FOREST COMPOSITION: MORE ALTERED BY FUTURE CLIMATE CHANGE THAN BY EURO-AMERICAN SETTLEMENT IN WESTERN NEW YORK AND PENNSYLVANIA?

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Abstract: The amount of forest compositional change that occurred due to Euro-American settlement over the past two centuries is compared with changes simulated to occur in the future under 2X and 3.5X atmospheric CO_2 scenarios. The comparison employs data from presettlement land survey records, modern forest inventory data, and future predictions from niche-based species distribution models. Comparisons are made in four independent study areas in western Pennsylvania and New York. Forest compositional changes in the recent past, attributed largely to anthropogenic factors other than climate change, are intermediate in size to changes predicted to occur as the result of climate change under the 2X CO_2 and 3.5X CO_2 scenarios. Results are similar across the four study areas, and are robust to variations in data collection and compilation methods. These results disagree with previous pollen-based estimates that suggested a greater relative influence of a 2X CO_2 climate change, but do indicate that a 3.5X CO_2 climate change may cause greater changes in forest composition than has already occurred due to anthropogenic impacts. [Key words: climate change, forest composition change, human impacts on the environment, Forest Inventory and Analysis, New York, Pennsylvania, presettlement land survey records, species distribution models.]

INTRODUCTION

Environmental change is an important focus of research in physical geography (Orme and Harden, 2008). In the context of global warming, researchers are especially interested in how anthropogenically induced changes compare with underlying natural ecosystem dynamics. Thus, researchers have reconstructed how ecosystems have changed in response to both past climate change and past human land use (e.g., Jackson and Hobbs, 2009; James, 2011), as well as predicted how

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they may change in the future in response to predicted future climate change and human land use (e.g., Ravenscroft et al., 2010). The relative magnitudes of naturally and anthropogenically induced changes are important because, although ecosystems have already survived several abrupt climate shifts during the Holocene (Peteet, 2000), present climate change is acting on forests that are already suffering from destruction, fragmentation, degradation, and increased rates of biological invasion due to human activities (Noss, 2001). Because change is ubiquitous, assessment of the role of human activities on the environment is a matter of degree, and a key component to its study is the quantification of how much change either has occurred or is predicted to occur (Overpeck et al., 1991). In this regard, it would be valuable to know if the amount of ecosystem change predicted to occur due to predicted future climate change is more, or less, than the amount of ecosystem change that has occurred in the recent past on a comparable time scale.

This question could be addressed using a variety of ecosystem structures, functions, or compositions; in this study we address it using forest tree community composition (hereafter referred to as forest composition). Changes in forest composition have been examined in retrospective studies using a variety of data types, including fossil pollen, land survey records, and tree rings (e.g., Egan and Howell, 2005; Hupy and Yansa, 2009). In this research we employ presettlement land survey records (PLSRs). These records are an accidental ecological survey, as land surveyors recorded trees while marking land for Euro-American settlement (Wang, 2005). PLSRs were employed in this study for three reasons. First, they are spatially extensive and spatially unbiased, being regularly distributed across the landscape along a rectilinear grid. Second, their use of individual trees as the resolution of observations makes them more compatible with modern forest surveys than other data such as fossil pollen percentages. Third, tree species were recorded at approximately the same proportion at which they occur in the forest; although species selection bias does occur (Mladenoff et al., 2002), the bias is not as large as it is in pollen records (Jacobson, 1981).

PLSRs have been compared with a variety of modern forest surveys, often using the Forest Inventory and Analysis (FIA) database created by the U.S. Department of Agriculture Forest Service. The FIA database consists of multiple trees from plots distributed across the landscape at a density of approximately one per 24.3 km^2 (Miles et al., 2001). Their spatial extensiveness and the stratified random manner in which they are gathered makes them a useful dataset for comparison with PLSRs. Comparisons of PLSRs with FIA records have found that the composition of present forests has been displaced from presettlement composition, with individual changes related to unique types of past land uses employed by humans (Dyer, 2001; Whitney and DeCant, 2003; Friedman and Reich, 2005). Although climatic factors may have played a role in changes in forest composition between presettlement and present (McEwan et al., 2011), most PLSR researchers have found evidence for the impacts of Euro-American settlement activities such as deforestation (Rhemtulla et al., 2007; Schulte et al., 2007; Wang et al., 2010), changes in fire frequency (Lorimer, 1977; Grimm, 1984; Whitney, 1986) and introduced tree diseases (Seischab, 1992; Mikan et al., 1994). For example, Wang et al. (2010) found that the difference between presettlement and present forests, as quantified using a multivariate distance metric, was directly related to the percentage of a landscape that had in the past been cleared for agriculture but was later abandoned and returned to forest. In contrast, analyses of changes in the abundances of species at the northern and southern ends of their geographical distribution yielded no significant results that might indicate change being related to climatic tolerance (unpubl. data). Therefore, forest compositional changes from presettlement to present have largely been the result of anthropogenic factors other than climate change.

