Effects of climate change, land-use change, and invasive species on the ecology of the Cumberland forests

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Abstract: Model projections suggest that both climate and land-use changes have large effects on forest biomass and composition in the Cumberland forests of Tennessee and Kentucky. These forests have high levels of diversity, ecological importance, land-use changes, and pressures due to invasive herbivorous insects and climate change. Three general circulation models project warming for all months in 2030 and 2080 and complex patterns of precipitation change. Climate changes from 1980 to 2100 were developed from these projections and used in the forest ecosystem model LINKAGES to estimate transient changes in forest biomass and species composition over time. These projections show that climate changes can instigate a decline in forest stand biomass and then recovery as forest species composition shifts. In addition, a landscape model (LSCAP) estimates changes in land-cover types of the Cumberlands based on projected land-use changes and the demise of eastern hemlock (*Tsuga canadensis* (L.) Carrière) due to the spread of the hemlock adelgid (*Adelges tsugae* Annand). LSCAP suggests that land-cover changes can be quite large and can cause a decline not only in the area of forested lands but also in the size and number of large contiguous forest patches that are necessary habitat for many forest species characteristic of the Cumberlands.

Résumé : Les projections des modèles indiquent que les changements tant climatiques que dans l'utilisation du sol ont des effets importants sur la composition et la biomasse des forêts des Cumberlands au Tennessee et au Kentucky. Ces forêts sont caractérisées par un degré élevé de diversité, d'importance écologique, de changements dans l'utilisation du sol et de pressions dues aux insectes herbivores invasifs et aux changements climatiques. Trois modèles de la circulation générale prédisent un réchauffement durant tous les mois en 2030 et 2080 et des changements complexes dans la configuration des précipitations. Les changements climatiques pour la période allant de 1980 à 2100 ont été élaborés à partir de ces projections et utilisés dans le modèle d'écosystème forestier LINKAGES pour estimer les changements passagers dans la biomasse forestière et la composition en espèces dans le temps. Ces projections montrent que les changements climatiques peuvent être à l'origine du déclin de la biomasse des peuplements forestiers et de sa récupération par la suite, à mesure que la composition en espèces forestières se modifie. De plus, un modèle de paysage (LSCAP) a été utilisé pour déterminer les changements qui pourraient survenir dans le type de couvert forestier des Cumberlands sur la base des changements prévus dans l'utilisation du sol et de la mortalité de la pruche du Canada (*Tsuga canadensis* (L.) Carrière) due à la progression du puceron lanigère de la pruche (*Adelges tsugae* Annand). Le modèle LSCAP indique que les changements dans le couvert pourraient être très importants et causer une diminution non seulement de la superficie du territoire forestier mais aussi de la dimension et du nombre de parcelles de forêt contiguës qui constituent des habitats pour plusieurs espèces forestières caractéristiques des Cumberlands.

[Traduit par la Rédaction]

Introduction

Global changes that affect ecological systems include alterations in climate, land use, invasive species, ultraviolet radiation, and atmospheric conditions (Intergovernmental Panel on Climate Change (IPCC) 2007). The effects of these changes on terrestrial biodiversity and ecosystem processes are of great concern. Many studies have examined the effects of single changes, but few have considered several effects. The most common combinations that have been examined include aspects of climate change and atmospheric conditions (e.g., Hanson et al. 2005) and invasive species and climate changes (e.g., Logan et al. 2007). Such studies call for more analyses to improve understanding and reduce the uncertainty of multivariate predictions of future ecosystem responses (e.g., Dermody 2006). Furthermore, Paine et al.

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(1998) demonstrated that unexpected and severe ecological consequences can result from compounded perturbations. The effects of regional differences in temperature and precipitation changes on US forest systems may best be understood in view of other pressures on ecological systems.

Some argue that land-use and climate changes may be the strongest environmental influences of our day (Dale 1997). In any case, there clearly is a relationship between change in land use and climate, for land use can cause local and global changes in climate and climate affects how the land is used and managed. For example, the clearing of forests, increased forest fire activity, and conversion of prairie grassland to agricultural land between 1900 and 1990 contributed to changes in annual surface air temperature in North America (Skinner and Majorowicz 1999). In a modeling study of the effects of both climate and land-use change on the rarity of plant species in the Proteaceae that are endemic to the Cape Floristic Region, South Africa, Bomhard et al. (2005) found that climate change has the most severe effects, but land-use change also affects some taxa.

Projected climate changes in the US are anticipated to include warming and changes in precipitation (IPCC 2007). These changes may affect US forests by altering forest processes, such as growth rates, patterns of nutrient uptake, and productivity (Aber et al. 2001; Shugart et al. 2003), as well as by altering forest species composition (e.g., Iverson and Prasad 2002). Watson et al. (1995) analyzed how different models project forest growth and decline in the face of climate change in the southeastern US and found that temperate mixed forest in the US undergoes a loss of leaf area (e.g., biomass decrease) of 12%–76% for the scenarios conducted without CO_2 effects conducted for the IPCC second assessment (Watson et al. 1995). However, different ecological models produce different results in response to climate (Vegetation/Ecosystem Modeling and Analysis Project (VEMAP) 1995; Malcolm and Pitelka 2000). The results of the study by Shugart et al. (2003) suggest that these differences are expected given the unique formulation and resolution of each model. The IPCC (2007) studies project to 2100 a general decline in forest productivity and a shift in species composition for Tennessee. The longevity of the southeastern trees and diversity of Tennessee forest systems make it unclear what the long-term forest composition and productivity might be.

The question that this paper addresses is how climate change, land-use change, and invasive species influence changes in forest species composition and structure. We focus on highly diverse forests of the northern Cumberland Plateau and Mountains of Tennessee because the region supports unique species combinations and habitats (e.g., Buehler et al. 2006), is undergoing major land-use changes, and is likely to be affected by the hemlock adelgid (*Adelges tsugae* Annand)[2]. The region is predicted to experience temperature increases for 2030 and 2080, but the changes in precipitation are expected to be less strong and less certain. Some models project wetter summers, and some project drier summers. Similar changes are projected for other areas of the world. It is therefore an ideal region in which to explore effects of land use, climate, and invasive systems on the forest ecosystems. We examine climate effects by using projections from three general circulation models (GCMs) that present medium trends for the region (extreme projections are not considered here). Monthly changes in temperature and precipitation projected to the year 2100 are used to drive the forest ecosystem model, LINKAGES (Post and Pastor 1996), which estimates changes in total biomass, species composition, and ecosystem conditions over time. In a companion analysis, estimates of land-use change and the death of all eastern hemlock (*Tsuga canadensis* (L.) Carrière) caused by the spread of the invasive hemlock adelgid are used to project changes in both the area and distribution of land-cover types of the Cumberlands using a landscape approach (LSCAP) (Druckenbrod et al. 2006). Together, these three models enable the examination of three factors that are anticipated to have major effects on the forests of the Cumberlands. The climate and land-use changes are not integrated into one model, which would be the next step in such an analysis.

