websoilsurvey.nrcs.usda.gov/.
GDD	Calculated from DayMet gridded daily climate dataset. Credit: Thornton, P.E., M.M. Thornton, B.W. Mayer, N. Wilhelmi, Y. Wei, R. Devarakonda, and R.B. Cook. 2014. Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 2. ORNL DAAC, Oak Ridge, Tennessee, USA. Accessed Month 03/2015. Time period: 2014-01-01 to 2014-12-31. Available: http://dx.doi.org/10.3334/ORNLDAAC/1219
Precipitation	DayMet gridded daily climate dataset.
Building Density	Digitized building footprints available by request from the Geospatial Management Office of the North Carolina (NC) Department of Public Safety and NC County GIS Offices
% Forest cover	Calculated from LIDAR dataset. Credit: NCDEM (North Carolina Division of Emergency Management). 2006. NC floodmapping: LIDAR Phase 3 all-returns data, French Broad River basin. Floodplain Mapping Program, NCDEM, Raleigh, North Carolina. Available: http://fris.nc.gov/fris/Download.aspx?ST=NC
% Shrub cover	Calculated from LIDAR dataset
Public land	United States Public Areas Database (PAD-US). Credit: US Geological Survey, Gap Analysis Program (GAP). November 2012. Protected Areas Database of the United States (PADUS), version 1.3 Combined Feature Class. Available: http://gapanalysis.usgs.gov/padus/data/download/
Roads and bike routes layer	Credit: NC Department of Transportation. Available: https://connect.ncdot.gov/resources/gis/pages/gis-data-layers.aspx
Trails layer	GroWNC 2013, available by request.

SM Table S4. Final regression models of overall flower species richness at 63 sites in the Southern Appalachians. The full (global) model included topoedaphic, climate, vegetation, development and land use variables, as well as 3 interaction terms. Models were compared using second-order Akaike information criteria (AICc) and models within ΔAICc < 2 were considered competing models. Bold indicates that confidence intervals did not overlap zero. Pseudo-R^2 calculated as the percentage of deviance explained by each model (1 – residual deviance/null deviance).

Predictor category	Predictor Variable	Overall flower species richness			
		Model1	Model2	Model3	Model4
	Intercept	2.35	2.35	2.38	2.27
Topoedaphic	Topographic wetness index				
	Slope (%)		-0.06		
	Topographic position index				
	Soil organic matter (%)	**-0.10**	**-0.11**	**-0.10**	**-0.10**
	Soil organic matter ^{2}	**0.22**	**0.23**	**0.21**	**0.21**
Climate	Growing degree days	-0.08	-0.09	-0.08	**-0.10**
	Precipitation	**-0.10**	**-0.13**	**-0.11**	**-0.14**
	Precipitation^2	-0.08	-0.08	-0.08	
Local vegetation & land use	Percent tree cover (100 m)	**-0.10**	-0.08	**-0.10**	**-0.11**
	Building density (100 m)	**-0.11**	**-0.13**	-0.05	**-0.10**
	Building density^2			-0.04	
Interactions	Growing degree days * % tree cover	**0.18**	**0.21**	**0.18**	**0.18**
	Growing degree days * building density	**-0.16**	**-0.16**	**-0.14**	**-0.16**
	pseudo-R^2	0.38	0.39	0.39	0.37
	AICc	438.36	439.85	439.92	438.38
	deltaAICc	0	1.49	1.55	0.01
	AICcWt	0.28	0.13	0.13	0.28

SM Table S5. Final regression models of subseason flower species richness at 63 sites in the Southern Appalachians. The full (global) model included topoedaphic, climate, vegetation, development and land use variables, as well as 2 interaction terms. Models were compared using second-order Akaike information criteria (AICc) and models within ΔAICc < 2 were considered competing models. Bold indicates that confidence intervals did not overlap zero. Pseudo-R^2 calculated as the percentage of deviance explained by each model (1 – residual deviance/null deviance).

		Early spring richness			Late spring richness					Summer richness	
		Model 1	Model 2	Model 3	Model 1	Model 2	Model 3	Model 4	Model 5	Model 1	Model 2
	Intercept	1.44	1.47	1.40	1.47	1.47	1.47	1.46	1.50	1.37	1.31
Topoedaphic	Slope (%)				**0.13**	**0.14**	**0.16**	**0.15**	**0.12**		
	Topographic position index	-0.11		-0.12	-0.08		-0.08	-0.07	-0.07		
	Soil organic matter (%)	**-0.15**	-0.13	**-0.16**	**-0.14**	-0.11	-0.12	-0.09	-0.13	-0.06	-0.07
	Soil organic matter^2				**0.13**	**0.13**	**0.13**	**0.14**	**0.13**	**0.19**	**0.21**
Climate	Growing degree days (GDD)	0.08	0.08	0.11	-0.11	-0.09	-0.12		**-0.14**	**-0.16**	-0.10
	Precipitation	**-0.27**	**-0.28**	**-0.29**							
Local vegetation & land use	Percent tree cover (100m)				**-0.22**	**-0.21**	**-0.22**	**-0.19**	**-0.20**	**-0.25**	**-0.29**
	Building density (100m)	0.12	0.16	0.05	-0.11	-0.10		-0.12	-0.07	**-0.21**	**-0.26**
	Building density^2	**-0.13**	**-0.15**	**-0.14**							
Interactions	GDD * % tree cover									**0.31**	**0.34**
	GDD * building density	-0.19	-0.22						-0.11	-0.19	
	Pseudo-R^2	0.39	0.37	0.37	0.34	0.32	0.32	0.31	0.35	0.36	0.34
	AICc	288.67	288.47	288.81	299.70	299.14	299.49	299.68	301.09	295.65	296.12
	deltaAICc	0.2	0.00	0.34	0.57	0.00	0.35	0.54	1.95	0.00	0.47
	AICcWt	0.25	0.28	0.24	0.18	0.23	0.20	0.18	0.09	0.34	0.27

SM Table S6. Final regression models of flower bloom abundance at 63 sites in the Southern Appalachians. The full (global) model included topoedaphic, climate, vegetation, development and land use variables, as well as an interaction term. Models were compared using second-order Akaike information criteria (AICc) and models within ΔAICc < 2 were considered competing models. Bold indicates that confidence intervals did not overlap zero. Pseudo-R^2 calculated as the percentage of deviance explained by each model (1- residual deviance/null deviance).

		Peak bloom abundance		Early spring	Late spring	Summer	
		Model1	Model 2	Model 1	Model 1	Model1	Model2
	Intercept	4.09	4.10	3.22	2.39	2.10	2.08
Topoedaphic	Soil organic matter (%)	0.00	0.00	**-0.34**	**-0.07**	**-0.28**	**-0.27**
	Soil organic matter^2	**0.31**	**0.31**	**0.30**	**0.23**	**0.23**	**0.23**
	Slope (%)	**0.13**	**0.12**	**0.12**	**0.19**	**-0.13**	**-0.13**
	Topographic position index	**-0.14**	**-0.14**	**-0.13**	**-0.25**	-0.04	
	Topographic wetness index	**0.37**	**0.36**	**0.30**		0.02	
Climate	Growing degree days	0.01	0.00	**-0.30**	**-0.40**	**-0.55**	**-0.56**
	Precipitation	**0.03**	0.02	0.04	**0.06**	**0.08**	0.05
	Precipitation^2	**-0.15**	**-0.15**	**-0.06**	**-0.07**	**0.11**	**0.13**
Local vegetation & land use	Site Type (open)	**2.10**	**2.07**	**2.02**	**2.83**	**2.70**	**2.71**
	Building density (100m)	**0.03**	**0.03**	**0.12**	-0.04	**-0.52**	**-0.52**
Interactions	Growing degree days * building density	0.04		**0.18**		**-0.64**	**-0.64**
	pseudo-R^2	0.74	0.74	0.35	0.86	0.68	0.68
	AICc	6020.47	6021.13	5638.20	1097.38	2159.60	2163.19
	deltaAICc	0.00	0.66	0.00	0.00	0.00	1.53
	AICcWt	0.58	0.42	0.87	0.74	0.63	0.29

SM Table S7. Final regression models for the proportion of overall species richness comprised of charismatic species at 63 sites in the Southern Appalachians. The full (global) model included topoedaphic, climate, vegetation, development and land use variables, as well as 2 interaction terms. Models were compared using second-order Akaike information criteria (AICc) and models within ΔAICc < 2 were considered competing models. Bold indicates that confidence intervals did not overlap zero. Pseudo-R^2 calculated as the percentage of deviance explained by each model (1 – residual deviance/null deviance).

		Charismatic species				
		Model 1	Model 2	Model 3	Model 4	Model 5
	Intercept	-0.84	-0.81	-0.83	-0.85	-0.79
Topoedaphic	Topographic wetness index	0.13	0.11		0.15	0.12
	Topographic position index	**-0.17**	-0.12	**-0.16**	**-0.17**	-0.13
	Soil organic matter (%)	-0.14		-0.10	-0.13	-0.07
Climate	Growing degree days	0.04	0.09	0.10	0.05	-0.01
	Precipitation	**0.29**	**0.26**	**0.26**	**0.29**	**0.31**
Local vegetation & land use	Percent tree cover (100 m)	0.09	0.09	0.10	0.07	0.05
	Building density (100 m)	0.15	0.14	0.16		0.12
Interactions	Growing degree days * % tree cover	-0.21	-0.14	-0.19	-0.18	
	Pseudo-R^2	0.30	0.27	0.26	0.26	0.25
	AICc	252.55	252.24	252.53	252.59	253.52
	deltaAICc	0.30	0	0.29	0.35	1.28
	AICcWt	0.19	0.22	0.19	0.19	0.12

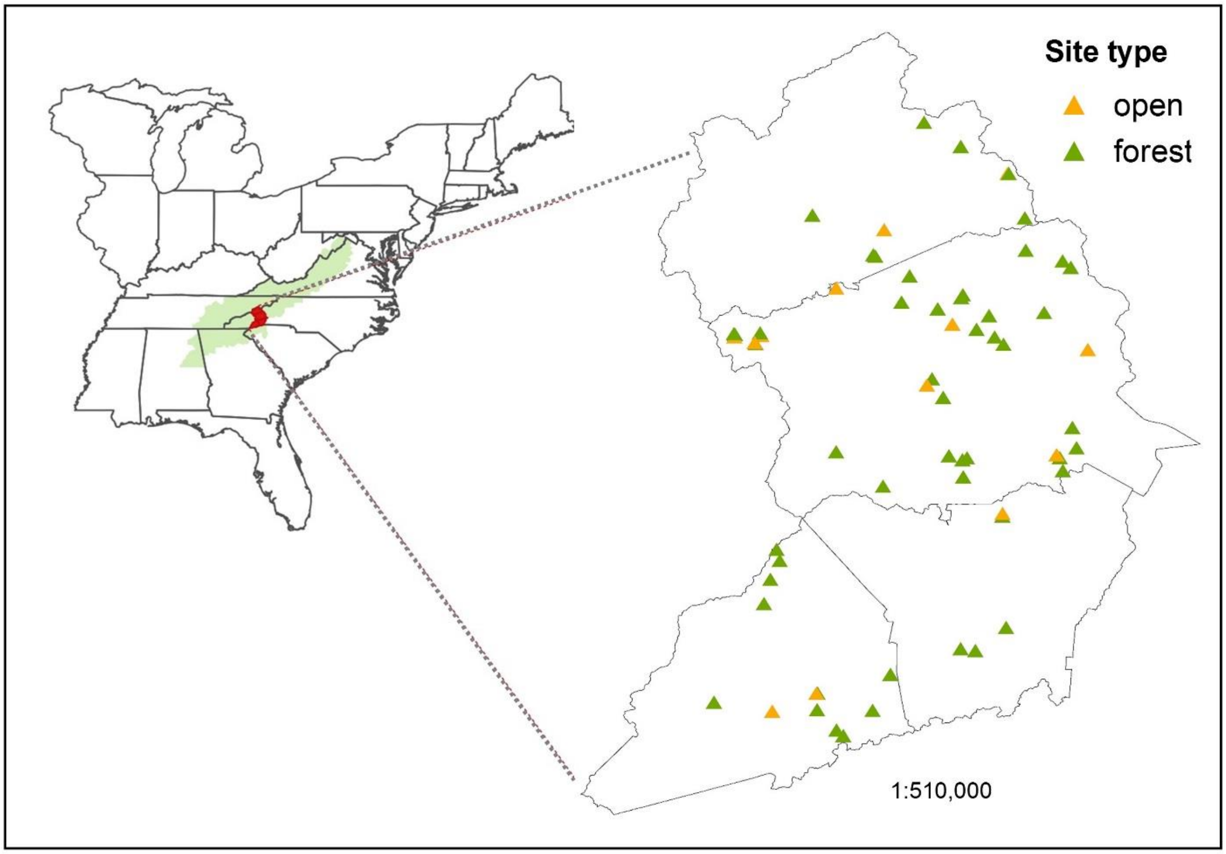
3. SUPPLEMENTAL FIGURES

SM Figure 1. Location of study area and study sites in the French Broad River Basin, North Carolina, USA. Open (n = 12) and forested (n = 51) sites were distributed throughout the study area.

SM Figure 2. Maps showing the standard error of projected floral resources values based on the top model predictions for (a) total flower species richness, (b) early spring flower richness, (c) late spring flower richness, (d) summer flower richness, (e) peak bloom abundance, (f) early spring flower abundance, (g) late spring flower abundance, and (h) summer flower abundance.

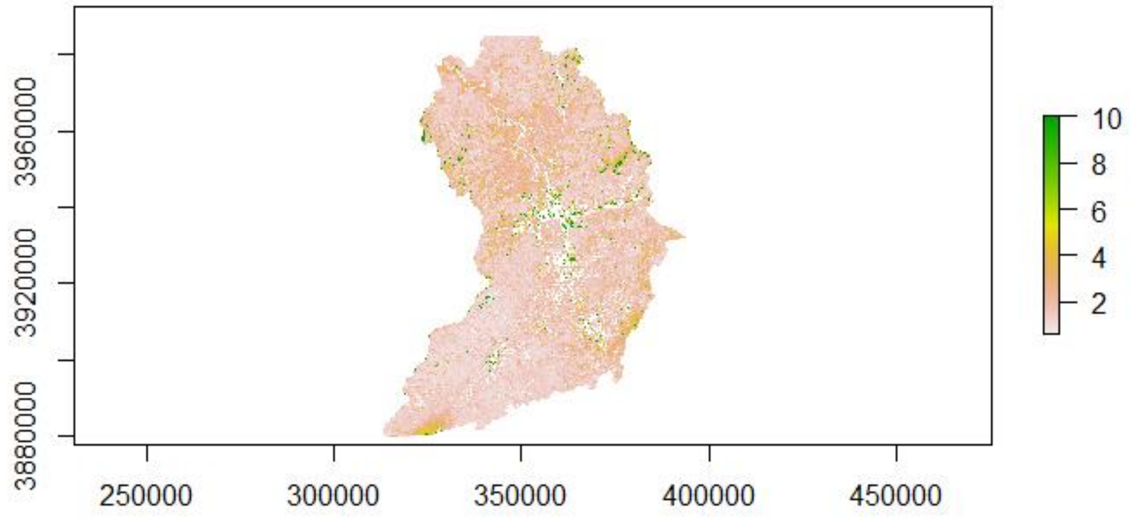
SM Figure 3. Cumulative frequency distributions of projected landscape (a) total flower species richness, (b) early spring flower richness, (c) late spring flower richness, (d) summer richness, (e) peak bloom abundance, (f) early spring abundance, (g) late spring abundance, and (h) summer abundance.

SM Figure 1

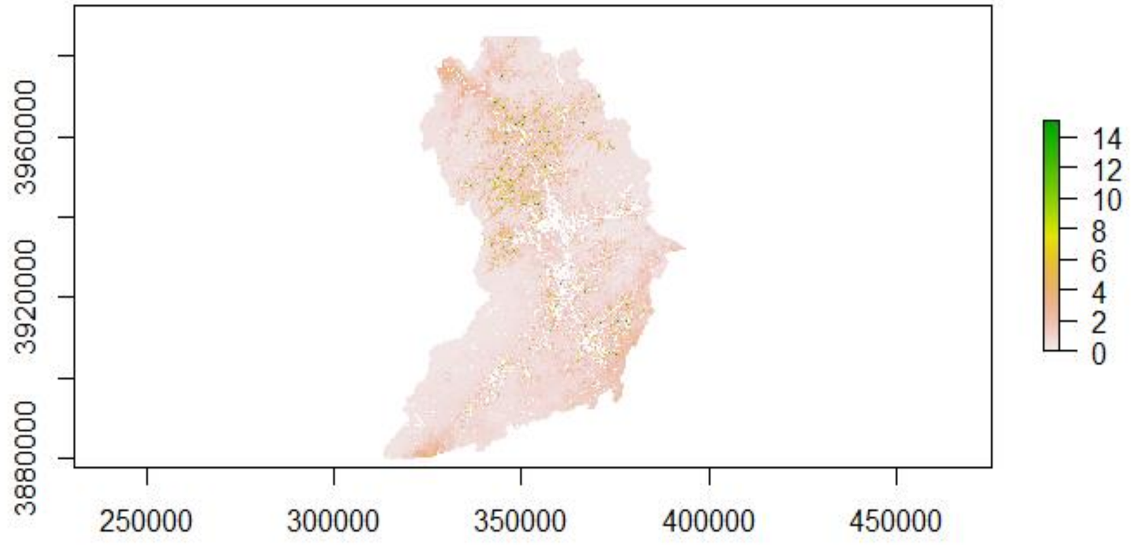


SM Figure 2

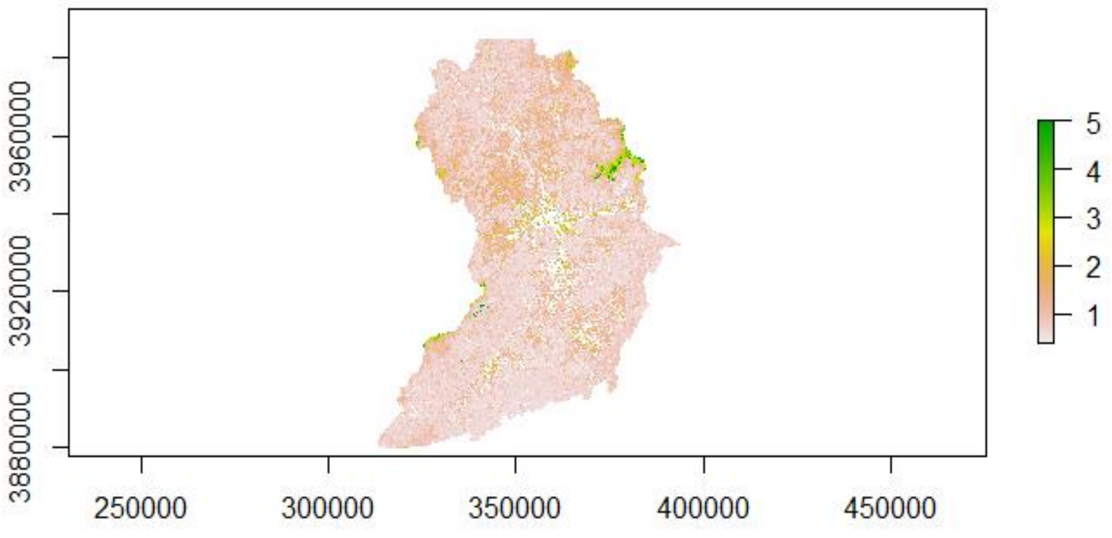
(a) SE of predicted total flower species richness