Changes in forest composition predicted to occur due to predicted future climate change have been explored at a variety of scales and using a variety of methods (Tang and Bartlein, 2008). These predictions include changes in the relative abundance of different species in individual locations, shifts in the geographic range of a species, and the development of non-analog communities (Iverson et al., 2008). Overpeck et al. (1991) predicted that the current vegetation of the eastern United States would be as different from the vegetation under a 2X CO_2 climate as it is to the vegetation of at least 7000 years ago. In addition, they predicted that the rate of change in vegetation would be at least twice as great as that which has occurred over any 250-year period during the past 18,000 years. Their predictions, however, were based on only seven pollen taxa, and used older climate model predictions. Surprisingly, we have not been able to find a study more recent than that of Overpeck et al. (1991) that calculates the amount of change in community composition between presettlement, present, and following future climate change.

In this study, we compare the present forest composition of four adjacent study areas in New York and Pennsylvania with their reconstructed presettlement forest composition and with their predicted future forest compositions. Four distinct areas are used to provide robustness to our results, because the four presettlement surveys were conducted by different agencies, included different types of PLSRs, and were compiled by different researchers. Changes in forest composition between presettlement and present are the result of climate and a variety of anthropogenic factors, including introduced tree diseases, fire suppression, and land-use changes (including old-field succession). However, the predicted forest composition under predicted future climate change that we employ is based solely on a change in climate (Iverson et al., 2008). Predictions made by such species distribution models (SDMs) have a number of limitations (Dormann, 2007; Elith and Leathwick, 2009), but are nonetheless essential for the exploration of ecological change (Elith et al., 2010). The hypothesis we test in this research is that future changes in forest composition that are predicted to occur due to predicted climate change will be greater than the changes in forest composition that have already occurred due to the combination of climate change and anthropogenic factors between presettlement and present.

STUDY AREA

This study examines forests within the geographic bounds of four distinct, but geographically adjacent areas that have had their PLSRs compiled and published (Fig. 1): northwestern Pennsylvania (NWPA) (Whitney and DeCant, 2003), northern Pennsylvania (NPA) (Black et al., 2006), western New York (WNY) (Wang, 2007),

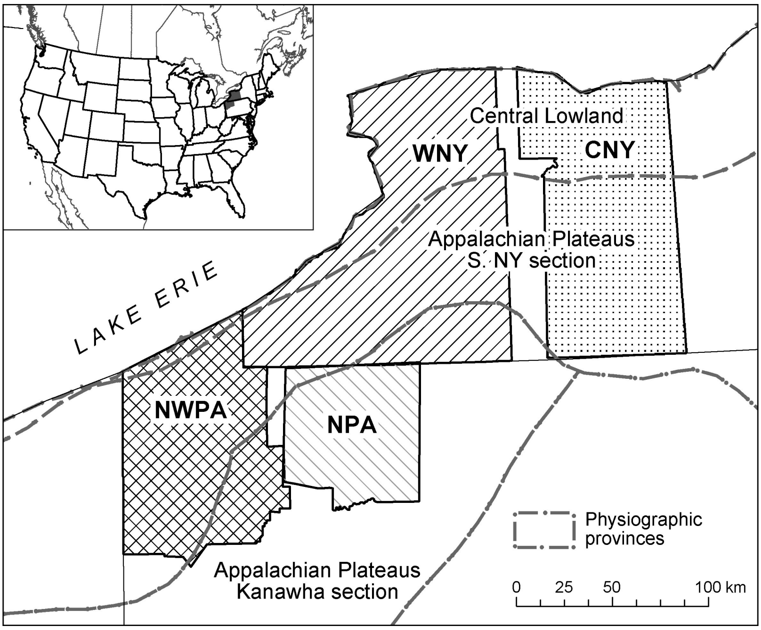

Fig. 1. Location of the four study areas across the three physiographic regions.

and central New York (CNY) (Seischab, 1990). The four areas range in size from 4828 km^2 in NPA to 14,400 km^2 in WNY (Table 1).

The four study areas are all within the temperate deciduous forest biome and contain a similar set of physiographic regions (Fenneman, 1938) (Fig. 1). Presettlement forests in the four areas were dominated by similar species (Table 2), with all having beech (*Fagus grandifolia*) as one of the two most abundant species.