Methods

Site description: Cumberland Plateau and Mountains

The mixed mesophytic forests of the Cumberland Plateau and Mountains in Tennessee and Kentucky are among the most diverse in North America (Ricketts et al. 1999) and are under increasing stress from climate change, land-use change, and invasive species. On the Cumberland Plateau and Mountains in Tennessee, few old-growth forests remain (Noss et al. 1995), yet these old-growth forests tend to have great botanical diversity and few nonnative species, which is indicative of high level of ecological integrity (McEwan et al. 2005). Previously disturbed forests of the Cumberlands contain as many as 110 nonnative species (>12% of the flora) (Fleming and Wofford 2004). About 72% of timberland is held in nonindustrial private forest land ownership (Schweitzer 2000). The Cumberland forests have been impacted by and remain threatened by changes in land use and are viewed as requiring critical habitat protection and restoration (Ricketts et al. 1999). In 2008, much of the forested land is up for sale following a broad-scale outbreak of the native southern pine beetle (*Dendroctunus frontalis* Zimm. (Coleoptera: Scolytidae)) and the death of many pines. Developers are looking at the rolling hills with an eager eye. Since the diversity of canopy species as well as forest associations across the Cumberland Mountains and Plateau prevents any single reserve from supporting the entire flora, a regional approach is necessary for effective forest conservation (Schmalzer 1989).

The region experiences mild winters and hot, humid summers. The Cumberland Plateau Climate Division of Tennessee reports annual temperatures of 13.6 ± 0.8 °C and a mean annual precipitation of 140.8 ± 19.5 cm from 1931 to 2000 (National Climatic Data Center 2002).

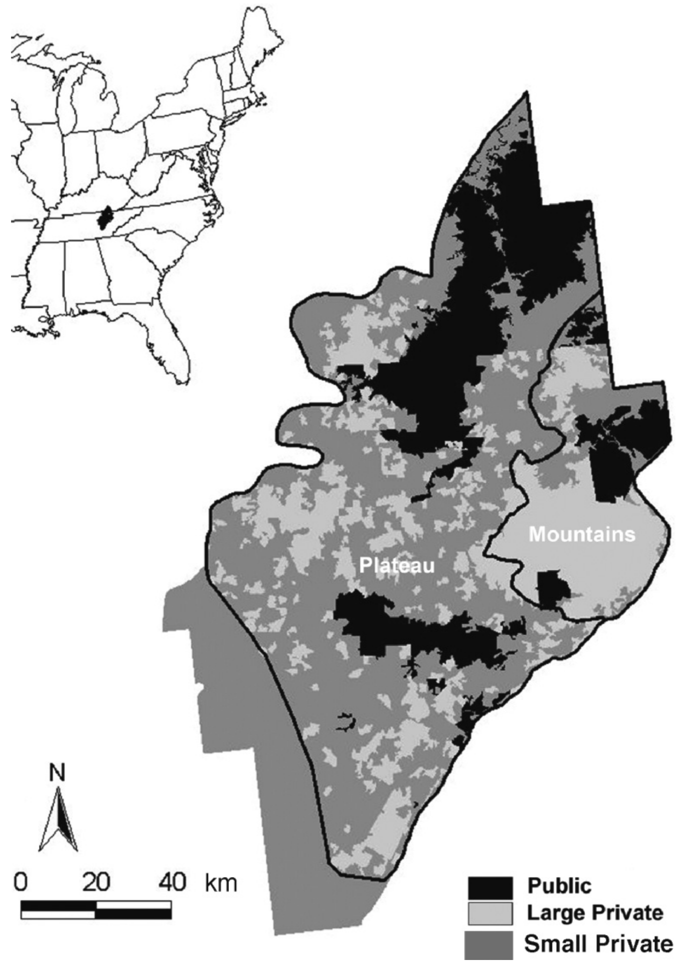
The Cumberland Mountains are underlain by shale, sandstone, siltstone, and coal and have an elevation range of more than 600 m. Some peaks extend above 1000 m. The

[2] S.W. Roberts, R. Tankersley, Jr., and K.H. Orvis. Preparing for the onset of hemlock mortality in Great Smoky Mountains National Park: an assessment of potential impacts to riparian ecosystems. Manuscript in review.

Cumberland Plateau has more sandstone, and its geology is less dissected than the Cumberland Mountains, with elevations generally between 350 and 600 m (Griffith et al. 1995); however, the northern part of the Plateau is more dissected northward (Smalley 1984).

The Cumberland Plateau and Mountains project areas of this study, encompassing 896 124 and 172 125 ha, respectively, support primarily mesic mixed and mesic deciduous forests on the plateau and mesic deciduous and xeric deciduous forests in the mountains (Druckenbrod et al. 2006). Anthropogenic land covers accounted for 23.7% of the plateau and 12.9% of the mountains region, with most cover in transitional and cleared classes. Ownership categories on the plateau (and mountains) are diverse, with 23% (20%) in public ownership, 21% (56%) in large private ownership, and 56% (24%) in small private ownership, in the early twenty-first century (Druckenbrod et al. 2006) (Fig. 1). Public lands on the plateau have greater amounts of natural forest cover in mesic evergreen, xeric mixed, and xeric evergreen forests but less cover in upland deciduous forests. In the mountains, both public and large private ownerships support greater amounts of natural cover mesic deciduous and xeric deciduous forests, and lessor of mesic evergreen and xeric evergreen forests. Large private ownerships on the plateau have more cover in mesic deciduous, upland deciduous, and upland mixed forests and less cover in xeric forest classes. Small private ownerships on both the plateau and mountains contain the greatest amounts of mesic deciduous, mesic mixed, and upland deciduous forest-cover classes but also have less cover in xeric forest-cover classes.

Fig. 1. Map of the Cumberland Plateau and Mountains of Tennessee and Kentucky.



Climate-change projections

The National Center for Atmospheric Research (NCAR) provided projections from three GCMs for the region that encompasses the Cumberland Plateau and Mountains. The GCM outputs represent three moderate projections of climate change for this region, which were selected to provide an envelope of possible future conditions. The "wet" scenario is from NCAR's Community Climate System Model (ccsm3) (Collins et al. 2006). The "middle" scenario comes from NCAR's Parallel Climate Model (PCM) (Washington et al. 2000). The "dry" scenario is from the Center Climate System Research (The University of Tokyo), National Institute for Environmental Studies, and Frontier Research Center for Global Change (JAMSTEC) Model for Interdisciplinary Research on Climate, medium resolution (MIROC medres model). More information about the GCMs, global climate modeling approaches, and uncertainty are provided by the IPCC (2007).

These GCM runs derive from the A1B storyline developed by the IPCC to build an underlying consistency in the social and physical relationships driving greenhouse gas emissions (Nakićenovic et al. 2000). The A1B storyline assumes rapid global economic growth (3%) and liberal globalization, as characterized by low population growth, very high gross domestic product growth, high to very high energy use, low to medium changes in land use, medium to high resource availability, and rapid technological advancement. This storyline emphasizes market-based solutions; high savings and investment, especially in education and technology; and international mobility of people, ideas, and technology. Other possible climate-change storylines developed by the IPCC (2007) emphasize more or less growth, energy use, land-use change, resource use, and technology change.