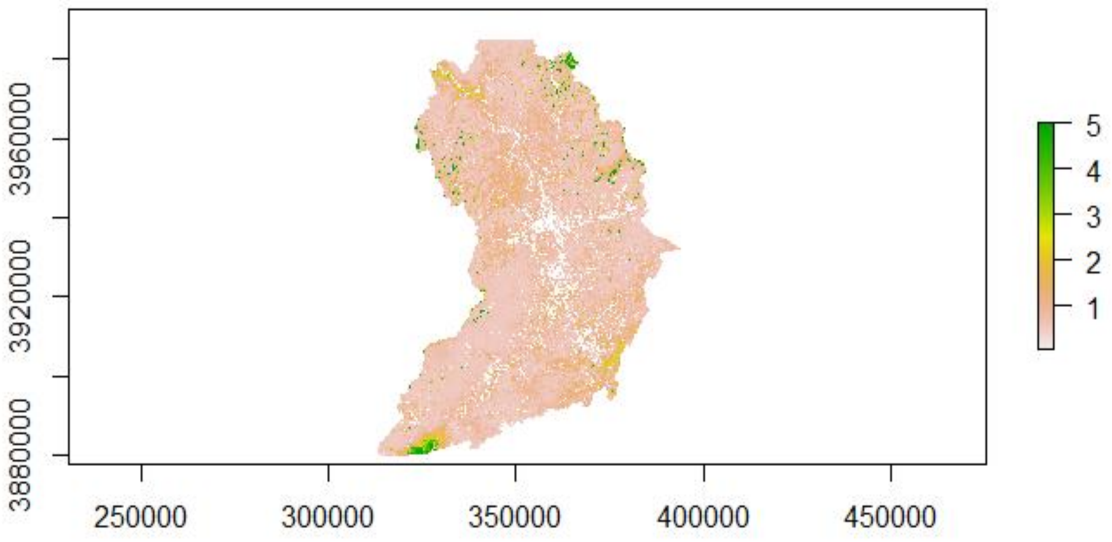
(b) SE of predicted early spring flower species richness



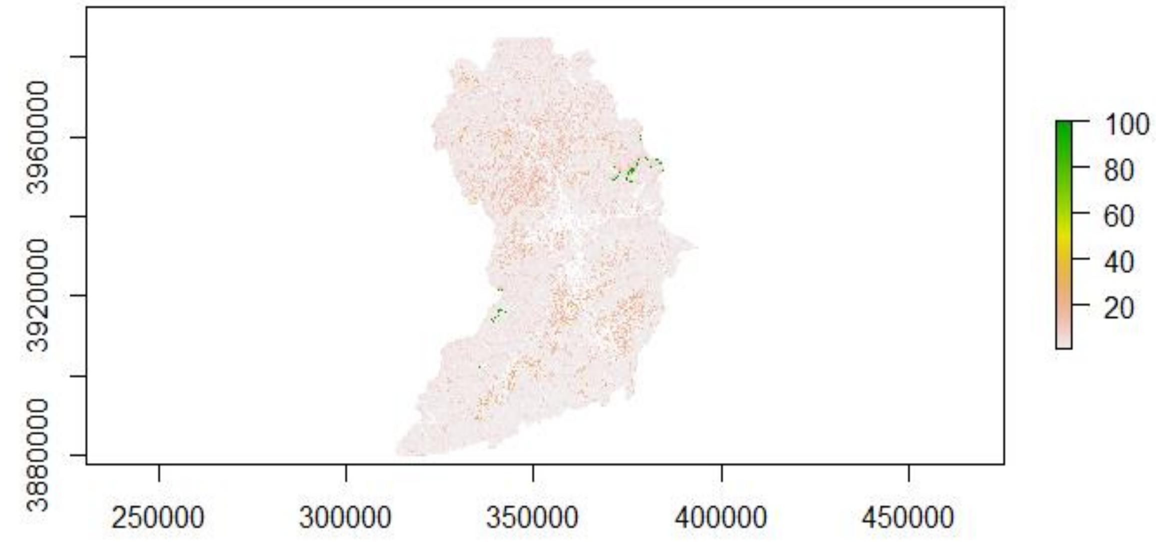
(c) SE of predicted late spring flower species richness



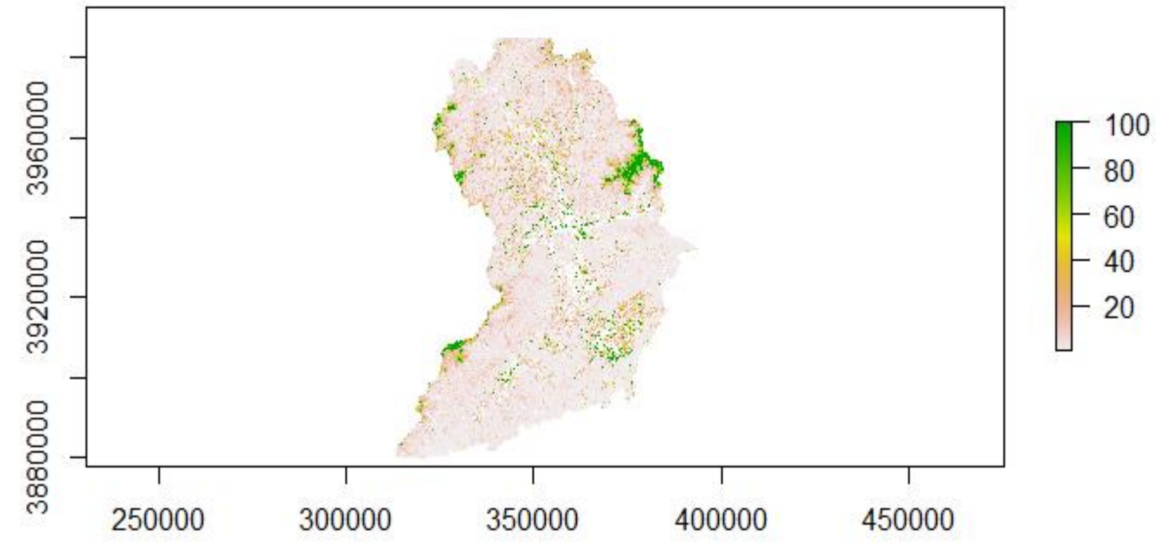
(d) SE of predicted summer flower species richness



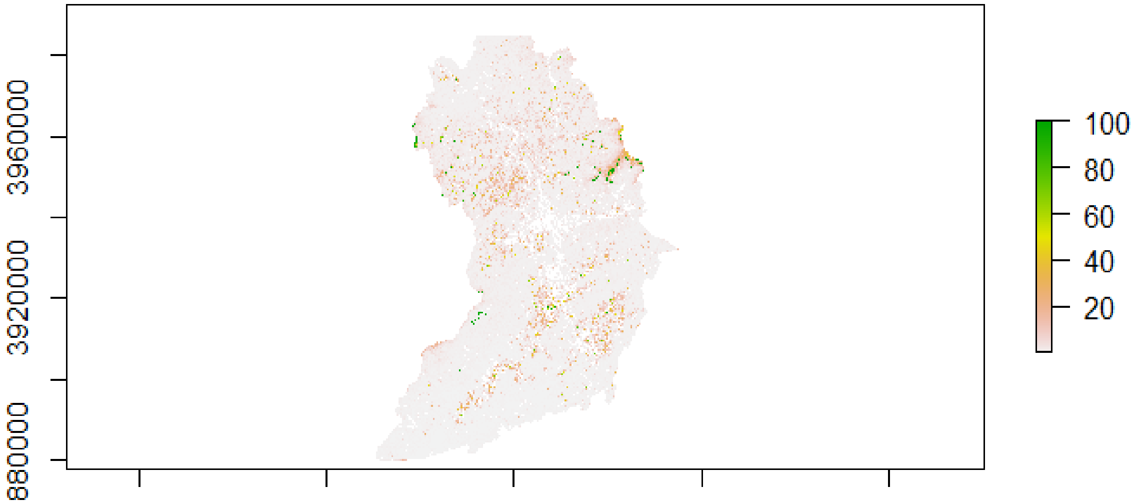
(e) SE of predicted peak bloom abundance



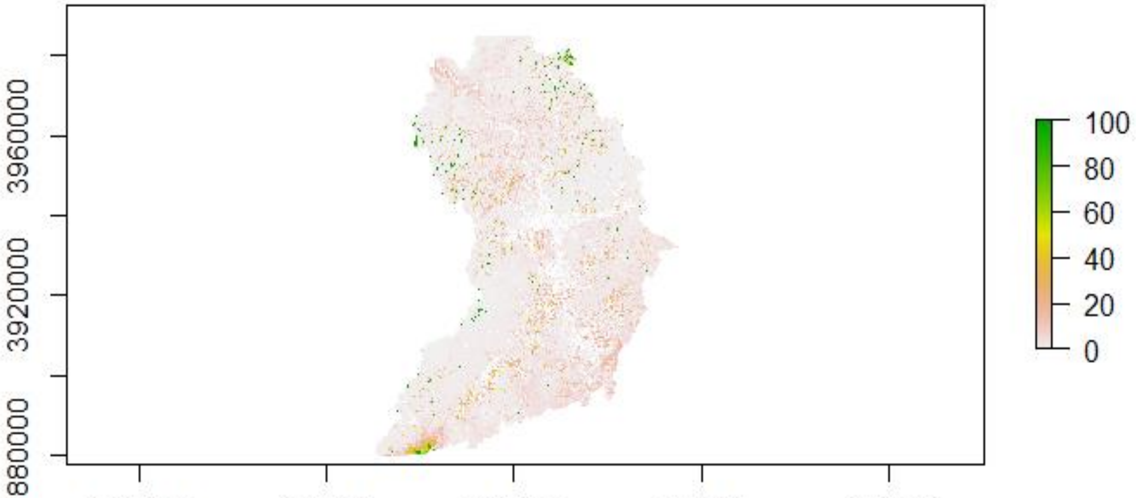
(f) SE of predicted early spring flower abundance



(g) SE of predicted late spring flower abundance

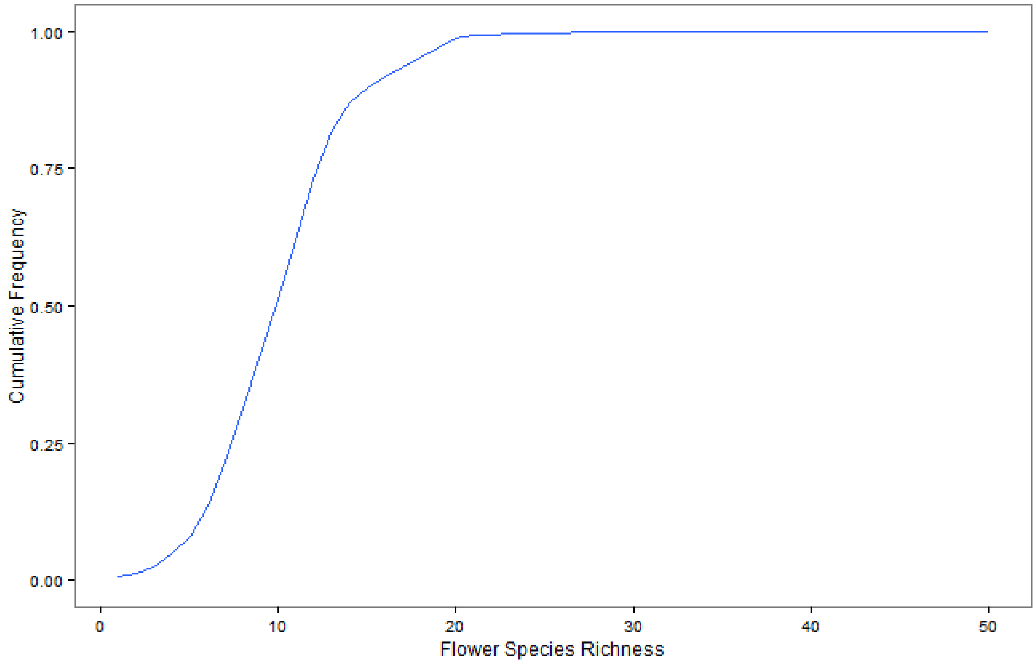


(h) SE of predicted summer flower abundance

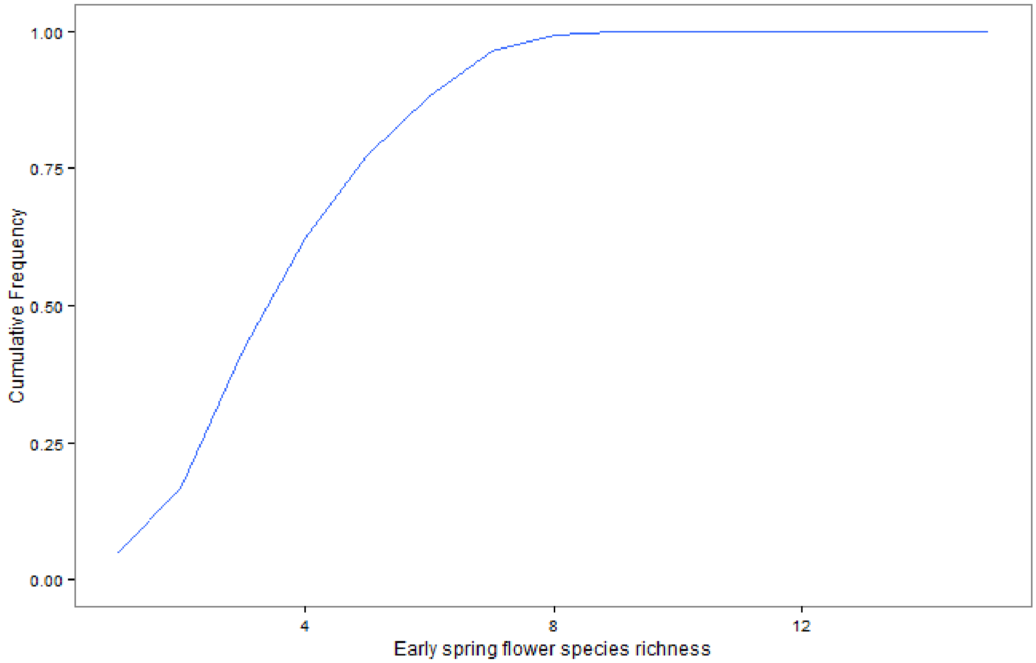


SM Figure 3

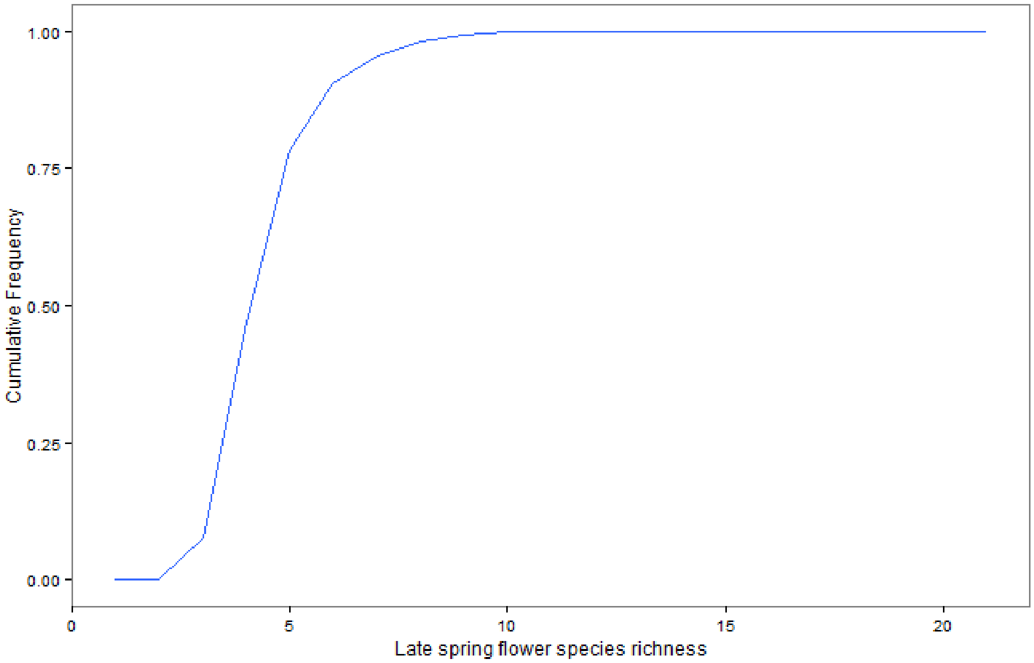
a)



b)



c)


Cumulative Frequency
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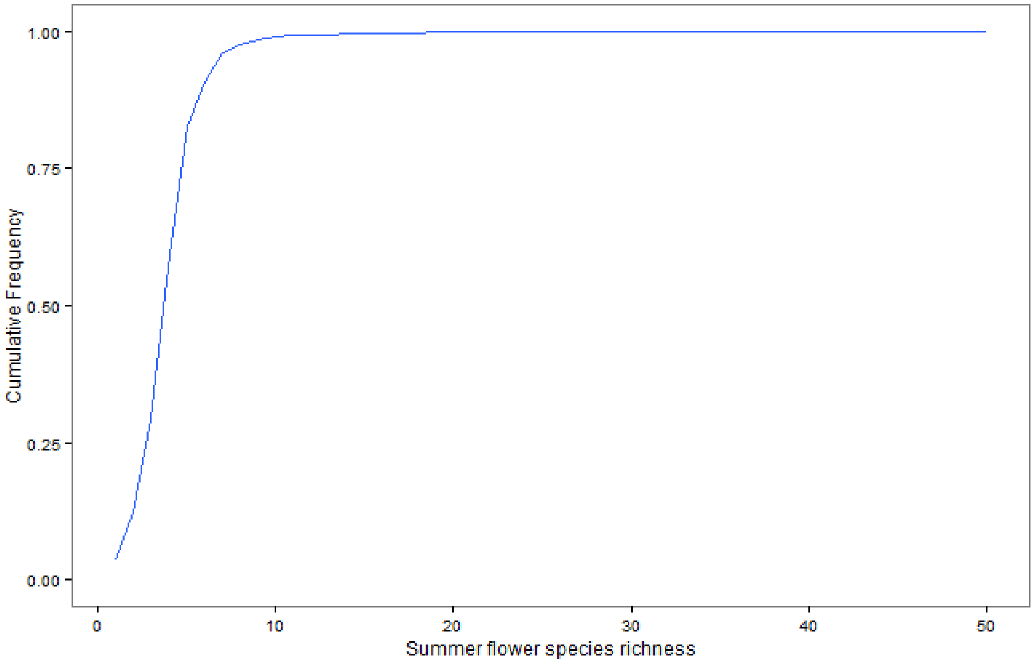
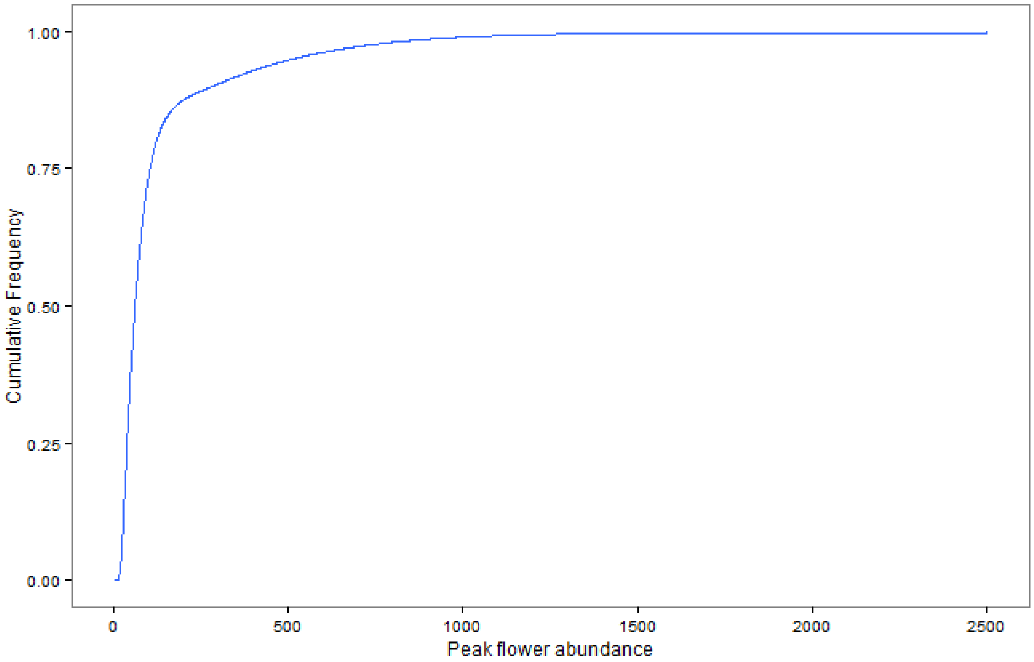
0.50
0.25
0.00
0
5
10
15
20
Late spring flower species richness