METHODS

Data Sources

Presettlement. The four areas were surveyed in a similar time period, all beginning between 1785 and 1797 (Table 1). Survey data from NPA and NWPA are for a longer period, as the PLSRs collected by the authors of those studies also included patent (lot) sales that were surveyed later, as late as 1840. The relative abundance of tree species for all study areas except CNY was given as the percent of bearing trees, with the number of bearing trees ranging between 1611 and 8792 (Table 1). For CNY, Seischab (1990) calculated the relative abundance of a species as a weighted estimate of the order in which a species was mentioned in the line-tree descriptions. It is expected that the weighted line data will provide a similar reconstruction as would bearing trees,[1] because, in the adjacent 14,400 km^2 WNY area, the species

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[1] Bearing trees consist of trees marked and recorded at regular distances when town and lot boundaries were surveyed (Wang, 2005).

Table 1. Data Attributes for the Four Study Areas and Different Time Periods

	NWPA	NPA	WNY	CNY
Area (km^2)	8320	4828	14,400	9510
Presettlement Land Survey Records				
Trees or lines	6000	1611	8792	1044 mile-lines
Year	1785–1840	1790–1820	1797–1799	1789–1792
Forest Inventory Analysis plot data				
Trees	1843	2517	2481	1719
Plots	186	176	210	160
Year	2002–2007	2002–2007	2002–2007	2002–2007
Climate change predictions				
Grids (full or part)	30	16	42	34

Table 2. The Two Most Abundant Species in Each of the Time Periods and Datasets, Determined Using Percent of Trees (%) or Importance Values (IV)

NWPA	NPA	WNY	CNY
Presettlement Land Survey Records (%)			
White oak	American beech	American beech	American beech
American beech	Eastern hemlock	Sugar maple	Sugar maple
Forest Inventory Analysis data plots (% and IV)			
Red maple	Red maple	Sugar maple	Sugar maple
Black cherry	Black cherry	Red maple	Red maple
Forest Inventory Analysis data (IV predictions)			
Red maple	American beech	White ash	White ash
Black cherry	Red maple	Sugar maple	Sugar maple
2X CO$_2$ climate (IV predictions)			
Red maple	Red maple	White ash	White ash
Sugar maple	Black cherry	Red maple	Red maple
3.5X CO$_2$ climate (IV predictions)			
Post oak	White oak	Post oak	Post oak
Black oak	Post oak	White oak	White oak

abundances from bearing-tree data (Wang, 2007) and from line data weighted in the same way as in CNY (Seischab, 1992) had an r^2 of 0.90 when regressed against each other. A georeferenced outline of each of the PLSR study areas was obtained by using the current political boundaries and, for sections of the study area that did not follow political boundaries, digitizing the study area map from the originating publication.

Predicted future climate change. Predictions of equilibrium forest composition for 134 tree species under different climate change scenarios, using 38 environmental variables (Iverson et al., 2008), were obtained from the authors. Their prediction for each species was made using a three-step approach. In the first step, they selected the tree species data that they would use from the FIA database and placed them in a 20 × 20 km grid. Second, they modeled the relationship between the Importance Value (IV) of a species and the 38 environmental variables using three methods: regression tree analysis (RTA), bagging trees (BT), and random forests (RF). They used the results from the RF model to predict the abundance of a species under climate change, as earlier studies had indicated that RF models provided superior results than RTA, BT, or multi-adaptive regression splines (Prasad et al., 2006). This niche-based species distribution model is really a model of potential habitat for the species, but if unrestricted dispersal is assumed, then it would also be the distribution of the species. Third, they created an overall assessment of the reliability of each species model by combining five measures of reliability from the RTA, BT, and RF models. Reliability ranges between a theoretical low of zero and a high of one, and they considered a reliability measure of 0.50 or greater to be good. The reliability of the 134 species models ranged from 0.07 to 0.75, and had a median value of 0.43.

Forest predictions employed climate predictions from two different greenhouse gas emissions scenarios and three different climatic models. The two emissions scenarios correspond to the equilibrium climate under atmospheric concentrations of roughly 2X (550 ppm) and 3.5X CO_2 (970 ppm), corresponding to low and high predictions of CO_2 concentrations at the end of the 21st century. Abundances of individual species were predicted by Iverson et al. (2008) as IVs that represent an equal weighting of basal area and relative abundance. They made such predictions using climate data from each of the three climate models and then created the average of those predictions that is used in this study. Although the predicted IVs for the 134 species should theoretically sum to a value of 100, they did not (mean sum for the four regions was 96 for FIA predictions, 106 for 2X CO_2, and 122 for 3.5X CO_2); the predicted IV of each species in a region was thus rescaled so that the sum of all species was 100. That the IVs did not sum to 100 is not surprising, as IVs were predicted for each species independently of all others and were thus not constrained to sum to 100. It is possible that the sum of IVs was progressively higher under 2X and 3.5X CO_2 conditions because they had progressively more species present (see the Results section).