NCAR provided data on changes in temperature and precipitation from a base period of 1980 to 1999 to 2030 and to 2080 (J.B. Smith and C. Wagner, Stratus Consulting, Boulder, Colorado, USA, personal communication, 2006). The 2030 years are model simulations of the years 2020–2039, and the 2080 years are model simulations of the years 2070–2089. The monthly temperature and precipitation data used in the forest simulation are a piecewise continuous curve beginning with average conditions for 1989 (derived from average conditions from 1980 to 1997), a linear extrapolation from 1989 to the 2030 climate projections from three GCMs, a linear extrapolation from 2030 to the 2080 GCM projections, and the constant value of the 2080 GCM projections to 2300.

The GCM output is a monthly average and does not indicate how daily or interannual variability can change. An appropriate way to use the GCM output is to combine it with an observed long-term historical weather database. In this study, the precipitation and temperature projections from the three climate-change models for 2030 and 2080 were related to the 1980–1997 monthly record of temperature and precipitation mean and standard deviation for each 1 km cell in the

Cumberland Plateau and Mountains. The 1980–1997 data are available from the Daily Surface Weather and Climatological Summaries (DAYMET http://www.daymet.org/). The DAYMET data were derived by using a digital elevation model and daily observations of minimum and maximum temperatures and precipitation from ground-based meteorological stations over the 18 year period. The data used in the study consist of temperature and precipitation at a 1 km resolution for the study region (Thornton and Running 1999). We averaged the observed 1 km DAYMET climate data for each region and combined them, as described in the next paragraph, with the monthly GCM output of temperature and precipitation mean and standard deviation to produce monthly climate projections for 2030 and 2080 for each region.

Monthly temperature and precipitation climate conditions used by the forest change model LINKAGES were derived from a piecewise curve. The average and standard deviation monthly conditions for the 1980–1997 period provided the base case for the 200 year LINKAGES model runs up to 1989 that allowed the model to equilibrate. Thereafter, the temperature and precipitation increased linearly to 2030, then increased linearly to 2080, and thereafter remained constant for each region. This piecewise continuous linear curve most directly relates to the climate projections and requires the fewest assumptions.

Projecting changes in forest stand structure and composition with the LINKAGES model

LINKAGES is a forest stand model that projects changes in forest composition and structure for a 1/12 ha plot (Post and Pastor 1996). It was developed from the family of gap models known as FORET (Shugart and West 1977) that tracks changes in individual trees according to their size and species as influenced by temperature and competition for light and moisture. The unique features of LINKAGES are that it models (*i*) the direct effects that monthly climate change can have on forest ecosystem production and hence carbon storage through temperature and soil moisture limitations and (*ii*) the indirect effects through the nitrogen cycle by affecting species composition (Post and Pastor 1996). Thus, the model captures the influences of spring temperatures and heterogeneity in soil moisture that Ibanez et al. (2007) found to be key drivers of tree recruitment in the southern Appalachian Mountains.

The 200 year spin-up time for LINKAGES was selected based on analysis with the FORET model reported by Shugart and West (1977). In simulations of 100 forest plots, starting from bare soil in East Tennessee and run for 1000 years, they found that by 200 years the leaf area, biomass, and number of stems had equilibrated.

The model projected changes over time from 1989 to 2100 in total stand biomass and biomass of key species, and for 2030 and 2080 in the diameter distribution of key species in 2 in. (5.08 cm) categories. Output from 100 stochastic model runs was averaged for each region.

Estimating landscape changes

The LSCAP used in this analysis compares the current conditions of forests with long-term perspectives, as expressed by the rules that define future conditions (Druckenbrod et al. 2006). These rules for land-cover change are based on detailed historical analysis of the Cumberland region, on estimates for current conditions by combining remote sensing analysis with the USDA Forest Service's Forest Inventory and Analysis data, and on future conditions derived from current short-term trends in East Tennessee. Because these social and economic trends are highly unpredictable and depend upon both local and global changes in timber prices, land values, and social choices, these future projections and rules should be considered as one possible scenario of land-cover change. However, they are consistent with the A1B storyline used in the climate-change scenarios and seem to contain the future trends toward which East Tennessee forests are now headed. We use these specific rules primarily to provide a comparison of how pressures from land-cover changes relate to influences of climate change in the Cumberland forests.

In the Druckenbrod et al. (2006) study, forest cover was classified with Landsat Thematic Mapper imagery and evaluated with the USDA Forest Service's Forest Inventory and Analysis data (Alerich et al. 2004). Those forest classes were combined with landforms to generate landform forest associations with a rule-based method (Biasi et al. 2001). Landform forest associations were characterized by combining forest cover, physiographic descriptions of remnant and historical forests, and forest structure and composition from the inventory data. These landform forest associations estimated and described current forest conditions of the Cumberlands (Druckenbrod et al. 2006).

The future conditions for this analysis are based on the assumption that much of the large private forest land becomes second-home development (especially on the plateau) and that all hemlock dies as a result of the hemlock woolly adelgid[2]. This change in land cover is consistent with a model of land parcelization developed for Morgan Country (within the Cumberlands) based on discussions with landowners (Fogel 2007). The hemlock woolly adelgid kills all sizes of hemlock; thus seed banks are likely to have little influence on survival of the species at any one location (Sullivan and Ellison 2006). Although distance to the closest stream, trail, and road affects the risk to hemlocks of the adelgid (Koch et al. 2006), it is most likely that in a short period of time all hemlock will succumb. The modeled changes in land cover will affect all the cover types on the plateau and mountains, including all anthropogenic cover types: upland evergreen, transitional, cleared, pasture/nonforest, and urban, with the exception that land is not allowed to change from urban to any other land-cover type. The basic rule is that if any land is in large private ownership, then it is considered for change. Of the land in large private ownership in the early twenty-first century, the scenario applies the rules shown in Table 1.

Results

Climate-change projections for the Cumberland region

Temperature is projected to increase in both the Cumberland Plateau and Mountains for all months in both 2030 and 2080 for all three GCMs (Fig. 2). Projected changes in precipitation are less consistent (Fig. 3). By 2030, the "wet" scenario estimates that the summers are wetter, and the "middle and "dry" scenarios project drier summers. By 2080, the differences among these scenarios are more pro-

Table 1. Rules for changes to large privately held land within the northern Cumberland Plateau and Mountains.

Landform	% Total area in large private ownerships	% Current land in large private ownership that changes to another landform		
		Transitional	Cleared	No change
Cumberland Plateau				
Steep slope N-NE	25.7	25	25	50
Steep slope S-SW	26.2	25	25	50
Slope crest	22.3	50	25	25
Upper slope	20.5	50	25	25
Flat summit	19.3	50	50	0
Sideslope N-NE	20.9	50	25	25
Cove or ravine N-NE	21.1	25	50	25
Sideslope S-SW	21.2	50	25	25
Cove or ravine S-SW	21.7	25	50	25
Flat	19.4	50	50	0
Slope bottom	18.7	25	50	25
Water	19.0	0	0	0
Total	**20.6**			
Cumberland Mountains				
Steep slope N-NE	64.4	25	0	75
Steep slope S-SW	64.1	25	0	75
Slope crest	58.7	25	0	75
Upper slope	55.6	25	50	25
Flat summit	45.7	0	100	0
Sideslope N-NE	51.9	25	25	50
Cove or ravine N-NE	56.0	25	50	25
Sideslope S-SW	53.5	25	50	25
Cove or ravine S-SW	57.1	25	50	25
Flat	25.5	0	100	0
Slope bottom	37.1	25	50	25
Water	50.1	0	0	100
Total	**56.1**			

Note: Note some areas will not change because they are already transitional or cleared. The current estimates are for the early twenty-first century (see details in Druckenbrod et al. 2006).

nounced, with slight differences in the winter and greater variation in the summer. All changes in precipitation fall within the current variability (one standard deviation) of monthly mean precipitation. These results are consistent with the estimates by Sheffield and Wood (2007) that drought is most likely in the Mediterranean, Southwest US, Central America, southern Africa, and Australia.

