Designing Sustainable Landscapes: Modeling Forest Succession and Disturbance

A project of the University of Massachusetts Landscape Ecology Lab

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1 Problem Statement

To accurately model landscape changes and the ecological consequences of the those changes overtime (McGarigal et al 2017), it is essential to account for vegetation disturbance processes and subsequent vegetation development (succession). Natural disturbances such as fire, wind, pathogens, floods, etc. and anthropogenic disturbances such as timber harvest are integral to determining the distribution of forest age/structure over the landscape. Disturbance models are therefore necessary to maintain a realistic distribution of stand age/structure overtime, preventing the landscape from uniformly succeeding to old-growth forest. Succession models then track changes of forest vegetation characteristics (e.g., biomass) as a forest undergoes succession following a disturbance. Specific forest vegetation characteristics are often important components of species-habitat models. Therefore, models of forest disturbance and succession are needed to account for the dynamic nature of forest vegetation characteristics in models that evaluate the effects of predicted changes in urban development and climate on a landscape's capability to support wildlife populations at future time steps.

2 Solution Statement

To model succession, we used FIA data to predict above-ground live biomass from stand age, growing degree days, growing season precipitation, soil pH, soil depth and soil available water supply by groups of similar forested ecological systems (hereafter, "macrogroup"). Thus, succession is implemented as a deterministic process in which each cell is attributed with the suite of ecological settings variables, and the predicted growth in biomass derived from a fitted statistical model for the corresponding macrogroup is added to the current biomass at each timestep.

To model disturbance, we used Forest Inventory and Analysis (FIA) data on total aboveground live biomass sampled at fixed locations over time to estimate the probability of vegetation disturbance per decade as a function of biomass by ecological region within forested ecological systems. We also used FIA data to model the severity of disturbance within each ecoregion, defined as the proportional loss of existing biomass. Lastly, we used the High-Resolution Global Maps of 21st-Century Forest Cover Change (Hansen et al. 2013) to model the disturbance patch size distribution. Thus, disturbance is implemented as a multi-stage stochastic process in which we first we randomly initiate disturbances within each ecoregion in forested ecological systems, and then randomly determine the severity of disturbance and patch size, and then grow the disturbance patch from the initiation cell.

3 Methods

3.1 FIA data

Given our reliance on FIA data in both the succession and disturbance model, a brief review of FIA is warranted. The FIA program of the U.S. Department of Agriculture Forest Service collects and makes publicly available detailed information of public and private forest stands within the U.S. Although FIA began collecting data in the early 1930's, FIA enhanced inventories from regional, periodic inventories to nationally consistent, annual inventories in the mid-1990's. Phase 2 of the enhanced FIA protocol samples fixed locations at a

density of one plot per 2,428 ha (intersections of a 5 km grid). Each plot consists of four, 18m radius subplots and 20% of plots within a state are sampled each year such that all plots within a state are sampled every 5 years (Bechtold and Patterson 2005). Typical FIA measurements describe:

- Tree diameter, length, damage, quality
- Tree regeneration
- Site quality
- Stocking
- Land use
- Forest type, stand age, and disturbance
- Tree growth, mortality and removals

FIA data is made publicly available (http://apps.fs.fed.us/fiadb-

<u>downloads/datamart.html</u>), however the geographic location of a plot is relatively confidential. Only the state in which a plot is located is made available. However, we were able to obtain permission to access the plot location data. FIA collects data for every tree within a plot and consequently the FIA database can be extremely complex. Therefore, we used the Forest Vegetation Simulator (FVS) to convert FIA data into the variable we were interested in: above-ground live biomass (Crookston 1997, Dixon 2003, Crookston and Dixon 2005).

3.2 Forest succession

We developed a statistical model of succession in forested ecological systems. This model was developed with the understanding (due to limited resources) that it was not intended to explicitly model the demographic processes that determine individual plant dispersal, establishment, growth, and mortality, or account for the community-level interactions among multiple competing species that ultimately determine the composition and structure of a forest stand. Rather, the intention of this model is to provide a simply but reasonably realistic representation of vegetation succession across the landscape that reflects the gross changes in forest structure over time due to vegetation development. In particular, we determined that it would be sufficient to model biomass change over time as an indicator of forest succession, and subsequently use biomass as a surrogate for successional stage in the wildlife-habitat relationships models.

3.2.1 Initial (current) biomass

A preprocessing step required for the vegetation succession model is to create the initial biomass grid for the current condition in 2010. For this purpose we used the Woods Hole NACP Aboveground National Biomass and Carbon Baseline Data V.2 (Kellndorfer et al. 2013) estimate of biomass and updated it with the High-Resolution Global Maps of 21st-Century Forest Cover Change (Hansen et al. 2013) and forest succession models to generate the current biomass grid (see biomass settings variable document for details, McGarigal et al 2017), as follows:

1) start with the NBCD dataset as the initial estimate of biomass for the year 2000;

- 2) convert biomass to expected stand age based on the appropriate regression model (as described below) for the corresponding macrogroup that describes biomass change as a function of stand age and a suite of ecological settings variables (growing degree days, growing season precipitation, soil pH, soil depth and soil available water supply). Note, any biomass value that exceeds the predicted value for stand age = 220 years (the maximum observed stand age in the FAI dataset) is assigned a stage age of 220;
- 3) advance stand age forward to 2012 (for consistency with the Hansen et al. data) by adding 12 years to stand age;
- 4) set stand age to the age since disturbance based on the Hansen et al. map of recent (2000-2012) stand-replacing disturbances. For example, a cell that was disturbed in 2005 would have an age of 7, whereas an undisturbed cell would have the predicted age in 2000 plus 12 years from step 3; and
- 5) apply the appropriate regression models to convert the adjusted stand ages in 2012 to predicted biomass.

The process above results in a map of predicted biomass for 2012, which we consider as the baseline condition in 2010.

