

Bioenergy production and forest landscape change in the southeastern United States

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Abstract

Production of woody biomass for bioenergy, whether wood pellets or liquid biofuels, has the potential to cause substantial landscape change and concomitant effects on forest ecosystems, but the landscape effects of alternative production scenarios have not been fully assessed. We simulated landscape change from 2010 to 2050 under five scenarios of woody biomass production for wood pellets and liquid biofuels in North Carolina, in the southeastern United States, a region that is a substantial producer of wood biomass for bioenergy and contains high biodiversity. Modeled scenarios varied biomass feedstocks, incorporating harvest of 'conventional' forests, which include naturally regenerating as well as planted forests that exist on the landscape even without bioenergy production, as well as purpose-grown woody crops grown on marginal lands. Results reveal trade-offs among scenarios in terms of overall forest area and the characteristics of the remaining forest in 2050. Meeting demand for biomass from conventional forests resulted in more total forest land compared with a baseline, business-as-usual scenario. However, the remaining forest was composed of more intensively managed forest and less of the bottomland hardwood and longleaf pine habitats that support biodiversity. Converting marginal forest to purpose-grown crops reduced forest area, but the remaining forest contained more of the critical habitats for biodiversity. Conversion of marginal agricultural lands to purpose-grown crops resulted in smaller differences from the baseline scenario in terms of forest area and the characteristics of remaining forest habitats. Each scenario affected the dominant type of land-use change in some regions, especially in the coastal plain that harbors high levels of biodiversity. Our results demonstrate the complex landscape effects of alternative bioenergy scenarios, highlight that the regions most likely to be affected by bioenergy production are also critical for biodiversity, and point to the challenges associated with evaluating bioenergy sustainability.

Keywords: biodiversity, bioenergy, biofuels, bottomland hardwood forests, forests, landscape change, longleaf pine, state-and-transition simulation models, timber supply model, wood pellets

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Introduction

Globally, policies and regulations aimed at increased production of woody biomass for bioenergy are becoming more numerous, but the ecological effects of that production have not been evaluated fully. Whether for wood pellets or liquid biofuels, much of the increased biomass production for bioenergy is likely to be from forests and nonfood agricultural crops such as switchgrass (Dale *et al.*, 2010; Goh *et al.*, 2013; Sedjo & Sohngen,

2013). Wood pellets from forest biomass are increasingly used for power generation in Europe and are expected to be a substantial part of the global renewable energy portfolio in the near future (Scarlat *et al.*, 2015). Second-generation cellulosic biofuels could be an important part of meeting the Renewable Fuel Standard set under the Energy Independence and Security Act (EISA) of 2007 in the United States (Energy Independence and Security Act, 2007). While research has shown that woody biomass production has the potential to maintain or increase carbon storage (Miner *et al.*, 2014; Ter-mikaelian *et al.*, 2015; Creutzburg *et al.*, 2016), in order to fully evaluate the sustainability of production, the full range of ecological effects must be considered (Dale *et al.*, 2010; Bosch *et al.*, 2015). In particular, bioenergy production

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could have profound effects on landscapes, ecosystems, and biodiversity, especially in the United States, because it requires more land per unit energy produced than traditional energy sources such as coal and petroleum (McDonald *et al.*, 2009; but see Parish *et al.*, 2013 for a global evaluation).

The production of woody biomass could lead to several types of landscape change, including more intensive forest management, conversion of existing agricultural lands to intensively managed forest, and conversion of marginal, or nonarable, forest and agricultural lands to woody crops (Wear *et al.*, 2010). The full set of effects of these types of changes are complex (Fletcher *et al.*, 2011; Dauber & Bolte, 2014) and are the subject of ongoing debate in the scientific community (e.g., see Dale *et al.*, 2015; and reply by Schlesinger, 2015). The actual landscape ecological effects of land-use change due to woody biomass production for bioenergy will depend on the amount and types of land used for biomass production, the location of that land, and the amounts and types of feedstocks being used (Dale *et al.*, 2011; Pedroli *et al.*, 2013).

Previous studies have shown that a bioenergy market based on woody biomass could lead to an increase in the total amount of forest on the landscape (Lubowski *et al.*, 2008; Wear *et al.*, 2010; Galik & Abt, 2016). An increase in forest land could be positive for forested ecosystems and the ecosystem services they provide, including support of biodiversity, wildlife habitat, and clean water. However, studies that project increased forest land assume that woody biomass to meet bioenergy demand comes from forests, but if woody agricultural crops such as switchgrass or sweet sorghum are planted to meet some biomass demand, there is potential for widespread land conversion. That land conversion could have concomitant effects on forests and habitats that support biodiversity, depending on which lands are converted to woody crops (Dauber *et al.*, 2010; Wear *et al.*, 2010; Wiens *et al.*, 2011). Furthermore, even if more total forest area is present on the landscape, if a large amount of naturally regenerating forest has been replaced by intensively managed forest, or forests that have altered structural or successional characteristics, the result could be substantial effects on forest ecosystems across landscape and regional extents (Littlefield & Keeton, 2012). Investigating a range of woody biomass production scenarios that take into account local landscape context and a set of realistic levels of demand will be critical to understanding the range of potential landscape effects of bioenergy production (Dale *et al.*, 2011).

Landscape and forest change due to woody biomass production will not occur in a vacuum; biomass production is one anthropogenic driver affecting

ecosystems amidst a backdrop of other change. In the United States, urbanization has been and will likely continue to be a dominant type of landscape change, while demand for agricultural land will also have a substantial effect on land-use change. Both high crop demand and conversion to urban land use could result in losses of forest in some places, including the southeastern United States, along with changes to ecosystems, including threats to biodiversity and reductions in wildlife habitat (Radeloff *et al.*, 2012; Martinuzzi *et al.*, 2013, 2015; Lawler *et al.*, 2014). In the southeastern United States, demand for forest land and conventional forest products like pulp, paper, and sawtimber also determines the rates of conversion between forest, agricultural, and urban land uses (Lubowski *et al.*, 2008; Wear *et al.*, 2013). Incorporating change due to bioenergy production in the context of these other background rates of land-use change, and determining whether there are specific places where bioenergy land-use change is likely to dominate the landscape over other drivers, will be critical for evaluating the sustainability of bioenergy production.

Our research examined the effects of potential alternative scenarios of bioenergy production for wood pellets and liquid biofuels on future land use and vegetation in the southeastern United States. The area of forest in the region was relatively stable through much of the 20th century because the amount of forest converted to urban land uses over time was offset by reforestation of agricultural land (Wear, 2002). In recent years, the reforestation of agricultural land in the region has lessened, and the net result has been the loss of forest land over time (Wear *et al.*, 2013). The region contains globally significant forest ecosystems and high levels of biodiversity, especially in longleaf pine and bottomland hardwood forests, and has recently been designated a global biodiversity hotspot (Peet & Allard, 1993; Mitchell *et al.*, 2009; Noss *et al.*, 2015). At the same time, the region is likely to be a substantial source of woody biomass for the global wood pellet as well as liquid biofuels, which could contribute to greater losses of forest land (Goh *et al.*, 2013). Yet, to date, studies of potential future landscape change under a range of biomass demand and feedstock scenarios in the region have been limited (but see Evans *et al.*, 2013).

We used state-and-transition simulation models, informed by timber supply modeling and published literature on biomass-to-bioenergy conversion, to project landscape dynamics across North Carolina (NC) through 2050. Projections were made under five bioenergy scenarios that incorporated the local mix of land uses and relevant feedstocks including forests and purpose-grown woody agricultural crops, compared to a

business-as-usual scenario without bioenergy production. The bioenergy scenarios we modeled aim to meet real-world, policy-relevant demand for wood pellets and liquid biofuels. Our work addressed these questions regarding landscape change, and especially forest change:

- What are the likely future effects of plausible woody biomass production scenarios on the mix of forest, agricultural and urban land uses, as well as the total areas, successional stages, and vegetation structures of forests?
- How will these scenarios affect forest habitats that are important for biodiversity?
- Under these scenarios, are there regions where bioenergy production alters the dominant type of land-use change?

Comparisons of modeled outcomes from the bioenergy scenarios allow insights into the range of future landscape changes expected under alternative biomass production approaches, and are a critical step in assessing the full set of ecological effects from bioenergy production.