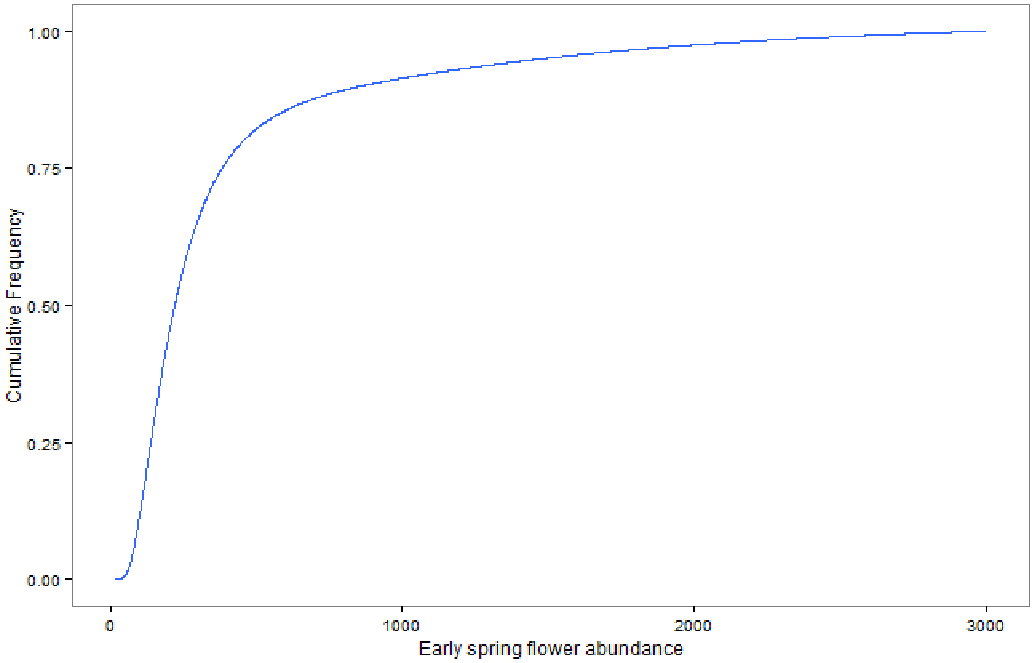
d)


Cumulative Frequency
1.00
0.75
0.50
0.25
0.00
0
10
20
30
40
50
Summer flower species richness

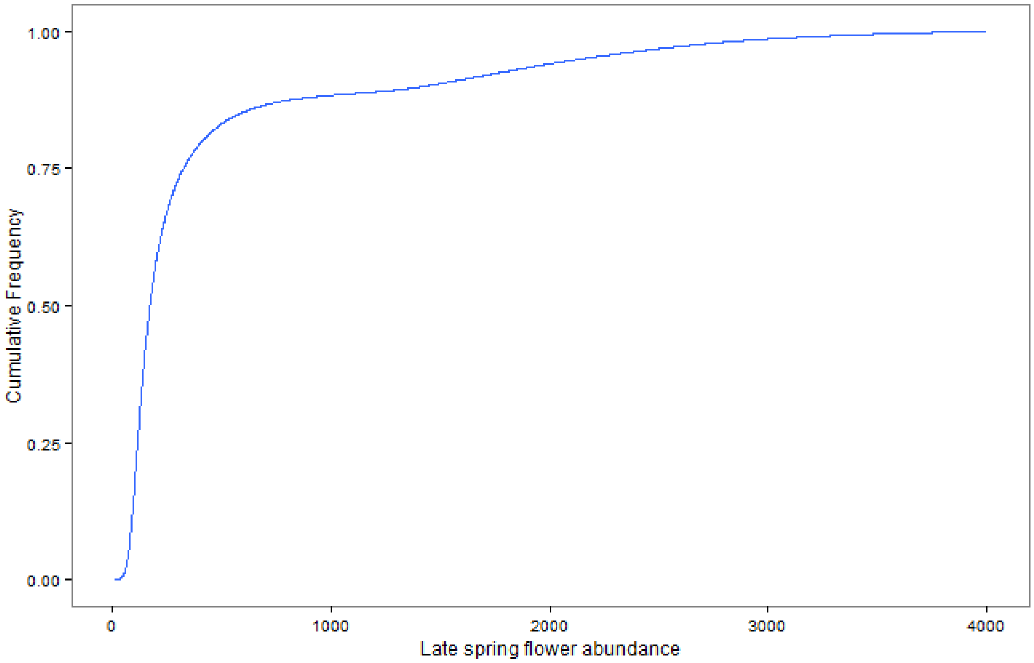
e)


Cumulative Frequency
1.00
0.75
0.50
0.25
0.00
0
500
1000
1500
2000
2500
Peak flower abundance

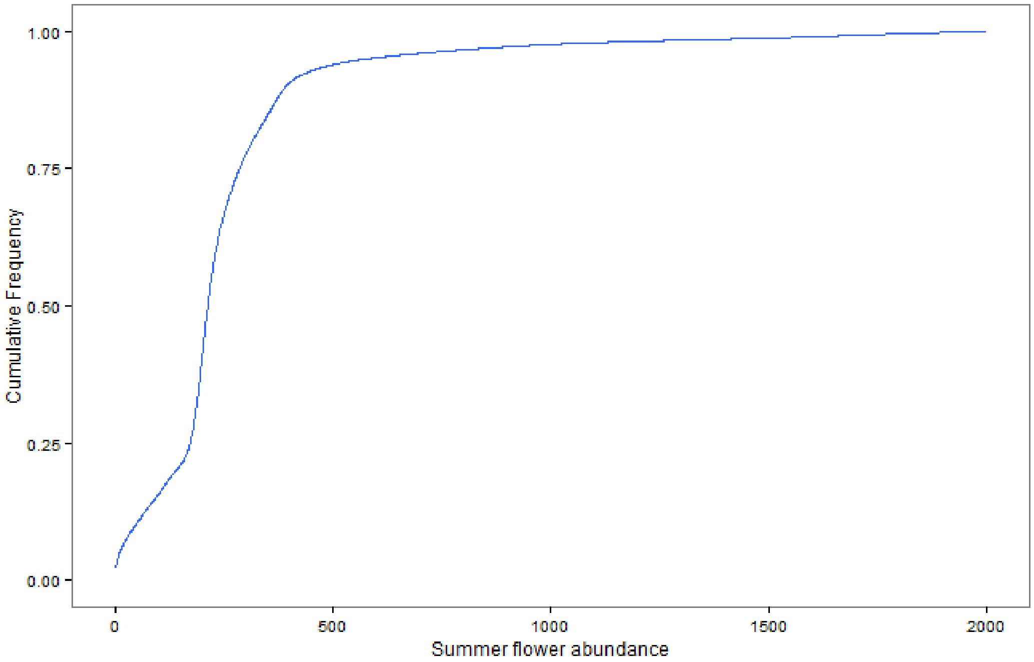
f)


Cumulative Frequency
1.00
0.75
0.50
0.25
0.00
0
1000
2000
3000
Early spring flower abundance

g)


Cumulative Frequency
1.00
0.75
0.50
0.25
0.00
0
1000
2000
3000
4000
Late spring flower abundance

h)


Cumulative Frequency
1.00
0.75
0.50
0.25
0.00
0
500
1000
1500
2000
Summer flower abundance

Chapter 3 – Species richness alone does not predict cultural ecosystem service value

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Abstract

Many biodiversity-ecosystem services studies omit cultural ecosystem services (CES) or use species richness as a proxy and assume that more species confer greater CES value. We studied wildflower viewing, a key biodiversity-based CES in amenity-based landscapes, in Southern Appalachian Mountain forests (USA) and asked (1) How do aesthetic preferences for wildflower communities vary with components of biodiversity, including species richness? (2) How do aesthetic preferences for wildflower communities vary across psychographic groups? (3) How well does species richness perform as an indicator of CES value compared to revealed social preferences for wildflower communities? Public forest visitors (*n* = 293) were surveyed during summer 2015 and asked to choose among images of wildflower communities in which flower species richness, flower abundance, species evenness, color diversity, and presence of charismatic species had been digitally manipulated. Aesthetic preferences among images were unrelated to species richness but increased with more abundant flowers, greater species evenness, and greater color diversity. Aesthetic preferences were consistent across psychographic groups and unaffected by knowledge of local flora or value placed on wildflower viewing. When actual wildflower communities (*n* = 54) were ranked based on empirically measured flower species richness or wildflower viewing utility based on multinomial logit models of revealed preferences, rankings were broadly similar. However, designation of hotspots (CES values above the median) based on species richness alone missed 27% of wildflower viewing utility hotspots. Thus, conservation priorities for sustaining CES should incorporate social preferences and consider multiple dimensions of biodiversity that underpin CES supply.

Significance Statement

Sustaining biodiversity and ecosystem services are common conservation goals. However, understanding relationships between biodiversity and cultural ecosystem services (CES) and determining the best indicators to represent CES remain crucial challenges. We combined ecological and social data to compare CES value of wildflower communities based on observed species richness versus revealed social preferences. Using a discrete-choice experiment with images of wildflower communities, we analyzed which aspects of biodiversity were associated with the aesthetic preferences of forest visitors. Although commonly used to indicate biodiversity-based CES, species richness did not predict aesthetic preference. This study suggests that successful management of CES requires understanding stakeholder preferences to determine conservation priorities.

Introduction

Sustaining ecosystem services is an emerging priority in sustainability science, and conservation plans increasingly emphasize joint protection or improvement of ecosystem services and biodiversity. Simultaneous concern for biodiversity and ecosystem services led to establishment of the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) as well as multiple national, regional, and local initiatives (1, 2). Despite recognition that the futures of biodiversity and ecosystem services are interconnected (3), understanding the direct links between biodiversity and ecosystem services and determining the best indicators to represent ecosystem services remain crucial challenges (4–7). Biodiversity is defined and measured in a multitude of ways, e.g., species richness, species evenness, genetic diversity, functional diversity, and community distinctness (8, 9). In biodiversity and ecosystem service (BES) research, species richness is the most frequent unit of measure (6) and hypotheses regarding increased biodiversity are often stated in terms of increased species number (e.g., more species confer greater CES value) (10, 11).

Studies of biodiversity-based ecosystem services rarely assess alternate metrics of biodiversity and seldom provide empirical links between biodiversity indicators and social preferences for ecosystem services (12). Cultural ecosystem services—the nonmaterial benefits provided by ecosystems (13)—are among the least quantified ecosystem services (14–16). Due to their normative nature and often abstract definitions (17), cultural ecosystem services (CES) can be challenging to study. They represent complex relationships between people and ecosystems, and the definition and valuation of a particular cultural service can vary across stakeholders (18, 19).

For biodiversity-based CES, common practice has been to map species richness as an indicator and use those maps to assess the spatial provision of CES (e.g., ref 17, 19). However, there is little known about whether maps of species richness correspond to actual social preferences for CES. Biodiversity conservation depends on the values that people attach to it (23, 24) and understanding people's preferences for biodiversity can facilitate communication between the public and land managers and help delineate publicly supported conservation goals (18). In particular, if social preferences can be translated to maps of CES indicators (25), a more complete assessment of conservation objectives targeted at maintaining biodiversity and CES is possible (26, 27).

Aesthetic beauty is a commonly cited CES in amenity-based landscapes (13, 28, 29) and is often assumed to be positively correlated with biodiversity (30, 31). Species-rich, flower-rich views improve the aesthetic value of landscapes, roadsides, field margins, and meadows (32–36), and increased flower color diversity may provide higher CES value, especially in rural landscapes (34, 37–40). Lindemann-Matthies et al. (40) demonstrated that aesthetic appreciation increased with perceived species richness. Moreover, aesthetic appreciation and perceived species richness also increased with evenness (i.e., the equitability of species in a community), suggesting compositional diversity may also be an important driver of aesthetic preference. Additionally, the presence of species with cultural significance or the presence of rare species can increase satisfaction among wildflower viewers (41) and the aesthetic value of particular species has been used as a reason for conservation (42, 43).

We studied the aesthetic preferences of public forest visitors for trailside wildflower communities to test whether species richness predicted CES value. We conducted the study in the Southern Appalachian Mountains (North Carolina, USA), where wildflower viewing and photographing is one of the fastest growing outdoor recreational activities (44). Wildflower blooms provide important CES to both residents and tourists (45). The region's high biodiversity, recognized globally, attracts both residents and visitors, many of whom visit public forests to participate in recreation and observe plants and animals (44, 46, 47). We asked three questions about the relationship of biodiversity to CES value: (1) How do aesthetic preferences for wildflower communities vary with components of biodiversity, including species richness? (2) How do aesthetic preferences for wildflower communities vary across psychographic groups? (3) How well does species richness perform as an indicator of CES value compared to revealed social preferences for wildflower communities?

Public forest visitors were asked to choose among digitally manipulated images of wildflower communities with varied levels of flower species richness, flower abundance, species evenness, color diversity, and presence of charismatic species, as identified from regional tourism websites (see SI text and 48) (Figure 1). Wildflower community preference was analyzed using multinomial logit models that were then used to predict wildflower viewing utility of actual wildflower communities. This analysis is consistent with Lancaster’s Theory of Value (49) and random utility theory (50), which assume that individuals prefer goods or services based on the utility derived from the attributes of those goods or services, and that individuals choose options based on their relative utility. Because individual preferences, beliefs and expertise may affect aesthetic preferences (51), we tested whether the effect of wildflower diversity on aesthetic preferences varied across psychographic profiles. Finally, using data collected from actual wildflower communities in the study region (48), we compared site prioritization for CES based on empirically measured species richness versus predicted aesthetic preference (i.e., wildflower viewing utility).

Results

We collected usable responses from 293 public forest visitors, representing a cross spectrum of ages, visitation characteristics, and attitudes (Table S3). Respondents tended to be white (90%) and well-educated (73%), which is representative of recreational visitors in this area (44). Respondents were grouped into segments ranging in size and psychographics based on their attitudes toward forest-based CES, measured along four attitudinal dimensions (Table 1a). Thirty-four percent of respondents were generalists, characterized by their high valuation of all forest-based CES (e.g., quiet relaxation, experiences, active escape, and collecting things) (Table 1b). The remaining respondents were divided among those that placed high value on active escape (26%), quiet relaxation (27%), or collecting (12%). Nearly half (46%) of respondents reported having visited a forest to view wildflowers within the past year (Table S4).

Aesthetic preferences for wildflower communities. People’s aesthetic preferences for wildflower communities varied with components of wildflower diversity but not with flower species richness. Flower species richness had no effect on respondents' aesthetic preference for images of wildflower communities (Table 2). The abundance of flowers was the most important predictor of aesthetic preference, followed by number of colors and evenness. Photographs displaying wildflower communities with higher bloom abundance, more colors, and higher evenness were more likely to be preferred.

Aesthetic preferences among psychographic segments. Results were remarkably consistent across all four psychographic segments of the respondents, indicating no difference in preference patterns among groups (Table 2, Table S5). Similarly, preference patterns did not differ based on a respondent's knowledge of local flora (i.e., novice, intermediate, or expert) or the value they placed on wildflower viewing (i.e., flowers more or less important) (Table S5).

Species richness vs. revealed CES value in actual wildflower communities. Empirically surveyed wildflower communities (n = 54) varied in flower species richness, flower abundance, evenness of species in bloom, number of colors, and whether charismatic species were present and blooming (Table S6). Overall flower species richness ranged from 2 to 34 ($\bar{x} =$ 11, sd =7.3). Wildflower viewing utility calculated using multinomial models of revealed preferences (Table S3) ranged from -0.11 to 13.29 ($\bar{x} = 2.2, sd = 2.5$). For surveyed wildflower communities, predicted CES value (i.e., wildflower viewing utility) was correlated with the overall species richness observed at a site (Spearman's rho = 0.66, Figure 2). Species richness was also correlated with aesthetic traits of flower abundance, evenness, color diversity, and number of charismatic species present (Pearson's r 0.48–0.77, all $P < 0.001$). When sites were classified as CES hotspots (CES values above the median) based on either wildflower viewing utility or overall species richness, classification broadly agreed, with 34 hotspots identified by both indicators. However, site classification based on species richness alone missed 27% (seven) of the sites predicted to have high wildflower viewing utility (Figure 2). Similarly, ranking sites based on wildflower viewing utility alone missed 29% (eight) of sites predicted to have the highest flower species richness.

Discussion

Conservation planning and management increasingly require consideration of both ecosystem services supply and maintenance of biodiversity. However, despite calls for holistic management of a full suite of ecosystem services to achieve landscape sustainability (52-54), CES have been largely absent from biodiversity and ecosystem service literature. We linked stakeholders' revealed preferences with empirical measurements of wildflower community diversity and demonstrated that only partial overlap exists between high species richness and high CES supply. Species richness *per se* was not a significant predictor of aesthetic preference, and site rankings based on empirically measured wildflower communities showed that the use of observed species richness as a CES indicator does not fully encompass sites with high predicted CES value. Thus, management of biodiversity-based CES and conservation of species diversity should be considered complementary, but different, goals when developing landscape conservation targets (55).

People's aesthetic preference for images of trailside wildflower communities was driven primarily by the abundance of flowers and not by species richness of flowers. However, people preferred wildflower communities with more colors, suggesting that, while respondents may not distinguish between flower species if they are the same color (e.g. Fig 1a-b), they recognize diversity in colors (e.g. Fig 1c-d). Our models suggest people respond to a complex combination of these floral traits, which were generally correlated with species richness in our study area, but not perfectly so. Since perceived species richness has been linked to aesthetic value and support for biodiversity conservation (40), misperceptions of the species richness in wildflower communities with lower color diversity could lead to biases in people's attitudes toward these wildflower communities. Our study did not test explicitly whether people judged wildflower communities with more colors to be more species rich, which limited our ability to judge whether visitors preferred wildflower communities that they perceived as more species rich. If people's perception and preferences are closely linked (56), and people's perception of species richness does not match actual species richness (57), promoting education that emphasizes knowledge about species diversity could increase appreciation of sites with high flower diversity but low color diversity.

Our study suggests that targeting management at sites with high wildflower viewing utility will yield benefits across a spectrum of visitors. People value nature for many different reasons including intrinsic, economic, emotional, spiritual, or psychological values that are not mutually exclusive (24). Landscape aesthetic preferences can vary based on age (56), gender (58), cultural and social groups (59-61) and recreation patterns (58, 60). However, preferences for wildflower communities in this study were remarkably similar across demographic, attitudinal, and recreational groups and were instead driven by the attributes of the wildflower communities. These results suggest that variation in aesthetic preference is greater among sites than across public forest visitors (61, 62). Since aesthetic appreciation and scenic beauty are desired conditions in recreation and outdoor tourism in amenity-based landscapes (44, 63, 64), understanding how to manage aesthetic CES can have positive impacts for residents and visitors to these areas.

Aesthetic preference varies among persons. While preferences among psychographic groups were similar, the discrete-choice models explained only about 30% of the variation among individual respondents. Cultural preference theories contend that the attitudes of each individual are in constant flux and are shaped by cultural and personal experiences (e.g. 65). Both biophysical and personal-social situational context affects aesthetic experience (30). In our study, we tested both the biological factors (i.e., wildflower community traits), as well as cultural factors (i.e., age, gender, botanical knowledge). Unmeasured factors related to a person's attitude, ethnic and cultural background could explain the remaining variation, but this information was beyond the scope of this study and impractical to collect under the field conditions.

In conservation and sustainability science, determining how to best conserve the biosphere while meeting the needs of humans has led to vigorous debate. While increasing recognition of ecosystem services and the contribution of ecosystems and biodiversity to human well-being has the potential strengthen conservation (1, 28, 66–69), some authors have suggested that increased emphasis on ecosystem services as a conservation goal may lead to unintended losses and inadequate protections for biodiversity (70–72). In part, this debate stems from lack of clarity about the multiple relationships between biodiversity and ecosystem services (see 66).