3.2.2 Biomass development

We model forest succession as the growth in biomass over time. For this purpose we used FIA data on biomass and stand age at 14,457 fixed locations to estimate the growth in biomass per decade by forested macrogroup as a function of stand age and a variety of static and dynamic ecological settings variables, as follows:

- 1) select FIA plots within forested ecological systems (based on the DSLland map) that were sampled at least once between 1982-2012 (N=14,910);
- 2) treat each sampling occasion at each plot as an independent observation (N=36,486). Note, 2,175 plots were sampled once, 5,182 twice, 6,345 three times, and 1,207 four times between 1982-2012;
- drop any observation in which age=0 and biomass>0, or age>0 and biomass=0, as these were suspect observations (adjusted N=33,560 observations at 14,470 locations);
- 4) drop any observation with missing biomass or stand age data (adjusted N=33,447 observations at 14,457 locations);
- 5) drop all but the last sampling occasion at each plot to avoid pseudo-replication (N=14,457 observations at 14,457 locations). Note, in contrast to the disturbance modeling, here we deemed multiple observations from the same plot as problematic given the nature of the model and opted to keep only a single observation from each plot, which we arbitrarily chose to be the last sampling occasion. Note, keeping all observations and pseudo-replicating does not change the results;
- 6) use non-linear least squares regression to estimate the parameters of a monomolecular function (a.k.a. asymptotic exponential function) that describes the increase in biomass with stand age for each macrogroup, and if the sample size for the

macrogroup is >30, allow the asymptote of the function to vary as a function of growing degree days (gdd), growing season precipitation (precipgs), soil pH (soil.ph), soil available water supply (soil.aws) and/or soil depth (soil.depth). Note, gdd and precipgs are dynamic covariates since their values change over time in the model, whereas soil.ph, soil.aws and soil.depth are static covariates since their values are treated as constant over time. First, fit a minimum model containing only stand age and no additional covariates. Next, for macrogroups with >30 observations, add a second covariate to the model allowing it to adjust the asymptote of the monomolecular function, but only if the additional covariate is significant and choosing the covariate that is most significant. Continue to evaluate the addition of covariates in a forward stepwise fashion until no additional significant predictors can be added to the model. Note, soil available water supply was fit as a quadratic polynomial since it was reasoned that within the range of conditions sampled that biomass (i.e., productivity) would be greatest at intermediate vales and would be depressed if the soil were too wet or too dry. The full model containing all significant predictors has the following form:

$$y = (a + c \cdot gdd + d \cdot precipgs + e \cdot soil.ph + f \cdot soil.depth + g \cdot soil.aws + h \cdot soil.aws^{2}) \cdot (1 - e^{-b \cdot age})$$

where y = biomass, a = parameter that controls the asymptote, *b*-*h* are parameters of the corresponding spatial covariates.

The process above results in a non-linear regression model for each forested macrogroup in which the predicted biomass increases monotonically to an asymptote as a function of stand age as modified potentially by one or more spatial ecological settings variables reflecting climate conditions during the growing season and soil conditions affecting productivity (**Table 1**). The ecological settings variables affect the height of the asymptote and thus determine whether a forest stand in a particular macrogroup will produce more or less biomass over time than the average stand for that macrogroup (**Fig. 1**). Note, we considered several other plausible functional response forms such as the Michaelis-Menton function, which is a common functional response used in ecology to define plant growth with competition over time, the hyperbolic function, which is a common functional response used in ecology to define plant density with competition over time, and the Holling type III function, which is similar to the Michaelis-Menton but has a sigmoidal shape (Bolker 2008), but the monomolecular produced superior fits as judged by the minimum least squares criterion. Lastly, we made a general comparison of our biomass growth trajectories to similar values in the literature to ensure that our estimates were within reason for the region (Brown et al. 1997).

We used the epi.ccc function in the R package epiR (Stevenson et al. 2011) to calculate the concordance correlation coefficient (CCC) (Lin 1989) between values predicted by the growth trajectory models and the observed values derived from FIA. An assessment of the correlation coefficients between fitted and observed values appears to be a reasonable

Table 1. Non-linear regression models based on a monomolecular function to predict above-ground live biomass (Mg/ha) as a function of stand age, growing degree days (gdd), growing season precipitation (precipgs), soil pH, soil depth and soil available water supply (soil.aws) for forested macrogroups in the Northeast; N is the number of FIA plot locations sampled between 1997-2012; a is a parameter of the monomolecular function that affects the rate of increase in biomass during the early years of growth; the value for each of the environmental covariates determines how the asymptote of the monomolecular function is affected, with positive values indicating an increase in the asymptote above the mean with an increase in the covariate (note, soil available water supply is given as a quadratic polynomial such that the asymptote is highest at intermediate values); R² is a measure of the percentage of variance in biomass explained by the model; CCC is the coefficient of concordance between observed and predicted values.

Macrogroup	Ν	а	Age	Gdd	Precipgs	Soil ph	Soil depth	Soil aws	Soil aws ²	R ²	ссс
Boreal Upland Forest	1,430	82.16	0.017	-	0.0006	-	-	-	-	0.20	0.29
Central Hardwood Swamp	29	195.96	0.019	-	-	-	-	-	-	0.22	0.28
Central Oak-Pine	4,543	-99.72	0.023	0.0004	0.0010	5.27	-	49.68	-5.25	0.26	0.39
Coastal Plain Peat Swamp	17	195.96	0.019	-	-	-	-	-	-	0.37	0.42
Coastal Plain Swamp	200	-543.16	0.030	0.0013	-	46.8	-	129.74	-16.58	0.27	0.41
Northeastern Floodplain Forest	28	195.96	0.019	-	-	-	-	-	-	0.14	0.23
Northern Hardwood & Conifer	7,455	-68.74	0.016	0.0006	0.0016	9.15	0.0946	-	-	0.25	0.37
Northern Swamp	659	-238.49	0.016	0.0009	0.0015	28.2	0.0969	-	-	0.23	0.33
Southern Bottomland Forest	68	-284.40	0.070	0.0019	-	-	-	-	-	0.10	0.15
Southern Oak-Pine	4	195.96	0.019	-	-	-	-	-	-	0.33	0.48
Tidal Swamp	24	195.96	0.019	-	-	-	-	-	-	0.20	0.28



Figure 1. Scatter plot of above-ground live biomass (Mg/ha) against stand age (years) for 7,455 Forest Inventory and Analysis (FIA) plots distributed throughout Northern Hardwood and Conifer forests in the Northeast, along with the fitted non-linear regression line based on the monomolecular function given in the title at the mean, minimum and maximum of the covariates (growing degree days, growing season precipitation, soil pH, and soil depth.

method to assess model fit (Hsieh et al. 2008, Glaser et al. 2011). Although we do report R^2 values in **table 1**, it can be a misleading indicator of model fit since residuals in nonlinear regression often do not add to zero (Ritz and Streibig 2008). Note, the R^2 and *CCC* values are relatively low, reflecting the fact that numerous unaccounted for factors (e.g., competition, herbivory, etc.) influence the realized biomass at a site at any point in time, but we feel that they are acceptable given our interest in representing the general pattern of vegetation development at the regional scale.