Materials and methods

Study area: North Carolina's landscape and likely bioenergy feedstocks

North Carolina spans four Environmental Protection Agency (EPA) Level III ecoregions: the Middle Atlantic Coastal Plain, the Southeastern Plains, the Piedmont, and the Blue Ridge (Fig. 2a; EPA 2004). Forest and woodland ecosystems occur across the state. Woodland ecosystems differ from forests in that the former contains lower tree cover; however, hereafter when we refer to forests and woodlands in aggregate, we use the term 'forests'. The major forests in the Middle Atlantic Coastal Plain and Southeastern Plains are longleaf pine forests and bottomland (river and stream floodplain) hardwood forests, while oak and oak-pine forests dominate in the Piedmont and Blue Ridge. Planted pine forests occur across 8% of the state and the majority of those forests are in the Middle Atlantic Coastal Plain and Southeastern Plains (Costanza *et al.*, 2015). The Piedmont contains the majority (52%) of the state's urban land, and that region is projected to experience the highest rates of future urbanization (Terando *et al.*, 2014). The Middle Atlantic Coastal Plain and the Southeastern Plains occur in a global biodiversity hotspot (Noss *et al.*, 2015), and the longleaf pine and bottomland hardwood ecosystems that occur in those regions contain particularly high levels of biodiversity (Peet & Allard, 1993; Mitchell *et al.*, 2009).

The state of NC has the potential for substantial forest-based biomass demand for bioenergy. Existing or announced wood pellet plants in NC could consume 3.45 million green tonnes (3.8 million green short tons) of forest biomass annually (Forisk Consulting LLC, 2014). In NC, like the rest of the southeastern

United States, biomass for bioenergy will likely be produced from harvesting or thinning of naturally regenerating or planted forests, all of which have been used in the past for other forest products (hereafter referred to collectively as 'conventional' forests). These conventional forests can supply biomass for biofuels or wood pellets. In addition to wood pellets, until recent changes in state policy, the state had a target of 10% of liquid transportation fuels from locally produced biofuels (Burke *et al.*, 2007). Biomass for biofuels could come from so-called purpose-grown crops, including cellulosic feedstocks such as sweet sorghum (*Sorghum bicolor* cultivars) and switchgrass (*Panicum virgatum*), as well as short-rotation trees grown at high densities (Dale *et al.*, 2010).

Methods overview

We simulated the spatial landscape dynamics resulting from biomass production for bioenergy across North Carolina from 2010 through 2050 using the following approach (Fig. 1). First, we developed five scenarios with alternative feedstocks and alternative types of lands converted to those feedstocks. Second, for each scenario, we used output from a timber supply model to determine annual amounts of forest harvest and change to and from broad forest types, urban, and agriculture. We used existing information on conversion of woody biomass to liquid biofuels to determine the amount of land needed for purpose-grown crops. Third, we created spatial data layers to represent initial conditions in 2010, and to set geographic constraints on biomass production and urbanization. Fourth, we input the aspatial projections of forest management and land-use change along with the spatial data into a state-and-transition simulation model (STSM) to produce spatially explicit landscape projections under the five scenarios, as well as a sixth, business-as-usual scenario. This work builds on our previous aspatial simulations that compared the business-as-usual scenario with two scenarios of biomass production from forests only (Costanza *et al.*, 2015).

Scenarios of woody biomass production

Each of the five bioenergy scenarios we developed met the potential wood pellet demand or the state's recent 10% biofuels target, or both (Costanza *et al.*, 2015). The scenarios varied in the feedstock types being used (conventional forests or purpose-grown crops, or both), and the types of land being converted to purpose-grown crops, if any (Table 1). As potential purpose-grown feedstocks, we included sweet sorghum, switchgrass, and short-rotation loblolly pine forests because those have potential to be grown in NC and have been shown to be economically feasible (Dale *et al.*, 2010; Gonzalez *et al.*, 2012; Treasure *et al.*, 2014). In addition to the five bioenergy scenarios, we also included a business-as-usual scenario that did not include bioenergy production (hereafter, 'Baseline').

The first bioenergy scenario incorporated woody biomass production from increased management of conventional forests only. This is hereafter the 'Conventional' scenario. Under this scenario, the demand for wood pellets is higher than for biofuels, and as a result, wood pellets are the primary bioenergy

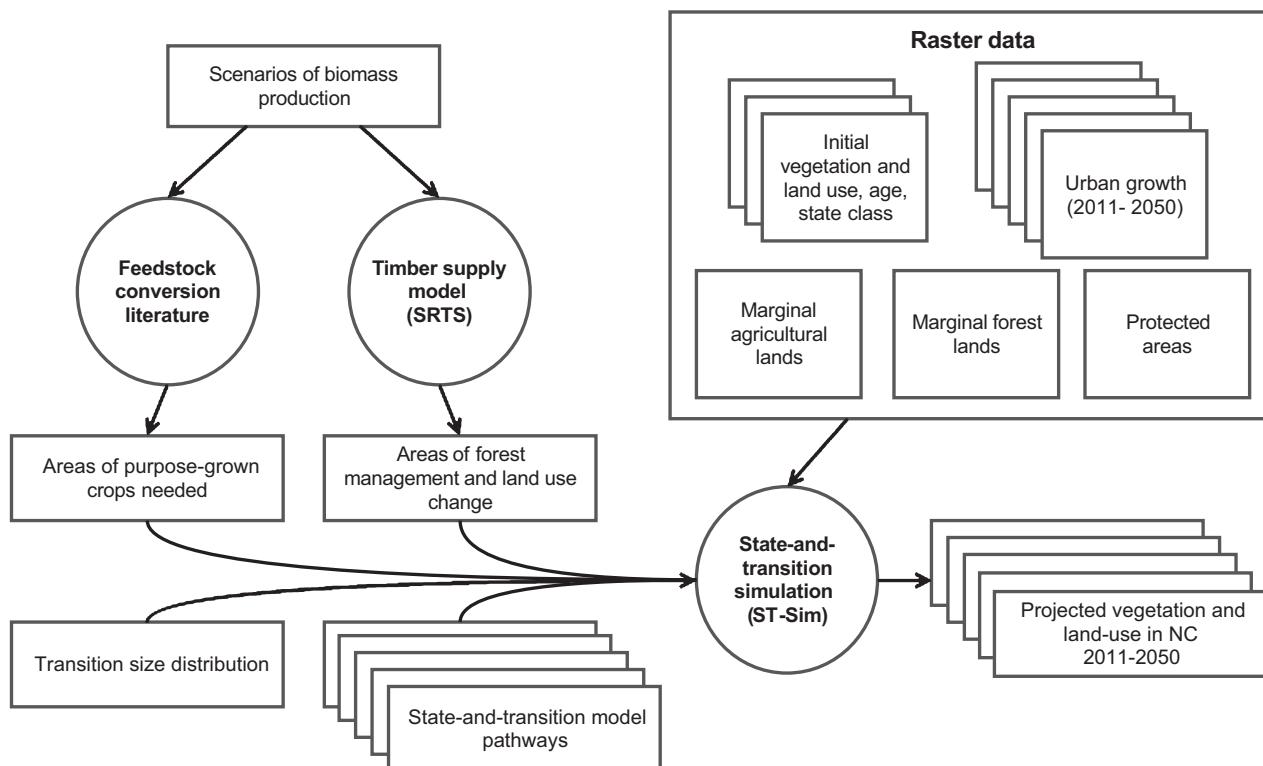


Fig. 1 Conceptual overview of model flow. Narrative scenarios about biomass production were translated into annual areas of land-use change and management via information in the feedstock conversion literature and the Sub-Regional Timber Supply model. Raster data sets were used to initialize the landscape, constrain purpose-grown crops to marginal agricultural or forest lands, direct urban growth, and exclude protected areas from biomass harvest. Raster data and areas of land-use change and management, along with transition size distributions, state-and-transition model pathways, were input into ST-Sim to produce maps of landscape change.

product being produced. In this scenario, we assumed that 3.63 million green tonnes (4.0 million green short tons) of wood-based bioenergy would be produced annually, which would meet 100% of wood pellet demand (see Costanza *et al.*, 2015 Supplementary Material for the conversion of conventional forest biomass to ethanol). Importantly, other forest products would continue to be produced under this scenario, but at a reduced level.