Studies have revealed both positive and negative relationships between priority areas for biodiversity and priority areas for the provision of ecosystem services, complicating landscape conservation planning (56-59). To preserve aesthetic beauty and the CES provided by wildflower communities, some maintenance of species diversity, which allows for a diversity of flower forms and colors, is important. However, despite correlations between richness and CES value in wildflower communities, conservation and management priorities based solely on maintaining species richness may not adequately conserve sites that supply biodiversity-based CES. Conservation priorities targeted at achieving sustainability of CES should use suitable indicators, beyond measures of species richness, that incorporate social preferences and recognize the multiple ways that biodiversity may contribute to the provision of ecosystem services.

Methods

Study area. We collected empirical data on wildflower communities (48) and people's aesthetic preferences in the French Broad River Basin (FBRB) in western North Carolina during the summers of 2014 and 2015. The FBRB, located within the southern Appalachian Mountains, covers an area of 7330 km^2 (Figure S1). The region is characterized by complex terrain, known for its high biodiversity, and popular for ecotourism (46, see SI Text for more detail). Approximately 75% of the FBRB is forested, mainly second growth, with spruce-fir (*Picea-Abies*) and northern hardwoods at high elevations, mixed hardwood species at lower elevations, and mixed mesophytic forests on lower slopes and coves (46). The regional economy changed in the last century from resource extraction (e.g., timber) and agricultural production to a nature-based, amenity-driven economy, leading to altered patterns of land use and increased exurban development (73-75). Land-use changes have altered plant communities within the region (74, 76-78) and likewise affect the location and abundance floral resources within the study area (48).

Aesthetic preferences for wildflower communities. We surveyed 295 public forest visitors using a convenience sampling approach at trailheads on National Forest and State Forest properties. Face-to-face surveys were conducted at trailheads and visitor information points during the summer of 2015. We varied the day of the week and time of day that each trailhead was visited, and individual surveys generally lasted less than 5 minutes. Once a survey was completed, the next visitor encountered was asked to participate in the study. At remote trailheads with limited use, we posted signs asking people to complete an online version of our survey. Online respondents accounted for 5% of our respondents.

The survey (see SI) consisted of three parts: (1) respondents' attitudes toward a set of CES provided by public forests; (2) respondents' recreational patterns, social and demographic data; and (3) a discrete-choice experiment to determine preferences for different wildflower communities. Respondents' attitudes toward forest-based CES were measured with the help of 15 statements about forest uses (Table S1). Respondents indicated their personal valuation of each service on a five-point Likert-type scale (1: unimportant, 2: somewhat important, 3: important, 4: very important and 5: extremely important). Respondents were asked to provide an estimate of the frequency with which they visited public forests in the last year and what activities they participated in while visiting public forests. We also asked them for their gender, age, race, highest level of education, and a self-assessment of their knowledge of plants in the area (1: no knowledge, 2: novice with some knowledge, 3: intermediate knowledge, and 4: expert knowledge).

Preferences for wildflower communities were obtained using a discrete-choice experiment where respondents were shown 8.5 x 11" photographs of near-view forest wildflower communities manipulated to contain different levels of diversity (i.e., flower abundance, flower species richness, number of colors, evenness or the distribution of abundance among species in a community, and presence of charismatic species). Respondents were asked to indicate their preferred alternative between pairs of digital images of wildflower communities. Each respondent was shown four pairs of images, or choice sets. The images were created using Adobe Photoshop and choice sets varied according to a D-efficient sampling design (79, 80), which maximizes the amount of information about each parameter through the most efficient number of choice sets. The choice model included 48 images organized in six blocks of four choice sets (see Table S2).

We used factor analysis to identify interpretable dimensions of attitudes toward forest-based CES. Factor analysis has been used previously to study psychographics of survey respondents in nature recreation, eco-tourism, and ecosystem service research (33, 81). Exploratory factor analysis identified a four-factor structure describing people's attitudes toward forest-based CES and accounted for 60% of the variance in the dataset (Table 1a). We performed K-means cluster analysis to identify segments of respondents with different psychographic profiles based on their attitudes toward forest-based CES, represented by their scores along the four factors (81, 82). The effect of biodiversity attributes on aesthetic preference for wildflower communities was modeled using multinomial logit models (see SI Text). We first analyzed the preferences of all respondents, without regard for psychographics or demographics, including only the wildflower community attributes. We tested whether the inclusion of interactive effects between the wildflower community attributes and respondents' attitudes toward forest-based CES improved the model fit. We then ran multinomial logit models for groups based on people's preference of different CES, knowledge of plants, demographics, and recreational patterns to determine if the effect of biodiversity attributes varied across segments. See SI Text for more details.

Indicators of CES value in actual wildflower communities. We used wildflower community data recorded in the study region (48) to evaluate differences between the designation of CES hotspots based on empirically measured flower species richness versus wildflower viewing utility predicted by the revealed preference models. Fifty-four forested sites were visited over the course of an 18-week growing season (April – August 2014) and richness, abundance, evenness of plants in flower were recorded, as well as the number of flower colors and presence of charismatic species (see SI Text for more details). Sites were visited multiple times, either weekly or tri-weekly. For each site visit, we calculated the predicted wildflower viewing utility, based on the discrete-choice multinomial logit models above. The maximum of the predicted wildflower viewing utility for each site was used as an indicator of CES value. We calculated overall flower species richness for each site using species accumulation curves, which allowed us to account for differences in observed species richness due to survey effort (e.g., weekly sampling versus tri-weekly sampling).

Lastly, we identified sites with the highest CES value, or “hotspots”. A variety of methods have been used to define ecosystem service hotspots (4, 83–85). We defined hotspots to be sites above the median value for flower species richness or wildflower viewing utility. We evaluated hotspot congruence based on the two CES indicators: overall flower species richness and maximum wildflower viewing utility. We compared site rankings and hotspot classifications based on these alternate indicators using Spearman rank correlation, Cohen’s kappa coefficient, and percent agreement.

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Figures.

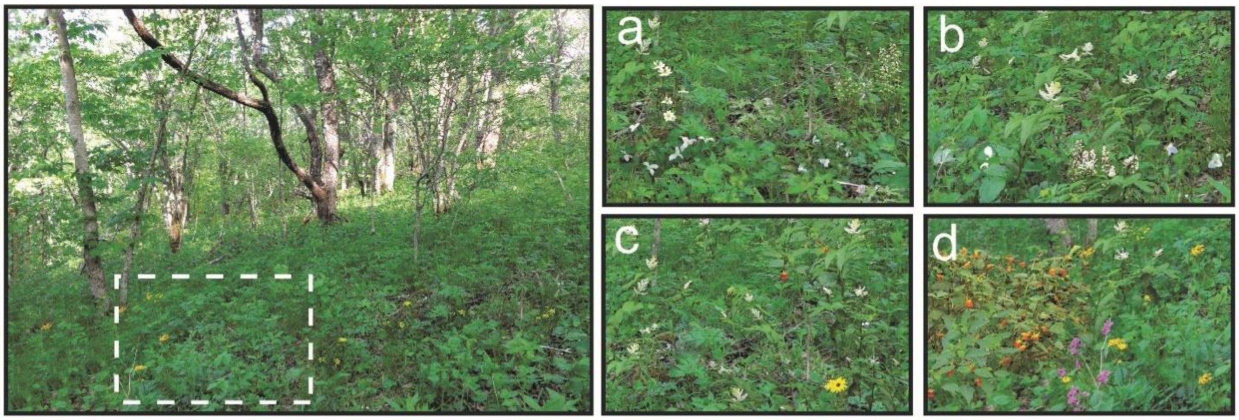

Figure 1. Examples of digitally manipulated images used in the discrete-choice experiment. A total of 48 images were used. Images all used the same background (see large panel) but varied in the flower species richness, flower abundance, the number of colors, and the evenness of the wildflower community. The cutouts displayed here (a – d) are illustrative of variation in the images and were selected from images that varied in the number of colors and evenness; species richness and flower abundance were held constant at five species and ninety flowers in these examples. Image (a) shows one color and low evenness, (b) one color and high evenness, (c) five colors and low evenness, (d) five colors and high evenness. Based on the results of the discrete-choice experiment, (d) would have the highest predicted wildflower viewing utility. See Figure S2 for uncropped image examples.

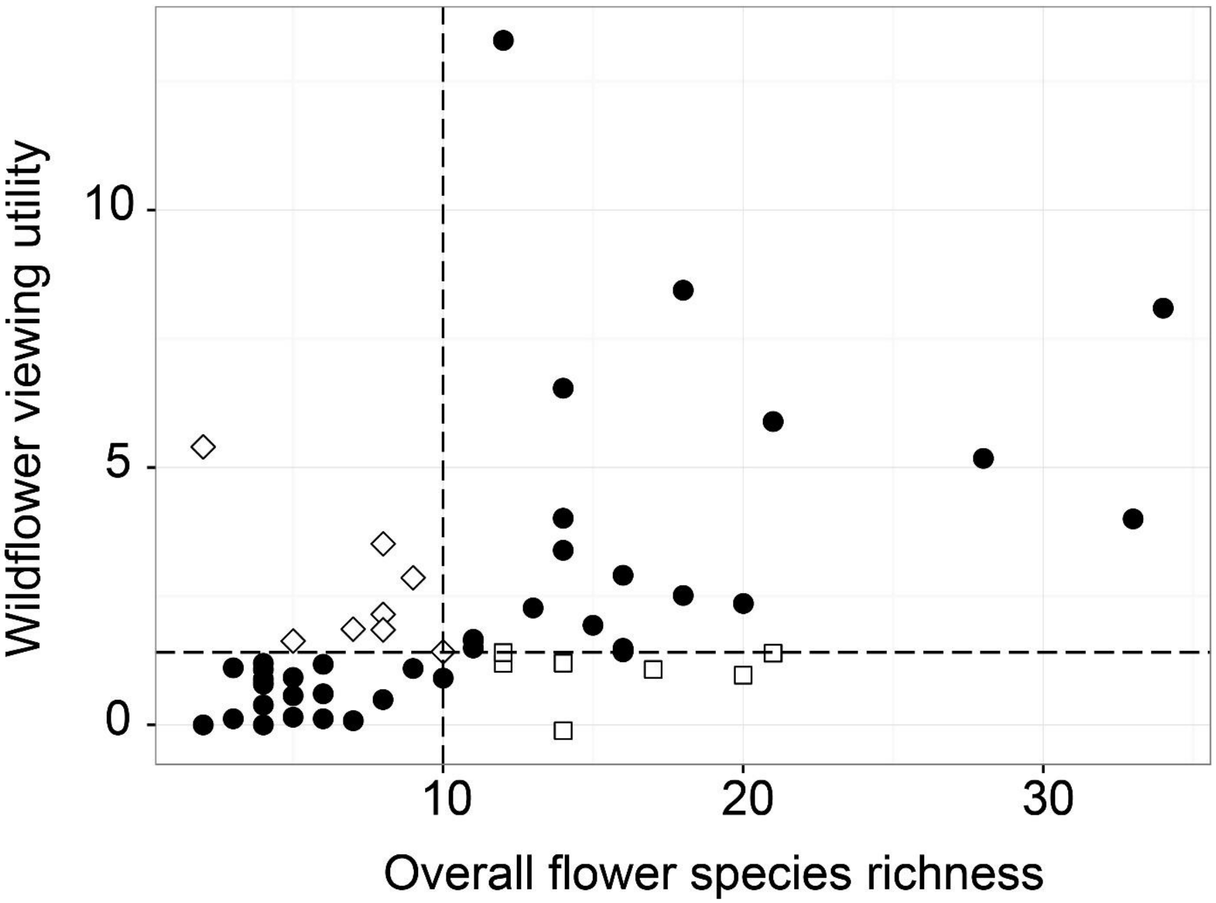

Figure 2. Predicted wildflower viewing utility correlated with overall flower species richness of 54 wildflower communities in the southern Appalachian Mountains. Dashed lines show the hotspot classification thresholds (median values) for each indicator. Sites were either not hotspots (below the median; bottom left quadrat), agreed upon hotspots (above the median; top right), or hotspots based on either wildflower viewing utility (top left) or species richness (bottom right) but not the other. Closed circles indicate agreement, open symbols indicate disagreement in hotspot classification. Wildflower community data were collected over an 18-week period between April and August 2014 (see (48) for details); discrete-choice data used to predict wildflower viewing utility were collected in 2015.

Table 1. (a) Factor loadings along four interpretable dimensions (*Quiet Relaxation, Experiences, Active Escape, Collecting*) of respondents' attitudes toward forest-based CES. Factors were extracted from survey response data using principal components solution with varimax rotation. The highest factor loadings for each forest-based CES are bolded. (b) Cluster analysis based on the attitudinal factors identified four psychographic segments of respondents. The segments differed in group size (*n*) and mean scores among the four attitudinal dimensions.

	Quiet relaxation	**Experiences**	**Active escape**	**Collecting**
(a) Forest-based CES		*Factor loadings*		
To find solitude	**0.80**	0.05	0.13	0.16
Spiritual value	**0.74**	0.17	0.14	0.09
To relax	**0.62**	0.18	0.31	0.12
To hear nature sounds	**0.57**	0.50	-0.07	0.07
To see scenic views	0.13	**0.73**	0.16	-0.14
To be with family and friends	-0.25	**0.65**	0.48	0.17
To view wildlife	0.27	**0.65**	-0.04	0.30
To view wildflowers	0.39	**0.64**	-0.10	0.01
To participate in recreation	0.05	0.02	**0.78**	0.06
To be physically active	0.24	-0.03	**0.68**	-0.12
To escape an urban setting	0.42	0.18	**0.43**	-0.02
Educational value	0.29	0.34	**0.40**	0.37
To hunt	0.04	-0.03	0.01	**0.80**
To collect food	0.16	0.09	-0.03	**0.77**
(b) Psychographic segment (*n*)		*Mean factor score*		
1: Active/experience seekers (77)	-1.27	0.13	0.16	-0.26
2: Quiet seekers (79)	0.48	-0.70	-0.89	-0.38
3: Collectors (36)	0.11	-0.27	-0.02	2.15
4: Generalists (101)	0.55	0.57	0.53	-0.26

Table 2. Relative importance of wildflower community attributes from multinomial logit models based on respondent preference for digital photos of wildflower displays. The first model is based on all respondents. The remaining models analyzed segments of the respondents based on their attitudes toward forest-based CES, attitudes toward wildflower viewing, and knowledge of local flora. Relative importance values provide a measure of the relative effect of each attribute. See Table S5 for full model results and coefficient estimates. Significant Wald (=) values indicate differences in the estimated coefficient of an attribute between segments.

	Relative importance of wildflower community attribute				
Model (*n*)	Species richness	Flower abundance	Number of colors	Evenness	Presence of charismatic species
All respondents (293)	0.02	0.53	0.24	0.12	0.09
Psychographic segments based on attitudes toward forest CES					
1 Active/experience seekers (77)	0.01	0.50	0.27	0.14	0.09
2 Quiet seekers (79)	0.05	0.56	0.18	0.12	0.09
3 Collectors (36)	0.05	0.50	0.28	0.13	0.05
4 Generalists (101)	0.01	0.49	0.28	0.11	0.11
Wald (=)	0.53	1.05	10.34	0.56	1.32
Segments based on attitude toward wildflower viewing					
Flowers less important (78)	0.11	0.54	0.11	0.15	0.08
Flowers mores important (210)	0.01	0.50	0.27	0.11	0.10
Wald (=)	2.96	0.02	8.33 $^{*p<0.05}$	0.34	0.19
Segments based on knowledge of local flora					
Novice (77)	0.02	0.59	0.18	0.15	0.07
Intermediate (174)	0.02	0.49	0.29	0.12	0.08
Expert (42)	0.03	0.49	0.23	0.08	0.17
Wald (=)	0.23	4.40	5.03	1.30	2.80

Supporting Information

Graves et al. Does species richness predict CES value?

SI Text

Study area description. From 1976 to 2006, the human population of the French Broad River Basin (FBRB) increased by 48% (86), accompanied by increased exurban, low-density housing development and increased forest land cover. Recent stakeholder interviews indicate that area residents strongly value biodiversity and are concerned for the futures of ecosystem services, particularly cultural ecosystem services (87). Several large tracts of public (e.g., federal, state, county, and municipal) land within the study area have trails, viewpoints, and other access areas for visitors and residents (Figure S1).

The North Carolina tourism office estimates that tourism’s impact increased from $269 million in 1991 to $901 million in 2013 in one urban center in the region, with combined visitor expenditures for 2014 over $1330 million for the FBRB (88, 89). While no data specifically report dollars generated by ecotourism, overnight visitors to the North Carolina Mountain Region reported participating in rural sightseeing (26%), visiting state/national parks (23%), wildlife viewing (14%), hiking/backpacking (10%), nature/ecotouring (9%), other nature (8%), and birdwatching (4%) during 2014 (90). Guidebooks specifically focused on wildflower hikes have been published for the area (91) and 2013 was named the “Year of the Wildflower” by North Carolina’s State Parks. An informal survey of tourism websites for the region revealed that 7 out of the top 10 website results mention wildflowers at least once in their tourism and marketing materials.

Visitor survey analysis. For each forest-based cultural ecosystem service, the ‘average importance’ attributed to that service was determined by calculating an ordinal mean across all respondents (Table S1). We used factor analysis to identify interpretable dimensions of attitudes toward forest-based cultural ecosystem services. Only factors with an eigenvalue > 1 were retained. The level for interpretation of factor loadings was 0.40, based on a significance level of 0.05 and a power of 80% (92). Items that loaded on more than one factor were included in the factor for which they had the highest factor-loading score. One item ("forests are important as a place to be outdoors") added no information and was dropped from the analysis based on communalities < 0.4 (93). We performed K-means cluster analysis with the four factors to identify groups of respondents, representing segments with different psychographic profiles, based on their attitudes toward forest-based cultural ecosystem services (81, 82). Factor and cluster analysis were conducted in R using packages *psych* and *vegan* (94, 95).

Discrete-choice and multinomial logit models. The effect of biodiversity attributes on aesthetic preference for wildflower communities was assessed using a discrete-choice experiment and modeled using multinomial logit models. Discrete-choice experiments are a quantitative technique for eliciting preferences from individuals by asking them to state their preference over alternative scenarios, good, or services. In this study, the discrete-choice experiment included alternative images of wildflower communities and asked individuals to indicate which image they preferred from each set of two images. A full factorial design consisting of all possible combination of wildflower community attributes was not feasible; with five attributes, three with four levels and two with two levels, a full factorial design would consist of $4^3 2^2 = 256$ experimental conditions. Since a full orthogonal array is not possible, we selected an efficient design, with trade-offs between the degree of orthogonality and balance (80). We assessed the sampling design using a measure known as D-efficiency. D-efficient sampling designs maximize the amount of information about each parameter through the most efficient number of choice sets

(80). The sampling design was created using NGene 1.02 (www.choice-metrics.com). The final sampling design included 48 images organized in six blocks of four choice sets and had a D-error = 0.13 (Table S2). Each choice set was a decision between two images.

The images were created using Adobe Photoshop and were representative of wildflower communities commonly encountered in the region. The base image was a photograph from a field site within the study area (48), and composition of the wildflower community was altered by adding or removing flowers. All species included in the digitally manipulated images are found within the study region. Images were shown to respondents as pairs of 8.5 x 11" images.