3.2.3 The succession model

The forest vegetation succession model consists of the following steps:

- 1) mask out areas that are not forested so that succession only occurs in forested cells;
- 2) convert current biomass to expected stand age based on the statistical model for the corresponding macrogroup and, depending on the model, accounting for the static and dynamic spatial ecological setting of the cell; and

3) for each timestep of the model, increment stand age by 10 years and covert stand age back to expected biomass based on the corresponding statistical model as in step 2 (as described below).

Note, because some of the ecological settings variables are dynamic (i.e., change over time; e.g., growing degree days and growing season precipitation), we convert current biomass to expected stand age based on the current ecological settings values and the appropriate statistical model, predict the growth for the next 10 years based on that statistical model, compute the delta biomass (i.e., difference in biomass over 10 years), and add the delta to the original biomass. In this manner, we ensure a smooth biomass growth curve while adjusting the growth rate for the changing ecological conditions.

It is important to note three things about the succession model:

- 1. <u>Stand age</u> is used internally as a convenient state variable to track to state of each cell over time, but we are not interested in stand age per se and thus it is not reported as an outcome of the model; rather, we are interested in modeling the change in biomass over time. Unfortunately, modeling the growth in biomass as a function of biomass was not successful due to the noise in the FIA biomass data, so we opted to model the growth in biomass as a function of stand age based on the underlying assumption that biomass should increase with stand age in a somewhat predictable manner (in the absence of disturbance).
- 2. Because we estimate biomass based on the predicted (or expected) value from the non-linear regression model, we end up modeling growth in biomass as a <u>deterministic</u> rather than stochastic process. The estimated biomass of a cell for any timestep is given by the predicted value from the non-linear regression model. Thus, given any particular stand age and values for the relevant spatial ecological settings variables, we get the same predicted biomass. We deemed this appropriate since we are more interested in the expected or long-term average patterns in biomass rather than the stochastic outcome of any single landscape change trajectory, but we recognize that this eliminates the stochasticity that is present in any real-world landscape change trajectory.
- 3. Because we convert current biomass to the expected biomass for the corresponding stand age and ecological setting, we eliminate the noise, or error, in the originally observed biomass. The original biomass data contains significant variability that cannot be explained by stand age and the chosen ecological settings variables. Unfortunately, there is no way to maintain this unexplained variability without projecting unrealistic biomass values in the future. Thus, the modeled biomass for both the baseline year of 2010 and the future decades (2010-2080) are much less heterogeneous than exists in reality.

3.3 Forest vegetation disturbance

We developed a multi-stage statistical model to initiate and spread disturbances in forested ecological systems. This model was developed with the understanding (due to limited resources allocated to this modeling component) that it was not intended to explicitly model specific disturbance drivers (e.g., fire, wind, floods, ice, timber harvest, etc.). Rather, the intention of this model is to provide a reasonably realistic representation of vegetation

disturbance across the landscape, with the intent to develop a more complex disturbance model that varies depending on the disturbance driver in a subsequent phase of this project. Note, this is a significant limitation in the current model. In particular, the current model does not account for policy differences among land ownerships with regards to vegetation management (e.g., timber harvest), which we know to be an important determinant of disturbance rate, severity and patch size. Despite this limitation, our goal in this phase of the project is to emulate the overall frequency, severity and size of forest vegetation disturbances characteristic of the past 10-20 years and provide the ability via scenario analysis to increase or decrease the overall disturbance rate to reflect future uncertainty in both natural and anthropogenic disturbance regimes.

The forest vegetation disturbance model consists of the following steps:

- 1) mask out areas that are not forested so that disturbances cannot initiate or spread into these cells;
- 2) within each ecoregion, pick a cell at random and determine whether to initiate a disturbance based on the corresponding probability of disturbance model (as described below);
- 3) if the cell initiates a disturbance, determine the severity of disturbance (i.e., the proportional reduction in existing biomass) based on the corresponding probability model (as described below);
- 4) determine the size of the disturbance patch based on the corresponding probability distribution (as described below);
- 5) create the disturbance patch using a resistant kernel from the initiation cell (as described below) and when disturbance events overlap retain the more severe disturbance; and
- 6) repeat steps 1-5 for each undisturbed cell.

3.3.1 Disturbance initiation

The first stage of the disturbance model is determining the initiation of individual disturbance events. For this purpose we used FIA data on biomass at 11,171 fixed locations to estimate the probability of vegetation disturbance per decade as a function of biomass by ecological region within forest ecological systems, as follows:

- 1) select FIA plots within forested ecological systems (based on the DSLland map, McGarigal et al 2017) that were sampled at least twice between 1997-2012 (N=11,180);
- 2) treat each sampling interval between 1997-2012 at each plot as an independent observation (N=14,254). Note, 8,384 plots have 1 sampling interval; 2,519 plots have 2 sampling intervals; and 276 plots have 3 sampling intervals. Note, selecting a single sampling interval for each plot or adding plot ID as a random effect in a mixed effects model to avoid pseudo-replication does not change the results, so we kept all sampling intervals and ignored the random effect of plot ID;
- 3) drop any observation with missing biomass data (N=14,239 observations at 11,171 locations);
- 4) truncate biomass at 500 Mg/ha, which represents a reasonable upper limit on biomass

for forests in the Northeast; values exceeding this threshold are more than likely errors in the database. Note, dropping all observations with biomass>500 does not change the results;