The second and third scenarios ('Conventional-Ag' and 'Conventional-Ag-Forest') assumed high demand for both wood pellets and liquid biofuels. These scenarios included the same level of demand for wood pellets as in the Conventional scenario, and thus the same amount of biomass production (3.63 million green tonnes), but also incorporated demand for liquid biofuels produced by purpose-grown crops. In each of these scenarios, 425 000 ha (1.05 million acres) of purpose-grown crops would be planted. One of these two scenarios, Conventional-Ag, assumed that purpose-grown crops would be planted on marginal agricultural lands only. The second, Conventional-Ag-Forest, assumed that in addition to marginal agriculture, marginal forest lands would also be converted to purpose-grown crops. Here, we define marginal lands as those that are poorly suited to traditional crops because of inherent edaphic or climate limitations, or because they are located in areas

vulnerable to erosion. These scenarios would meet 100% of the wood pellet demand as well as 84–118% of the liquid biofuels target depending on the liquid conversion pathway (see Table S1 for biomass-to-ethanol conversion and regional marginal land conversion areas). It is worth noting that here, we assume demand for biofuels would be relatively low, and thus, conventional forests would be used for wood pellets and not for biofuels. If biofuel demand increased substantially in the future, it is possible that both conventional forests and purpose-grown crops could both be used to produce biofuels, which would meet 100–140% of the biofuel target and thus 0% of the wood pellet demand. Regardless, the destination of the woody biomass from conventional forests and purpose-grown crops does not affect our modeled landscape results.

The third and fourth scenarios ('Ag' and 'Ag-Forest') assumed that demand for liquid biofuels would increase, but at the same time, conventional forests would be used to supply pulpwood and would not be used to supply biomass for wood pellets. All biomass for bioenergy would come from purpose-grown crops planted on marginal lands. In these scenarios like the previous two, purpose-grown crops would be planted on either marginal agricultural lands only (Ag scenario), or marginal agricultural and forest lands (Ag-Forest scenario). In these scenarios compared with the previous two, a slightly

Table 1 Overview of five bioenergy scenarios and one business-as-usual, or Baseline, scenario

Scenarios	Assumed bioenergy target(s)	Biomass from conventional forests (mill. green tonnes)	Portion of harvest residues used (%)	Other forest products from conventional forests	Marginal ag converted (ha)	Marginal forest converted (ha)	Portion of biofuels 10% goal met (%)*	Portion of wood pellet demand met (%)
Baseline	N/A	None	N/A	Business-as-usual	0	0	0	0
Conventional	Wood pellets	3.63	40	Reduced	0	0	0	100
Conventional-Ag	Wood pellets, biofuels†	3.63	40	Reduced	425 000	0	84–118	100
Conventional-Ag-Forest	Wood pellets, biofuels†	3.63	40	Reduced	212 500	212 500	84–118	100
Ag	Biofuels	None	N/A	Business-as-usual	504 000	0	100–140	0
Ag-Forest	Biofuels	None	N/A	Business-as-usual	252 000	252 000	100–140	0

*The range of the state's goal met by each scenario depends on liquid fuel conversion pathway. The low end is for a biochemical pathway, and the high end is for a thermochemical pathway. See Table S1 for conversion calculations.

†If all biomass from conventional forests goes to wood pellet production, purpose-grown crops are assumed to go to production of biofuels. If demand for biofuels becomes high in the future, conventional forests and purpose-grown crops could both be used to produce biofuels, in which case 100–140% of the biofuels goal would be met.

greater area of marginal land in NC, 504 000 ha (1.25 million acres), would be converted to the same three purpose-grown crops. These scenarios would meet at least 100% of the state-wide liquid biofuels target.

Landscape dynamics models and state-and-transition pathways

To model landscape dynamics under the six scenarios, we used the spatially explicit *STSM* software *ST-Sim* version 2.3.0 (Apex Resource Management Solutions, 2014; Daniel et al., 2016). In *ST-Sim*, state classes are defined for each vegetation or land-use type based on characteristics such as successional stage and canopy cover. Transitions include ecological succession; disturbances such as wildfire; forest management, including thinning and harvest; and conversion from one land-use or vegetation type to another. Initial conditions define the starting point for the model, and the simulation proceeds from the initial landscape on an annual time step. At each pixel in the landscape at each time step, transitions occur based on rules and probabilities set in aspatial state-and-transition model pathways. Transitions can also have areal targets, which are set by input time series, and spatial constraints, which are set based on input raster data. When a given pixel experiences a transition such as a management event, neighboring pixels may also experience the transition, depending on the state of neighboring pixels and the size distribution rules set in *ST-Sim*. Therefore, we developed four main types of inputs to *ST-Sim*: (1) a set of aspatial state-and-transition model pathways for all vegetation and land-use types in NC, (2) time series of annual areas of land-use change, forest management, and conversion to purpose-grown feedstocks, (3) raster data that describe

initial landscape conditions and direct where biofuel production and urbanization occur, and (4) rules about sizes of transitions. We discuss (1) below and (2), (3), and (4) in subsequent sections.

The aspatial state-and-transition pathways we used for most vegetation types were modified from the models developed for the *LANDFIRE* project (Rollins, 2009; <http://www.landfire.gov>). In those models, state classes are defined for each vegetation type in terms of their successional stage (early, mid-, or late succession), and their vegetation structure (open or closed canopy, or 'all', which is the structure that corresponds to most early-successional stages). The *LANDFIRE* models describe successional and disturbance dynamics in those systems that were likely present prior to European settlement. We modified this set of models to reflect current conditions and biofuels scenarios by (1) adding new pathways for anthropogenic land uses that were not modeled by *LANDFIRE*, such as urban land, agriculture (includes row crop and pasture), and pine plantations, as well as the three purpose-grown biofuel crops; (2) adding state classes and transitions for conversion to biofuel crops, forest thinning, and harvest; (3) adding transitions among vegetation and land-use types to reflect land-use change, including urbanization and conversion to/from agricultural land, and conversion to/from forest; and (4) reducing wildfire probabilities to reflect contemporary fire suppression. Except for the addition of purpose-grown crops, these modifications are described in Costanza *et al.* (2015), and the pathways are included as Supplementary Material in that publication. For each of the three purpose-grown crops included here, we added pathways with a single state class and transitions to each from any forest or agriculture state class.

Annual areas of land-use change, forest management, and purpose-grown feedstocks

For all scenarios, previous forest economics modeling for NC (Costanza *et al.*, 2015) with the Sub-Regional Timber Supply (SRTS) model (Abt *et al.*, 2009) was used to generate time series of forest harvest and thinning, as well as conversion among forest and land-use types except for purpose-grown crops. The SRTS model combines economic resource allocation with biological growth to link timber markets (price and harvest for a range of timber products) with forest and land-use dynamics for groups of counties. The model simulates the annual impact of exogenous demand scenarios on the areas of five broad forest types in five-year age classes that are harvested or thinned, along with the total areas of forest types and the total areas of other land uses. The broad forest types in SRTS are lowland hardwood, mixed pine–hardwood, natural pine, planted pine, and upland hardwood. Each broad type except planted pine is naturally regenerating and all correspond to one or more vegetation types for which we had developed state-and-transition pathways.

The SRTS model was run in four subregions of NC for 2011–2050 at annual time steps under two levels of exogenous forest biomass demand (see Costanza *et al.*, 2015 for subregions). The first level of demand simulated in SRTS assumed that forest-based biomass production continues according to past trends, and was used in the Baseline, Ag, and Ag-Forest scenarios. The second, used in the Conventional, Conventional-Ag, and Conventional-Ag-Forest scenarios, included 3.63 million green tonnes of biomass from conventional forests for bioenergy production and assumed that 40% of forest residues were harvested for biomass. In that case, biomass demand was increased in SRTS starting in 2015 until the target demand was reached in 2019. The SRTS simulations projected slightly greater annual areas of thinning and harvest when biomass for bioenergy came from conventional forests, versus the scenarios without conventional forest biomass (Costanza *et al.*, 2015). Much of the increased thinning came from planted pine forests, while the majority of the increased harvest came from natural pine forest types.

For the four biomass scenarios that included biomass from purpose-grown crops, we developed annual time series of marginal land areas converted to purpose-grown crops. We assumed that the area converted to those crops would increase 20% annually starting in 2015 and reach 100% of the total area needed under each scenario by 2019, after which there would be no further conversion to or from purpose-grown crops. For scenarios that included the conversion of both marginal forest and agriculture, we assumed that equal amounts of each would be converted. In all cases, we assumed that equal proportions of the three purpose-grown crops (switchgrass, sweet sorghum, or short-rotation loblolly pine plantation) would be planted across the state. We assumed that each subregion's contribution to the statewide total marginal land converted was proportional to the relative occurrence of marginal lands in that subregion. We recognize that many of our assumptions are likely oversimplifications and we return to them in the Discussion.