Projected changes in forest stand structure, composition, and evapotranspiration

Projected changes in total biomass suggest there will be a decline in stand biomass for all scenarios for both the Cumberland Mountains and Plateau (Fig. 4). The projected climate changes induce slower growth and demise of some trees in the simulation. The model was run to 2300 so that we could examine the long-term implications of this change in biomass. Both the middle and wet scenarios for the plateau and mountains reestablish biomass close to their original levels by 2150 and 2100, respectively. In both regions, the dry scenarios are slower to reestablish stand biomass and do so by model year 2170 for the plateau and 2125 for the mountains. The projected climate changes have differential effects on tree species. For the Cumberland Plateau, American basswood (*Tilia heterophylla*) and shagbark hickory (*Carya ovata*) become greater contributors to biomass for all scenarios, and chestnut oak (*Quercus prinus*), black oak (*Quercus velutina*), and yellow buckeye (*Aesculus octandra*) become less important (Fig. 5). In addition, over time there is a slight increase in the biomass of red maple (*Acer rubrum*), pignut hickory (*Carya glabra*), black hickory (*Carya texana*), mockernut hickory (*Carya tomentosa*), and hackberry (*Celtis laevigata*)—especially in the dry scenario.

The changes in biomass by species are quite different in the Cumberland Mountain projections (Fig. 6). American basswood and shagbark hickory increase in all scenarios. Chestnut oak does not have a major change in biomass in the wet or middle scenarios, but in the dry scenarios it increases and then declines. Black oak remains stable in all three cases. Sugar maple (*Acer saccharum*) declines in all cases, but its loss from the forest occurs slower in the middle scenario. Yellow buckeye increases in the middle case but increases and then declines in both the dry and wet scenarios.

Actual evapotranspiration (AET) is the amount of soil moisture exiting via evaporation and transpiration, and it de-

Fig. 2. Projected changes in temperature for the Cumberland Plateau and Mountains.

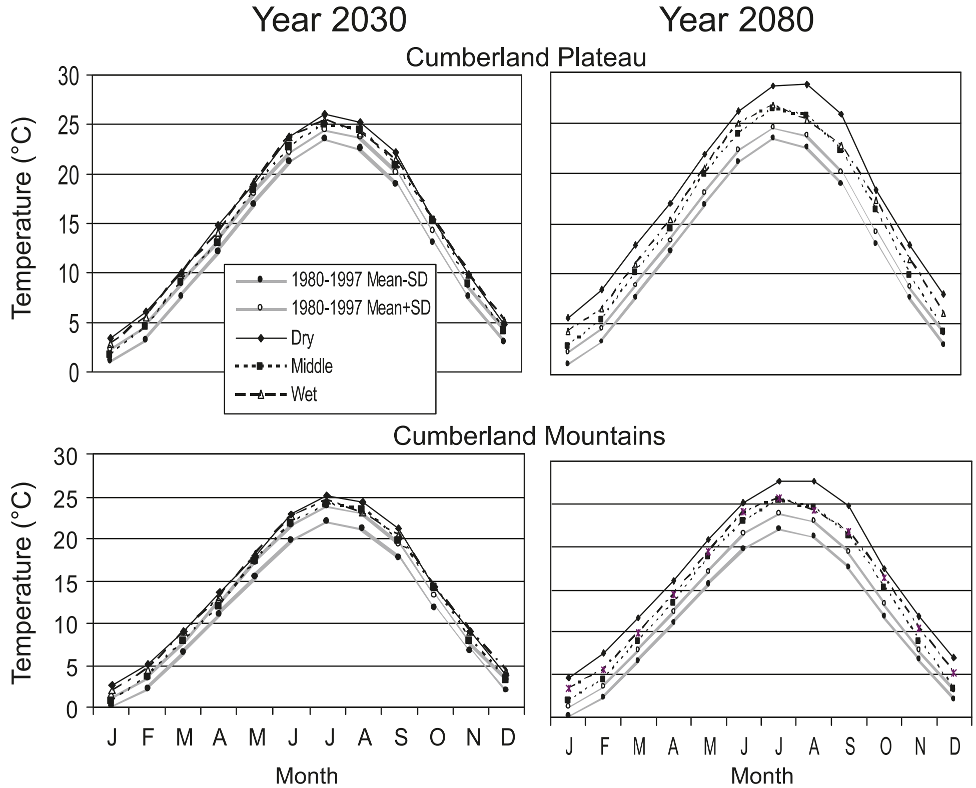


Fig. 3. Projected changes in precipitation for the Cumberland Plateau and Mountains.