Each respondent was randomly assigned one of six choice blocks and was asked to evaluate four choice situations. According to random utility theory (49), an individual *n*, chooses alternative, *i*, from a choice set, *C*. The utility derived from alternative, *i*, is assumed to be great than any other choice (*j*) within the choice set. The formula below specifies the utility derived from any particular option (e.g., wildflower community) as:

$$U_{ni} > U_{nj} \rightarrow V_{ni} + \varepsilon_{ni} > V_{nj} + \varepsilon_{nj} \quad \forall\, j \neq i;\ \ i, j \in C_n$$

$$V_{ni} = \beta x_{ni} + \gamma z_{ni}$$

Here, U_{ni} represents the latent utility of a chosen wildflower community, *i*, for respondent, *n*. V_{ni} represents the explainable, or systematic, component of utility and ε_{ni} is random, or unexplainable, component of utility. Moreover, V_{ni} can be a function of the wildflower community attributes and their levels (x_{ni}) as well as other covariates (z_{ni}) thought to influence aesthetic preference (e.g., demographic information, recreation patterns, and respondent characteristics). Finally, β and γ are the vectors of coefficients associated with x_{ni} and z_{ni}. Multinomial logit analysis was conducted using Latent Gold software (96). These models can be thought of as simultaneously estimating binary logits for all comparisons among the alternatives. Each choice is treated as an observation, with a binary response variable and alternative specific explanatory variables.

We first analyzed the preferences of all respondents, without regard for psychographics or demographics (i.e., single-class model). Flower species richness and abundance were modeled as continuous variables while number of colors, evenness, and charismatic species presence were effect coded as categorical values. We tested whether the inclusion of interactive effects between the wildflower community attributes and respondents' attitudes toward forest-based CES improved the model fit. We then ran multinomial logit models for groups based on people's preference of different cultural ecosystem service, knowledge of plants, demographics, and recreational patterns to determine if the effect of biodiversity attributes varied across segments. Models based on segments were compared using the Wald statistic (96) which tests the restriction that parameter estimates in one segment are equal to the corresponding estimates within each of the other groups. In other words, the Wald statistic tested the equality of the regression effects across all the groups.

Characteristics of public forest visitors. We collected usable responses from 293 public forest visitors. Respondents were 55% male, predominantly white (90%), and ranged across age groups (Table S3). The largest group of respondents were the 25 – 34 age group (22%). Respondents were well-educated; 44% had completed at least a 4-year college degree and 29% had advanced degrees. Respondents ranged in the frequency that they visit public forests from visiting public forests only a few times a year (22%) to visiting several times a week or more (26%). The respondents participated in a range of activities and most commonly reported hiking on trails and viewing waterfalls as the main motivations for visiting the public forests (Table S4). Nearly half

(46%) of respondents reported having visited a forest to view wildflowers within the past year and 8% of respondents participated in viewing wildflowers during the visit in which they were surveyed.

Exploratory factor analysis identified a four-factor structure describing people’s attitudes toward forest-based cultural ecosystem services and accounted for 60% of the variance in the dataset (Main Text Table 1a). Based on factor composition, we labelled the factors “Quiet Relaxation”, “Experiences”, “Active Escape”, and “Collecting”. Respondents’ gender was not related to their scores along either the “Quiet Relaxation” or “Active Escape” axis. However, females scored higher on the “Experiences” axis ($t = -2.93$, $p=0.004$) and males scored higher along “Collecting” ($t = 2.89$, $p=0.004$). Respondents who visited public forests more frequently tended to have higher ratings for “Quiet Relaxation” and “Collecting” and lower ratings along the “Experiences” factor than those who visited public forests less frequently. Older people tended to score lower along the axis “Active Escape” (Kruskal-Wallis $H=26.07$, $p<0.001$) and higher on “Experiences” (Kruskal-Wallis $H=20.53$, $p<0.001$). Respondents’ education level was unrelated to factor scores. Respondents’ preferences for images were strongly influenced by flower abundance, evenness, and number of colors. Preference did not vary across segments of public forest visitors (Table S5).

Wildflower community field data collection. Wildflower community data were collected at 54 forested sites in the FBRB during summer 2014. We stratified the study area by elevation, building density, and land use. Sites were in forested areas and within 150 m of trails or roads to characterize floral resources likely to be visible to people. Sites were located on both public and private property, and sampling design is described in detail in another study (48). In brief, we established a 50 x 2 m belt transect at each site and surveyed for wildflower blooms at least three times between April 1 to August 8, 2014. During each visit, we tallied the number of flowering individuals, identified each flowering individual to species, and estimated percent cover of flowers along the transect. We classified each species as charismatic or not (48) and recorded the color. For each site visit, we tallied the number of species in flower (flower species richness), the number of flowers (flower abundance), and the number of flower colors. Charismatic species presence was recorded as a binary variable (1= present, 0=not present). We calculated evenness of the flower community using Simpson's evenness (E) (97). Overall flower species richness (for the whole sampling period April – August 2014) was calculated using species accumulation curves and the *vegan* package in R (94), which allowed us to account for differences in observed species richness due to survey effort (e.g., weekly sampling versus tri-weekly sampling).

Table S1. Respondents' rating of the importance of different forest-based ecosystem services. All values measured on five-step rating scales, with 1: unimportant, 2: somewhat important, 3: important, 4: very important, 5: extremely important. Mean scores and SEM derived from raw data. Survey question was phrased to read "How important is it to you personally that a public forest is a place to…"

Forest-based cultural ecosystem service	Mean importance rating	Std. error
Be outdoors	4.51	0.04
Be physically active	4.25	0.06
See scenic views	4.25	0.05
Participate in recreation	4.15	0.06
Hear nature sounds	4.12	0.06
Escape an urban setting	4.11	0.06
Relax	4.02	0.06
See wildlife	3.93	0.06
Find solitude	3.87	0.07
Be with family and friends	3.72	0.07
Spiritual value	3.47	0.08
Educational value	3.42	0.08
See wildflowers	3.36	0.07
Collect food	1.55	0.06
Hunt or fish	1.29	0.05

Table S2. Wildflower community characteristics of the 48 images used in the discrete-choice experiment. Wildflower community characteristics varied per a D-efficient design. Respondents were randomly assigned to a block, which consisted of four choice sets. Each choice set included a pair of images of which respondents indicated their preferred alternative. Evenness had two levels: low (<0.5) coded as 0, and high (>0.5) coded as 1. Charismatic species presence is binary where 1 = present, 0 = not present.

		Alternative 1					Alternative 2				
Choice set	Block	Species richness	Abundance	No. colors	Evenness	Charismatic species	Species richness	Abundance	No. colors	Evenness	Charismatic species
1	1	5	90	3	0	1	10	10	1	0	0
2	1	3	35	3	1	1	5	90	2	0	0
3	1	3	5	3	1	0	10	90	2	1	1
4	1	3	35	3	1	0	5	5	2	0	1
5	2	3	10	3	0	1	5	5	5	1	0
6	2	5	90	1	0	1	3	5	2	1	0
7	2	5	5	2	0	0	3	10	3	1	1
8	2	10	10	3	1	1	1	35	1	0	0
9	3	1	90	1	0	1	3	35	3	0	0
10	3	1	5	1	0	0	5	10	2	1	1
11	3	10	90	2	0	0	5	10	3	0	1
12	3	3	10	2	0	1	5	90	5	0	0
13	4	10	90	1	1	0	1	90	1	0	1
14	4	3	90	2	1	0	10	90	1	0	1
15	4	10	35	3	0	0	5	90	1	1	1
16	4	1	10	1	1	0	3	90	3	1	1
17	5	3	5	1	1	1	1	10	1	0	0
18	5	10	90	5	1	1	3	90	2	0	0
19	5	5	10	5	0	0	3	35	3	1	1
20	5	3	35	1	0	0	1	5	1	1	1
21	6	5	90	5	1	0	10	35	3	0	1
22	6	3	5	3	0	1	5	35	3	1	0
23	6	3	35	2	0	1	10	10	3	1	0
24	6	1	35	1	1	1	3	5	3	0	0

Table S3. Characteristics of the sample population.

Gender	Male	55%
	Female	45%
Age	18 to 24 years	6%
	25 to 34 years	22%
	35 to 44 years	20%
	45 to 54 years	17%
	55 to 64 years	16%
	65 years and over	18%
Education	High School or equivalent	9%
	Some college/2-year degree	18%
	4-year college degree	44%
	Advanced degree	29%
Race	African American/Black	2%
	Asian	2%
	Caucasian/White	90%
	Hispanic	4%
	Native American	2%
	Pacific Islander	< 1%
	Other	< 1%
Frequency of visits to public forest annually	One to a few times per year	23%
	About once per month	17%
	A couple times per month	18%
	About once per week	16%
	Multiple times per week	26%

Table S4. Visitors' reported participation in a range of activities during visits to public forests within 1 year of being surveyed and motivations for visiting on the day of the survey.

Activity	Past Year	This visit
Hiking on trails	92%	51%
Viewing waterfalls	72%	26%
Walking for pleasure or exercise	81%	24%
Viewing scenery	79%	17%
Nature viewing	83%	16%
Swimming	65%	15%
Mountain biking	35%	14%
Photographing nature	64%	10%
Camping	60%	9%
Picnicking	54%	8%
Wildflower viewing	46%	8%
Fishing	39%	8%
Running on trails	33%	7%
Wildlife watching	54%	4%
Birdwatching	27%	3%
Backpacking	29%	3%
Collecting fruits or berries	30%	1%
Collecting things (e.g. sticks/rocks)	27%	1%
Canoe/kayak/boating	42%	1%
Collecting mushrooms	9%	<1%
Horseback riding	6%	<1%
Collecting medicinal plants	4%	<1%
Hunting	10%	0%
Geocaching	5%	0%

Table S5. Model estimates for the discrete-choice model based on all respondents (i.e., single-class) or segments based on respondents' attitudes toward forest-based cultural ecosystem services, attitude toward wildflower viewing, and knowledge of local flora. Significant Wald (=) values indicate differences in the estimated coefficient of an attribute between segments.

		Segments based on attitudes toward forest-based CES					Classes based on attitude toward wildflower viewing			Classes based on knowledge of local flora			
Attributes and levels	All respondents	1	2	3	4	Wald (=)	Less important	More important	Wald (=)	Novice	Intermediate	Expert	Wald (=)
Flower species richness	-0.01	0.00	-0.02	-0.02	0.00	0.53	-0.05	0.01	2.96	-0.01	-0.01	-0.01	0.23
Flower abundance	0.02†	0.03†	0.02†	0.02†	0.03†	1.05	0.02†	0.02†	0.02	0.03†	0.02†	0.02†	4.4
No. of colors						10.34			8.33*				5.03
1	-0.61†	-0.79†	-0.29	-0.67†	-0.74†		-0.23†	-0.76†		-0.52†	-0.70†	-0.46†	
2	0.08†	0.16†	-0.03	-0.02†	0.16†		-0.15†	0.18†		0.06†	0.11†	0.01†	
3	0.24†	0.27†	0.33	0.36†	0.10†		0.20†	0.24†		0.25†	0.18†	0.50†	
5	0.29†	0.35†	-0.01	0.33†	0.49†		0.18†	0.34†		0.21†	0.41†	-0.04†	
Evenness						0.56			0.34				1.3
low	-0.24†	-0.30†	-0.21†	-0.23†	-0.25†		-0.29†	-0.23†		-0.31†	-0.24†	-0.16†	
high	0.24†	0.30†	0.21†	0.23†	0.25†		0.29†	0.23†		0.31†	0.24†	0.16†	
Charismatic species						1.32			0.19				2.8
present	-0.18†	0.19†	0.15†	0.09†	0.23†		-0.16†	-0.20†		-0.15†	-0.16†	-0.34†	
absent	0.18†	-0.19†	-0.15†	-0.09†	-0.23†		0.16†	0.20†		0.15†	0.16†	0.34†	
Pseudo-R^2	0.25	0.28	0.21	0.23	0.28		0.23	0.26		0.32†	0.23†	0.26	
n	293	77	79	36	101		82	211		77	174	42	

Significance: † p <0.001; ** p<0.01; *p<0.05

Table S6. Summary statistics for wildflower communities (*n* = 54) surveyed during April – August 2014. Data are summarized across all sites for the visit that resulted in maximum wildflower viewing utility.

	Median	Mean	Std. dev	min-max
Flower species richness	4	4	2.2	1 -11
Flower abundance	44	82	102	4 - 550
Evenness	0.71	0.62	0.28	0 - 1
No. of colors	2	3	1	2 - 5
Charismatic species presence	*na*	0.89	0.32	0 - 1
Predicted maximum utility	1.41	2.2	2.50	-0.11 - 13.29

Figure S1. Study area and public forest locations in the French Broad River Basin, North Carolina, USA.

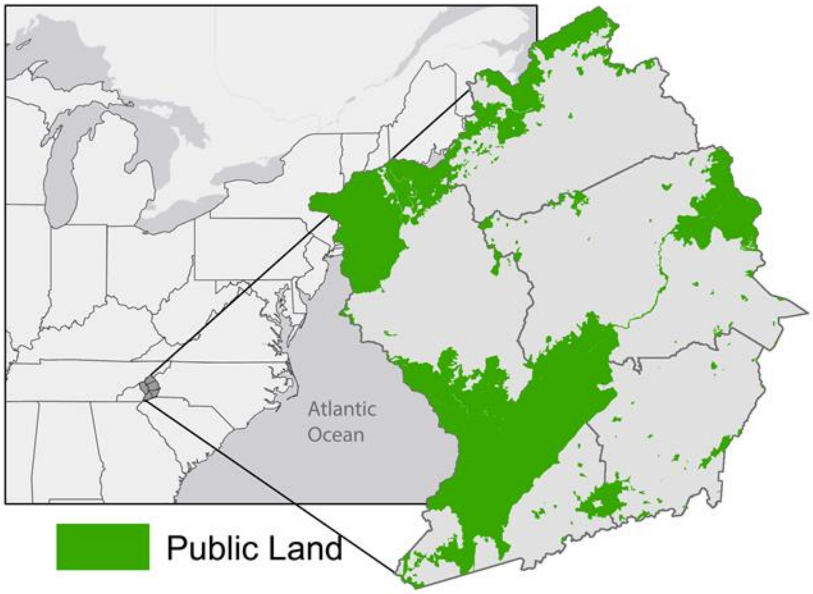

Figure S2. Four example images showing differences in wildflower community. Images vary only in the number of colors and evenness, with species richness and flower abundance held constant at five species and ninety flowers, respectively. Image (a) shows one color and low evenness, (b) one color and high evenness, (c) five colors and low evenness, (d) five colors and high evenness. Based on the results of the discrete-choice experiment, (d) would have the highest predicted wildflower viewing utility.

Chapter 4 – Bird community dynamics change the seasonal distribution of a cultural ecosystem service in a montane landscape

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ABSTRACT

Many cultural ecosystem services (non-material benefits to people from nature) depend directly on biodiversity, and temporal dynamics of biotic communities thus can affect the landscape supply of these services. Birdwatching, a biodiversity-based cultural ecosystem service, has been steadily increasing in popularity. Bird community composition varies across space and over time in relation to multiple environmental variables. However, models of birdwatching supply are largely static, relying on single estimates of species richness or simple land-use/land-cover proxies, and may be insufficient to quantify cultural ecosystem service dynamics. We sampled bird communities across topographic and land-use gradients in the southern Appalachian Mountains (USA) and asked (1) How do projected patterns of birdwatching supply vary among bird functional groups and over space and time? (2) How do changing landscape patterns of birdwatching supply affect public access to birdwatching? (3) How well does birdwatching supply align with direct estimates of birdwatching (i.e., eBird locations)? Repeated point-counts were conducted at 69 sites in the French Broad River Basin (North Carolina) from April through August 2014, and a total of 96 bird species was recorded. We developed spatial-temporal models of five indicators of birdwatching supply (total bird species richness, and richness of migratory, infrequent, synanthrope and resident species), and mapped each indicator (1-ha resolution) across the landscape in early spring, late spring, and summer. Landscape patterns of total and synanthrope bird species richness were similar through time, but landscape patterns of resident, migratory, and infrequent species richness changed substantially. Projected birdwatching supply differed among models of different components of the bird communities, leading to sometimes opposing conclusions regarding the places with the highest supply of bird CES. Hotspots for these three groups varied among time periods by 10%, 14%, and 27% of the landscape, respectively. Hotspots of total species richness seldom overlapped with hotspots of migratory or infrequent species richness; only 7-9% of the landscape was a hotspot for at least 4 indicators in any time period. Changes in bird communities led to differential access to hotspots of birdwatching supply as the season progressed. For migratory and infrequent species, 31-41% of hotspot area was publicly accessible. Areas of high supply for total, resident, and synanthrope bird species richness were largely on private lands. Observations of actual bird watching were reported from both public and private lands. Overlap between eBird observations and hotspots of birdwatching supply were greatest for migratory species in spring and for synanthrope species in summer. Studies that rely only on simple, static metrics of biodiversity may overlook seasonal and spatial dynamics important to users of CES and future studies should consider multiple facets of biotic communities.

Keywords: avian diversity, biodiversity, spatial model, recreation, birdwatching

INTRODUCTION

Sustaining ecosystem services has become a priority in landscape management and environmental policy worldwide (MA 2005, Díaz et al. 2015). Cultural ecosystem services (CES), or the non-tangible benefits from nature, are among the least studied ecosystem services (Daniel et al. 2012, Hernández-Morcillo et al. 2013, Milcu et al. 2013) and, despite substantial development in the theory and practice of ecosystem service assessment, empirical and biophysical models of CES remain rare (Troy and Wilson 2006, Kareiva et al. 2011, Bagstad et al. 2015). Knowing where, when, and how landscapes provide cultural ecosystem services is a crucial step to help decision-makers evaluate tradeoffs between different societal needs and sustaining multiple-use landscapes (Fisher et al. 2009, Plieninger et al. 2012, 2013). Thus, CES assessments need to be developed that can more effectively contribute to decision making and conservation planning (de Groot et al. 2010, Fish et al. 2016).

Cultural ecosystem services, which include mental health benefits, recreational opportunities and aesthetic enjoyment (e.g. beauty of the landscape, the smell of a flower, sound of the birds), can be challenging to quantify because the capacity for an ecosystem to deliver CES depends both on biophysical characteristics of the ecosystem as well as the experience of the ES user or beneficiary (Chan et al. 2012, Martín-López et al. 2012). Furthermore, many CES depend on biodiversity (e.g., bird watching, fall foliage, wildlife photography) but have not been included in many biodiversity-ecosystem service studies (Cardinale et al. 2012, Daniel et al. 2012). The supply of biodiversity-based CES (i.e., the potential of an ecosystem to provide a given ES, Tallis et al. 2012) may rely on the presence, abundance, diversity, and/or functional traits of biota or ecological communities (Lavorel et al. 2017). Depending on the ES, life history traits of the underlying biota, like phenology (the timing of species life cycle events like flowering in plants) or animal behavior, affect supply and cause patterns of supply to change over time (Kremen et al. 2007, Grêt-Regamey et al. 2014, Graves et al. 2017a). Therefore, to manage and provide better estimates of biodiversity-based CES supply, CES models need to incorporate a strong understanding of the underlying ecology (Kremen 2005, Luck et al. 2009). However, most CES studies have used simple indicators or proxies and static data sources that ignore underlying temporal dynamics in biotic communities (Martínez-Harms and Balvanera 2012, Graves et al. 2017a).

Birdwatching is a key biodiversity-dependent CES that has steadily been increasing in popularity (Puhakka et al. 2011, Villamagna et al. 2014), especially in the US, where approximately one in five Americans report participating in birdwatching (Carver 2013). Bird diversity contributes to the amenity value in semi-rural landscapes (Lepczyk 2005, Carver 2009, Fuller et al. 2012) and birdwatching has large economic impacts. For example, in 2011, 47 million birders in the US spent $41 billion on birding related expenditures (Carver 2013).

Birdwatching supply, when included in CES assessments, has typically been represented by static, coarse measurements of species richness (Bateman et al. 2013, Villamagna et al. 2014, Dallimer et al. 2015). While these estimates demonstrate that bird-based CES have strong spatial trends, they ignore temporal dynamics in bird communities. Bird communities vary even within a single season (Boulinier et al. 1998, Leveau and Leveau 2012, Brambilla et al. 2012, Frey et al. 2016, Zuckerberg et al. 2016), and such dynamics are likely to affect spatial patterns of birdwatching supply. Thus, static species richness models, which often accumulate all species possibly present in an area, may not equate to the well-being benefits received by birdwatchers and may not represent the number and types of bird species likely to be observed during an average birdwatching visit (Cumming and Maciejewski 2017).

