

## Research Article

# Developing Species-Age Cohorts from Forest Inventory and Analysis Data to Parameterize a Forest Landscape Model

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Simulating long-term, landscape level changes in forest composition requires estimates of stand age to initialize succession models. Detailed stand ages are rarely available, and even general information on stand history often is lacking. We used data from USDA Forest Service Forest Inventory and Analysis (FIA) database to estimate broad age classes for a forested landscape to simulate changes in landscape composition and structure relative to climate change at Fort Drum, a 43,000 ha U.S. Army installation in northwestern New York. Using simple linear regression, we developed relationships between tree diameter and age for FIA site trees from the host and adjacent ecoregions and applied those relationships to forest stands at Fort Drum. We observed that approximately half of the variation in age was explained by diameter breast height (DBH) across all species studied ( $r^2 = 0.42$  for sugar maple *Acer saccharum* to 0.63 for white ash *Fraxinus americana*). We then used age-diameter relationships from published research on northern hardwood species to calibrate results from the FIA-based analysis. With predicted stand age, we used tree species life histories and environmental conditions represented by ecological site types to parameterize a stochastic forest landscape model (LANDIS-II) to spatially and temporally model successional changes in forest communities at Fort Drum. Forest stands modeled over 100 years without significant disturbance appeared to reflect expected patterns of increasing dominance by shade-tolerant mesophytic tree species such as sugar maple, red maple (*Acer rubrum*), and eastern hemlock (*Tsuga canadensis*) where soil moisture was sufficient. On drier sandy soils, eastern white pine (*Pinus strobus*), red pine (*P. resinosa*), northern red oak (*Quercus rubra*), and white oak (*Q. alba*) continued to be important components throughout the modeling period with no net loss at the landscape scale. Our results suggest that despite abundant precipitation and relatively low evapotranspiration rates for the region, low soil water holding capacity and fertility may be limiting factors for the spread of mesophytic species on excessively drained soils in the region. Increasing atmospheric temperatures projected for the region could alter moisture regimes for many coarse-textured soils providing a possible mechanism for expansion of xerophytic tree species.

## 1. Introduction

Over the past twenty years, a number of studies have documented the potential impacts of climate change on forest biomes, broad forest cover types, and the ranges of individual tree species in eastern North America [1–4]. Most of this research was based on correlations between current bioclimatic conditions and current distributions of forest types or tree species, which were then extrapolated into the future using outputs from global or regional climate models

to characterize future distributions. These projections either implicitly or explicitly assumed that the current distributions of tree species approximate the range of environmental tolerances the species have adapted to over thousands of years and that absence of a species or community suggests the presence of bioclimatic conditions unsuitable for sustained regeneration and growth. A number of authors have noted limitations of the “climatic envelope” approach as the basis for species distribution models (SDM), including reliance on temporally and spatially limited climate data,

incomplete information on the distribution of tree species, and lack of detailed information on adaptations to wide ranging biophysical conditions [5–8]. Often, species distribution models are based on a few observed or modeled climate variables from the past 100–150 years that do not encompass the complete range of climatic conditions, whereby species evolved during the Holocene. Moreover, complicating our current perspective on tree distributions, this recent period widely is recognized as warmer and wetter in comparison to long-term climatic variation in North America.

A number of different approaches and tools are available to model changes in forest structure and function over time and space including tree and stand-level models (e.g., traditional growth and yield models [9], Climate-Forest Vegetation Simulator [10], species-specific niche models [11], process models [12], and dynamic global vegetation models (MC1) [13]. Trade-offs inherent in these different approaches have been well summarized using characteristics such as application scale, spatial versus nonspatial approaches, complexity in constructing parameters, availability of adequate input data, applicability across different ecoregions, statistical approach, and interpretation of model outputs [6, 7, 14, 15]. LANDIS-II (landscape disturbance and succession) is a stochastic forest landscape simulator that can incorporate site adaptations and biological interactions such as competition for light, reproductive strategies, and disturbance from fire, wind, and timber harvesting within a spatially explicit context to model change in forest communities over time [16–18]. Species-age cohorts and site types that define limitations on establishment and growth are specified for each cell in a raster data structure, and life history attributes for each species of interest are used to model change in species composition and biomass over time. Cohorts of trees age and senesce compete for light and reproduce based on life history attributes such as species longevity, shade tolerance, age when seed is produced, and seed dispersal strategies. Unless killed by a disturbance such as timber harvesting or fire, an age-dependent mortality function is used to remove cohorts from the model. Raster maps and associated attribute files are produced that allow visualization and analysis of model results. LANDIS-II has been shown to be a flexible and accurate tool for modeling changes in species composition and distribution over time as a function of climate change by accounting for a variety of natural and anthropogenic disturbances [19, 20].