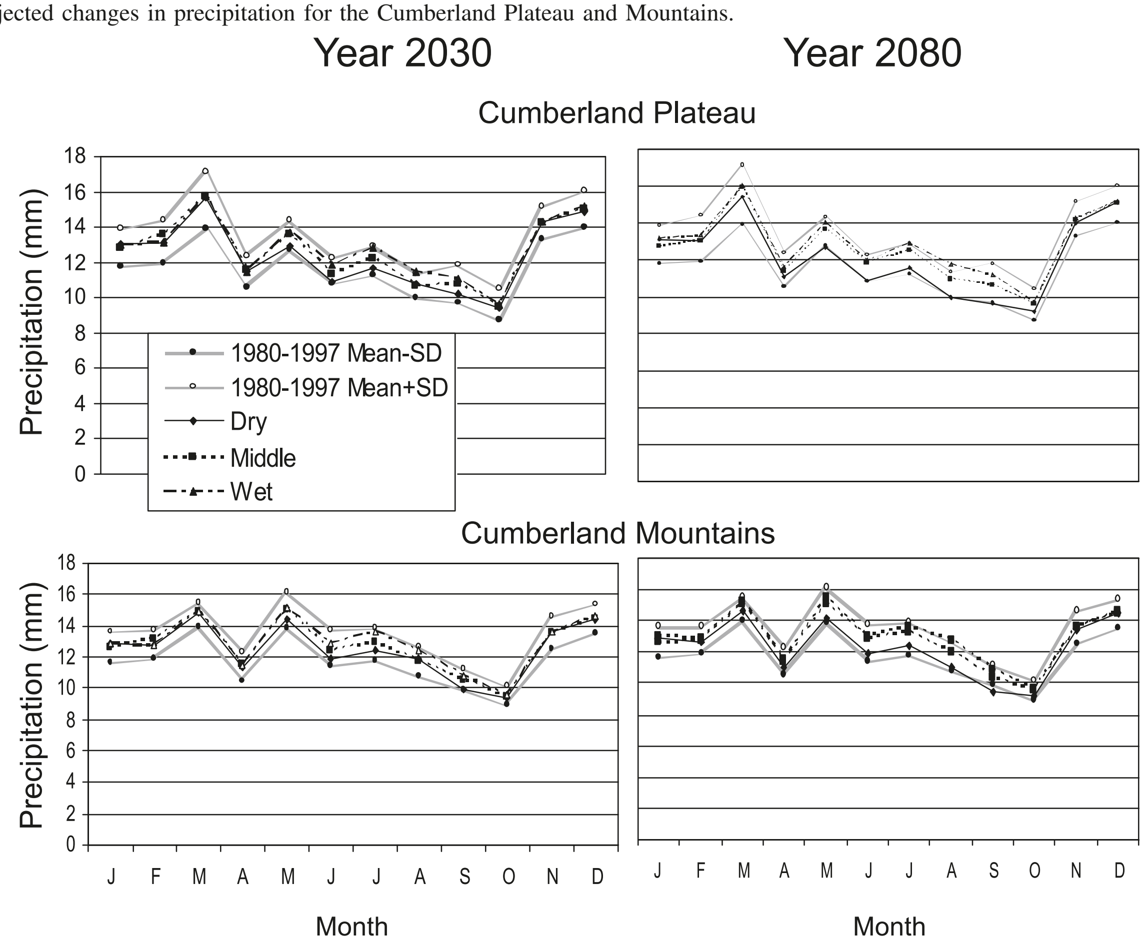
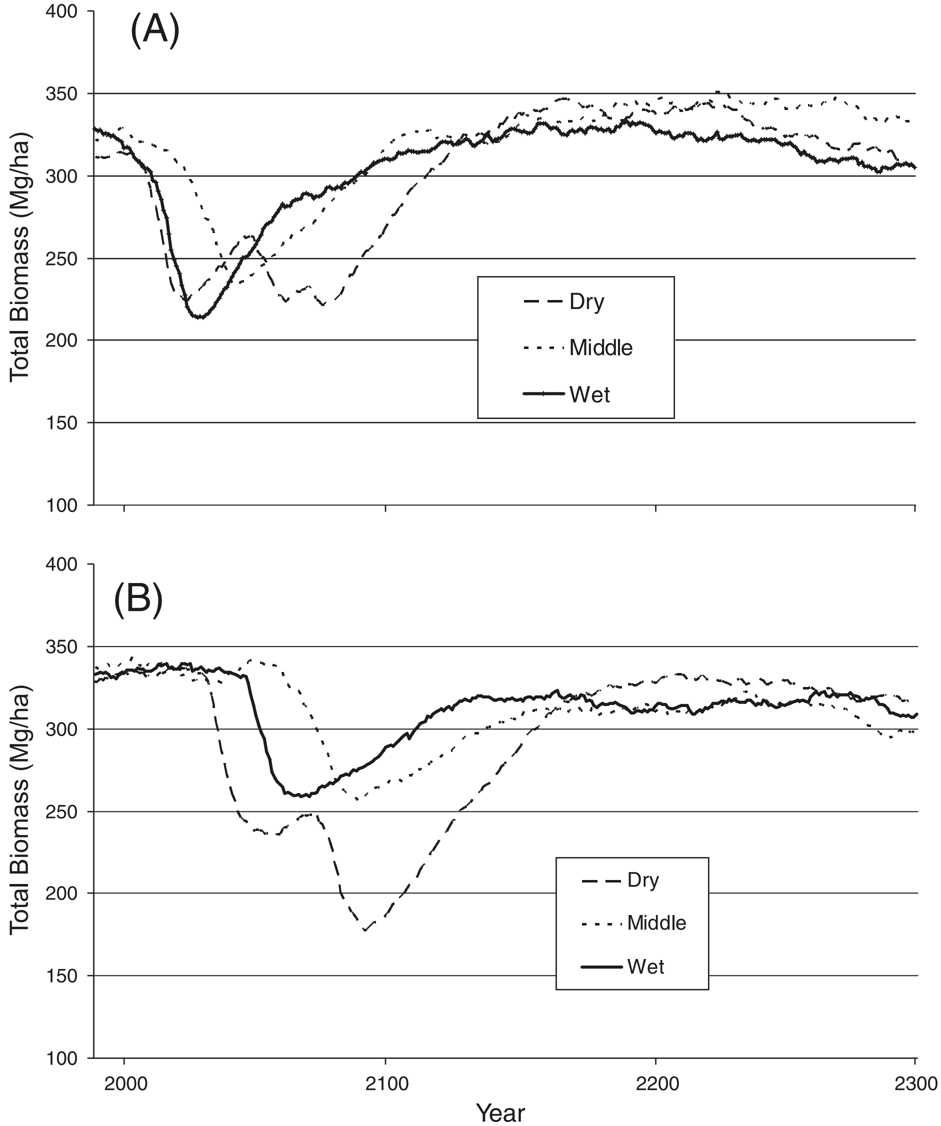


Fig. 4. Projected changes over time in total biomass for the Cumberland (A) Plateau and (B) Mountains.



pends on both precipitation and temperature. Model projections show an increase in AET over time and then a leveling off for all scenarios as climate conditions stabilize (Fig. 7).

Landscape changes

The projected changes in the landscape result in large changes in the area and distribution of transitional and cleared lands (Fig. 8). An examination of the changes in area by land-cover types shows that most types decrease (Table 2). We also examined patch size because it is an important indicator of habitat and forest continuity in the face of future disturbance. At the same time, the mean patch area of mesic deciduous forest on the plateau declines by 30% and in the mountains declines by 77%. All other forest types experience a decline in mean patch area, but the change for the mesic deciduous forest is the greatest. Even the transitional and cleared lands have a decline in mean patch areas of 25% and 49%, respectively, for the plateau and 48% and 13%, respectively, for the mountains. A decline in forest patch size is likely to have negative impacts on interior forest animals, such as the cerulean warbler (Buehler et al. 2006).

Hemlock is an important species in the mesic mixed and mesic evergreen forest types of both the Cumberland Plateau and Mountains. Its loss from those forest types will primarily cause changes in the cove forests where eastern hemlock can dominate.

Discussion

These analyses report different ways that forests in the Cumberland Plateau and Mountains can be affected by projected changes in environmental conditions. Clearly the effects of climate, land use, and hemlock woolly adelgid will all be important to consider both singly (as shown here) and in combination (the focus of future work). Climate changes instigate declines and then reestablishment of stand biomass as species composition within a stand shifts to that more suitable for the changing temperature and precipitation re-

Fig. 5. Projected changes over time in percentage of biomass of major species under three general circulation models for the Cumberland Plateau.