Importantly, for scenarios in which marginal forest lands were converted, we assumed that vegetation types

corresponding to natural pine, mixed pine–hardwood, and hardwood upland forest were twice as likely to be converted as lowland hardwood forests, and four times as likely as planted pine. Hardwood forests were less likely to be converted because their hydric soils prevent drainage and make planting of agricultural crops difficult. Pine plantations were least likely to be converted because, on the whole, their owners have invested in timberland for economic gains and many are not likely to change management practices in response to a novel market (i.e., bioenergy; Dorning *et al.*, 2015).

Spatial landscape inputs

Spatial inputs to ST-Sim included raster data sets to describe initial landscape conditions, locate biomass production and urban growth, and define rules for the sizes of all transitions. All raster inputs had a spatial resolution of 60 m (0.36 ha per pixel). Previous work found that resolution was appropriate for modeling urbanization in the region (Terando *et al.*, 2014). Other land-use changes and management actions such as conversion to purpose-grown crops or forest thinning likely occur on larger parcels, and spatial aggregation of pixels was accounted for in the transition rules described below.

To define initial conditions, each pixel in the NC was assigned to a state class within a state-and-transition model pathway based on three initial condition rasters: vegetation or land-use type, state class, and age. The initial vegetation and land-use raster was based on recent land cover (Southeast Gap Analysis Project (SEGAP), 2008), updated to reflect urbanization as of 2010 (Terando *et al.*, 2014; see Fig. 2b for example). We applied a spatial smoother to the land cover data by identifying landscape patches in circa 2001 Landsat imagery based on image objects, and assigning the land cover value as to each patch using a majority rule. The state class raster was a combination of canopy cover and successional stage. We used LANDFIRE 2008 succession class (s-class) data (LANDFIRE, 2012) in combination with the 2011 National Land Cover Database (NLCD) canopy cover data (Multi-Resolution Land Characteristics Consortium (MRLC), 2014) to label canopy cover class and successional stage. We assigned ages to pixels within each successional stage to match the distribution of ages in forest types across each SRTS subregion according to data from the USDA Forest Service Forest Inventory and Analysis (FIA) database (USDA Forest Service, 2012a). For more details on assigning ages, and structural and successional stages, see Costanza *et al.* (2015).

Raster layers showing marginal agricultural and forest lands that could be converted to purpose-grown crops were developed based on soil characteristics and land cover types. Lands were first classified as marginal if they were in nonirrigated soil capability classes 3 or 4 according to gridded Soil Survey Geographic Database (Soil Survey Staff, 2013; following Wright & Wimberly, 2013). Those marginal lands were labeled as forest or agricultural based on their land-use type in the 2006 National Land Cover Database (Fry *et al.*, 2011). Marginal agricultural lands included both row crops and pasture. A protected lands raster was used to exclude biomass production and conversion to urban or agricultural land, based on GAP PAD-US data (U.S. Geological Survey National Gap Analysis

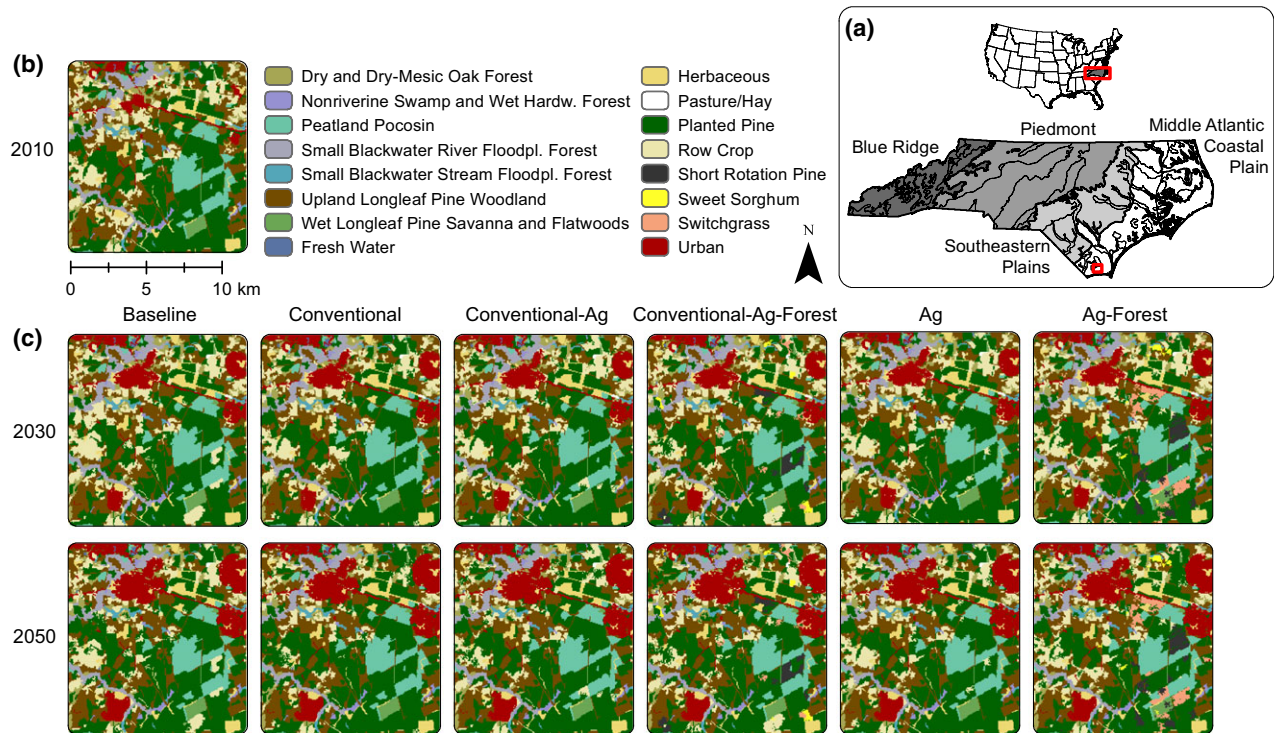


Fig. 2 (a) North Carolina ecoregions used in this analysis (EPA 2013). Thin black lines delineate Level IV ecoregions, which were used to quantify landscape change (Fig. 6); shading and labels indicate Level III ecoregions, which were used to describe overall trends in the text. (b) Initial conditions in 2010 near Wilmington, NC, where longleaf pine woodlands and bottomland hardwood forests exist. (c) Landscape projections under all six scenarios. Scenarios differed in the types and amounts of land used for biomass; thus, projections differ in the amounts and spatial patterns of forest vegetation, agricultural, and purpose-grown crop land. Because urbanization was only minimally affected by biomass production, urban growth patterns through time are nearly identical among scenarios.

Program, 2013). A series of rasters indicating locations of future urbanization from a previous study (Terando *et al.*, 2014) was used to direct future urbanization.

A set of rules for the sizes of all disturbance, management, and land conversion transitions except for urbanization determined the spread of those transitions to adjacent eligible pixels based on the distribution of patch sizes in the initial vegetation and land-use raster. In the rules, no transitions were smaller than 2.0 ha (5 ac), approximately the minimum patch size in the initial conditions. Ninety percent of all transitions were between 2.0 ha and 202.3 ha (500 ac; twice the mean initial patch size). Ten percent of transitions were larger than 202.3 ha.

Landscape simulation

We simulated landscape dynamics under each scenario on an annual time step from 2011 to 2050 across the four regions of NC corresponding to those simulated in SRTS, then mosaicked the regional results into statewide projections. All spatial outputs from ST-Sim had a spatial resolution of 60 m.

In ST-Sim, time series of SRTS outputs were used as annual target areas for land-use changes (transitions among naturally regenerating forest, planted forest, and agriculture), and forest management transitions (harvest and thinning). The SRTS

outputs by major forest type and age class were applied to state classes within one or more state-and-transition models based on the crosswalk between forest types and vegetation types, as well as the ages assigned to each state class in ST-Sim. In most cases, land-use change transitions from SRTS could apply to more than one vegetation or land-use type, and in those cases, transitions were distributed among types based on the proportion of the landscape in a given time step. Vegetation types that are not forested (e.g., Atlantic Coastal Plain Northern Tidal Salt Marsh) or would likely not be managed for biomass (e.g., Atlantic Coastal Plain Central Maritime Forest) were included in simulations, but were not matched to a SRTS forest type and did not contribute to biomass production. We assumed that the demand for purpose-grown crops would be greater than that for any other land use, and thus once converted, land would remain in purpose-grown crops for the rest of the simulation. Simulations did not include places that were sparsely vegetated, or already urbanized in 2010, but we added those areas back to outputs for visualization and data summaries. See Costanza *et al.* (2015) for more information about linking ST-Sim and SRTS.