Furthermore, while there is clear evidence that birdwatching can contribute to human well-being (Curtin 2009, Ratcliffe et al. 2013), how bird species richness relates to the benefits received by birdwatchers is not well known (Belaire et al. 2015, Cumming and Maciejewski 2017) and may vary with birdwatcher motivation and expertise (Scott et al. 2005, Cox and Gaston 2015). While more casual birdwatchers may be motivated by observing "many types of birds" (Cordell and Herbert 2002), avid birders are more likely to plan birding trips to around the likelihood of observing particular types species, such as migratory birds, or ascribe more importance to seeing rare birds or birds they have not seen before (McFarlane 1994, Hvenegaard 2002, Scott et al. 2005, Booth et al. 2011, Deason et al. 2015). By focusing solely on overall avian species richness, CES models may misrepresent the spatial distribution of bird CES and limit managers' ability to manage landscapes for multiple ecosystem services and multiple beneficiaries.

Managers need not only to know where CES, such as birdwatching, are produced but also where CES can be accessed and where they are used. Robust CES assessments should include both the biophysical and social components of the CES (Chan et al. 2012). For example, CES supply will depend on the presence or abundance of species (i.e., biophysical) but also on the demand for key species and the ability for people to access locations with high CES supply (Burkhard et al. 2012, Villamagna et al. 2013, 2014). By comparing the spatial-temporal supply of CES with public access and use of CES, managers may be able to identify opportunities for increasing the availability of CES (Villamagna et al. 2014), educating people about important CES in their own backyard (Cox and Gaston 2015), and incentivizing management to maintain CES across the landscape (Raudsepp-hearne and Peterson 2016).

In this study, we sampled bird communities across topographic and land use gradients in the southern Appalachian Mountains and developed spatial-temporal models of five indicators of birdwatching supply (i.e., richness of all bird species, and richness of rare species, migratory species, synanthropic and resident species). We asked (1) How do projected patterns of birdwatching supply vary among bird functional groups and over space and time? (2) How do changing landscape patterns of birdwatching supply affect public access to birdwatching? (3) How well does birdwatching supply align with direct estimates of birdwatching (i.e., eBird locations)? We hypothesized that bird community dynamics driven by the arrival of migratory species and habitat specialization during the nesting season would generate distinct patterns of supply for different bird-watching variables. For example, species richness was expected to increase in higher elevations during the late spring as both migratory and resident species moved into these areas. Migratory species richness was expected be greater in areas with low building density and increased forest cover; that pattern was expected to be strongest during the late spring after nesting territory establishment. Further, we expected that spatial-temporal patterns of birdwatching supply would result in changing public access for birdwatching and that birdwatching use would reflect those patterns.

METHODS

Study Area

This study was conducted within the Blue Ridge Mountain physiographic region in the southern Appalachian Mountains (USA), an ecotourism destination with over $1330 million in combined visitor expenditures for the region in 2014 (SAMAB 1996, Strom and Kerstein 2015, VisitNC 2016). Overnight visitors to the region during 2014 reported using recreational ecosystem services including rural sightseeing (26%), visiting state/national parks (23%), wildlife viewing (14%), hiking/backpacking (10%), nature/ecotouring (9%), other nature (8%) and birdwatching (4%) (VisitNC 2015). Stakeholder interviews indicate that area residents value biodiversity and cultural ecosystem services (GroWNC 2013).

We sampled bird communities in the French Broad River Basin (FBRB), a 7330 km^2 watershed in western North Carolina (Figure 1), dominated by secondary forest, with strong topographic variation in forest type and climate (Whittaker 1956, Bolstad et al. 1998). Elevation ranges from 300 to 2100 m. The region's landscape heterogeneity and long evolutionary history have led to a high diversity of both flora and fauna (Whittaker 1956, Delcourt and Delcourt 1998) as well as relatively high vegetation productivity (Spruce et al. 2016). Regional avian species richness (i.e., gamma diversity) is estimated to be as high as 141 species (Mckerrow et al. 2006) and bird communities within the study area are diverse and influenced by topography, climate, land use and development patterns (Haney et al. 2001, Lumpkin et al. 2012, Lumpkin and Pearson 2013).

The region is dominated by forest (75%), mainly secondary growth, ranging from spruce-fir and northern hardwood forest types at high elevation to mixed-deciduous forests at lower elevations (Stephenson et al. 1993, White et al. 1993). Agricultural use comprises 12% of the landscape, the majority (> 70%) of which is managed as meadow or pasture. Urban areas account for 12% of the landscape with the remainder comprised of shrubland, water, or barren land (all <1%) (Homer et al. 2012). Population has increased in the region by 48% between 1976 and 2006, accompanied by increased exurban and low-density housing development and afforestation (Gragson and Bolstad 2006).

Bird CES supply

Data collection. Bird communities were surveyed at 69 sites located on both public and private property. Sites were stratified by elevation and development intensity (e.g., building density) and were located within 150 m of trails and roads. The same sites were used to collect data on wildflower communities for a concurrent study and detailed site selection methods are published in that study (Graves et al. 2017a). Bird surveys were conducted at sites at least once every three weeks, and a subset of sites was visited weekly, from April 1 to August 8, 2014.

Bird surveys consisted of standard 10-minute point counts and were conducted between 05:45 to 10:30. One of three trained observers performed each point count and all study sites were surveyed by at least 2 different observers throughout the study. Surveys were not conducted on rainy days or days with high wind. Each bird detected by sight or song within 100 m of the point location (i.e., site center) was identified to species and recorded. Birds observed outside the 100-m radius were recorded but not included in the primary analysis.

A variety of remotely sensed and GIS data were used to derive variables related to the environmental factors that we hypothesized to be important in predicting the distribution bird communities (Table 1). Environmental variables included elevation, tree cover, vegetation structural diversity, local and neighborhood building density, land cover diversity, and estimated annual productivity. Survey variables recorded included the time of the survey, estimated wind speed and cloud cover as well as observer ID.

Building density (building units per hectare) was quantified by counting the number of buildings located within 100 m and 1000 m of the center of each study site (i.e., local and neighborhood building density). Digitized building footprints were provided and used with permission from county governments to locate each building (Graves et al. 2017). Building density at local scales (100 – 200 m) has a significant effect on breeding bird occupancy within the study area (Lumpkin and Pearson 2013). We also tested for effects of building density within 1000 m of the study site center, since birds may be responding to broader scale habitat variables.

Vegetation structure and tree cover were calculated from LIDAR (light detection and ranging) data. Discrete-return LIDAR data were collected in 2005 (NCDEM 2006) for the entirety of the study area during winter. Vegetation height was measured from LIDAR first returns by subtracting the elevation of a bare-earth digital terrain model, derived from the same LIDAR data set, from the elevation of each return (Graves et al. 2017). We excluded returns within digitized building footprints. Vegetation structural diversity was calculated using the Shannon Evenness index ($E_H = \frac{-\sum_{i=1}^{S} p_i \ln p_i}{\ln S}$) using the proportion ($p_i$) of LIDAR returns in each of four vegetation strata (i.e., herb, shrub, subcanopy, and canopy layers) within 100 m of the site center. Tree cover was recorded as the proportion of LIDAR returns at each study site (100-m radius around site center) that were within the subcanopy or canopy layers (i.e., >2.0 m above ground) (Graves et al. 2017).

Land-cover diversity was calculated as the Simpson's diversity index ($SIDI = 1 - \sum_{i=1}^{m} {P_i}^2$) using six land-cover categories (grassland/herb, shrubland, cropland, forest, developed and other/water) within 200 m of each study site. SIDI ranges from 0 to 1.0 and can be interpreted as the probability that two points chosen at random within a given area will land in different land cover types (McGarigal et al. 2012). We used data from the 2014 Cropland Data Layer (CDL) and calculated SIDI using Fragstats (McGarigal et al. 2012).

Annual vegetation productivity was extracted from a smoothed and gap-filled MODIS Normalized Difference Vegetation Index (NDVI) dataset (Spruce et al. 2016). We calculated the 10-year (2004 – 2014) median of annual vegetation productivity for each study site. Elevation was extracted from the National Elevational Dataset-Digital Elevation Model (NED-DEM, data available from the U.S. Geological Survey).

Data analysis. Bird species were classified based on (1) migratory status (short-, long-distance migrants, and resident), (2) synanthrope status (following Johnston 2001), and (3) conservation status (SI Table 1). Because the uniqueness or rarity of bird species can also be important for birdwatcher satisfaction (Booth et al. 2011), we also calculated an index of relative species rarity using the frequency of sighting of each species in the eBird dataset for the FBRB. Species with sighting frequencies in the lowest quartile (i.e., the lowest 25% of sightings) were considered ‘infrequent’. For each site survey, five bird CES indicators were tallied: (1) total number of species, (2) migratory species richness, (3) resident species richness, (4) synanthrope species richness, and (5) ‘infrequent’ species richness. Instead of modeling the total potential bird species richness at a site, we modeled the average species richness observed during a survey visit. Average observed species richness, rather than richness estimates corrected for detectability (Nichols et al. 2000), may better represent the experience of a casual birdwatcher and, from a birdwatching perspective, would be equivalent to the average number of species that a birder might expect to observe in a short birding trip (~ 10 minutes).

Bird CES indicators were modeled during each of three time periods (i.e., early spring, late spring, and summer) to explore how temporal dynamics in bird communities affected the spatial distribution of birdwatching supply. Early spring (i.e., April 1 to May 13) roughly corresponds to the migration/pre-breeding season, late spring (i.e., May 13 – June 24) is representative of the breeding season and overlaps with existing bird surveys, and summer (i.e., June 24 – Aug 6) corresponds with post-breeding season (Shriner et al. 2002, Sauer et al. 2013). Our target was to sample each site at least twice during each period, for a minimum of six surveys across the season. Fifty-six out of 69 sites met this criterion; these data comprised the model training dataset. The remaining 13 sites (~19% of data) were retained as a validation dataset.

For each site and each time period, means were calculated for each of the five bird CES indicators across site surveys. Then, generalized linear models (GLM) were constructed for each bird CES indicator with the mean bird CES as the response variable and all environmental variables as possible predictor variables. Time period (early spring, late spring, and summer) and the potential interaction effects of time period with tree cover, building density, and elevation were included as predictor variables. Models were fitted first to the full model and variables were progressively eliminated from the model by means of backward selection. Models were compared based on AICc and top models were defined as having the lowest AICc (Burnham and Anderson 2002). To ensure the most robust models as possible, we retained all models within delta-AICc < 2.0. Goodness-of-fit was assessed for each model using AICc values, residual deviance, and McFadden's pseudo-R^2. We also inspected the correlation between observed and predicted values for each model. Finally, we assessed the prediction accuracy for each model using the retained validation dataset.

The resulting GLMs were used to map the projected supply of each bird CES in each time period: early spring, late spring, and summer. Maps were produced using the *predict* function in the raster package in R (Hijmans and van Etten 2015) and the best-fitting models identified in the analysis above. To be conservative in our estimate of bird CES supply, projected bird CES was defined as the predicted value from the GLM minus one standard error. For response variables with competing top models, we first mapped the projected bird CES (i.e., predicted value minus the standard error) from each of the competing top models. Final maps were created by calculating the weighted-average of the top model projections, using the corresponding AICc model weights, rather than using model-averaged coefficients (Grueber et al. 2011, Cade 2015). All input layers were standardized to z-scores based on the mean and variance of the training dataset (n=56) and referenced to the same projection (Albers Equal Area) and 100-m grid cell. For more detail on preparation of input data layers, see Appendix A. For maps of the standard error of each predicted response, see supplemental material (Figure A1).

Areas of high birdwatching supply (i.e., hotspots) were identified for each bird CES indicator in each time period as areas where projected bird CES supply exceeded the mean in our training dataset (Table 2). Hotspots of total species richness were compared to hotspots for alternate bird CES indicators by calculating the percent overlap in each season. Hotspots for multiple bird CES were identified by overlaying hotspot maps of each response variable (sensu Qiu and Turner 2013). Hotspots were mapped for each time period and the temporal consistency of hotspots was analyzed by overlaying hotspots for each time period and calculating the percent of spatial concordance among time periods.

Bird CES and public access

Maps of projected bird CES supply were compared to maps of public access to examine how access to bird CES changed over time using two levels of public access across the landscape. ‘Highly accessible’ included locations within 100 m of public-use trails (e.g., hiking trails, greenways), access points (e.g., overlooks, view points), or the Blue Ridge Parkway, a highly-traveled scenic byway in the area. ‘Moderately accessible’ included any publicly owned lands (e.g., federal, state, or municipality-owned forests and parks); these areas are considered open to access but off trail. The remainder of the landscape was considered private land or to have limited and/or controlled access. For each time period and bird CES, we calculated the area overlap between hotspots and public access.

Bird CES supply and bird CES use

Maps of bird CES supply were compared to demonstrated use of birdwatching CES using data from eBird, an online citizen science bird-monitoring project (Sullivan et al. 2009, 2014). Point locations of eBird observations for the years 2009 to 2014 were mapped using ArcGIS. Observations were limited observations to those between April 1 and August 31 of each year, to better capture bird CES use during the time periods for which we sampled bird CES supply. The eBird observations were classified into early spring, late spring, and summer based on the same time periods as the bird CES supply above. To determine how well bird CES use corresponded with projected bird CES supply, the proportion of eBird points within hotspots of bird CES supply was calculated for each time period.

RESULTS

Over 700 individual bird surveys were conducted from April 1 to August 6 across 69 sites, and the training dataset consisted of 656 surveys at 56 sites. A total of 96 bird species were detected and used in the training dataset (Table A1). The most commonly occurring species (observed at 90% or more of the study sites) were Tufted Titmouse (100%), Carolina Chickadee (98%), Northern Cardinal (96%), American Robin (93%), Blue Jay (93%), Rufous-sided Towhee (93%), and Carolina Wren (91%). We observed 65 migratory species, 31 resident species, and 44 synanthropic species. Of the synanthropic species, 21 were migratory species and 23 were resident species. Forty-six of our observed species were classified as ‘infrequent’ (i.e., low relatively frequency of sighting in the full eBird dataset for the FBRB), 38 of which were migratory species and 8 of which were resident species.

The total number of species observed during each survey varied from 1 to 21 species (mean = 8 species). Observed migratory species richness varied from zero to 10 (mean = 3 species) and both observed resident species and observed synanthropic species ranged from zero to 15 species (mean = 5 species). The number of ‘infrequent’ species observed ranged from zero to 9 (mean = 3 species). Mean migratory species richness and mean ‘infrequent’ species richness were significantly higher during the late spring (Table 2) but there was no difference in mean total bird species richness, mean resident species richness, and mean synanthrope species richness among the three time periods (Table 2).

The top models for each bird CES indicator (Table 3) explained between 23 and 48% of the variance in bird CES indicators. Elevation was included in top models for total species richness (negative effect), resident species richness (negative effect), and ‘infrequent’ species richness (positive effect) but not included in models of migratory species richness. Local building density had a positive effect on all bird CES, but neighborhood building density had negative effects on total, migratory, and ‘infrequent’ species richness. Neighborhood building density was not included in models for resident and synanthrope species richness. Tree cover was negatively related to all bird CES, with stronger effects on total, resident, and synanthrope species richness, relatively weak effects on ‘infrequent’ species richness, and only slight effects on migratory species richness. Vegetation structural diversity was an important predictor in models of resident and synanthrope species richness, with positive effects, and was included in one of the top models for ‘infrequent’ species, with negative effects. Land-cover diversity was not included in the models of total bird species richness; however, migratory species richness and ‘infrequent’ species richness was negatively affected by land cover diversity while resident and synanthrope species richness were positively related to land cover diversity. Effects of time period were included in all top models for migratory, resident, synanthrope, and ‘infrequent’ species richness. Time period was included in one model of total bird species richness, but effects were weak. The interaction effect between time period and building density was included in top models of migratory and ‘infrequent’ species richness. Finally, the interaction between time period and tree cover was included in models of resident, synanthrope, and ‘infrequent’ species richness.

Bird CES supply

The spatial distribution of bird CES supply varied across time periods and among bird CES indicators (Figure 2, Table 4). For total bird species richness and synanthrope species richness, the landscape percentage with high birdwatching supply (i.e., hotspots) remained consistent across the time periods (32 – 34% and 26 – 29%, respectively). For migratory bird species richness, the majority of the landscape was projected to have high birdwatching supply (>60%) and projected hotspot area was highest in the late spring (78% of the landscape projected above the observed mean). For high resident bird species richness, the landscape percent declined from early spring (37%) to summer (27%); similarly, ‘infrequent’ bird species richness hotspots declined from early spring (71%) to summer (45%).

Hotspots for total bird species richness were consistent across time periods (Table A2), with 66% of the landscape consistently predicted to have low supply and locations of high supply shifted on less than 5% of the landscape. Hotspots of resident and synanthrope species richness were similarly consistent (Figure 2), with 63 – 67% of the landscape predicted to have low supply and locations of high supply shifting on only 8% of the landscape. Migratory and ‘infrequent’ bird species richness had the most dynamic patterns of bird CES supply and spatial patterns of these hotspots were different than for total, resident, and synanthrope species richness (Figure 2). Hotspots of migratory bird species richness consistently comprised 63% of the landscape, and a further 15% of the landscape was projected to have shifting supply of migratory species richness. Similarly, hotspots of ‘infrequent’ bird species richness consistently comprised 45% of the landscape, with an additional 32% of the landscape projected to have high supply of ‘infrequent’ bird species richness during only one or two of the time periods.

Hotspots of total species richness were not often spatially co-located with hotspots of migratory or infrequent species richness (Figure 2, Table 6). However, total species richness hotspots overlapped substantially with resident and synanthropic bird species richness (over 50% overlap, Table 6). Nearly all (98%) of the landscape supplies high levels of at least one bird CES indicator, but hotspots of at least four CES indicators were rare (7 – 9% of the landscape) (Table 4).

Public accessibility of bird CES

Up to 27% of the study area is publicly accessible, with 5% ‘highly accessible’ and 22% ‘moderately accessible’ (Figure 3). For total, resident, and synanthrope species richness, areas of high bird CES supply tended to be in the privately owned or limited access areas and both the proportion of these bird CES hotspots located on publicly accessible land (6 – 9%) and the total percent of the landscape with high supply of these bird CES and within publicly accessible land remained relatively stable across time periods (Figure 4, Table A3). For migratory and ‘infrequent’ species richness, a larger percent (31 – 41%) of hotspot area was located on publicly accessible land and, for ‘infrequent’ bird species richness, the percentage of hotspot area located on publicly accessible land increased (8%) from early spring to summer for the (Table A3). However, the total percent of the landscape with high supply of ‘infrequent’ species richness and located on public land declined by 5% from early spring to summer (Figure 4) indicating that ‘infrequent’ species richness hotspots contracted to publicly accessible lands over the time periods.

Bird CES supply and bird CES use

There were 4347 eBird observations within our study area during the spring/summer (i.e., April – August) of 2009 to 2014 and were located on both publicly accessible and private land (24% ‘highly accessible’, 17% ‘moderately accessible’, and 59% private/limited access). Forty-three percent were recorded within the early spring, 23% within the late spring, and 34% within the summer time periods (as defined in our study) (Figure 5). On average across the time periods, a higher percent of eBird points were located within projected bird CES supply hotspots for resident (62%) and synanthrope (53%) species richness than for migratory (45%), all species (48%), and ‘infrequent’ (33%) species richness. Correspondence between eBird observations and projected migratory and ‘infrequent’ bird CES supply hotspots were higher in the early and late spring than the summer (Table 8). Conversely, the percent overlap of eBird observations with hotspots of bird CES supply was highest for synanthrope species richness in the summer.

DISCUSSION

Landscape models of birdwatching supply in the Southern Appalachians revealed seasonal variation in birdwatching supply for five bird CES indicators. Birdwatching supply for at least one bird CES was high across much of the landscape, but only a small percent of the landscape provided high supply for all bird CES. Spatial variation in hotspots of birdwatching supply for different bird CES suggested that public accessibility of birdwatching may differ depending on a birder’s motivations. Shifts in birdwatching supply were accompanied by shifts in use of bird CES, highlighting that the spatial-temporal patterns of biotic communities underlying CES supply as well as the patterns of CES users are important considerations to fully understand landscape provision of CES.