An important input to initialize and model succession in LANDIS-II is the spatial distribution and structure of species-age cohorts across the landscape. However, the age of individual trees or forest stands may be lacking for many forest landscapes, and determining age from increment cores requires a substantial amount of fieldwork and laboratory analysis of tree growth rings [21]. Equations to predict tree age from diameter are not abundant in the literature, and it is uncertain whether age can be accurately predicted from tree diameters in mixed species stands with different developmental histories and site characteristics [22, 23]. Differences in shade tolerances and growth rates between tree species in mixed stands as well as the effects of

past disturbances and silvicultural treatments can make it difficult to establish reliable age-diameter relationships. However, several studies have shown that a significant proportion of the variation in tree age can be explained by stem diameters for some important northern hardwood species. Tubbs [24] analyzed a mature northern hardwood stand dominated by sugar maple (*Acer saccharum*) in the Upper Peninsula of Michigan after 50 years of selection cutting and found that diameter measured from cut stumps explained 88% of the variation in tree age. A similar study based on 60 sugar maple trees harvested from a managed forest in Wisconsin indicated that 64% of variation in age was explained by diameter [25]. Leak [26] developed regression equations based on basal diameters for several northern hardwood and conifer species at two old-growth sites in New Hampshire that explained 47%, 79%, and 86% of the variation in age based on diameter measured at breast height (DBH) for sugar maple, yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*), respectively. Kenefic and Nyland [27] reported an  $r^2$  of 0.81 for age-DBH relationships in a managed, uneven-aged stand of 96 sugar maple trees in central New York. Collectively, these studies provide reasonable evidence that age can be approximated from stem diameters for sugar maple-dominated stands with differing stand histories and site conditions, albeit with unexplained variation in predicted ages ranging from 12% to as much as 53%.

Northern red oak (*Quercus rubra*) is less shade tolerant and generally faster growing than sugar maple that largely overlaps in range with northern red oak [28–31]. As with sugar maple, several studies have developed age-diameter relationships for northern red oak in the northeastern U.S. and southern Canada. Rentch [32] studied five old-growth stands on the Allegheny Plateau of Ohio, Pennsylvania, and West Virginia, but tree ages derived from increment cores were not strongly correlated with DBH ( $r^2 = 0.34$ ). Conversely, data derived from a managed, northern red oak stand in Connecticut showed a very high degree of correlation between age and DBH ( $r^2 = 0.93$ , [33]). Analysis of data from northern red oak stands in southeastern New York [34] and southern Quebec [35] resulted in age-DBH correlations of  $r^2 = 0.42$  and  $r^2 = 0.49$ , respectively. Best fit lines from an old-growth stand in North Carolina [36] and managed stands in West Virginia [37] illustrated similar age-diameter relationships. As with sugar maple, age predictions from published age-diameter relationships for northern red oak are highly variable, but approximately half of the variation in age can be explained by stem diameter across a large portion of the range of northern red oak in the northeastern U.S. Additionally, variability in age predictions might be reduced if predictions are limited to dominant and co-dominant trees and not applied to shade-tolerant species in the understory that may be of similar age but have significantly smaller diameters.