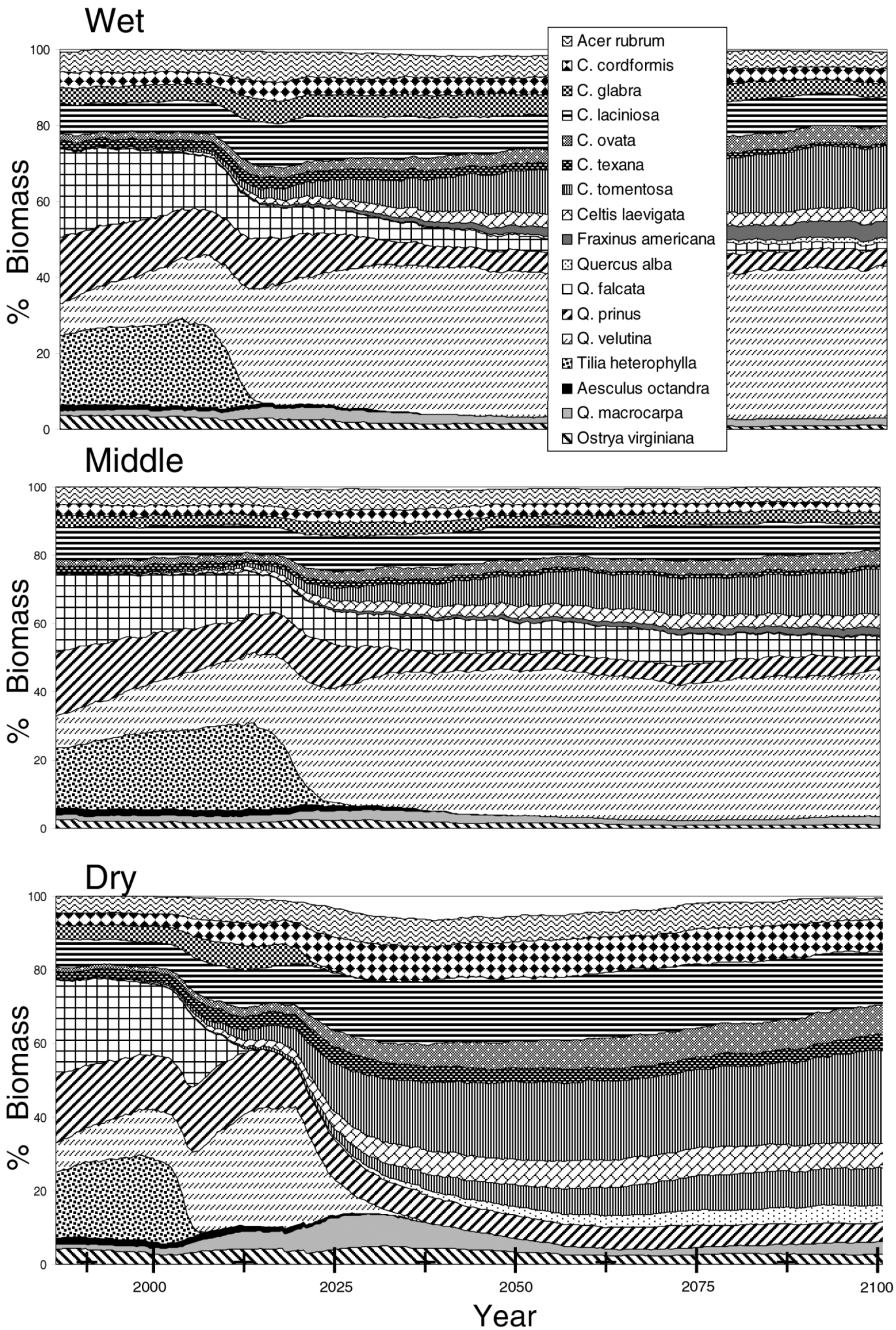


Fig. 6. Projected changes over time in percentage of biomass of major species under three general circulation models for the Cumberland Mountains.

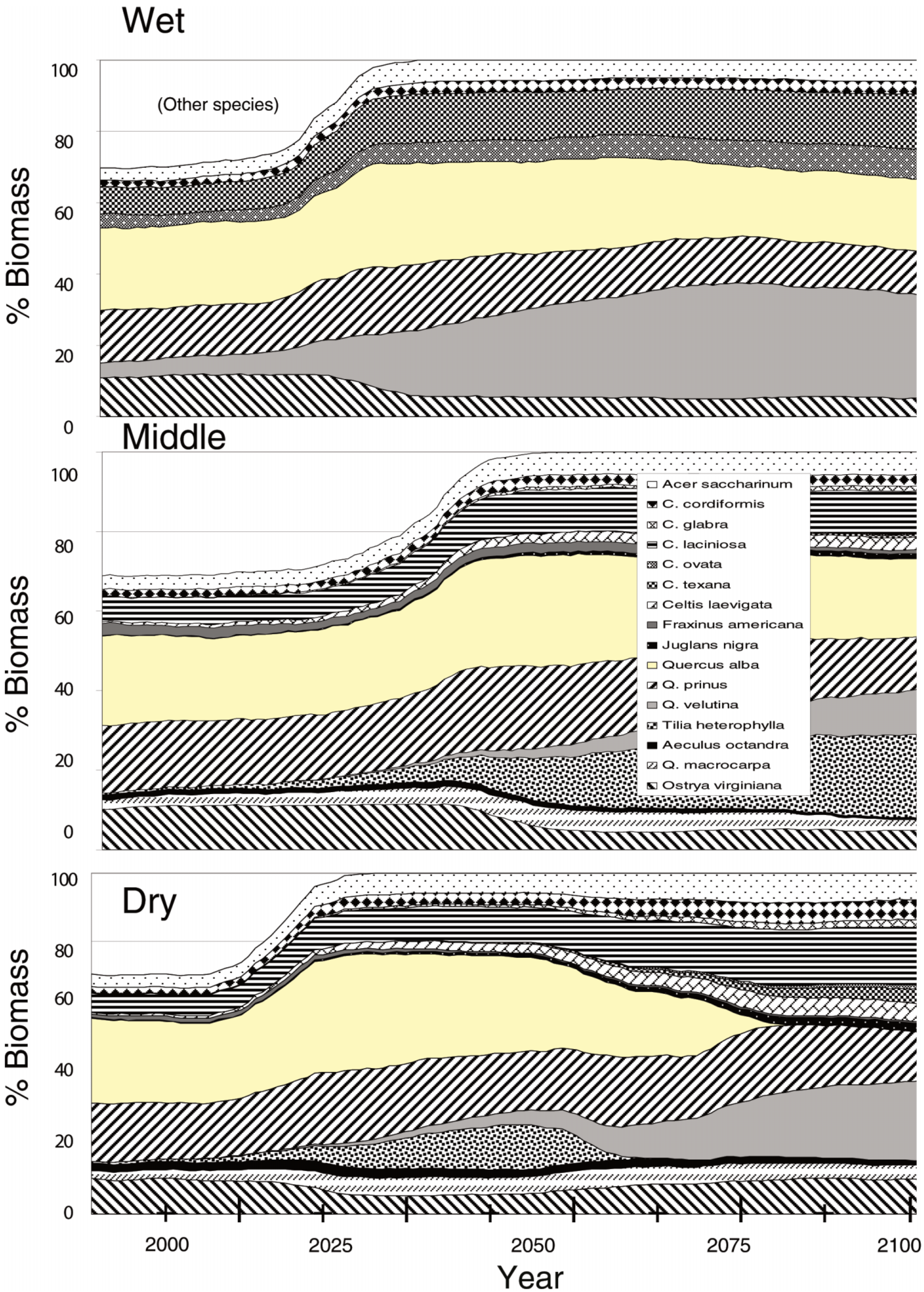
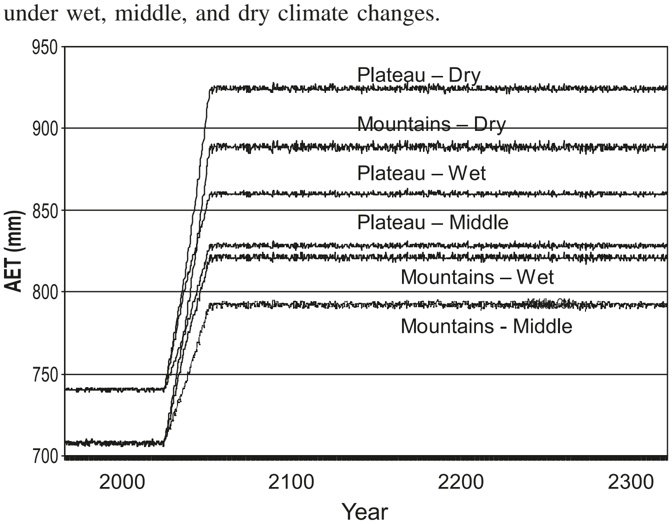


Table 2. Current and potential land cover in the northern Cumberland Plateau and Mountains.