Biodiversity-based CES provision may be driven by more than total species richness, and users of CES may be interested in other aspects of biotic communities (Cumming and Maciejewski 2017, Graves et al. 2017b). We developed landscape projections of birdwatching supply that account for different components of the bird community (e.g., where are the birds vs. where are the migratory birds). Projected birdwatching supply differed among models of different components of the bird communities, leading to sometimes opposing conclusions regarding the places with the highest supply of bird CES. In particular, hotspots of total bird species richness, a commonly used metric for birdwatching supply (Bateman et al. 2013), did not often overlap with high supply of migratory or infrequently sighted species richness. However, total bird species richness was a reasonable surrogate for common (i.e., resident and synanthrope) species richness. Studies that rely only on simple, static metrics of biodiversity may overlook seasonal and spatial dynamics important to users of CES and future studies should consider multiple facets of biotic communities.

Spatial-temporal variation in birdwatching supply was driven by bird community response to land use/land cover and development patterns within the study area. In the Southern Appalachians, abundant forest cover provides habitat for several species of Neotropical migrants and forest-specialists (Haney et al. 2001). From a birdwatching perspective, the extensive forest cover resulted in high supply of migratory birds over a large percentage of the landscape.

Exurban development occurs widely within the study area (Gragson and Bolstad 2006) and individual bird species response to local building density varies depending on habitat and migratory guild (Lumpkin and Pearson 2013). Birdwatching supply increased with local building density, reflecting community-level versus species-level responses to building density. Increased avian species richness with increased low-level and exurban building density is not uncommon (Marzluff 2005, 2014, Luck 2007). In the predominantly forested Southern Appalachians, local increases in building density provides habitat heterogeneity that can enhance avian diversity (Willson and Comet 1996), consistent with the idea that human settlement acts as an intermediate disturbance on the landscape (McDonnell et al. 1993, McKinney 2002). However, birdwatching supply of migratory and infrequently-sighted species declined with increased neighborhood building density. For these groups of birds, community-level responses to building density are complex and stronger at the neighborhood scale, suggesting that birdwatching supply for these groups and may be driven by threshold responses to landscape level human settlement.

Birdwatchers’ expectations may be an important driver of final CES provision and the geographic location that birders choose may be a function of the bird community in addition to public accessibility or other landscape features, such as mountain views, waterfalls, or wildflowers (Potschin and Haines-Young 2013, Cumming and Maciejewski 2017). We found that only about half of eBird observations were located on publicly accessible land, and that the degree to which birding locations overlapped with different bird CES shifted across time periods. The demonstrated shift in birder location suggests that birdwatchers are choosing to bird at locations projected to have high migratory bird species richness during the migration and nesting season, and then concentrating on other locations throughout the summer. The shifts in birder locations suggest that people may be adjusting their expectations based on landscape context

(Cumming and Maciejewski 2017), which leads to different patterns of social demand for bird CES across time periods. In addition, since over half the birding locations were located on private or limited access lands, our study highlights the importance of backyard birdwatching and private lands in the provision of a key CES.

Given the extensive supply of birdwatching across the landscape, public access may be the limiting factor for the provision of bird CES to birdwatchers in the Southern Appalachians. For instance, while over 60% of the landscape was projected to have high supply of migratory and infrequently sighted species, less than 25% of the landscape provided high supply and was also publicly accessible. For total species richness, synanthrope and resident species, less than 5% of the landscape provided high birdwatching supply and was also publicly accessible. Since evidence suggests that watching birds can increase the connection people feel with nature (Zelenski and Nisbet 2014, Cox and Gaston 2015) and being connected to nature is linked to people’s awareness of nature around them and support for conservation issues (Miller 2005, Restall and Conrad 2015), enhancing public accessibility in locations projected to have high birdwatching supply could lead to increased human well-being as well as benefits for biodiversity conservation.

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Table 1. Summary of environmental variables used in multiple regression models of bird cultural ecosystem service indicators. Data were extracted from a variety of GIS and remotely sensed datasets.

PREDICTOR VARIABLE	**MEAN (MIN – MAX)**
Elevation (m a.s.l.)	788 (530 – 1475)
Building density (#/ha) w/in 100 m	0.43 (0 – 2.23)
Building density w/in 1 km	0.63 (0 – 5.20)
Tree index (Proportion of LIDAR returns in canopy)	0.52 (0.11 – 0.81)
Vegetation diversity index (based on LIDAR returns)	0.65 (0.41 – 0.87)
Landcover diversity index (Simpson's Diversity Index or SIDI)	0.34 (0.00 – 0.65)
Annual vegetation productivity	2231 (1885 – 2440)
Season: early spring, late spring, or summer	Factor: 1, 2, 3

Table 2. Summary of observed bird cultural ecosystem service (CES) indicators at 56 total sites across time periods and results from repeated measures ANOVA. Super-script letters indicate post-hoc groupings.

Bird CES indicator	Overall mean	Early spring mean (Min – Max)	Late spring mean (Min – Max)	Summer mean (Min – Max)	ANOVA (F, p)
Total species richness	8.11	8.29 (4.33 - 14.83)	8.23 (4.0 – 17.0)	7.8 (2.5 – 13.5)	F = 1.34, p = 0.265
Migratory species richness	3.34	3.09 (1.00 – 8.00)^{ab}	3.77 (0.5 – 6.67)^{b}	3.15 (1.0 - 7.0)^{a}	F = 7.87, p < 0.001
Synanthrope species richness	4.85	4.73 (1.25 - 11.00)	4.78 (1.5 -9.5)	5.04 (1.5 - 8.6)	F = 1.39, p = 0.26
Resident species richness	4.77	5.2 (1.00 - 11.67)	4.46 (1.00- 11.00)	4.66 (1.0 - 9.0)	F = 0.521, p = 0.595
‘Infrequent’ species richness	2.74	2.91 (1.0 - 7.5)^{a}	3.02 (0.5 - 6.5)^{b}	2.28 (0.5- 5.0)^{a}	F = 8.20, p < 0.001

Table 3. Summary of top models for bird cultural ecosystem service indicators. Models were selected using AICc and backward variable elimination.

	ΔAICc	Elev.	Local building density	Neighborhood building density	% Tree	Veg. structure	LU/LC diversity	Time period: Late spring	Time period: Summer	Time period x %Tree	Time period x local building	AICc wt.	pseudo-R2
Total species richness	0.00	-0.41	0.87	-0.43	-0.54							0.78	0.23
	2.04	-0.41	0.87	-0.43	-0.54			-0.06	-0.48			0.22	0.24
Migratory species richness	0.00		0.26	-0.69				0.68	0.06		Late spring: -0.49 Summer: 0.16	0.42	0.27
	0.35		0.29	-0.64			-0.14	0.68	0.06		Late spring: -0.49 Summer: 0.16	0.4	0.28
	1.78		0.29	-0.63	-0.07		-0.19	0.68	0.06		Late spring: -0.49 Summer: 0.16	0.17	0.28
Resident species richness	0.00	-0.64	0.64		-0.36	0.36	0.48	-0.74	-0.54			0.61	0.47
	0.86	-0.64	0.64		-0.57	0.36	0.48	-0.74	-0.54	Late spring: 0.11 Summer: 0.53		0.39	0.48
Synanthrope species richness	0.00	-0.38	0.76		-0.65	0.2	0.31	0.05	0.31	Late spring: 0.30 Summer: 0.59		1	0.47
‘Infrequent’ species richness	0.00		0.26	-0.57	-0.14		-0.29	0.12	-0.62	Late spring: 0.41 Summer: 0.04	Late spring: -0.49 Summer: -0.05	0.45	0.37
	0.67	0.13	0.27	-0.52	-0.16		-0.29	0.12	-0.62	Late spring: 0.41 Summer: 0.04	Late spring: -0.49 Summer: -0.05	0.32	0.37
	1.41	0.16	0.29	-0.51	-0.16	-0.12	-0.33	0.12	-0.62	Late spring: 0.41 Summer: 0.04	Late spring: -0.49 Summer: -0.05	0.22	0.38

Table 4. Summary of bird cultural ecosystem service (CES) hotspots across time periods. Locations were considered hotspots if the predicted bird CES value was above the mean observed for that indicator.

Time Period	Percent of landscape classified as hotspot					
	Total bird species richness	Migratory species richness	Resident species richness	Synanthrope species richness	‘Infrequent’ species richness	Hotspot of 4 or 5 CES
Early spring	34%	66%	37%	29%	71%	9%
Late spring	34%	78%	26%	26%	70%	7%
Summer	32%	64%	27%	27%	45%	2%

Table 5. Overlap of projected bird cultural ecosystem service hotspots with hotspots of total bird species richness during three time periods.

Time Period	Percent overlap with total species richness hotspots			
	Migratory species richness	Resident species richness	Synanthrope species richness	‘Infrequent’ species richness
Early spring	10%	73%	82%	13%
Late spring	15%	68%	68%	7%
Summer	8%	62%	58%	2%

Table 6. Percent of eBird observations that overlap with projected bird cultural ecosystem service (CES) supply hotspots during early spring, late spring, and summer. All eBird observations from April to August for the years 2009 – 2014 were included (n = 4347).

	Bird CES hotspot				
Time Period	Total bird species richness	Migratory species richness	Resident species richness	Synanthrope species richness	‘Infrequent' species richness
Early spring (n = 1888)	47%	53%	69%	50%	45%
Late spring (n = 990)	45%	59%	54%	47%	50%
Summer (n = 1469)	51%	23%	64%	63%	5%

Figure Captions

Figure 1. Land use/land cover in the French Broad River Basin and the location of the bird point count study sites. Sites were located on both public and private property and were surveyed during April – August, 2014.

Figure 2. Maps of projected bird CES supply and hotpots of multiple CES during early spring, late spring, and summer. High/low values differed for each bird CES indicator: all species (range: 2 – 13 species), migratory species (0 – 5 species), resident species (0 – 11 species), synanthrope species (0 – 11 species), and ‘infrequent’ species (0 – 5 species).

Figure 3. Distribution of publicly accessible areas classified by three levels of access (high, moderate, and limited) within the study area.

Figure 4. Percent of landscape with high supply of each bird CES and located within publicly accessible land during early spring, late spring, and summer.

Figure 5. Locations of eBird observations during early spring, late spring, and summer. All observations during these time periods in the years 2009 to 2014 are included.

Figure 1.

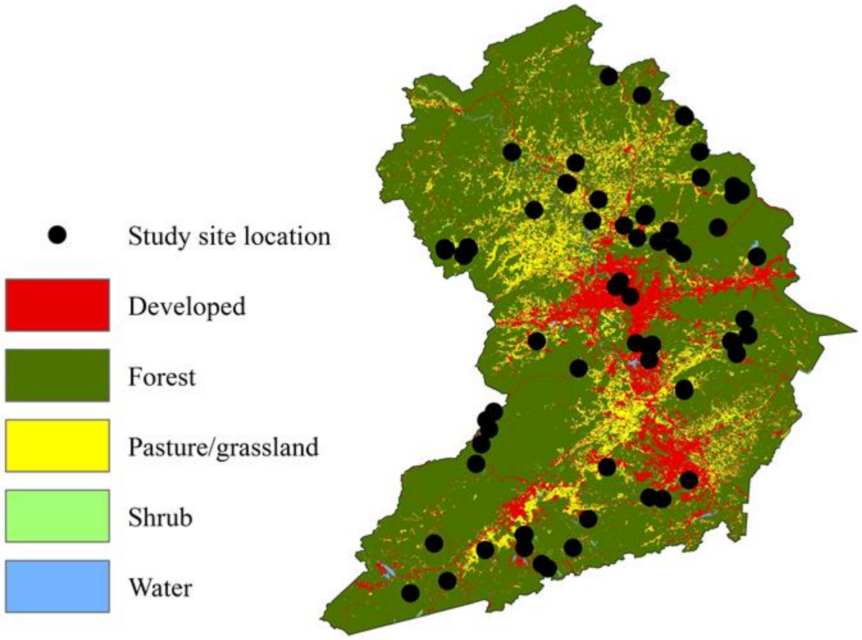
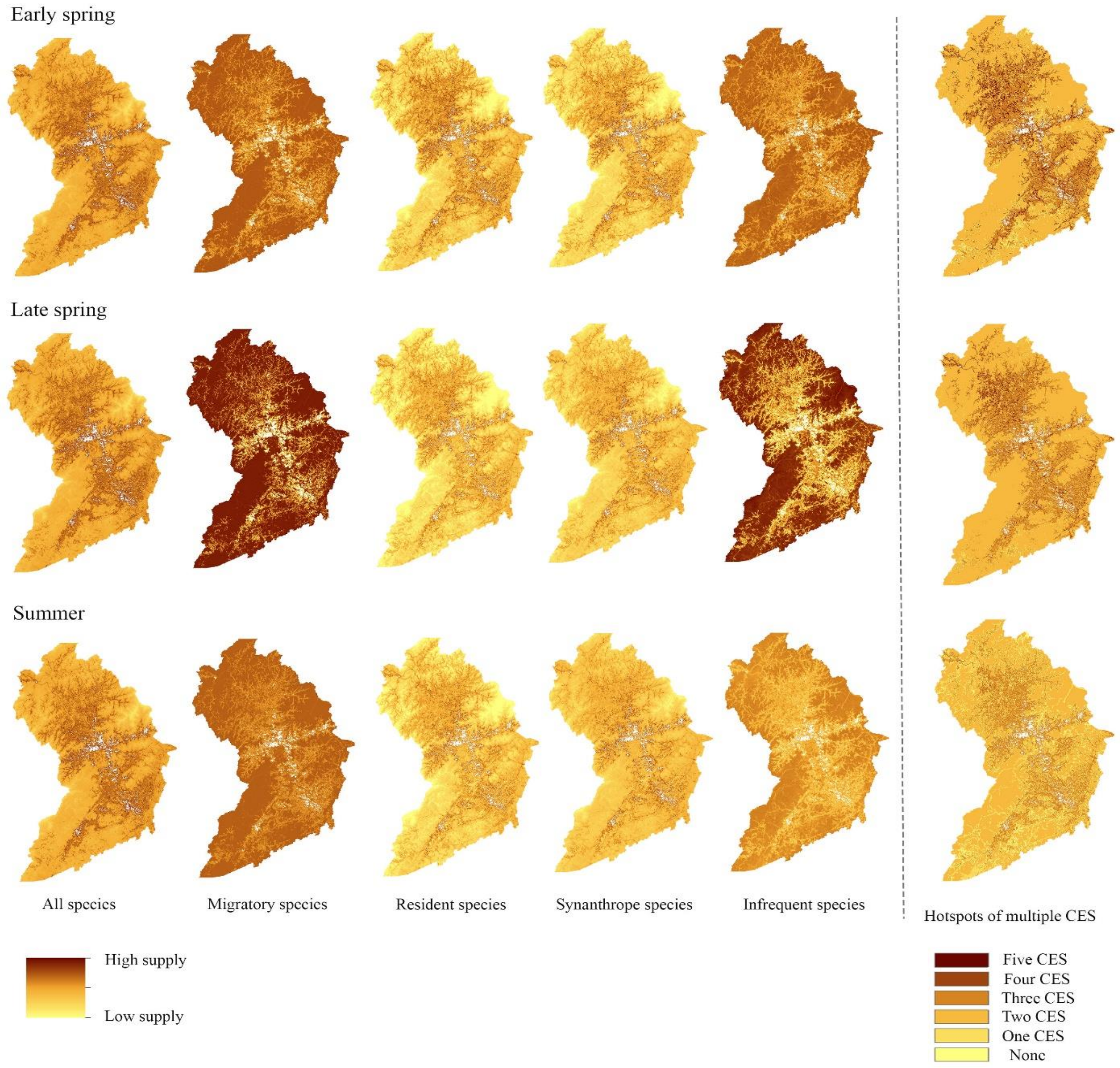

Study site location
Developed
Forest
Pasture/grassland
Shrub
Water

Figure 2


Early spring
Late spring
Summer
All species
Migratory species
Resident species
Synanthrope species
Infrequent species
Hotspots of multiple CES
High supply
Low supply
Five CES
Four CES
Three CES
Two CES
One CES
None

.

Figure 3.

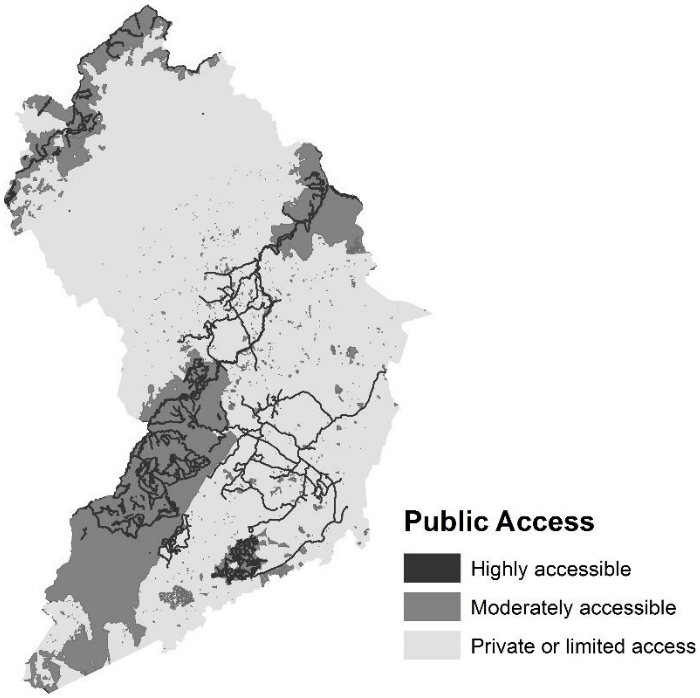

Public Access
Highly accessible
Moderately accessible
Private or limited access

Figure 4.

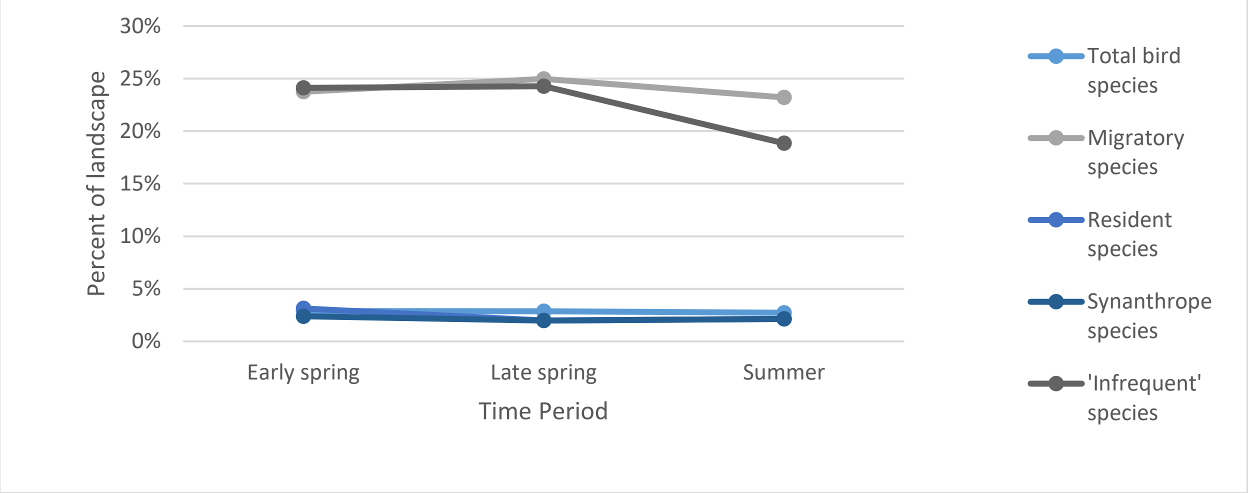
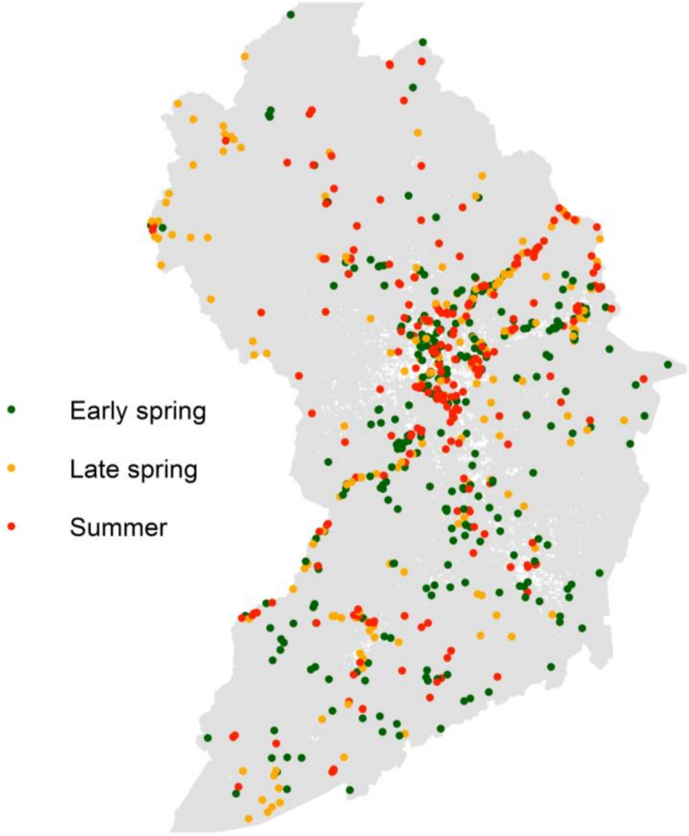

30%
25%
20%
15%
10%
5%
0%
Percent of landscape
Early spring
Late spring
Summer
Time Period
Total bird species
Migratory species
Resident species
Synanthrope species
'Infrequent' species

Figure 5.