- 5) create a disturbance indicator variable to treat as the dependent variable in a binary logistic regression based on whether biomass increased during the sampling interval (0) or decreased during the sampling interval indicative of a disturbance (1);
- 6) fit a binary logistic regression with binomial errors separately for each ecoregion to predict the annual probability of disturbance as a function of biomass. Here, disturbance indicator is the dependent variable, biomass at the start of the sampling interval is the independent variable, and the sampling interval in number of years is the trial size. Note, trial size (or sampling interval) varied from 1-10 years with a mean of 5 years. Here, we are forced to assume that if a disturbance was recorded (i.e., an observed decrease in biomass) that it happened in a single year during the sampling interval, which is entirely reasonable for anthropogenic disturbances and may slightly under estimate the frequency of natural disturbances. The fitted model predicts the annual probability of disturbance given the current biomass;
- 7) convert the model predictions to decadal probabilities of disturbance. Specifically, use the fitted models to predict the probability of not being disturbed for 10 years, and take the compliment;
- 8) convert the decadal probability of disturbance to the probability of initiation by dividing by the expected mean disturbance size for the corresponding ecoregion to account for the fact that disturbances spread from the initiation cell to surrounding cells (equal to on average the number of cells in an average disturbance event); and
- 9) lastly, adjust the cell-level probability of initiation to correct for the downward bias in disturbance that occurs when disturbances overlap.

The process above results in a fitted logistic regression for forested systems within each ecoregion (**Table 2**), and the conversion to decadal probability of disturbance results in the logistic curves shown in **figure 2**. It is important to note a few things about these results. First, the p-values are highly significant for most ecoregions, indicating that biomass has a significant effect on the probability of disturbance, which is logical since disturbances (especially anthropogenic disturbances) and generally more likely to occur in older stands with greater biomass. However, in 4 of the 13 regions the scale parameter was not significant, indicating that biomass was not a major factor. Nevertheless, we opted to keep biomass in the model in these ecoregions for consistency and because the trends were intuitive and similar to the other ecoregions. Second, the proportion of deviance (analogous to variance) explained and the Kappa (chance-corrected correct classification rate) statistics are both quite low, indicating relatively weak ability to discriminate between disturbance events and non-disturbance events. However, this is not surprising and should not be alarming given the extremely low prevalence and highly stochastic nature of disturbances. Lastly, the logistic curves in **figure 2** all indicate that the probability of disturbance increases with increasing biomass and moreover that it varies substantially among ecoregions. Not surprisingly, the Northern Appalachian/Acadian ecoregion has the highest predicted disturbance rate owing to the extensive industrial forest lands that are managed intensively for timber products.

Table 2. Logistic regression models to predict annual probability of disturbance as a function of above-ground live biomass (Mg/ha) by ecoregion for forest ecosystems in the Northeast. N is the number of FIA observations of biomass change over an average 5-year sampling interval between 1997-2012; a (location) and b (scale) are parameters of a standard 2-parameter logistic function; P-val is the p-value or significance of the scale parameter which determines the steepness of the logistic function; D² is the proportion of the deviance explained; and Kappa is the chance-corrected correct classification rate.

Ecoregion	Area (ha)	Ν	а	b	P-val	D ²	Карра
Central Appalachian Forest	9,664,780	1912	-3.77	0.0053	<0.001	0.042	0.142
Chesapeake Bay Lowlands	4,398,613	398	-3.172	0.001	0.444	0.002	0.019
Cumberlands and Southern Ridge and Valley	2,415,159	407	-4.172	0.0063	<0.001	0.06	0.216
Great Lakes	3,223,530	278	-3.639	0.0052	< 0.001	0.057	0.033
High Allegheny Plateau	6,836,508	1,670	- 3.908	0.005	<0.001	0.038	0.147
Lower New England / Northern Piedmont	9,414,710	1,545	-3.651	0.0031	<0.001	0.013	0.071
North Atlantic Coast	5,073,767	349	-3.933	0.0039	0.009	0.013	0.09
Northern Appalachian / Acadian	13,214,337	5,408	-3.614	0.0074	<0.001	0.063	0.217
Piedmont	4,113,189	769	-3.965	0.0065	< 0.001	0.058	0.215
Southern Blue Ridge	530,811	103	-3.768	0.0022	0.467	0.008	0.094
St. Lawrence - Champlain Valley	1,608,227	227	-3.465	0.0035	0.101	0.017	0.044
Western Allegheny Plateau	5,709,297	1,037	-3.725	0.0048	<0.001	0.035	0.154
Mid-Atlantic Coastal Plain	891,912	136	-3.065	0.0029	0.193	0.014	0.187



Figure 2. Predicted decadal probability of disturbance as a function of above-ground live biomass (Mg/ha) by ecoregion for forest ecosystems in the Northeast. Note, the probability of disturbance gives the probability that a disturbance event will occur during 1 of 10 years, but it does not reveal the severity of the disturbance; i.e., the proportional reduction in biomass.

3.3.2 Disturbance severity

The second stage of the disturbance model is determining the severity of the disturbance event once initiated. For this purpose we again used FIA data on biomass at 11,171 fixed locations to estimate the proportional reduction in biomass for a disturbance event by ecological region within forest ecological systems, as follows:

- 1) start with the data set derived above in step 3 containing 14,239 observations;
- 2) keep all observations that record a loss of biomass, which we interpret as a disturbance (N=3,340 or 23.45% of all sampling observations);
- 3) compute the proportional loss of biomass for the observations above by taking the delta-biomass divided by the initial biomass, and multiplying by -1 to make the result positive; and
- 4) fit a beta distribution (which is appropriate for proportional response data) to the distribution above for each ecoregion. Note, the beta distribution contains two

Table 3. Beta error models to determine the severity of disturbance, defined as the proportional reduction in above-ground live biomass (Mg/ha), by ecoregion for forest ecosystems in the Northeast; N is the number of FIA observations of biomass loss over an average 5-year sampling interval between 1997-2012; Y.mean equals the mean proportional loss of biomass; Shape1 and Shape2 are parameters of the beta probability density function.