Forest resource managers on military installations in the United States need tools and approaches that can provide installation-specific context from global and regional climate change assessments. Our challenge in this study was to develop preliminary forest succession models using

LANDIS-II to evaluate if available information resources were adequate to inform simulations and therefore produce credible models of successional patterns over the next 100 years as a prerequisite for subsequent modeling of potential climate change impacts. Given the general lack of information on tree and stand age at many military installations, we chose to derive age-diameter relationships from site tree records in the USDA Forest Inventory and Analysis database [38] and integrate these relationships with available forest stand data to parameterize the LANDIS-II model.

## 2. Methods

**2.1. Study Area.** Fort Drum is a U.S. Army installation covering over 43,000 ha near Watertown, New York, USA, approximately 25 km east of Lake Ontario (latitude 44.10°N, longitude 75.65°W; Figure 1). The installation lies primarily in the Saint Lawrence Glacial Lake Plain physiographic region [39] with elevations ranging from 126 m to 280 m. The region has a humid, cool temperate climate with an average annual temperature of 7.9°C and mean annual precipitation of 1100 mm. Average monthly precipitation is highest in the late fall (114 mm in November) and lowest in mid-winter (70 mm in February), but it is distributed evenly throughout the growing season. A substantial amount of precipitation falls as snow during the winter months averaging 2847 mm per year over the past 35 years. The average frost-free growing season runs from May 15 through September 25 [40].

Three physiographic units characterize the majority of the installation: relatively flat, low elevation plains derived from fine-textured glacial lacustrine deposits (28% of total area), slightly more elevated and coarse-textured sand terraces and plains derived from glacial outwash and wind-blown deposits (25% of total area), and bedrock-controlled uplands covered by coarse glacial till in the northeastern third of the installation (27% of total area, [41]). Topography is a general level to gentle rolling, and both alluvial and depressional wetlands are common throughout the installation. Soils in the western and southern portions of the base formed from postglacial, fine-textured lacustrine deposits and sandy outwash plains underlain by sandstone and limestone bedrock. Mesic to wet, circumneutral soils are common on lowland plains, while excessively drained soils predominate on higher sand plains and terraces. Intermediate to the above are relatively narrow terraces of mesic, loamy fine sands. There are significant areas of calcareous glacial till covering lower elevation landscapes that have given rise to soils with relatively high base saturation and pH. The northeastern upland portion of the installation is dominated by acidic, coarse-textured soils derived from glacial till underlain by bedrock comprised of gneiss, schist, and granite. Most upland soils are mesic, relatively shallow to bedrock, and have a frigid temperature regime (mean annual temperature <8°C and difference between summer and winter temperature means >6°C, [42]). Organic soils associated with bogs and alluvial wetlands cover approximately 6% of the installation and are especially common in the northeastern uplands as a result of glacial erosion of underlying bedrock during the latter stages of the Pleistocene [41].

Prior to European settlement in the 18th century, the area was covered by mixed pine-eastern hemlock (*Tsuga canadensis*) and northern hardwood forests typical of cool temperate regions in northeastern North America [43, 44]. Beginning in the late 1700s, much of the land in the St. Lawrence River Valley, including the Fort Drum area, was converted to agriculture with forests remaining in relatively isolated patches on soils either too wet or too rocky to farm [45]. The U.S. Army began acquiring land in the early 1900s and expanded the installation to over 35,000 ha during World War II. Fort Drum reached its current extent in the 1980s. Concurrent with the growth of Fort Drum, agricultural acreage in the region in general declined substantially during the latter half of 20<sup>th</sup> century [46]. These lands have largely reverted to old field, shrub, and early successional forest communities that characterize much of the local landscape.