	Early twenty-first century				Projected landscape changes			
	Area (ha)	Area (%)	Mean patch area (ha)	Median patch area (ha)	Area (ha)	Area (%)	Mean patch area (ha)	Median patch area (ha)
Cumberland Plateau								
Natural cover								
Mesic deciduous	168 471	19.7	1.026	0.18	143 572	16.8	0.709	0.18
Mesic mixed	204 930	24.0	0.896	0.18	178 193	20.8	0.667	0.18
Mesic evergreen	52 022	6.1	0.446	0.18	47 754	5.6	0.416	0.18
Upland deciduous	94 355	11.0	0.551	0.18	78 017	9.1	0.475	0.18
Upland mixed	101 310	11.8	0.402	0.18	84 294	9.9	0.363	0.18
Xeric mixed	17 700	2.1	0.218	0.18	15 070	1.8	0.213	0.09
Xeric evergreen	4 814	0.6	0.181	0.09	4 380	0.5	0.181	0.09
Anthropogenic cover								
Upland evergreen	25 846	3.0	0.314	0.18	23 226	2.7	0.308	0.09
Transitional	86 041	10.1	0.627	0.27	132 308	15.5	0.469	0.18
Cleared	66 911	7.8	0.994	0.27	117 514	13.7	0.506	0.18
Pasture or nonforested	30 216	3.5	0.625	0.18	28 288	3.3	0.599	0.18
Urban	2 416	0.3	4.773	0.45	2 416	0.3	4.773	0.45
Total	855 031				855 031			
Cumberland Mountains								
Natural cover								
Mesic deciduous	75 704	45.6	2.3	0.18	41 205	24.8	0.528	0.09
Mesic mixed	15 143	9.1	0.3	0.09	9 789	5.9	0.219	0.09
Mesic evergreen	3 030	1.8	0.3	0.09	1 963	1.2	0.216	0.09
Xeric deciduous	36 708	22.1	1.0	0.18	25 963	15.6	0.481	0.18
Xeric mixed	12 472	7.5	0.3	0.18	9 022	5.4	0.249	0.09
Xeric evergreen	858	0.5	0.2	0.09	614	0.4	0.169	0.09
Anthropogenic cover								
Transitional	11 188	6.7	0.4	0.18	30 425	18.3	0.207	0.09
Cleared	10 896	6.6	0.7	0.18	47 018	28.3	0.612	0.18
Urban	99	0.1	1.9	0.18	99	0.1	1.85	0.18
Total	166 097				166 097			

Note: Water not shown.

Fig. 7. Actual evapotranspiration (AET) projected over time with the LINKAGES model for the Cumberlands Plateau and Mountains under wet, middle, and dry climate changes.



gimes. Field studies in other temperate forests have also found an increase in the rate of tree mortality coincident with climate change (van Mantgem and Stephenson 2007) and likely in response to changing AET. As simulated here, land-use effects are largely expressed as change in the area and the pattern of forest types across the landscape. In addition, hemlock's demise causes a change in the composition of forests in which it is now a part. Together, the loss of forest area, forest fragmentation, the death of hemlock, and the changes in stand and species biomass will result in a greatly different forest ecosystem than is currently present on the Cumberland Plateau and Mountains.

It is unclear how changes in forest species composition, changes in nutrient conditions, and turnover rates affect the overall ecosystem. Prior changes in Cumberland forest composition due to the death of the chestnut trees have been documented to affect both the canopy and subcanopy trees (Myers et al. 2004).

The loss of hemlock from the mesic mixed and mesic evergreen forest types is likely to have effects on the entire system. Similar to these projections, Fuller (1998) reported that a rapid and synchronous hemlock's decline in southern Ontario about 5400 years ago that was likely the result of a pathogen outbreak caused a long-term shift in forest composition. Furthermore, Stadler et al. (2006) suggested that associated progressive needle loss and changes in needle chemistry are likely to produce a normal dissolved organic