Ecoregion	Ν	Y.mean	Shape1	Shape2
Central Appalachian Forest	434	0.224	0.342	1.184
Chesapeake Bay Lowlands	89	0.342	0.345	0.665
Cumberlands & Southern Ridge and Valley	77	0.209	0.439	1.659
Great Lakes	72	0.184	0.381	1.687
High Allegheny Plateau	349	0.176	0.370	1.729
Lower New England / Northern Piedmont	298	0.225	0.277	0.951
North Atlantic Coast	50	0.243	0.285	0.886
Northern Appalachian / Acadian	1,484	0.261	0.533	1.512
Piedmont	168	0.267	0.358	0.984
Southern Blue Ridge	16	0.199	0.861	3.474
St. Lawrence - Champlain Valley	49	0.231	0.416	1.383
Western Allegheny Plateau	213	0.234	0.378	1.237
Mid-Atlantic Coastal Plain	41	0.298	0.247	0.580

parameters, shape 1 and shape 2, but an alternative parameterization is given in which shape 2 is specified in terms of the mean and shape 1. Here, we used the alternative parameterization, fixed the mean at the observed mean proportional loss of biomass for the corresponding ecoregion, and estimated shape 1.

The process above results in a fitted beta error distribution for forested systems within each ecoregion (**Table 3**) and the corresponding fitted curves shown in **figure 3**. It is important to note a few things about these results. First, the mean overall disturbance severity across ecoregions is 0.24, indicating that on average approximately 1/4 of the biomass is lost in a disturbance event, although the average varies from 0.18-0.34 among ecoregions. Second, the probability of a low severity disturbance is considerably greater than that of a high severity disturbance across all ecoregions, as depicted in figure 2. Consequently, most disturbances will result in a small reduction in biomass, perhaps reflecting the loss of scattered canopy trees typical of a windstorm or ice damage. Lastly, whereas the rate of disturbance varies considerably among ecoregions (**Fig. 2**), the severity of disturbance per event is relatively similar among ecoregions, although a couple of ecoregions show a "U-shaped" distribution with a slightly increased probability of a complete stand-replacing or high severity disturbance (**Fig. 3**).



Figure 3. Predicted probability density of disturbance severity (defined as the proportional loss of above-ground live biomass, Mg/ha) by ecoregion for forest ecosystems in the Northeast based on the beta error models given in **table 2**. Note, the density gives the relative probability that a disturbance event will be of a particular severity, but it does not indicate the frequency or rate of disturbance. The relatively high probability density for very small proportional loss of biomass values reflects the fact the most disturbances are of low severity.

3.3.3 Disturbance spread

The final stage of the disturbance model is determining the size of the disturbance and creating the disturbance patch. For this purpose we used the High-Resolution Global Maps of 21st-Century Forest Cover Change (Hansen et al. 2013) (see description of the biomass settings variable for details, McGarigal et al 2017) to estimate the disturbance patch size distribution, as follows:

 generate a list of disturbance patch sizes by ecoregion from the Forest Cover Change dataset, in which a disturbance patch is defined as contiguous cells (based on the 8neighbor rule; i.e. ,touching either orthogonally or diagonally) having the same recorded age since disturbance. Note, the Forest Cover Change data set is based on severe disturbances that result in complete or nearly complete loss of canopy cover. Unfortunately, there is no dataset available for determining patches of low-severity

Table 4. Generalized Pareto error models to derive the size of disturbance patches by ecoregion for forest ecosystems in the Northeast; N is the number of discrete disturbance patches and the corresponding mean, minimum and maximum patch sizes (in hectares) recorded in the High-Resolution Global Maps of 21st-Century Forest Cover Change (Hansen et al. 2013) for disturbances between 2000-2012; Scale and Shape are parameters of the generalized Pareto probability density function.

		Pate	ch size			
Ecoregion	Ν	Mean	Min	Max	Scale	Shape
Northern Appalachian / Acadian	592,943	0.99	0.09	489.87	2.093	-0.243
St. Lawrence - Champlain Valley	19,699	0.50	0.09	45.00	1.927	-0.306
North Atlantic Coast	62,072	0.55	0.09	1433.70	1.785	-0.184
Lower New England / Northern Piedmont	234,951	0.52	0.09	116.91	1.801	-0.251
Great Lakes	28,819	0.30	0.09	45.09	1.485	-0.238
High Allegheny Plateau	99,332	0.59	0.09	235.80	1.841	-0.233
Western Allegheny Plateau	137,508	0.54	0.09	559.71	1.678	-0.192
Central Appalachian Forest	184,186	0.69	0.09	135.18	1.988	-0.271
Chesapeake Bay Lowlands	88,895	1.45	0.09	308.25	2.458	-0.302
Piedmont	201,134	2.10	0.09	282.96	2.798	-0.347
Cumberlands And Southern Ridge And Valley	78,512	0.97	0.09	229.23	2.146	-0.273
Mid-Atlantic Coastal Plain	42,704	2.42	0.09	769.95	2.913	-0.321
Southern Blue Ridge	12,899	0.73	0.09	86.58	2.186	-0.317

disturbances, so we are forced to use the distribution of high-severity disturbances as representative of all disturbance patch sizes; and

2) fit a generalized Pareto distribution to the patch size distribution above for each ecoregion. Note, the generalized Pareto distribution contains two parameters, shape and scale, and is a heavy-tailed distribution commonly used to fit heavily right-skewed distributions with a long right tail (i.e., very few very large values). However, because the observed distribution of patch sizes was so heavily skewed, we fit the distribution to the log-transformed patch sizes instead of the raw-scale patch sizes, and then back-transform (via exponentiation) to get the random patch size for the disturbance event.

The process above results in a fitted generalized Pareto error distribution for disturbance patch sizes in forested systems within each ecoregion (**Table 4**) and the corresponding fitted curves shown in **figure 4**. It is important to note a few things about these results. First, the mean overall patch size across ecoregions is only 11 cells (1 ha), although it varies



Figure 4. Predicted probability density of disturbance severity (defined as the proportional loss of above-ground live biomass, Mg/ha) by ecoregion for forest ecosystems in the Northeast based on the beta error models given in **table 4**. Note, the density gives the relative probability that a disturbance event will be of a particular severity, but it does not indicate the frequency or rate of disturbance. The relatively high probability density for very small proportional loss of biomass values reflects the fact the most disturbances are of low severity.

among ecoregions from roughly 3 cells (0.27 ha) to 27 cells (2.5 ha). Second, the vast majority of disturbance patches are quite small; the median patch size across the region is only 2 cells (0.18 ha) and the 75th percentile is only 6 cells (0.54 ha) owing to the highly right-skewed distribution. Lastly, the patch size distribution varies somewhat among ecoregions, especially with respect to the size and probability of the largest disturbances.