To determine how the modeled biomass scenarios affected forests, we summarized the total area of forests, the total areas of planted pine and naturally regenerating forests separately, and the areas of forest in each successional stage and structure

class in the ST-Sim output. For each bioenergy scenario, we assessed the differences in each of these values compared with Baseline in 2050. To determine how bioenergy scenarios would affect important ecosystems, we summarized the changes in areas of modeled state classes that harbor high diversity in bottomland hardwood and longleaf pine vegetation types: mid- and late-successional open state classes in the longleaf pine, and the late-successional closed state class in bottomland hardwoods (Mitchell *et al.*, 2009). To examine the local importance of bioenergy production versus other drivers of land-use change, we summarized the predominant type of land-use change between 2010 and 2050 for each scenario within the U.S. Environmental Protection Agency's (EPA) Level IV ecoregions (U.S. EPA 2013; Fig. 2a).

Results

We simulated landscape dynamics in response to five bioenergy scenarios and one Baseline scenario for the period 2011 to 2050 (Fig. 2c). The simulated landscape included 52 vegetation and land-use types (49 initial types, plus three woody biomass crops), across 11 508 462 ha (115 085 km²), or 91% of the land area of

the state. Throughout the simulation period in all scenarios, the total areas of forest and agriculture decreased, while the area of urban land increased (Table 2, Fig. 3). Because we used the same urbanization projections in each of the six scenarios, there was little difference among the scenarios in the area of urban land by 2050. The only differences in urbanization among scenarios were slightly smaller (2–3% smaller) urban land areas by 2050 in the four scenarios that included purpose-grown crops, because those lands were prevented from being urbanized. However, there were larger differences among scenarios in the amount of change by 2050 for agricultural and forest land. The Baseline scenario resulted in the smallest decrease in agricultural land across the simulation period, with a decrease of 24.5% from 2010. The four scenarios that included the conversion of agricultural land to purpose-grown crops had less agricultural land by 2050 than the both the Baseline scenario and the Conventional scenario, which did not include purpose-grown crops. Of the four scenarios that included the conversion of agricultural land, the Conventional-Ag scenario resulted in the

Table 2 Areas of general land-use types, forest types, forest successional stages, and forest vegetation structures in 2010, 2050, and change between 2010 and 2050 for each modeled scenario. Forest types, successional stages, and vegetation structures are alternative ways of parsing the same total forest area. All areas are in hectares

Type	2050						
	2010	Baseline	Conventional	Conventional-Ag	Conventional-Ag-forest	Ag	Ag-forest
General type							
Agriculture	3 147 665	2 375 242	2 229 480	1 926 323	2 033 758	2 013 968	2 145 443
Barren	16 479	16 479	16 479	16 479	16 479	16 479	16 479
Forest	7 728 902	7 112 180	7 257 950	7 261 268	7 066 638	7 119 153	6 890 989
Grass/shrubland	272 285	271 864	271 864	271 864	271 487	271 864	271 864
Purpose-grown crop	0	0	0	343 980	427 278	406 758	503 248
Urban	1 418 669	2 809 107	2 809 100	2 764 958	2 763 025	2 756 650	2 756 850
Water	1 273 035	1 273 035	1 273 035	1 273 035	1 268 972	1 273 035	1 273 035
Wetland	104 194	103 321	103 321	103 321	103 303	103 321	103 320
Forest type							
Lowland hardwood	657 241	642 321	639 124	638 909	637 537	641 850	639 477
Mixed pine–hardwood	2 136 636	1 870 209	1 914 903	1 918 123	1 889 900	1 869 019	1 846 211
Natural pine	1 031 782	1 059 113	1 069 375	1 068 969	1 036 341	1 062 824	1 024 698
Planted pine	1 064 429	977 622	1 066 958	1 067 889	959 099	982 327	842 609
Upland hardwood	2 093 399	1 824 483	1 829 157	1 828 946	1 805 361	1 824 700	1 799 567
Forest successional stage							
Recently Thinned	0	590 769	704 083	705 131	679 653	643 793	621 298
Recently Harvested	0	421 930	420 574	398 271	430 308	359 461	377 429
Early	592 802	1 192 106	1 288 720	1 310 206	1 319 117	1 144 434	1 147 836
Mid	5 403 444	2 903 900	2 915 283	2 907 533	2 800 995	2 920 534	2 793 234
Late	1 732 655	3 016 174	3 053 947	3 043 529	2 946 527	3 054 185	2 949 919
Forest vegetation structure							
All	592 947	670 986	749 097	788 556	775 350	679 004	675 621
Open	194 865	374 507	361 538	369 002	370 270	373 739	379 174
Closed	6 941 089	5 053 989	5 022 658	5 000 308	4 811 057	5 063 155	4 837 467

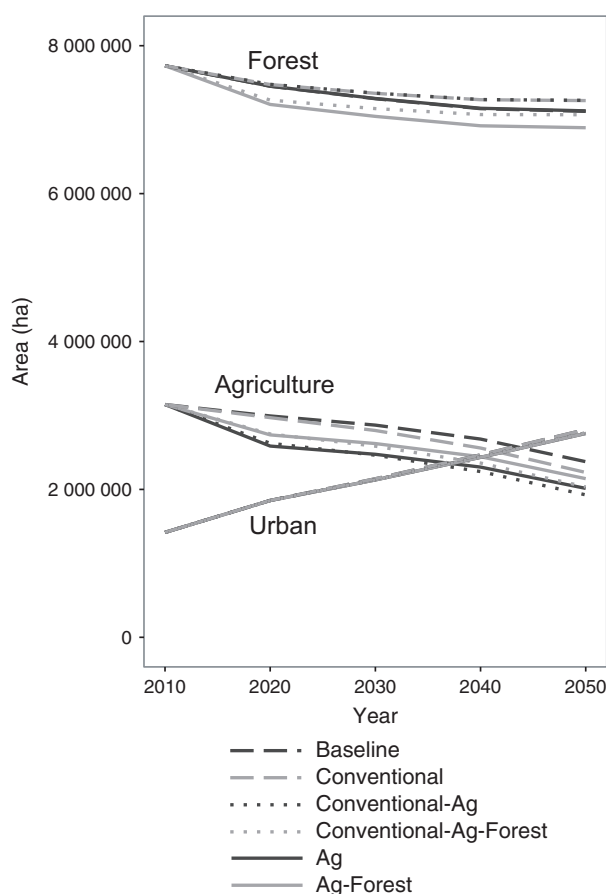


Fig. 3 Total areas of three major general land-use types over time under the five bioenergy scenarios and one Baseline scenario. Modeled ecosystems and land uses were aggregated into these land-use types according to Costanza *et al.* (2015).

smallest area of agriculture by 2050, a decrease of 38.8% from 2010, and 18.9% less than the Baseline scenario in 2050.

Loss of forest land by 2050 was greatest for the two scenarios that included the conversion of marginal forest to purpose-grown bioenergy crops. Of those two scenarios, the Ag-Forest scenario resulted in the greatest loss, a decrease of 10.8% in forest land compared to 2010, and 3.1% less than the Baseline scenario in 2050 (Figs 3 and 4). The Conventional-Ag-Forest scenario resulted in a decrease of 8.5% of forest land compared with 2010, and 0.6% less forest than the Baseline scenario in 2050. Total forest area in 2050 under the Ag scenario, which did not include biomass from conventional forests or marginal forest conversion, was similar to (0.01% more than) the Baseline scenario. Under that scenario, 7.9% of forest was lost between 2010 and 2050, whereas under the Baseline scenario, 8.0% of forest was lost. The final two scenarios, Conventional and Conventional-Ag, which included biomass from conventional

forests, but not the conversion of marginal forests, resulted in the smallest loss of forest land by 2050, and more forest on the landscape by 2050 than under the Baseline scenario. By 2050 under both of those scenarios, there was a loss of 6.1% of forest land compared to 2010, resulting in 2.0% (Conventional) and 2.1% (Conventional-Ag) more forest on the landscape compared to the Baseline scenario in 2050.

Statewide in all scenarios including the Baseline, loss of mid-succession forests and forests with a closed vegetation structure occurred by 2050, while all other successional stages and structures gained area over the simulation period (Table 2). Compared with the Baseline scenario, for bioenergy scenarios by 2050 there was little difference (<5% difference; Fig. 4) in the areas of many forest successional stages and vegetation structures with some notable exceptions. For the three scenarios that included biomass from conventional forests (Conventional, Conventional-Ag, and Conventional-Ag-Forest), there was between 8.1% and 10.1% more early-succession forest, and between 15.0% and 19.4% more recently thinned forest compared with the Baseline scenario (Fig. 4). The Ag scenario also resulted in more recently thinned forest compared with the Baseline scenario by 2050, with a difference of 9.0%. That scenario and the Ag-Forest scenario resulted in 14.8% and 10.5% less recently harvested forest, respectively, compared to Baseline in 2050.