Approximately 30% of the undeveloped lowland landscapes at Fort Drum remains in open old field-woody shrub cover types that developed following abandonment or displacement of agricultural activities over the past 50–100 years. Grass (*Schizachyrium scoparium*, and *Avenella flexuosa*) and sedge (*Carex pensylvanica*, *C. rugosperma*, and *C. lucorum*) communities with scattered stands of eastern white pine (*Pinus strobus*) and red pine (*Pinus resinosa*) as well as northern red oak and white oak (*Quercus alba*) dominate dry sand plains [47]. In addition to occurring on the most xeric sites at Fort Drum, these communities are maintained in an open, early successional state through mowing and occasional ground fires that occur because of military training exercises. On more mesic old field sites with fine-textured soils, early successional grass-sedge-herb and woody shrub communities are common with species composition varying depending on time since abandonment, type of disturbance, and soil drainage [47]. Common species include bluegrasses (*Poa pratensis* and *P. compressa*), several introduced grass species (e.g., *Elymus repens*, *Bromus inermis*, and *Dactylis glomerata*), sedges (*Carex* spp.), and a diverse herb layer comprised of goldenrods (*Solidago altissima*, *S. nemoralis*, and *S. rugosa*), New England aster (*Sympyotrichum novae-angliae*), evening primrose (*Oenothera biennis*), Queen Anne's lace (*Daucus carota*), ragweed (*Ambrosia artemisiifolia*), and common chickweed (*Cerastium arvense*). Woody shrub cover ranges from 10% to 50% and includes species such as speckled alder (*Alnus incana*), shrub dogwoods (*Cornus amomum* and *C. racemosa*), sumacs (*Rhus glabra* and *R. typhina*), and raspberries (*Rubus* spp.) along with shrubby red maple (*Acer rubrum*), green ash (*Fraxinus pensylvanica*), and willow (*Salix* spp.). Other relatively open cover types at Fort Drum include recently harvested tracts dominated by early successional tree species such as trembling aspen (*Populus tremuloides*), big-tooth aspen (*P. grandidentata*), gray birch (*Betula populifolia*), black cherry (*Prunus serotina*), and red maple [47].

Broadleaved deciduous forests cover approximately 33% of Fort Drum and are comprised of two primary northern hardwood types: beech-maple forest and maple-basswood (*Tilia americana*) rich mesic forest [43, 47]. Beech-maple forests occur on upland sites with relatively shallow, coarse-

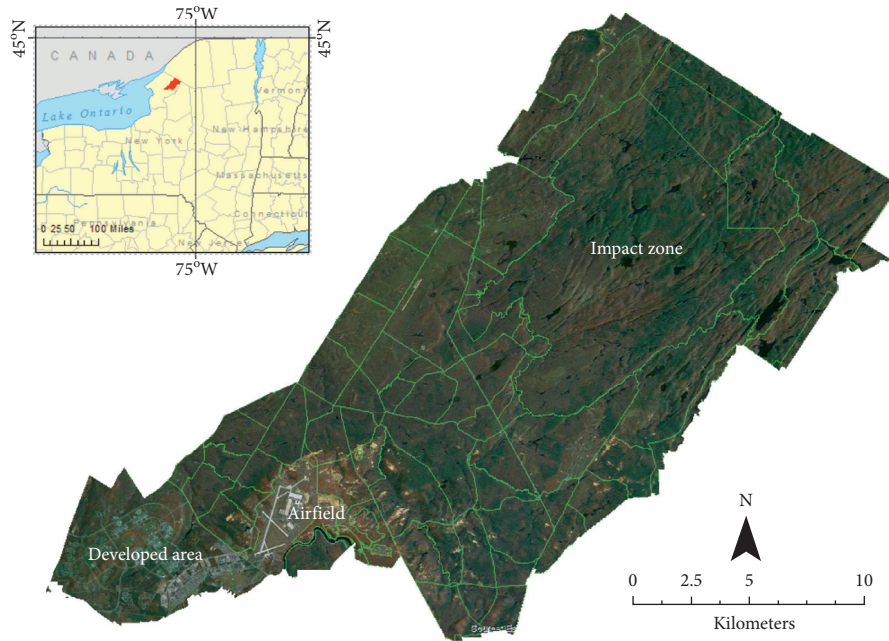


FIGURE 1: Study site location (inset) and location of military infrastructure (training areas shown in green outline) at Fort Drum, New York, USA. Training areas are comprised of over 1,500 forest stands managed to support military training requirements, timber and fiber production, game and nongame wildlife management programs, and ecosystem sustainability. The “Impact Zone” and developed areas were excluded from the study.