To create the disturbance patch once the patch size is determined, we use a resistant kernel from the initiation cell, as follows:

 create a resistance surface out of biomass and slope near the initiation cell (i.e., an area large enough to contain the patch). For this purpose, non-forest cells are assigned high resistance (sufficient to prevent any spread), while forest cells are assigned a resistance equal to:

resistance = 1 + (biomassRes * deltaBiomass + deltaLog(slope+1)* slopeScaler)

where biomassRes is a parameter that defines the increase in resistance per unit difference in biomass (currently=0.01); deltaBiomass is the difference between each cell's biomass and the initiation cell's biomass; deltaLog(slope +1) is a measure of the difference in slope between each cell and the initiation cell; and slopeScaler is a parameter that regulates the effect of slope on resistance (currently=1);

- 2) build a resistant kernel by spreading outward from the initiation cell using an initial bank account sufficient to spread 24 times the desired patch area over a minimally resistant surface. The result is a kernel where the initiation cell has that bank account value and every other cell's value is the bank account minus the least cost path between the cell and the initiation cell (or 0 if the spread did not reach the cell);
- 3) identify the threshold in the spread kernel height that yields the kernel size closest to the target patch size and slice the kernel at that threshold value to create the disturbance patch; and
- 4) set the biomass of each cell within the disturbance patch to the previously selected proportion of its current biomass.

The process above results in a disturbance patch that is confined to forested cells and has a shape that corresponds roughly to the spatial distribution of biomass and slope, such that patches tend to spread into similar aged cells on similar slopes. Note, the severity of the disturbance is treated as constant across the patch, which translates into a constant proportional reduction in the current biomass. Consequently, the final biomass preserves the original spatial heterogeneity in biomass within the patch even as the amount of biomass is reduced. This may or may not reflect real-world disturbances in all cases. However, in most real-world cases evidence suggests that a single disturbance event will typically result in heterogeneous severity, and thus we sought to maintain not reduce the heterogeneity within patches.

4 Model Evaluation

Given the stochastic nature of the disturbance-succession model, it is important to evaluate various outcomes of the model for adherence to our expectations. In this regard, we evaluated four things: 1) difference between the expected and simulated probability of disturbance; 2) difference between the expected and simulated severity of disturbance; 3) difference between the initial biomass distribution and the simulated biomass distribution over time; and 4) difference in the spatial configuration of biomass between the initial condition in 2010 and the last timestep of the simulation in 2080.

4.1 Probability of disturbance

If each cell was disturbed independently of all other cells, there would be no need to calibrate the probability of disturbance, as it would be determined exactly by the specified cell-level probability of disturbance given by the empirically determined model parameters. However, given that disturbances initiate in a focal cell and then spread to surrounding cells in a contagious manner, and that individual disturbance events within a single timestep (10 years) can overlap each other, it is necessary to evaluate the simulated or realized disturbance probability and if necessary adjust the cell-level probability of initiation to accommodate any realized bias. Overall, the calibrated probability of



Figure 5. Expected (empirical) and simulated (model) probability of disturbance per decade (y-axis) as a function of biomass (Mg/ha, x-axis) for forest ecosystems by ecoregions in the Northeast. The expected values were derived by fitting a logistic function to the presence of disturbance and biomass data for a set of Forest Inventory and Analysis (FIA) plots within each ecoregion. The simulated probability of disturbance is the realized values after adjusting the cell-level probability of initiation to correct for the observed downward bias in disturbance that occurs when disturbances overlap.

disturbance does a reasonably good job across ecoregions of emulating the expected probability disturbance based on the fitted relationships from the FIA data, with a couple of exceptions (**Fig. 5**): the Southern Blue Ridge ecoregion exhibits an upward bias, whereas the Mid-Atlantic Coastal Plain exhibits a downward bias, both for unknown reasons. Lastly, the simulated relationships between probability of disturbance and biomass exhibit much shallower slopes than expected because of the spread of disturbance from the initiation cell (in which the relationship with biomass is maintained exactly) to surrounding cells that differ in biomass from the initiation cell. In other words, the strong biomass affect at the



Figure 6. Expected (red) and simulated (black) density (y-axis) of disturbance severity (x-axis) for forest ecosystems by ecoregions in the Northeast. Note, the density gives the relative probability that a disturbance event will be of a particular severity and severity is given as the proportional reduction in biomass (i.e., severity=1 when current biomass is reduced to zero). The expected values were derived by fitting a beta distribution to the observed biomass loss between surveys for a set of Forest Inventory and Analysis (FIA) plots within each ecoregion.

initiation cell is weakened by forcing disturbance events to spread to surrounding cells that differ in biomass.

4.2 Disturbance severity

Because individual disturbance events within a single timestep can overlap, and we chose to retain the more severe disturbance where overlap occurs, the simulated or realized distribution of disturbance severity does not perfectly mirror the expected distribution based on the fitted relationships from the FIA data. Specifically, because we retained the more severe disturbance where overlap occurs, we realize an upward bias in the simulated distribution of severity (**Fig. 6**). Thus, we simulate fewer cells of very low severity

disturbance and more cells of higher severity disturbance than expected based on the FIA data. In general, however, the upward bias is very slight in most ecoregions.

4.3 Biomass distribution

Simulated succession (the development of biomass) and disturbance (the loss of biomass) processes interact to affect the simulated distribution of biomass over time. **Figure 7** depicts the changes in the simulated biomass distribution over time (by decade) for each ecoregion, from which several patterns emerge.