The predictions were made for 20 × 20 km (400 km^2) grids. The total areas of the grids and portions of grids in each of the four study areas were determined by overlaying them with the georeferenced PLSR study area outline. The gridded area was the same as the PLSR area for NPA, but because partial grids along the Great Lakes were not used by Iverson et al. (2008), it was smaller than the PLSR area by 7.3% in NWPA, 12.6% in WNY, and 6.1% in CNY. The overall abundance for species under a climate scenario was calculated by multiplying its abundance in a grid by the portion that grid represented of the total study area.

Present. Information on present forests was obtained by using the United States FIA database (Bechtold and Patterson, 2005). The FIA program distributes inventory plots in a spatially stratified random manner across the county, with a density of one plot every 24.3 km^2 (6000 acres). The data were collected by the FIA annual inventory program that inventories approximately 20% of the plots in each state each year. Of the plots within the outline of each PLSR study area, only those coded as having a natural origin were selected. From those FIA plots, only trees with a diameter at breast height of greater than 22.9 cm (9 inches) were selected, to approximate the selection criteria of presettlement surveys. Since diameters were not recorded in the PLSRs used in this study, this 9-inch-diameter cutoff was inferred through a comparison of presettlement corner-to-tree distances and those that occur in modern WNY forests that are greater than 100 years in age (Kronenfeld and Wang, 2007; Wang et al., 2009).

The resulting FIA plot data for each PLSR study area contained a minimum of 160 plots and 1719 trees (CNY) and a maximum of 210 plots (WNY) and 2517 trees (NPA) (Table 1). Because the 20 × 20 km climate-change grids of Iverson et al. (2008) did not completely cover three of the PLSR study areas, FIA plots were identified that were in both the study area and the climate change grids. The number of FIA plots in this gridded area was unchanged for NPA, and less than that in the total PLSR study area by 6.5% in NWPA, 5.7% in WNY, and 5.6% in CNY.

The following six tree species and four tree genera were removed from the FIA plot data, as they were introduced or cultivated, and thus were not present in either the PLSR or climate change databases: *Acer platanoides*, *Larix* spp., *Malus* spp., *Picea abies*, *Picea pungens*, *Picea rubens*, *Pinus sylvestris*, *Prunus avium*, *Prunus* spp. and *Salix* spp. If *Larix*, *Prunus,* or *Salix* were identified to species, they were retained; but if not, they were deleted as they might have been non-native. The sum of exotic trees removed was: zero in NPA, 1.3% in NWPA, 3.4% in WNY and 4.3% in CNY. Following their removal, the percentages and IVs of all remaining species were rescaled to sum to 100.

The trees in all plots in a PLSR study area were used to calculate relative abundance in two ways: as a percentage of all trees to compare with the percentages available for the PLSRs, and as IVs to compare with the IVs available for the climate change predictions. Those empirical records of the FIA plot data were complemented by the use of IVs predicted for the present using the same environmental models that were employed to predict IVs under future climate change scenarios (Iverson et al., 2008). Because these predictions employ the overall environment of the study area, they might provide a better general representation of the abundance of a species than was suggested by averaging the abundances of trees in individual plots within the study area.

Analytic Methods

Analyses took place in three steps: aggregating tree species to a common taxonomic level, measuring compositional change between time periods for each study area, and comparing amounts of change between different types of transition.

Aggregating tree species. The taxonomic resolution of the PLSRs was not always to the species level. For example, while the surveyors in WNY (Wang, 2007) recognized the same two species of walnut that are identified in the FIA and climate change data, *Juglans nigra* and *Juglans cinera*, the surveyors in NPA (Black et al.,

2006) only recognized the genus *Juglans*. To enable our analyses, this required that the FIA and the climate change species data be aggregated to the same taxonomic resolution as used in the corresponding PLSRs for that study area. Thus, while walnut retained its taxonomic resolution of two species for the FIA and climate change data in WNY, it was aggregated to the level of one genus for the FIA and climate change data in NPA. The taxonomic correspondences that were employed came from the originating papers for each of the four studies. If a species present in the FIA or climate-change data was not mentioned in the taxonomic correspondences used in the original author's paper, the species was retained for analyses but was not aggregated with any other species. Differences in species aggregations in different PSLR study areas disallow comparisons between them.