textured, and frigid soils derived from acidic glacial till. Common associates include yellow birch, white ash, American hophornbeam (*Ostrya virginiana*), and red maple. Depending on the level of disturbance, understories are comprised of seedlings from the above species along with striped maple (*Acer pennsylvanicum*), American hornbeam (*Carpinus caroliniana*), viburnums (*Viburnum lantanoides* and *V. acerifolium*), and eastern hemlock. Extensive diameter-limit timber harvests have occurred in the upland forests at Fort Drum over the past 10 to 20 years, which has apparently resulted in a much higher component of red maple, black cherry, white ash, and northern red oak than might be expected for typical northern hardwood stands at this latitude. In addition, beech bark disease (fungal pathogens *Neonectria faginata* and *N. ditissima*) has reduced the prevalence of American beech at Fort Drum [13]. Maple-basswood forests occur at lower elevations and on fine-textured mesic soils derived from glacial lacustrine deposits and till derived from limestone bedrock. Dominant tree species include sugar maple, red maple, American basswood, and white ash, but American elm (*Ulmus americana*), bitternut hickory (*Carya cordiformis*), and black cherry are also common associates. Understory vegetation is generally more diverse than upland forests due to base-rich soils, abundant soil moisture, and warmer temperatures and includes woody species such as American hophornbeam (*Ostrya virginiana*), alternate-leaved dogwood (*Cornus alternifolia*), mountain maple (*Acer spicatum*) and witch-hazel (*Hamamelis virginiana*), ferns (*Athyrium filix-femina* and *Dryopteris*

*marginalis*), and a rich herb layer [47]. Red maple, black ash (*Fraxinus nigra*), green ash, and cottonwood (*Populus deltoides*) increase in frequency on poorly drained floodplains, stream terraces, and depressions within the maple-basswood type (red maple-hardwood swamp forest and floodplain forest types [47]). Dutch elm disease (*Ophiostoma* spp.) has killed most mature American elm trees at Fort Drum, but elm regeneration remains abundant on mesic, fine-textured soils throughout the installation.

Evergreen coniferous forests and evergreen-deciduous mixtures occur on approximately 25% of Fort Drum. Eastern white pine and eastern hemlock form mixed stands with northern hardwoods on both upland and lowland sites (pine-northern hardwood and hemlock-northern hardwood forests, [47]). Eastern hemlock is significantly more common on lowland soils derived from coarse loamy glaciofluvial deposits and in forested wetlands where it forms dense stands with northern white cedar (*Thuja occidentalis*), red maple, and yellow birch (hemlock-hardwood swamp forest, [47]). Pine plantations (eastern white pine, red pine, jack pine *Pinus banksiana*, and Scotch pine *Pinus sylvestris*) predominate on excessively drained sand plains. Overall, eastern white pine, eastern hemlock, red maple, sugar maple, and black cherry comprise more than 70% of the total basal area and are among the most abundant species on the installation. In conjunction with the species listed, trembling aspen, gray birch, American elm, white ash, and northern red oak comprise the top ten species in terms of relative abundance (84%) and relative frequency at Fort Drum (Table 1).

TABLE 1: Relative frequency, density, and abundance of the 22 most common tree species at Fort Drum, New York, USA.

Species	Number of plots where present	Relative frequency	Relative basal area	Relative abundance
<i>Acer rubrum</i>	3734	55.8	13.7	20.0
<i>Prunus serotina</i>	2983	44.6	8.9	11.0
<i>Pinus strobus</i>	2385	35.6	31.4	16.7
<i>Populus tremuloides</i>	1702	25.4	5.0	7.2
<i>Acer saccharum</i>	1624	24.3	9.2	8.2
<i>Ulmus americana</i>	1168	17.4	1.4	3.3
<i>Fraxinus americana</i>	1080	16.1	1.9	3.0
<i>Betula populifolia</i>	1057	15.8	0.6	3.7
<i>Tsuga canadensis</i>	1018	15.2	9.2	8.2
<i>Quercus rubra</i>	754	11.3	5.2	3.2
<i>Betula alleghaniensis</i>	691	10.3	1.2	1.9
<i>Fagus grandifolia</i>	583	8.7	1.2	1.5
<i>Tilia americana</i>	505	7.5	1.6	2.0
<i>Populus grandidentata</i>	433	6.5	1.7	1.9
<i>Ostrya virginiana</i>	345	5.2	0.1	0.9
<i>Quercus alba</i>	332	5.0	1.0	0.8
<i>Amelanchier laevis</i>	279	4.2	0.1	0.7
<i>Fraxinus nigra</i>	273	4.1	0.3	1.0
<i>Pinus resinosa</i>	229	3.4	1.7	1.2
<i>Betula papyrifera</i>	194	2.9	0.2	0.5
<i>Thuja occidentalis</i>	163	2.4	0.6	1.2
<i>Carya cordiformis</i>	117	1.7	0.3	0.4