First, the initial (2010) biomass distribution is distinctly bimodal, with modes at very low biomass and moderately high biomass, and this pattern is consistent across all ecoregions, although it is more pronounced in some (e.g., Cumberlands and Southern Ridge and Valley) than others (e.g., Central Appalachian Forest). The low biomass mode is likely due to a combination of confounded factors. In part, this mode may reflect a real pulse of high-severity disturbances during the past couple of decades (e.g., due to increased forest cutting). However, it may also reflect GIS errors in the creation of the initial biomass layer. Indeed, there is good evidence for the latter resulting from disagreement between the forest cover mask used to create the initial biomass layer (Kellndorfer et al 2013) and the forest cover mask used in our simulation (DSLland). Unfortunately, it is difficult to discern between these two possible sources for the cause of the low biomass mode.

Second, the relative probability of very high biomass is maintained over time in the simulation. In other words, the simulation does not result in a notable increase in the proportion of very high biomass cells.

Third, over time the simulation gradually converts the bimodal distribution in biomass to a unimodal distribution, with considerably more early- to mid-successional forest and an overall mode at moderate biomass that equates roughly to an early mature forest stand. However, the shifting distribution between 2010-2080 is much more pronounced in some ecoregions (e.g., Northern Appalachian/Acadian) than others (e.g., Piedmont). It is important to note that the initial bimodal distribution is impossible to maintain overtime without introducing periodic or intermittent surges in the proportion of high-severity disturbances.

4.4 Spatial configuration of biomass

Our final evaluation of the disturbance-succession model involves visually comparing the initial (2010) spatial configuration of biomass to the configuration at the end of the simulation (2080). We noted several patterns:

First, we fit and then applied the probability of disturbance, disturbance severity and patch size distribution at the ecoregion level. However, the underlying processes driving disturbance are not necessarily distributed evenly throughout each ecoregion. For example, the Northern Appalachian/Acadian ecoregion includes the Adirondacks, the higher elevations and more northerly portions of Vermont and New Hampshire, and all but the southern tip of Maine. Much of Maine is subject to industrial forestry and an intensive disturbance regime while the Adirondacks and the White Mountains have much less anthropogenic disturbance. This is evident in the initial biomass which shows much higher values in the Adirondacks and White Mountains than in Maine (**Fig 8**). Our model then



Figure 7. Simulated density (y-axis) of biomass (x-axis) per decade between 2010-2080 for forest ecosystems by ecoregions in the Northeast. Note, the density gives the relative probability that a cell will have a particular biomass.

applies the average of these two regimes everywhere, ultimately over disturbing the Adirondacks and under disturbing the industrial forest of Maine, and by 2080 the biomass is homogenized across the ecoregion (**Fig. 8**). In other ecoregions this issue is less evident. For example, in the Piedmont the initial spatial configuration of biomass largely reflects intensive forest management with relatively consistent management practices applied across relatively homogeneous forest cover, and in this situation the simulation does a relatively good job of emulating the spatial configuration in biomass over time (**Fig. 9**).

Second, although our models for predicting the occurrence and severity of disturbances across all forest types with an ecoregion were statistically better than using separate models for each forest type, it is clear that this results in over- or under-estimating biomass in some forest types. For example, in the Mid-Atlantic Coastal Plain ecoregion, the universal model appears to overestimate biomass accumulation over time for the Pine Barrens (**Fig. 10**). Note, this is another example of the coarse-scale heterogeneity in disturbance processes within an ecoregion discussed above.

Lastly, our generic disturbance model does not appear to adequately capture the spatial autocorrelation in disturbance probability or severity that results in very irregular disturbance patch shapes. Unfortunately, the real-world shape complexity of disturbance patches is determined by different factors affecting different disturbance processes. For example, ownership parcels, which are rectilinear in shape, strongly determine anthropogenic disturbance patches such as those produced from timber harvesting, but ownership parcel data is not incorporated into our model yet due to the lack of available regional data.

5 Conclusions and Recommendations

Due to limited resources, our succession and disturbance model was intended to be a generic model; i.e., one that would account for vegetation development (i.e., succession) and disturbance without considering the separate disturbance processes that affect real-world vegetation patterns. To this end, we developed a fully empirically-based landscape disturbance-succession model (LDSM) that successfully meets this goal. However, after evaluating the model outcomes (see above), we have reached the following important conclusions and recommendations.

The architecture to model fully empirically-based disturbance and succession processes is now developed and in implemented in the DSL LCAD (Landscape Change, Assessment and Design) model. Indeed, the succession model does an excellent job of capturing the expected development of biomass over time in the absence of disturbance, and accounts nicely for differences among forest types and several ecological settings variables as warranted by the empirical data. The stochastic disturbance model simulates individual disturbance events and incorporates the steps of disturbance initiation, spread and severity, and each step allows for geographic differences and the incorporation of ecological settings variables as warranted by the empirical data (although the latter was largely not supported on statistical grounds based on the FIA data). Thus, we are well poised to extend this model as described below in future phases of this project.



Figure 8. Initial (2010) biomass and simulated biomass in 2080 for the Northern Appalachian/Acadian ecoregion.



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Figure 9. Initial (2010) biomass and simulated biomass in 2080 for the Piedmont ecoregion.



Figure 10. Initial (2010) biomass and simulated biomass in 2080 for the Pine Barrens in the Mid-Atlantic Coastal Plain ecoregion.

Unfortunately, the intentional confounding of unique disturbance processes into a single generic disturbance model ignores important differences among different disturbance processes that in the real world give rise to multi-scale spatial patterns in disturbance rate, severity and patch configuration. After evaluating the model outcomes, we conclude that the simulated spatial patterns in biomass are too unrealistic in this regard to be useful at this time as inputs to the focal species landscape capability models.

Lastly, we emphasize that the modeling machinery is now in place to decouple the different dominant disturbance processes (e.g., wind, insects/pathogens, fire, timber harvest), but it will be necessary to model each process separately (allowing for interactions among processes) to produce realistic spatial patterns in biomass over time. Moreover, even with decoupled disturbance processes, the best use of the disturbance-succession model is in scenario analysis, for example comparing alternative future scenarios involving differences in disturbance rate, severity and/or spatial configuration.