Assessing reliability of species predictions. The model reliability for all of the species abundances predicted by Iverson et al. (2008) to occur in any one area *k* in any one time period *A*, can be combined to create a weighted forest compositional reliability (WFCR):

$$\mathrm{WFCR}_k = \sum_{i=1}^{n} A_{ki} \cdot R_i \tag{1}$$

where *n* is the number of taxa, A_{ki} is the IV of taxon *i* in region *k* during time period A, and R_i is the reliability of the model for species *i* (from Supplement 1 in Iverson et al., 2008). The WFCR was calculated for each of the FIA, 2X CO_2, and 3.5X CO_2 predictions made by Iverson et al. (2008), following the aggregation of species abundances to match the PLSR tree taxonomies for each study area. Note that the WFCR, like the measure of reliability for individual species, ranges from a theoretical low of 0 to a high of 1.

Calculating forest compositional turnover. The forest change between any two time periods *A* and *B* for any study area *k*, was calculated as the forest compositional turnover (FCT):

$$\mathrm{FCT}_k = \frac{\sum_{i=1}^{n} |A_{ki} - B_{ki}|}{2} \tag{2}$$

where *n* is the number of taxa, *A* and *B* are two time periods, and A_{ki} and B_{ki} are two datasets of either percentages or IVs of taxon *i* in region *k* (Wang et al., 2010). The numerator is the sum of the absolute differences between the abundance of a taxon in the two datasets; the denominator is two, so that the FCT has a maximum value of 100% rather than the less intuitive 200%. For example, assume that a study area contained three species (*a*, *b*, and *c*); in time period *A* taxon *a* = 60%, *b* = 38%, and *c* = 2%, and in time period *B* taxon *a* = 30%, *b* = 56%, and *c* = 4%. For this example, the FCT would be equal to (|60-30| + |38-56| + |2-4|)/2 = (30 + 18 + 2)/2 = 25.

FCTs were calculated for each of the four study areas for three different time intervals: presettlement (PLSR) to present (FIA), present (FIA) to 2X CO_2, and present (FIA) to 3.5X CO_2. FCTs were not calculated between different study areas as they had different levels of taxonomic aggregation, and in the case of Seischab (1990) employed different types of PLSR data.

FCTs were calculated using several variants of the data to assess the robustness of the results. First, the FIA data were expressed in three ways: measured percentages from plot data, measured IVs from plot data, and IVs predicted from environmentally modeled data. For the FIA plot data, percentages and IVs were both used, as the published PLSR data were in percentages and the published climate change data were in IVs. The predicted IVs were also used, as they were predicted in the same manner as were the climate change predictions, and differences between the results for the FIA plot IVs and predicted IVs might provide information on the influence of the prediction methods on the data.

Second, to assess the influence of minor taxa that are more common for the FIA-predicted IVs than for the measured presettlement and FIA data (Table 3), FCTs were also calculated following removal of minor values. Values of a taxon were considered minor if its abundance was less than 1.00 (% or IV); if a taxon had an observation of less than 1.00 in one time period (e.g., presettlement) and greater than 1.00 in another (e.g., present), then the presettlement observation would be deleted and the one for the present would be retained. The sum of the values of minor taxa that were removed varied greatly by location and time period. For example, for the NWPA study area (Whitney and DeCant, 2003), the sums of the minor taxa that were removed were 2.5% for PLSRs, 6.9% for FIA plot percent, 7.9% for predicted FIA IVs, and 15.8% for the 3.5X CO_2 climate. Such differences might strongly influence the relative size of FCTs between different time periods, and thus the results of the hypothesis tests. To remove this influence, following removal of minor values, all remaining values were rescaled so that all remaining taxa for that time period summed to 100 (% or IV).

Comparing forest compositional turnovers. The hypothesis was tested by calculating the numerical difference between pairs of FCTs. To assess the influence of different degrees of predicted climate change, two sub-hypotheses were tested: that the FCT from PLSR to FIA was greater than the FCT from FIA to 2X CO_2 and that the FCT from PLSR to FIA was greater than the FCT from FIA to 3.5X CO_2. The hypotheses were tested using the three forms of FIA data, and for each of them using all native taxa (NA) and only data with a value of $\geq$ 1.00 (% or IV) (NA1).

RESULTS

Forest Composition

Forests in the four areas show some consistency in the changes in the two most abundant species over the four time periods (Table 2). In the presettlement period, American beech was one of the two most abundant species in all four areas. In the current time period, represented by the FIA plot data, all four of the study areas had red maple (*Acer rubrum*) as one of the two most abundant species. Also for the current time period, at least one of the two most abundant species in each of the four study areas for the predicted IV data was also one of the two most abundant species in the FIA plot data. Under the 2X CO_2 climate, red maple was one of the two most abundant tree species in each of the four areas. Under the 3.5X CO_2 climate, post oak (*Quercus stellata*) was one of the two most abundant tree species in each of the four areas.