Graves et al. Bird community dynamics change the seasonal distribution of a cultural ecosystem service in a montane landscape

Appendix A: Supplemental Materials

Maps of predictor variables

Input layers were created for each predictor variable in order to project landscape floral resources using the *predict* function in the *raster* package for R. All input layers were standardized to z-scores based on the mean and variance of the training dataset (n=56) and referenced to the same projection (Albers Equal Area) and 100-m grid cell. The 100-m grid cell was chosen to correspond with the 100-m National Elevation Dataset digital elevation model (available from the U.S. Geological Survey: https://catalog.data.gov/dataset/100-meter-resolution-elevation-of-the-conterminous-united-states-direct-download). The NED DEM layer was also used to extract the elevation predictor layer.

We created maps of tree cover and vegetation diversity within each 100-m pixel and used a moving window analysis to calculate the landcover diversity (SIDI) within 200 m and local and neighborhood building density for each 100-m pixel. Building footprints were obtained from county government GIS offices and converted to point locations. Local building density (building units per hectare) was quantified using the point-density tool with a 100-m circular moving window in ArcMap 10.4, with the output raster specified as a 100-m grid matching the NED DEM, and points/ha as the output value. Similarly, neighborhood building density was quantified using the point-density tool with a 1-km circular moving window, with the output raster specified as a 100-m grid matching the NED DEM, and points/ha as the output value.

We used 30-m raster data from the 2014 National Crop Data Layer (CDL; USDA NASS 2014) to create maps of landcover diversity within 200 m of each 100-m grid cell using a moving window analysis in GIS. We first reclassified the CDL to six land-cover categories (grassland/herb, shrubland, cropland, forest, developed and other/water). Land-cover diversity was calculated as the Simpson's diversity index ($SIDI = 1 - \sum_{i=1}^{m} {P_i}^2$) using six land-cover categories (grassland/herb, shrubland, cropland, forest, developed and other/water) within 200 m of each cell center.

Forest canopy cover maps were created using the proportion of LIDAR returns within each 100-m grid cell within the subcanopy or canopy layers (i.e., >2.0 m above ground). Discrete-return LIDAR data were collected in 2005 (NCDEM 2006) for the entirety of the study area during winter. Vegetation height was measured from LIDAR first returns by subtracting the elevation of a bare-earth digital terrain model, derived from the same LIDAR data set, from the elevation of each return. Only first returns were used, and we excluded returns within digitized building footprints. Vegetation structural diversity was calculated using the Shannon Evenness index ($E_H = \frac{-\sum_{i=1}^{S} p_i \ln p_i}{\ln S}$) using the proportion ($p_i$) of LIDAR returns in each of four vegetation strata (i.e., herb, shrub, subcanopy, and canopy layers) for each 100-m grid cell.

Annual vegetation productivity was extracted from a smoothed and gap-filled MODIS Normalized Difference Vegetation Index (NDVI) dataset (Spruce et al. 2016). We calculated the 10-year (2004 – 2014) median of annual vegetation productivity for each study site and subsampled to a 100-m resolution.

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Table A2. List of species observed and their classification at 56 sites during April – August 2014 in the French Broad River Basin, NC. Migratory status was determined using Rodewald 2015; synanthrope status follows Johnston 2001; and infrequent species were classified as the least frequently recorded species for the French Broad River Basin in the eBird dataset (Sullivan et al. 2009).

Common Name	**Code**	**Species name**	**Migratory status**	**Synanthrope status**	**Listed in NC Wildlife Action Plan**	**Infreq-uent species**
Acadian flycatcher	ACFL	Empidonax virescens	neotropical	NA	0	1
American crow	AMCR	Corvus brachyrhynchos	resident	Tangential	0	0
American goldfinch	AMGO	Spinus tristis	resident	NA	0	0
American kestrel	AMKE	Falco sparverius	short-distance	Tangential	1	1
American redstart	AMRE	Setophaga ruticilla	neotropical	Tangential	0	0
American robin	AMRO	Turdus migratorius	resident	Casual	0	0
Baltimore oriole	BAOR	Icterus galbula	neotropical	NA	0	1
Barn swallow	BARS	Hirundo rustica	neotropical	Tangential	0	0
Black-and-white warbler	BAWW	Mniotilta varia	neotropical	NA	0	0
Bay-breasted warbler	BBWA	Setophaga castanea	neotropical	NA	0	1
Blue-gray gnatcatcher	BGGN	Polioptila caerulea	neotropical	NA	0	0
Brown-headed cowbird	BHCO	Molothrus ater	short-distance	Tangential	0	0
Blue-headed vireo	BHVI	Vireo solitarius	short-distance	NA	0	0
Blackburnian warbler	BLBW	Setophaga fusca	neotropical	NA	0	1
Blue grosbeak	BLGR	Passerina caerulea	neotropical	NA	0	1
Blue jay	BLJA	Cyanocitta cristata	resident	Tangential	0	0
Blackpoll warbler	BLPW	Setophaga striata	neotropical	NA	0	1
Brown thrasher	BRTH	Toxostoma rufum	short-distance	NA	0	0

Black-throated blue warbler	BTBW	Setophaga caerulescens	neotropical	NA	0	0
Black-throated green warbler	BTNW	Setophaga virens	neotropical	NA	1	1
Broad-winged hawk	BWHA	Buteo platypterus	neotropical	NA	0	1
Carolina chickadee	CACH	Poecile carolinensis	resident	Tangential	0	0
Carolina wren	CARW	Thryothorus ludovicianus	resident	NA	0	0
Canada warbler	CAWA	Cardellina canadensis	neotropical	NA	1	1
Cedar waxwing	CEDW	Bombycilla cedrorum	resident	NA	0	0
Cerulean warbler	CERW	Setophaga cerulea	neotropical	NA	1	1
Chipping sparrow	CHSP	Spizella passerina	neotropical	Tangential	0	0
Chimney swift	CHSW	Chaetura pelagica	neotropical	Full	1	1
Cape May warbler	CMWA	Setophaga tigrina	neotropical	NA	0	1
Common grackle	COGR	Quiscalus quiscula	short distance	Tangential	0	0
Cooper's hawk	COHA	Accipiter cooperii	resident	NA	1	1
Common raven	CORA	Corvus corax	resident	Tangential	0	1
Common yellowthroat	COYE	Geothlypis trichas	short-distance	Tangential	0	1
Chestnut-sided warbler	CSWA	Setophaga pensylvanica	neotropical	NA	0	0
Dark-eyed junco	DEJU	Junco hyemalis	resident	Tangential	0	0
Downy woodpecker	DOWO	Picoides pubescens	resident	Tangential	0	0
Eastern bluebird	EABL	Sialia sialis	short-distance	Tangential	0	0
Eastern kingbird	EAKI	Tyrannus	neotropical	NA	1	1
Eastern meadowlark	EAME	Sturnella magna	resident	Tangential	1	1
Eastern phoebe	EAPH	Sayornis phoebe	resident	NA	0	0
Eastern screech-owl	EASO	Megascops asio	resident	NA	0	1
Eastern wood-pewee	EAWP	Contopus virens	neotropical	NA	0	0
European starling	EUST	Sturnus vulgaris	resident	Full	0	0
Field sparrow	FISP	Spizella pusilla	short-distance	NA	1	1
Great crested flycatcher	GCFL	Myiarchus crinitus	neotropical	NA	0	1

Golden-crowned kinglet	GCKI	Regulus satrapa	short-distance	NA	0	0
Gray catbird	GRCA	Dumetella carolinensis	neotropical	Tangential	0	0
Hairy woodpecker	HAWO	Picoides villosus	resident	Tangential	1	1
Hermit thrush	HETH	Catharus guttatus	short-distance	NA	0	1
House finch	HOFI	Haemorhous mexicanus	resident	NA	0	0
Hooded warbler	HOWA	Setophaga citrina	neotropical	NA	1	1
House wren	HOWR	Troglodytes aedon	neotropical	Tangential	0	1
Indigo bunting	INBU	Passerina cyanea	neotropical	NA	0	0
Kentucky warbler	KEWA	Geothlypis formosa	neotropical	NA	1	1
Louisiana waterthrush	LOWA	Parkesia motacilla	neotropical	NA	0	1
Mourning dove	MODO	Zenaida macroura	resident	Tangential	0	0
Northern bobwhite	NOBO	Colinus virginianus	resident	Casual	0	1
Northern cardinal	NOCA	Cardinalis	resident	Tangential	0	0
Northern flicker	NOFL	Colaptes auratus	short-distance	Tangential	0	0
Northern mockingbird	NOMO	Mimus polyglottos	resident	Tangential	0	0
Northern parula	NOPA	Setophaga americana	neotropical	NA	0	0
Northern pintail	NOPI	Anas acuta	short-distance	NA	0	1
Northern rough-winged swallow	NRWS	Stelgidopteryx serripennis	neotropical	Tangential	0	1
Ovenbird	OVEN	Seiurus aurocapilla	neotropical	NA	0	1
Palm warbler	PAWA	Setophaga palmarum	short-distance	NA	0	1
Pine warbler	PIWA	Setophaga pinus	short-distance	NA	0	1
Pileated woodpecker	PIWO	Dryocopus pileatus	resident	NA	0	0
Rose-breasted grosbeak	RBGR	Pheucticus ludovicianus	neotropical	NA	1	1
Red-breasted nuthatch	RBNU	Sitta canadensis	resident	Tangential	0	1
Red-bellied woodpecker	RBWO	Melanerpes carolinus	resident	Tangential	0	0
Ruby-crowned kinglet	RCKI	Regulus calendula	short-distance	Tangential	0	1
Red-eyed vireo	REVI	Vireo olivaceus	neotropical	Tangential	0	0

Red-shouldered hawk	RSHA	Buteo lineatus	short-distance	NA	0	0
Rufous-sided towhee	RSTO	Pipilo maculatus/erythr	short-distance	Tangential	0	0
Red-tailed hawk	RTHA	Buteo jamaicensis	resident	Tangential	0	0
Ruby-throated hummingbird	RTHU	Archilochus colubris	neotropical	Tangential	0	0
Ruffed grouse	RUGR	Bonasa umbellus	resident	Casual	0	1
Red-winged blackbird	RWBL	Agelaius phoeniceus	short-distance	Tangential	0	0
Scarlet tanager	SCTA	Piranga olivacea	neotropical	NA	0	0
Song sparrow	SOSP	Melospiza melodia	resident	Tangential	0	0
Swainson's warbler	SWWA	Limnothlypis swainsonii	short-distance	NA	1	1
Tree swallow	TRES	Tachycineta bicolor	resident	Tangential	0	0
Tufted titmouse	TUTI	Baeolophus bicolor	resident	Tangential	0	0
Veery	VEER	Catharus fuscescens	neotropical	NA	0	1
White-breasted nuthatch	WBNU	Sitta carolinensis	resident	Tangential	0	0
White-eyed vireo	WEVI	Vireo griseus	short-distance	NA	0	1
Worm-eating warbler	WEWA	Helmitheros vermivorum	neotropical	NA	1	1
Wild turkey	WITU	Meleagris gallopavo	resident	Casual	0	0
Winter wren	WIWR	Aix sponsa	short-distance	Casual	0	0
Wood thrush	WOTH	Hylocichla mustelina	neotropical	NA	1	1
White-throated sparrow	WTSP	Zonotrichia albicollis	short-distance	Tangential	0	0
Yellow-billed cuckoo	YBCU	Coccyzus americanus	neotropical	Tangential	0	1
Yellow-bellied sapsucker	YBSA	Sphyrapicus varius	short-distance	NA	1	1
Yellow-rumped warbler	YRWA	Setophaga coronata	neotropical	NA	0	0
Yellow-throated vireo	YTVI	Vireo flavifrons	neotropical	NA	0	1
Yellow-throated warbler	YTWA	Setophaga dominica	neotropical	NA	0	1

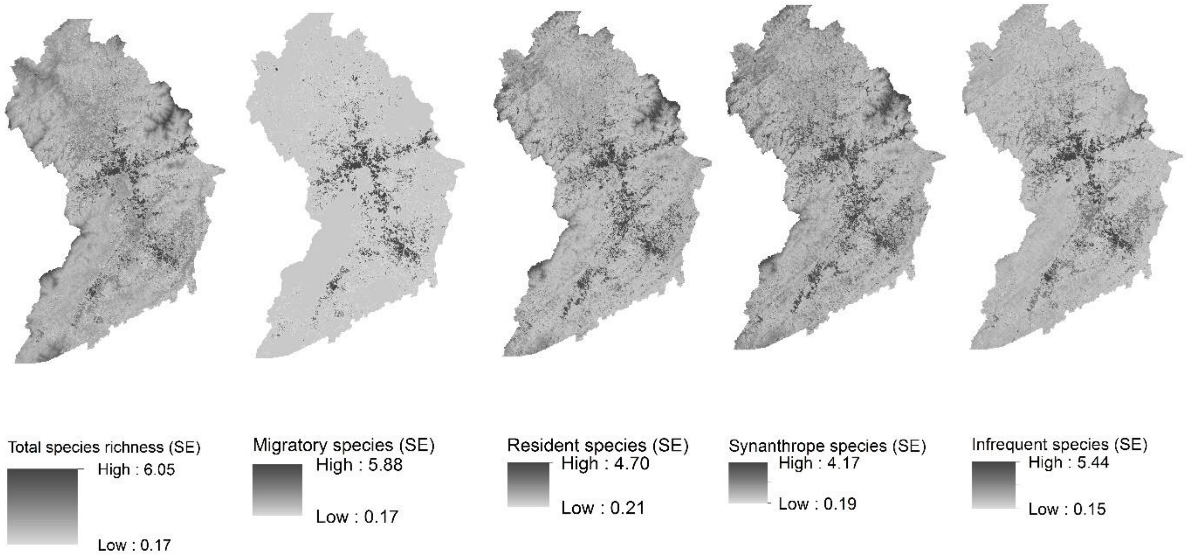
Table A2. Temporal consistency of bird CES hotspots.

	Percent of landscape in each category				
Temporal consistency category	All bird species richness	Migratory species richness	Resident species richness	Synanthrope species richness	'Infrequent' species richness
Never classified as hotspot	66%	21%	63%	67%	23%
Hotspot during one time period	<1%	12%	8%	8%	12%
Hotspot during two time periods	2%	3%	3%	3%	20%
Always classified as hotspot	32%	63%	25%	23%	45%

Table A3. Overlap of projected hotspots of bird CES supply and public accessibility, measured as the percent of the bird CES hotspot contained within public accessibility categories, during three time periods from April to August.

		Percent of hotspot area		
Bird CES indicator	Time period	Highly accessible	Moderately accessible	Private or limited access
All species richness	Early spring	4%	5%	91%
	Late spring	4%	5%	91%
	Summer	4%	5%	91%
Migratory species richness	Early spring	6%	29%	65%
	Late spring	5%	26%	69%
	Summer	5%	31%	64%
Resident species richness	Early spring	4%	5%	91%
	Late spring	3%	3%	94%
	Summer	4%	4%	92%
Synanthrope species richness	Early spring	4%	4%	91%
	Late spring	4%	4%	92%
	Summer	4%	5%	91%
Rare species richness	Early spring	5%	28%	67%
	Late spring	5%	29%	66%
	Summer	5%	36%	59%

Figure A1. Maps of standard error of projected bird CES for total, migratory, resident, synanthrope, and infrequent species richness (left to right in each row). Standard error did not change across time periods.



Dissertation Conclusion

Overall, this research provides insights into the spatial dynamics of ecosystem services in the Southern Appalachian Mountains, which can be used to inform the management of multi-functional landscapes in this amenity-based region. Furthermore, this research contributes to increased understanding about the effects of biodiversity and climate on spatial dynamics of ecosystem services and advances the inclusion of stakeholders in ecosystem service research. Understanding the dynamics of ecosystem service supply and demand, as well as better incorporating biodiversity into ecosystem service models, are key priorities in ecosystem service research and management agendas (Bennett et al. 2015, Braat and de Groot 2012, Daniel et al. 2012). Several key findings are summarized below:

1. Ecosystem service supply is not likely to remain static under future conditions, and spatial shifts in ecosystem service provision may lead to increased land-use competition and tradeoffs among ecosystem services in the future. Despite concern over the future of ecosystem services and human well-being (MA 2005, Steffen et al. 2015), few studies have considered future scenarios in the assessment of ecosystem services. Results from Chapter 1 demonstrate that effects of climate change on crop productivity are likely to shift the locations with the highest supply of ecosystem services (i.e., hotspots) and that these changes in hotspot distribution will lead to increased land-use competition between bioenergy provision and continued exurban/suburban development. Despite overall increases in projected bioenergy productivity by 2100, landscape production of this provision service would be substantially decreased if development patterns continue as predicted. These findings suggest that future climate conditions will alter current patterns of ecosystem service supply, and decision-makers should consider both current and future ecosystem service distributions when evaluating landscape management goals.

2. The spatial dynamics of biodiversity-based cultural ecosystem services vary over time, depending on the underlying biotic community, and these changes lead to differential public access to cultural ecosystem services. Few contributions in the ecosystem services literature fully integrate the ecology of organisms with the spatial and temporal dynamics of ecosystem service supply. Using empirical data on wildflower and bird communities, this dissertation (Chapters 2 and 4) showed that seasonal variation biotic communities results in variable ecosystem service hotspot locations over time and leads to changes in the proportion of cultural ecosystem service hotspots accessible to the public. Models that incorporate seasonal dynamics revealed changing relationships between landscape gradients, biodiversity and ecosystem services, and identified important locations for sustaining biodiversity-based cultural ecosystem services otherwise obscured by static models.

3. Species richness, although commonly used as an indicator of biodiversity-based cultural ecosystem services, may not adequately reflect these services as perceived by beneficiaries. Results from the discrete-choice experiment in Chapter 3 showed that species richness was not an important predictor of people’s aesthetic preferences for wildflower communities; instead, other aspects of the biotic community (i.e., wildflower abundance, number of colors, and evenness) predicted the cultural ecosystem service value of wildflower communities. When total species richness was used as an indicator of the birdwatching cultural ecosystem service provided by bird communities, projected hotspots did not overlap with hotspots for particular bird groups that may be preferred by birdwatchers (i.e., migratory or infrequently seen birds; Chapter 4). Together, these results suggest that successful management of cultural ecosystem services requires understanding stakeholders’ preferences and basing conservation priorities on species richness alone may not be adequate to sustain cultural ecosystem service benefits.

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