Change in the total area of conventional planted pine forest differed substantially among scenarios. Planted pine decreased under the Baseline scenario, as well as under the Conventional-Ag-Forest, Ag, and Ag-Forest scenarios (Table 2). By 2050, the Ag-Forest scenario, in which all biomass came from the conversion of marginal forest lands to purpose-grown crops, showed the largest reduction in planted pine forest area over the simulation period. That scenario resulted in 13.8% fewer hectares of planted pine by 2050 than the Baseline scenario (Fig. 4). The Conventional-Ag-Forest and Ag scenarios showed smaller differences in total planted pine area compared to Baseline, with differences of -1.8% and 0.4% under those scenarios, respectively. Conversely, the area of planted pine forest increased under the Conventional and Conventional-Ag scenarios (Table 2), which included conventional forest biomass but not biomass from purpose-grown crops on marginal forest lands. Under those scenarios, respectively, there were 9.1% and 9.2% more planted pine on the landscape by 2050 than under the Baseline scenario (Fig. 4). As a whole, the total area of naturally regenerating forest (all forest that is not planted pine) decreased under all scenarios including the Baseline scenario. The amount of change in naturally regenerating forest area was not as sensitive to scenario as the change in planted

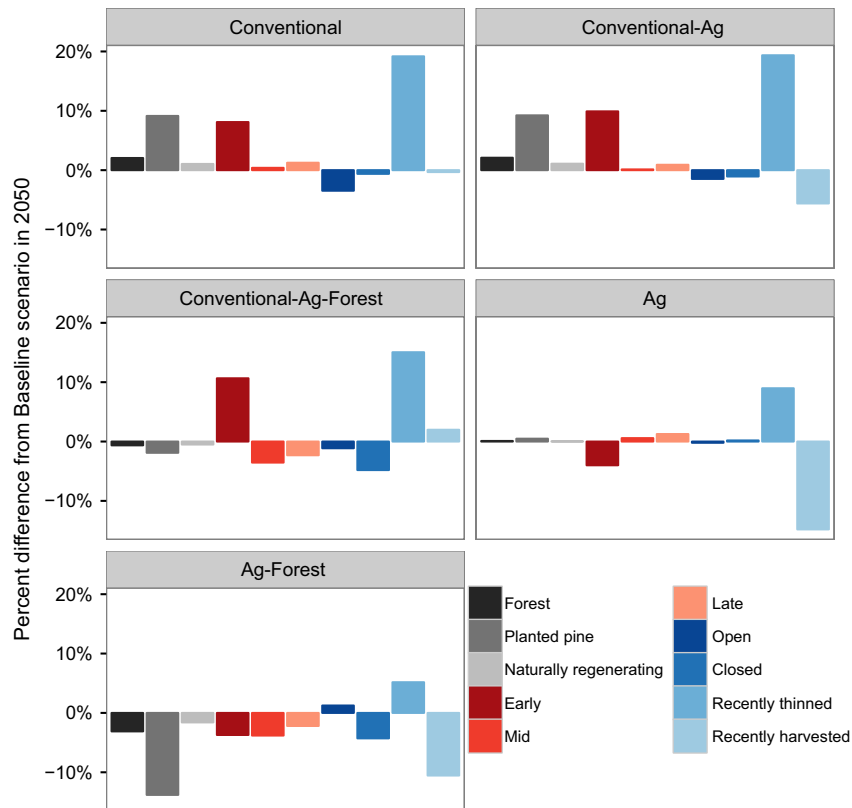


Fig. 4 Differences in total forest area, planted pine, naturally regenerating forest, and forest successional stages and structures across NC in 2050 for each biomass scenario, compared with Baseline in 2050. All forest ecosystems besides planted pine forest are included in naturally regenerating forest.

pine, and there was little difference among scenarios in the total areas of all naturally regenerating forest (Fig. 4).

We present here the results for the three bottomland hardwood (Fig. 5a–c) and two longleaf pine (Fig. 5d, e) ecosystems that comprise >1% of the simulated area in NC (Fig. 5). Results for two additional longleaf pine and seven additional bottomland hardwood ecosystems each comprise <0.5% of North Carolina and are included in Table S2 and File S3, as are results for all state classes in each vegetation and land-use type in our analysis. Under all bioenergy scenarios, the total areas of each of the three bottomland hardwood ecosystems showed little difference from the Baseline scenario by 2050. However, there were differences among scenarios for the late-successional closed forest state classes that are important for supporting biodiversity. The three bioenergy scenarios that included biomass from conventional forests (Conventional, Conventional-Ag, and Conventional-Ag-Forest) led to fewer hectares of late-successional closed forest in 2050 for both bottomland hardwood forest ecosystems than under the Baseline scenario. The difference was greatest for the Atlantic Coastal Plain Small Blackwater Stream Floodplain

Forest under the Conventional-Ag scenario, in which there was a 13.2% fewer hectares of late-successional closed forest, but across all three ecosystems, those scenarios resulted in at least 7.2% fewer hectares of late-successional closed forest. Under the other two bioenergy scenarios that included purpose-grown crops only (Ag and Ag-Forest), differences from Baseline in the amount of late-successional closed forest in these three ecosystems were relatively small (within $\pm 1.2\%$).

For the two longleaf pine ecosystems, there was also relatively little difference in total area between each bioenergy scenario and Baseline by 2050. However, the two scenarios that included the conversion of marginal forest lands (Conventional-Ag-Forest and Ag-Forest) did lead to between 2.4% and 4.9% fewer hectares of each longleaf ecosystem than Baseline by 2050. The three scenarios that included conventional forest biomass (Conventional, Conventional-Ag, and Conventional-Ag-Forest) generally resulted in fewer hectares of mid- and late-successional open state classes by 2050 than the Baseline scenario. These scenarios resulted in a difference of as much as -18.8% for the mid-succession open state class in the Atlantic Coastal Plain Upland Longleaf Pine Woodland type under the Conventional-