6 Alternatives Considered and Rejected

Prior to selecting the methods described above, we considered and rejected other options, as follows:

- Complete disturbance model Initially, once a disturbance was initiated, stand age and biomass were set back to zero throughout the entire disturbance patch. We rejected this approach for two reasons. First, it was an inaccurate representation of many disturbance processes in the Northeast being that most natural disturbances in the Northeast only partially disturb a stand and many forest management practices consist of partial cuts. Therefore, reducing the biomass by a proportion of the current biomass and setting the stand age back to a correspondingly younger age, 9 for example instead of zero, we felt was a better representation of actual disturbances. Second, by setting all disturbed areas to age zero, future age class distributions did not approximate the current age class distribution in which young stands are rare.
- 2) No disturbance model In this alternative, we considered two options. The first was not to model disturbance at all and let stands grow over time. This resulted in all forests reaching considerably old age classes with essentially no early to mid-succession classes. We deemed that this alternative resulted in a completely unrealistic representation of the landscape and thus rejected it. The second approach was not to model disturbance explicitly, but to keep the current biomass (and age) distribution as represented in the current landscape condition static over time. This approach maintained the current biomass/age class distribution, a goal we achieve in our preferred approach; however it completely omitted the dynamic nature of the landscape and thus we rejected this approach.
- 3) FVS growth model We originally considered using FVS (Forest Vegetation Simulator) to develop growth trajectories. FVS is an individual tree-based forest growth simulator that deterministically grows forests at the stand level. Our original consideration was to grow each FIA plot, indexed by ecological system, for 100 years using FVS. The result of the simulation would be a data point for each FIA stand every 10 years for 100 years for each of the forest characteristics of interested such as biomass. We would then use these data as the dependant variable in the nonlinear

least squares regression to develop growth trajectories. Upon extensive exploration of this alternative, it was rejected because FVS consistently produced unrealistic growth trajectories for older forest stands for which growth was expected to have levelled off. This appeared to be caused by relatively high numbers of seedlings given stand age, particularly for plots located in ME. The cause of the high seedling counts given age may have two potential sources:

- a) Difficulty in accurately estimating stand age on FIA plots may have led to stands of a primarily young age being aged as relatively old stands. FIA defines the age of a stand as the weighted average age of two or three dominant or codominant trees in the overstory (Smith 2002). Therefore, a stand which may primarily be in an early successional stage with just a few old trees would be given an age reflective of the few older trees in the stand.
- b) Although an FIA plot may be classified as forested and stocked, it's possible that the proportion of the plot stocked is quite low (i.e., one or more of the subplots may not be forested). This could have been causing expansion errors when FVS expanded the data to a per acre basis. Much of this insight was derived from a discussion with Dr. Coeli Hoover, Research Ecologist, USFS, Northern Research Station, Durham, NH.

Although FVS is an individual tree-based growth model, it functions (i.e., accepts and reports data) at the stand level and is typically used to understand the implications of a particular harvest on an individual stand. For this reason, making specific adjustments, at the stand level, within FVS is quite common to derive realistic results. Since we were considering >1,000 FIA plots in our analysis, refinement at the plot level was unrealistic and we ultimately decided that using the raw FIA plot data provides us with the most accurate representation of stand development.

4) LANDFIRE state-based transition model — We also briefly considered using statebased transition (or simply "state transition") models to model succession, based on models developed for the LANDFIRE project (www.landfire.gov). Briefly, state transition models, such as those developed for LANDFIRE, identify discrete states of development for each ecological system (or biophysical setting) and pathways by which states transition over time from one state to another either in the absence of disturbance or following particular disturbances. These models are typically constructed and parameterized based on expert opinion and often vary dramatically in detail by region and development team. These models have the advantage of being intuitive and simple to understand, as ecologists and managers often conceive of vegetation development as a progression through discrete stages — a somewhat dogmatic perspective that has been facilitated by many seminal publications on vegetation development. The use of existing state transition models for the ecological systems within the NALCC has the additional practical advantage that the work has largely been done by the LANDFIRE project. However, the use of discrete state transition models has the disadvantage of producing potentially artificially abrupt changes in the state of vegetation and thus in the seral stage distribution of the landscape. Moreover, most ecologists recognize that vegetation development is in fact a continuous process and that discretizing the process, while having great heuristic value, is perhaps not the best way to represent vegetation development in a model

when empirical data allow otherwise. Lastly, it is our intent in the project to empirically base as much of the model processes as possible given extant data. In this case, we believed that the FIA data allowed us to develop an empirically based approach to modeling continuous vegetation development and, by so doing, eliminate the subjectivity of the expert based state transition modeling approach.

7 Major Risks and Dependencies

The succession and disturbance model is empirically based and thus reliant on the availability and sufficiency of relevant extant data. In this regard, our model is heavily reliant on FIA data, which is used to model the growth in biomass (succession) by forest type (macrogroup) in addition to the probability of disturbance initiation and severity by ecoregion. Errors in the FIA data introduce "noise" to the statistical relationship being evaluated and make it more challenging to accurately model the process being considered. For example, we found no statistical support for including forest type in the models of disturbance probability and severity, but this may have been due to the excessive noise-to-signal ratio in the FIA data rather than the absence of a true real-world relationship. In addition, the limited number of FIA plots in some forest types (e.g., Table 1) makes it difficult to model relationships for forest types separately, again weakening our ability to model real-world spatial patterns. Nevertheless, FIA is the only rigorous, regionally consistent assessment of forest structural characteristics available.

Similarly, as noted previously, our estimate of disturbance patch size distributions by ecoregion was derived from the High-Resolution Global Maps of 21st-Century Forest Cover Change (Hansen et al. 2013). Unfortunately, the Hansen et al data represent high-severity disturbances resulting in nearly complete forest loss, but we are applying it to all disturbances of any severity. This was necessary because there is no empirical dataset of partial forest loss.

It should be noted again that the current disturbance model was intentionally a generic disturbance model and thus did not explicitly model specific disturbance processes. Our intention was to implement a reasonable disturbance model that resulted in a relatively realistic representation of the landscape, i.e., maintaining the current stand age distribution over time. Unfortunately, our evaluation of the current model results suggest that it is necessary to model different disturbance processes separately to obtain realistic and thus useful results.

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