Table 3. Numbers of Tree Taxa with Values in Each Study Area for Six Types of Data and Three Data Standards[a]

	NWPA			NPA			WNY			CNY		
Type	N	NA	NA1	N	NA	NA1	N	NA	NA1	N	NA	NA1
PLSR	22	22	19	25	25	10	38	38	15	39	39	13
Plot%	46	36	15	29	23	13	41	33	17	47	39	15
PlotIV	46	36	16	29	23	14	41	33	17	47	39	15
PredIV	56	44	20	49	38	16	57	51	20	58	47	19
2X CO_2	64	55	29	50	41	26	72	63	29	71	59	26
3.5X CO_2	68	58	27	61	52	29	78	70	34	74	62	33

[a] The six types of data are: Presettlement Land Survey Records (PLSRs); percent of stems in FIA plot data (Plot %); importance values (IVs) in FIA plot data (Plot IV); predicted IVs (Pred. IV) made using environmental models by Iverson et al. (2008); and IVs for forests predicted under equilibrial 2X CO_2 and 3.5X CO_2 climates. The three data standards are the number of native taxa identified in the whole dataset (N); the number following aggregating of native taxa into the taxonomic groups used in the PLSRs (NA); and the number of native, aggregated taxa with observations of greater than or equal to 1.00 (% or IV) (NA1).

The forests also showed some temporal resilience in terms of the two most abundant species. First, sugar maple (*A. saccharum*) was one of the two most abundant species in WNY and CNY during both the presettlement and in the FIA plot and predicted data. Second, red maple was the most abundant species in both the FIA plot data and under the 2X CO_2 climate in NWPA, NPA and WNY. Third, white ash (*Fraxinus americana*) was the most abundant species in the FIA predicted data and under the 2X CO_2 climate for WNY and CNY.

The total number of all species (*N*) observed in each of the four areas increased in this order: PLSR, FIA Plot percentage and Plot IV, FIA Pred IV, 2X CO_2, and 3.5X CO_2 (Table 3). This pattern was the same when species were aggregated as in the presettlement data (NA). Following removal of minor observations (NA1), the number of taxa became similar for the PLSR, FIA Plot (% and IV), and predicted FIA data, but were typically still progressively higher under the 2X CO_2 and then 3.5X CO_2 climates.

The WFCRs for the three time periods were highest for FIA Pred IV (ranging between 47.5 and 55.6 for four study areas) intermediate for the 2X CO_2 predictions (45.9 to 49.3), and lowest for the 3.5X CO_2 predictions (44.4 to 45.9). For each time period the WFCR was lowest for WNY (median = 45.9) and highest for NWPA (median = 49.3).

Forest Compositional Turnovers

The FCTs ranged from a low of 31.4 to a high of 71.7 (Table 4). The smallest FCTs for all four areas were for the FIA to 2X CO_2 transition, when using predicted FIA IVs with NA for NWPA and NPA, and when using predicted FIA IVs with NA1 for WNY and CNY. The largest FCTs for NWPA, NPA, and WNY were for the FIA to 3.5X CO_2 transition, when using NA1 with predicted FIA IVs for NWPA, when using NA1 with plot FIA percentages for NPA, and when using NA with plot percentage for WNY. The largest FCT for CNY was for the PLSR to FIA transition, when using NA1 and predicted FIA IVs.

Comparing Forest Compositional Turnovers

Difference pairs were calculated to compare the relative size of the FCTs between two different time periods. The difference pairs between PLSR to FIA and FIA to 2X CO_2 were all positive (Table 5). Thus, changes from presettlement to present were greater than predicted changes from present to predicted future under 2X CO_2 climate change scenarios. The difference pairs between PLSR to FIA and FIA to 3.5X CO_2 were all negative, except for those in CNY using predicted FIA IVs. Thus, the current forest is less different from the presettlement forest than it is to the predicted future 3.5X CO_2 forest.