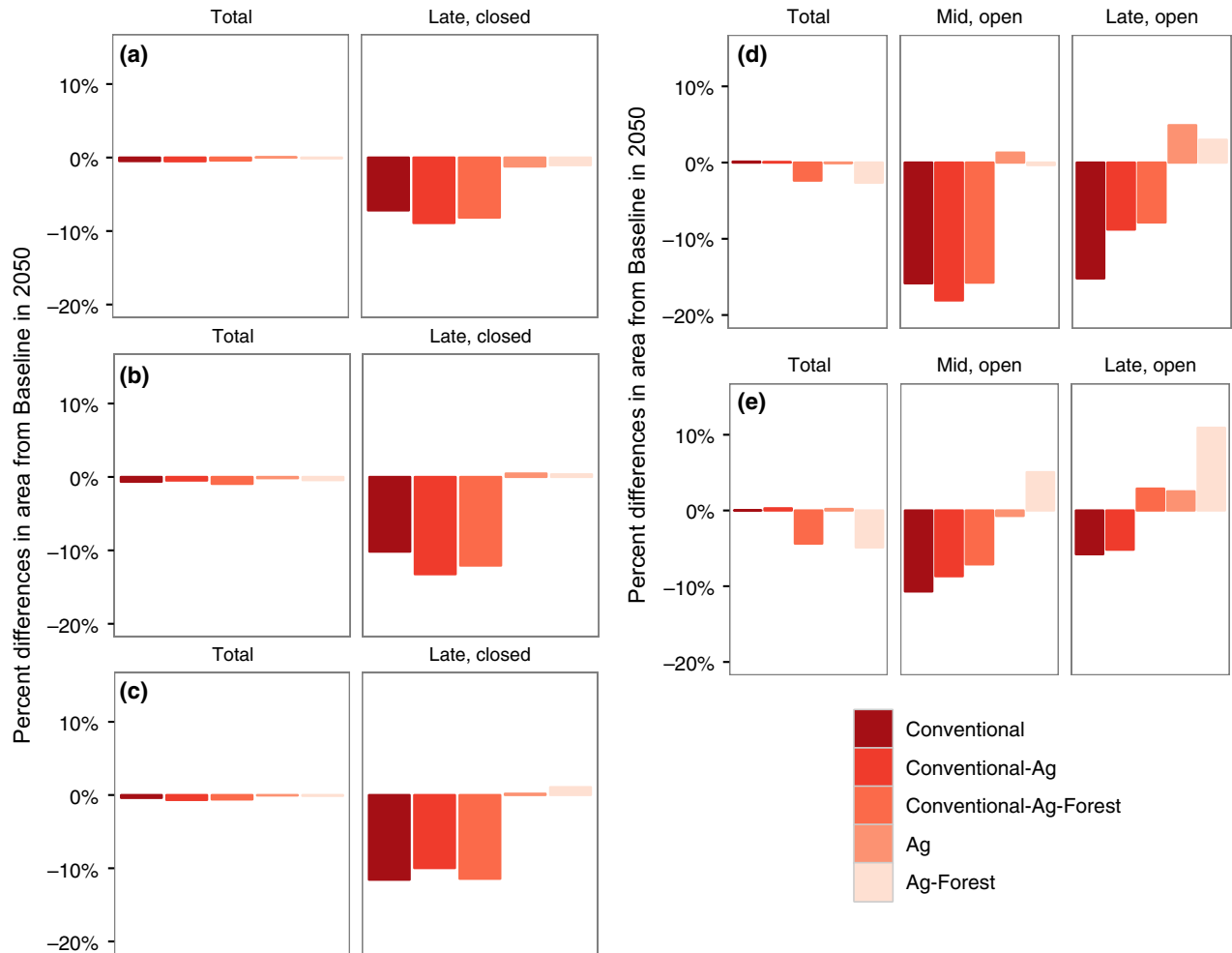


Fig. 5 Differences between bioenergy scenarios and Baseline for the total areas and areas of state classes that are critical for supporting biodiversity in bottomland hardwood forest and longleaf pine woodland ecosystems in 2050. Ecosystems in the left column are bottomland hardwood ecosystems: (a) Atlantic Coastal Plain Small Blackwater River Floodplain Forest; (b) Atlantic Coastal Plain Small Blackwater Stream Floodplain Forest; and (c) Atlantic Coastal Plain Small Brownwater River Floodplain Forest. The right column shows longleaf pine ecosystems: (d) Atlantic Coastal Plain Fall-line Sandhills Longleaf Pine Woodland, (e) Atlantic Coastal Plain Upland Longleaf Pine Woodland.

Ag scenario. The one exception was the late-successional open state class for the Atlantic Coastal Plain Fall-line Sandhills Longleaf Pine Woodland type, which had 2.8% more hectares by 2050 under the Conventional-Ag-Forest scenario compared to Baseline. The two scenarios that incorporated biomass from purpose-grown crops only (Ag and Ag-Forest) led to larger areas of many, but not all, mid- and late-successional longleaf pine state classes by 2050 compared with Baseline. The largest difference from Baseline was 10.9% more hectares of the late-successional open state class of the Atlantic Coastal Plain Fall-line Sandhills Longleaf Pine Woodland under the Ag-Forest scenario compared to the Baseline scenario.

Across the state for every scenario from 2010 to 2050, changes from one state class to another within the same

vegetation type due to succession, disturbance, and management were more common than changes from one land-use type to another. However, when considering the change among major land-use types, in every modeled scenario, transition from forest to urban land use dominated many ecoregions of the state, especially in the Piedmont and Blue Ridge regions (Fig. 6). However, there were important differences in the dominant types of land-use change among modeled scenarios for some regions of the state, especially in the Southeastern Plains and Middle Atlantic Coastal Plain. Under the Baseline scenario, change in the Southeastern Plains was dominated by transition from agriculture to urban land use. In the three scenarios that included biomass from conventional forests (Conventional, Conventional-Ag, and Conventional-Ag-Forest), transitions from

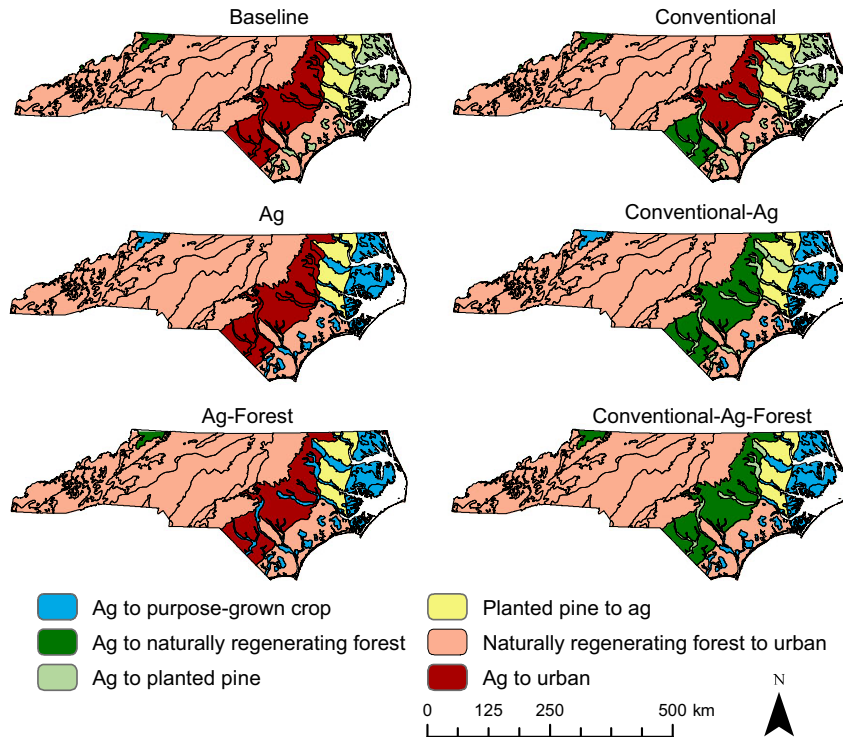


Fig. 6 Major land-use changes from 2010 to 2050 by scenario, summarized by EPA Level IV ecoregion. Maps indicate the most frequent type of change between two land uses in each ecoregion. Transition from naturally regenerating forest to agriculture was the predominant change in a single ecoregion in the eastern Blue Ridge under all scenarios except Ag and Conventional-Ag. That transition is not symbolized in the legend because the small scale of this figure prevents showing shading within that ecoregion.

agriculture to naturally regenerating and planted pine forests dominated a greater number of ecoregions in the Southeastern Plains. In the four scenarios that included purpose-grown crops (Conventional-Ag, Conventional-Ag-Forest, Ag, and Ag-Forest), transitions to those crops from agriculture dominated several ecoregions, especially in the northern portions of the Middle Atlantic Coastal Plain under all scenarios and in portions of the Southeastern Plains under the Ag-Forest scenario. Many of those ecoregions were dominated by transitions from agriculture to planted pine under the Baseline scenario.

Discussion

We modeled landscape dynamics under a set of policy-relevant, demand-driven woody biomass production scenarios that incorporated a portfolio of regionally appropriate feedstocks. Across the simulation period statewide, all bioenergy scenarios as well as the Baseline scenario lost forest and agriculture and gained urban land. However, our results emphasize that choices about the bioenergy feedstocks used and the types of land converted influence the degree of forest land loss, the relative loss or gain of planted pine forest, the structural and successional characteristics of the remaining

forest, and the effects on ecosystems that are important for biodiversity. Furthermore, in some regions, the mix of feedstocks used for bioenergy production is likely to have a substantial effect on land-use change and forest dynamics.

In general, scenarios that included the production of biomass from conventional forests avoided some loss of forest by 2050 compared with the Baseline and other scenarios. That result confirms the findings of previous studies that have suggested that a strong market for products from conventional forests will result in the retention of forest land in the southeast (Wear *et al.*, 2013; Galik & Abt, 2016). Indeed, more forest land implies the potential to benefit many forest ecosystem services, including water quality, erosion control, and wildlife habitat (USDA Forest Service, 2012b). However, the structural and successional characteristics of the remaining forests all influence ecological processes and habitat quality within forests. By examining the dynamics within the remaining forests under all scenarios, our work provides an important extension of those previous results. The simulated dynamics within forests indicates that by 2050, if biomass is sourced from conventional forests, remaining forests will likely be composed of more planted pine, more recently thinned, and more

early-successional habitat than under a Baseline, non-bioenergy future. Furthermore, while the use of biomass from conventional forests does not change the overall area of longleaf and bottomland hardwood forests by 2050 compared with a nonbioenergy future, it does result in smaller areas of the mid- and late-successional habitats within longleaf pine woodland and bottomland hardwood that are critical for biodiversity. Therefore, even though forest land area may be greater by 2050, critical habitats and the species that depend on them may face more threat in the future if conventional forests are used for bioenergy.