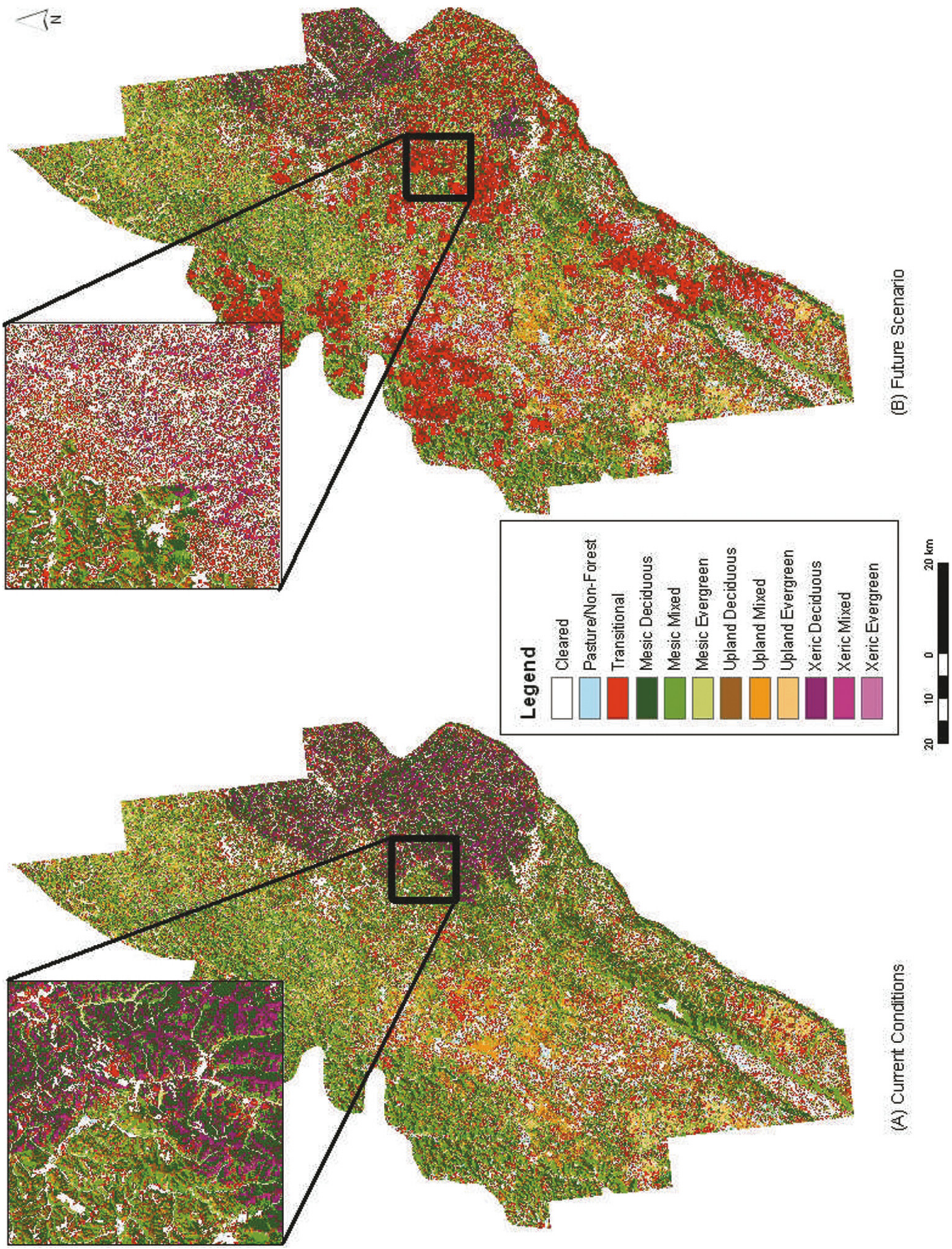


Fig. 8. Maps of land cover in the Cumberlands under (A) current conditions and (B) future scenarios, as defined in Table 1.

carbon curve, while nitrogen fluxes are likely to initially decrease as infestation continues but may rise as hemlock declines and hardwood species immigrate. These changes are greatly influenced by soil moisture levels (Cobb et al. 2006) and thus would be affected by climate change. In addition, just as the northern spread of hemlock woolly adelgid may be slowed or prevented by cold temperature (Skinner et al. 2003), warmer temperatures may enhance its spread. In a study of the effects of the hemlock woolly adelgid, Small et al. (2005) found that, as the hemlock basal area declined, there was a shift in canopy dominance to oak and mixed hardwoods, much understory development, and an expansion of several invasive shrubs and woody vines. These model results are consistent with the observations of Small et al. (2005). These changes will affect the structural and compositional conditions of the mesic evergreen landform associations on both the Cumberland Mountains and the Plateau, but the mesic evergreen landform will continue to exist. Fuller (1998) suggested that pathogenic outbreaks may be rare but extremely important events in forest dynamics. Dale et al. (2001) emphasized that disturbances that affect how forests respond to climate change include a variety of surprise events, such as introduction of invasive species, hurricanes, tornadoes, and fires.

Furthermore, Stadler et al. (2006) suggested that it is important to examine connections between fast and small-scale processes, such as changes in nutrient cycling in tree canopies, and slow and integrative processes, like shifts in composition of forest stands and landscapes, to fully understand the effects of hemlock woolly adelgid on forest ecosystem structure and function. We can expand these comments to include the effects of broad-scale alterations such as occur with climate and land-use changes. For example, changes in species composition and land-use distribution may create new habitats across the landscape and promote a greater diversity of animal species across the broad landscape (e.g., Bulluck and Buehler 2006).

These results show the importance of considering climate-change effects on forests in view of other changes to the region. Because trees are so long-lived and climate changes are occurring so rapidly, the research must combine modeling, experimental, and management approaches to be able to address complexities and scales of the challenge. We recognize that adapting to this need often requires a change in planning perspectives. A management approach engaged with research provides an appropriate way for decision makers to deal with the uncertainties inherent in climate change. Management actions can be treated as experiments that test hypotheses, answer questions, and thus, provide future management guidance. This approach requires that both conceptual models be developed and used and relevant data be collected and analyzed to improve understanding as the system changes.

There are key factors not included in this analysis. We did not consider the effects of increasing CO_2 on stand structure. Hanson et al. (2005) simulated increased temperatures and wetter winters in a model that includes elevated CO_2 and projected an 11% increase in stand biomass over 100 years and little change in species composition of an East Tennessee forest dominated by tulip poplar (*Liriodendron tulipifera*), white oak (*Quercus alba*), chestnut oak, and red maple. It is not clear how the more recent IPCC (2007) climate change estimates that include changes in summer precipitation would affect those projections.

Other disturbances are not included in our projections. For example, outbreaks of the native southern pine beetle occur at decadal intervals in the Cumberlands, and the most recent wide-scale death of pines is now affecting land use and managements, as much of the private forestry land is now for sale. In fact, the 1999–2001 outbreak that killed pine occupying over 155 000 ha in Tennessee (www.state.tn.us/agriculture/publications/forestry/forestinsectpests.pdf) is one reason why the Cumberlands are expected to undergo large changes in land use and management. Global climate change could intensify southern pine beetle infestation risk by 2.5–5 times and could account for 4–7.5 times higher mortality than the current number of trees killed annually (Gan 2004). Forest fire intensity, extent, and frequency may also increase with climate change (Flannigan et al. 2000; Dale et al. 2001). Fire initiation and spread depend on the amount and frequency of precipitation, the presence of ignition agents, and the prevailing environmental conditions (e.g., lightning, fuel availability and distribution, topography, temperature, relative humidity, and wind velocity). Yet, surprisingly there were no large-scale fires in the Cumberlands after the recent bark beetle outbreak left the landscape covered with standing, and later downed, dead trees. Earlier climate-change projections for a warmer and drier southeastern US produced a 30% increase in seasonal severity rating of fire hazard for the region (Dale et al. 2001). Fire can affect forests by altering nutrient cycling, killing trees, shifting successional direction, inducing seed germination, losing soil seed bank, increasing landscape heterogeneity, changing surface-soil organic layers and underground plant root and reproductive tissues, and volatilizing soil nutrients. Furthermore because trees can live for so long, climate-change impacts are expressed in forests, in part, through alterations in disturbance regimes (Dale et al. 2000). However, experimental studies that explored the effects of prescribed fire on the Cumberland Plateau on oak regeneration found that fire does reduce mid-story stem density, particularly of fire-sensitive species such as red maple (Gilbert et al. 2003), but there were no positive effects on oaks (Blankenship and Arthur 2006).

There are uncertainties in any model study. Because trees live so long, it is difficult to perform experiments to confirm or refute the model projections. It is not clear how combined perturbations will affect the forest system.

Conclusions

The climate-change projections for the Cumberlands suggest that temperature will increase in all regions for all months in both 2030 and 2080 for all three GCMs and that projected changes in precipitation are less strong and less consistent. The forest projections suggest that abrupt declines in total stand biomass will be followed by a gradual increase to prior levels. The long-term recovery of biomass occurs beyond the IPCC (2007) projection period and thus adds to our understanding of how these forest systems respond over the long run to climate changes. At the same time, changes in forest stand species composition will occur for both the Cumberland Plateau and Mountains.

Changes in land use and spread of invasive species will also have major effects on forest composition and distribution in the Cumberlands. Land-use changes will also influence the type and distribution of habitats in the Cumberlands. The loss of eastern hemlock will likely affect soil nutrient and moisture conditions in mesic forests of the region. In summary, tools to examine direct effects of climate and land-use changes on forest systems suggest these changes can be quite significant, but to fully understand the effects, interactions should be considered.

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