DISCUSSION

Our results suggest that while there is much concern about the impact of climate change on forest composition (e.g., Iverson et al., 2008; Tang and Bartlein, 2008),

Table 4. Forest Compositional Turnovers (FCTs) between Presettlement (PLSR), Present (FIA), and Forests Predicted under Equilibrial 2X CO_2 and 3.5X CO_2 Climates[a]

	NWPA		NPA		WNY		CNY	
FIA data	NA	NA1	NA	NA1	NA	NA1	NA	NA1
PLSR to FIA								
Plot %	50.8	53.4	53.9	57.9	46.3	47.2	42.1	44.3
Plot IV	49.4	51.3	54.4	58.7	47.4	48.1	42.1	44.5
Pred. IV	47.6	51.7	49.4	54.2	56.4	53.5	56.5	58.2
FIA to 2X CO_2								
Plot %	44.3	46.2	37.3	37.0	44.0	43.8	38.1	36.3
Plot IV	43.3	44.7	37.1	37.2	44.0	43.9	38.6	36.7
Pred. IV	38.3	39.1	32.0	35.6	34.8	33.8	32.1	31.4
FIA to 3.5X CO_2								
Plot %	67.7	**71.7**	**68.0**	69.0	66.5	71.5	54.3	53.2
Plot IV	**67.9**	71.0	**68.0**	69.2	**66.6**	**71.7**	54.3	53.0
Pred. IV	67.3	71.4	65.4	**72.5**	61.9	61.8	54.8	56.1

[a] FCTs were calculated using all native species aggregated to the PLSR taxa (NA), and using only those taxa with a percent abundance or IV greater than or equal to 1.00 (NA1), the sums of which for that data type were then rescaled to sum to 100%. The largest value in each column is indicated in bold type.

the amount that has already occurred due to Euro-American settlement is more than that predicted to occur in the future from a predicted 2X CO_2 climate (Tables 4 and 5). These results differ from those of Overpeck et al. (1991), who suggested that the amount of change due to a predicted 2X CO_2 climate would be more than that which occurred due to Euro-American settlement and equal to that which occurred due to climate change over the past 7000 years. The different results are likely largely a result of them using only seven pollen taxa, rather than the large number of tree species that make up a forest, in combination with the non-linear relations between the abundance of a pollen taxon and the vegetation that created it (Webb et al., 1981). A further limitation of their study was that their most recent pollen samples contained a mixture of pollen from pre- and post-settlement (St. Jacques et al., 2008) that disallowed them from estimating the amount of change between presettlement and present, as we have done, and also influenced the rate of change they suggest between present and predicted future vegetation.

The amount of compositional change that has already occurred in each of the four study areas between presettlement and present, though greater than predicted from a 2X CO_2 climate scenario, is substantially less than that predicted from a 3.5X CO_2 climate scenario (Tables 4 and 5). Temporal rates of change are more difficult to compare. The future climate change scenarios we used are based on predicted CO_2

Table 5. Differences in the Size of Pairs of Forest Compositional Turnovers (FCTs) from Table 4, Using the Acronyms Given in Tables 3 and 4[a]

FIA	NWPA		NPA		WNY		CNY	
	NA	NA1	NA	NA1	NA	NA1	NA	NA1
(PLSR to FIA) minus (FIA to 2X CO_2)								
Plot %	6.5	7.2	16.6	20.9	2.3	3.4	4.0	8.0
Plot IV	6.1	6.6	17.3	21.5	3.4	4.2	3.5	7.8
Pred. IV	9.3	12.6	17.4	18.6	21.6	19.7	24.4	26.8
(PLSR to FIA) minus (FIA to 3.5X CO_2)								
Plot %	**–16.9**	**–18.3**	**–14.1**	**–11.1**	**–20.2**	**–24.3**	**–12.2**	**–8.9**
Plot IV	**–18.5**	**–19.7**	**–13.6**	**–10.5**	**–19.2**	**–23.6**	**–12.2**	**–8.5**
Pred. IV	**–19.7**	**–19.7**	**–16.0**	**–18.3**	**–5.5**	**–8.3**	1.7	2.1

[a] For example, the value of 6.5 in this table for the Plot% NA data in NWPA was calculated using the FCT values from Table 4 of 50.8 (the FCT from PLSR to FIA for the Plot % NA values in NWPA) minus 44.3 (the FCT from FIA to 2X CO_2 for the Plot % NA values in NWPA). All differences with a negative value are indicated in bold type.

levels for the year 2100, so these changes would occur in less than a century if forest composition were to adjust to climate instantaneously. However, because species dispersal is restricted, there may be a significant lag in forest response to climate change, and, as a result, an equilibrium species composition would not be achieved instantaneously if ever (Morin et al., 2008). This restricted dispersal might result in FCTs being lower than those predicted following climate change, though it is possible that if extant species are weakened by the changed climate, then they might be lost in favor of invasive and early successional native species, and thus still result in a high FCT. A further problem with the predictions is that they exhibit progressively lower WFCRs (Eq. 1) under progressively more climate change in these study areas, suggesting that FCTs could vary markedly around the value that we calculated. Relatedly, changes in species composition from presettlement to present did not occur gradually, with most of the resultant FCT appearing to be due to agricultural land clearance that began to slow in the late 19th century (Wang et al., 2010).