And, what happens to forests under futures in which biomass for bioenergy is sourced from purpose-grown crops grown on formerly marginal agricultural or forest lands, alone or in combination with biomass from conventional forests? Our results indicate that the initial use of the marginal lands being converted to purpose-grown woody crops for biomass influences the effects of land conversion. Meeting demand for biomass via purpose-grown woody crops on marginal agricultural lands alone, or in combination with conventional forest biomass, may not change the total area of forest substantially over scenarios without the conversion of marginal agricultural lands. However, according to our results, including biomass from marginal agricultural lands will likely affect the levels of forest harvest and thinning, leading to larger areas of thinned forest and smaller areas of harvested forest by 2050.

In contrast, meeting a portion of demand for bioenergy via the conversion of marginal forest land to biomass crops is likely to result in fewer hectares of total forest, planted pine, and all naturally regenerating forest in 2050 compared to a nonbioenergy future. In addition, the conversion of marginal forest land is also likely to lead to somewhat fewer hectares of longleaf pine ecosystems by 2050 compared to a future without bioenergy. In our results, reductions in total areas of forest and longleaf pine ecosystems were greatest for the scenario that did not include biomass from conventional forests to offset some of the forest loss. However, even in the Conventional-Ag-Forest scenario, which included conventional forest biomass, the decrease in forest land due to the conversion of marginal forest was larger than any increase in forest land area from conventional forest biomass production, and the net result was a reduction in forest area by 2050 compared with Baseline.

Our results also demonstrate that dynamics within longleaf pine and bottomland hardwood forest ecosystems may be most influenced by the inclusion of biomass from conventional forests. Including conventional forest biomass, whether alone or in combination with purpose-grown crop biomass, led to larger reductions in the critical longleaf pine and bottomland hardwood

forest habitats by 2050. These reductions in mid- and late-succession habitats are the result of more forest harvest in scenarios that included conventional forest biomass. The result of this reduction in important habitats could affect the overall biodiversity as well as the plant and wildlife species that depend on that habitat. For example, the federally endangered Red-cockaded Woodpecker, which makes its home in late-successional, open longleaf habitat, is already threatened by habitat loss (VanLear *et al.*, 2005) and could be further threatened if additional habitat is lost. To avoid the negative effects on critical habitats, restrictions on biomass harvesting in longleaf pine and bottomland hardwoods would be necessary, especially if biomass from naturally regenerating forests is to be used for bioenergy. However, because our work did not explicitly model changes in habitat for specific species, additional work to determine the precise effects of land management practices for bioenergy production on this and other species is warranted.

While urbanization or management of conventional forests for traditional forest products may otherwise be dominant drivers of landscape change across the southeastern United States (Lubowski *et al.*, 2008; Terando *et al.*, 2014; Martinuzzi *et al.*, 2015), our results indicate that in some localized regions, bioenergy production may also become a dominant driver of landscape change, implying increased competition for land and natural resources in those regions. Specifically, in our scenarios, bioenergy production influenced the major landscape dynamics in most ecoregions in the Southeastern Plains and Middle Atlantic Coastal Plain. In those regions, biomass from conventional forests led to a predominance of change from agriculture to planted pine or naturally regenerating forests, especially in ecoregions that were otherwise dominated by agriculture-to-urban transitions. We do not suggest that urbanization would be prevented under scenarios that include conventional forest biomass, but rather that urbanization may be superseded as the dominant type of change in some ecoregions. In addition, including biomass from purpose-grown crops tended to result in a predominance of agriculture-to-purpose-grown crop conversion, especially in ecoregions that were otherwise dominated by agriculture-to-planted pine transitions. In this case, the change is likely the result of conversion to purpose-grown crops on lands that would otherwise be converted to planted pine. These spatial results reiterate an important aspect of the geography of the southeastern United States: The coastal plain ecoregions are where the majority of biomass production may occur and are also the most important for biodiversity (Evans *et al.*, 2013; Lendemer & Allen, 2014; Noss *et al.*, 2015). Thus, developing and implementing best practices for

sustainable production of biomass will be crucial for maintaining that biodiversity.

The use of biomass for bioenergy globally hinges on its sustainability (Bosch *et al.*, 2015). While there is no consensus on how to define and measure sustainability of biomass, and sustainability likely includes multiple ecological, social, and economic factors (Bosch *et al.*, 2015), minimizing overall loss of forests and biodiversity and maximizing the area of habitat for taxa of special concern have been suggested as indicators or criteria for sustainable bioenergy production (McBride *et al.*, 2011; VanDam & Junginger, 2011; Davis *et al.*, 2013). Furthermore, sustainability criteria should be refined based on local context and should avoid areas with high biodiversity (European Commission, 2009; Efrogmson *et al.*, 2013; Joly *et al.*, 2015). Because the Southeastern Plains and Middle Atlantic Coastal Plain occur in a global biodiversity hotspot, and longleaf pine woodlands and bottomland hardwood forests are reservoirs of biodiversity, achieving positive effects or at least avoiding negative effects to the regions and ecosystems that support biodiversity are important criteria for sustainable production of bioenergy in the region.

Results from the scenarios we examined suggest that simultaneously achieving the best outcomes for these sustainability criteria under a single biomass production future may not be possible. No single scenario led to more forest overall as well as more of each of the longleaf pine and bottomland hardwood habitats that support biodiversity. However, some scenarios may lead to a middle ground. For example, including only the conversion of marginal agricultural lands to purpose-grown crops for biomass resulted in as much loss of forests and important bottomland hardwood habitats as the Baseline scenario, while leaving more of the mid- and late-successional open habitats that support biodiversity in the longleaf pine ecosystem. Alternatively, including harvest of conventional forest biomass, but not the conversion of marginal forest lands, led to more total forest area in 2050 compared with Baseline, but the loss of important habitats in the longleaf pine and bottomland hardwood ecosystems generally occurred under those scenarios. Future work should prioritize sustainability indicators based on their relevance to local ecological goals and examine alternative landscape designs using an optimization approach to maximize sustainability (Efrogmson *et al.*, 2013; Ekroos *et al.*, 2014; Dale *et al.*, 2016).

We have modeled landscape dynamics under a set of demand-driven biomass production scenarios that incorporated a set of regionally appropriate feedstocks. While we incorporated the best available knowledge about future feedstocks, scenarios, and effects on timber

supply and demand, we made several assumptions about landscape change that should be further assessed and refined. One critical assumption was that land harvested or thinned in a specific ecosystem in a given year would be the result of the total area of a broad forest type harvested in that year according to the SRTS model, modified by the proportion of land in the specific ecosystem. That assumption is likely an oversimplification, and there are other factors that contribute to the likelihood of harvest, such as proximity to a biomass processing facility and landowner demographics (Evans *et al.*, 2013; Dorning *et al.*, 2015; Young *et al.*, 2015). Refining the spatial distribution of land-use conversions and management actions will be important for better understanding the potential effects on ecosystems. In addition, given the uncertainties and assumptions made in these models, it will be critical to quantify the effects of these assumptions on modeling results via sensitivity analysis.

Our simulations of landscape change did not incorporate details about specific land management practices and their effects on ecological processes. For example, little work has examined the effects of potential intensification of land management for biomass production, including the use of fertilizer (Immerzeel *et al.*, 2014). Knowing the effects of such practices is critical to fully assessing ecological impacts. Furthermore, assessing all social and environmental effects of these bioenergy scenarios beyond the landscape ecological effects examined here, including changes to carbon emissions and storage and effects on water quality, is essential for informing sustainable biomass production.

Our results indicate that while outcomes varied by region and with the combination of feedstocks examined, each resulted in trade-offs in terms of the amount and characteristics of remaining forest. Conventional forest biomass tended to retain more forest on the landscape, but the remaining forest had a lower proportion of critical habitats for biodiversity, while converting marginal agricultural lands to purpose-grown biomass crops retained less forest land, but resulted in fewer alterations to overall forest composition and characteristics. Converting marginal forest resulted in the loss of forest as well as altered forest characteristics. Further testing assumptions about future scenarios as well as continuing field-based research to examine the specific effects on ecological processes will be essential to ensure sustainability of bioenergy production.

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Table S1. Biomass-to-ethanol conversion for purpose-grown crops in scenarios that include conversion of marginal lands to purpose-grown crops.

Table S2. Changes in area from 2010 to 2050 for all state classes in all modeled ecosystems and land-use types in all bioenergy scenarios and the Baseline scenario.

File S3. Area differences from the Baseline scenario in 2050 for all state classes in all modeled ecosystems and land-use types for all bioenergy scenarios.