The finding that forest compositional change due to Euro-American settlement is intermediate in magnitude relative to those predicted to occur due to 2X CO_2 and 3.5X CO_2 climate scenarios (Tables 4 and 5) is robust to at least five variants of the input data and methods of analysis. First, similar results were obtained in all four areas, even though the PLSRs from CNY were weighted line data, while those from the other three study areas were bearing-tree data. Second, similar results were obtained from all four areas, despite unknown differences in presettlement species identifications made by different surveyors within and between the four study areas. Third, similar results were obtained when the present forest was represented using FIA plot percentage data, FIA plot IV data, and predicted FIA IV data. Fourth, similar results were obtained when FIA plot data from the older periodic survey system were employed (NWPA and NPA from 1989, WNY and CNY from 1993) (results not shown). Fifth, similar results were obtained when analyses employed all taxa or only taxa present at a value of 1.00 (% or IV).

The species abundances predicted for the 2X and 3.5X CO_2 climates must also be considered in terms of the potential uncertainties addressed. Recent reviews have pointed out a number of factors that can introduce uncertainty into SDMs (Heikkinen et al., 2006; Dormann, 2007; Elith and Leathwick, 2009) and that should thus be considered in good SDM studies. In this regard, the predictions made by Iverson et al. (2008) compared different modeling techniques, measured model reliability, used ecologically relevant variables, used appropriate models for both explanation (RTA) and prediction (RF), and used a method of prediction (RF) that deals well with multi-collinear data and, in their estimation, extrapolates well into novel environments. Their modeling did not, however, explicitly address issues of spatial scale. In addition, and acknowledged by Iverson et al. (2008), their approach to SDM involves the use of what are called correlative or niche models that simply predict suitable habitat for a species, not the actual locations that they will occupy. These niche SDMs, unlike mechanistic SDMs (Kearney and Porter, 2009), do not include dynamic processes such species interactions, disease, disturbance, or CO_2 fertilization, the inclusion of which can markedly change predictions for future vegetation relative to those from niche-based models (e.g., Morin et al., 2008; Keenan et al., 2011).

While our results suggest that the FCT will be higher between present and presettlement than it will be between present and 2X CO_2 (Tables 4 and 5), the two situations will differ across the landscape. While climate change will influence the composition of all forests, Euro-American forest clearance left relict patches that retained their natural species composition and were thus able to influence the species composition of forests that developed after adjacent cleared land was later abandoned (Wang et al., 2010). Thus, the current landscape displays a heterogeneity of FCTs relative to the presettlement (Wang et al., 2010), while the predicted future landscape will likely have a homogeneity of FCTs relative to presettlement, unless maintained by continued land clearance and abandonment. If fire suppression in many forests of the eastern U.S. continues, then mesophication (Nowacki and Abrams, 2008) should result in those that had much presettlement fire having higher FCTs than will occur in study areas such as ours that had little presettlement fire.

The comparisons of vegetation composition between presettlement, present, and following climate change might differ if the predictions of vegetation under climate change were created using different approaches. For example, the predictions made by the niche-based statistical model of Iverson et al. (2008) might differ if the statistical model were calibrated and validated using presettlement data rather than current forest data, as presettlement species are primarily late successional whereas current forest species are primarily early successional. Indeed, the finding of resilience of red maple in NWPA and NPA and of white ash in WNY and CNY, between the FIA predictions and the 2X CO_2 predictions, may reflect the use by Iverson et al. (2008) of the predominantly early successional FIA forest data to parameterize their models. Although it would have been valuable to have included non-native species in the

FCT calculations, it was not possible, as their abundances under climate change were not predicted by Iverson et al. (2008).

Although our results suggest that historical rates of change in forest composition may be equal to or greater than the rates of change that will be induced by climate change over the next century (Tables 4 and 5), it should be remembered that changes in climate will occur in conjunction with continuing pressures from land-use change, introduction of new tree species and pathogens, fire suppression, and other anthropogenic factors (Noss, 2001). The combined effects of all anthropogenic factors will likely add to those from climate change, even though restricted species dispersal might reduce those effects and, as a result, the FCTs under an equilibrial 3.5X CO_2 climate scenario may be larger than we calculated. Although this does not diminish concern over the potential impact of climate change on forests in the region, it does highlight the importance of reducing existing anthropogenic stresses through good forest management.

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