2.2. *Developing Species-Age Cohorts.* Detailed stand histories were not available for Fort Drum, but a systematic, variable-plot timber inventory completed in 2009–2011 provided basic information on species composition, abundance, DBH, and basal area distributions for 1,450 stands covering approximately 25% of the installation. However, the Fort Drum inventory was largely designed to produce a one-time estimate of commercial forest product volume and did not contain data on total tree height or site index that could be used to estimate stand ages from site index curves. Accordingly, we extracted age and DBH for site trees from regional USDA Forest Service Forest Inventory and Analysis (FIA) program plots (2002–2012) from the host and adjacent level IV ecoregions in New York [39, 48] for 13 species characteristic of major forest types at Fort Drum [38]. Each standard FIA plot is comprised of four circular subplots covering 0.4 hectares on which attributes are collected or computed for all trees greater than 5 inches in diameter. A standard FIA plot represents approximately 2,429 hectares (6,000 acres), and 15–20% of each state is assessed annually. Aggregate statewide reports are produced every 5 years that summarize key findings and compare trends over time [38]. Statistical details about the sampling framework, attributes collected at each plot, data processing procedures, and accuracy of FIA data are reported by Bechtold and Patterson [49]. Site trees are dominant or codominant trees located on FIA subplots that are used to estimate site index and stand age. The age of site trees is determined by counting growth rings on increment cores extracted at 1.37 m above the ground, and each tree is assigned a weighting factor that approximates the proportion of overstory trees represented by each site tree [50]. If FIA site trees are representatives of the diameters and ages of dominant and codominant species that comprise

the majority of the overstory in their respective stands, then age-diameter relationships derived from these trees should approximate the mean age of stands at Fort Drum when applied to the dominant species in each stand as defined by the relative basal area. It is important to note that the goal in developing age-diameter relationships was not to determine the precise ages of individual trees with a high degree of accuracy but to develop generalized age-diameter relationships that would support assignment of broad age classes to stands at Fort Drum in order to parameterize the LANDIS-II base succession model. Insufficient data were available for two overstory tree species at Fort Drum, American beech and white oak, so we excluded these species from the analysis. All plots had a forested condition class and elevation less than 500 m; the latter excluded trees located in higher elevations of the Adirondack Mountains and Tug Hill Plateau to the northwest and west, respectively, that were less likely to reflect site conditions at Fort Drum. We initially limited the FIA plot section to those located in counties containing the installation to approximate site conditions as much as possible. However, in order to obtain minimal samples sizes to support development of regression equations, we obtained data from additional nearby counties for three species, eastern hemlock, black cherry, and northern red oak, and a statewide sample was required for two species, American basswood and American elm. We filtered all site tree records to remove duplicate records from multiple inventory years. Tree age (years) and DBH (mm) were analyzed using simple linear regression (SAS JMP 13.1.0, SAS Institute 2016); diameter distributions for all species or species groups were not significantly different from normal based on the Shapiro–Wilk  $W$  test ( $W < 0.05$ ), and all outliers were retained in the analysis.

We then applied age-diameter regression equations to forest stands on Fort Drum by using the mean DBH for the most dominant species in each stand as the explanatory variable. Because the diameter distribution for all trees was negatively skewed (Figure 2(c)) and over 80% of the stands had a mean DBH less than 218.4 mm (8.6 in), we assumed that mean DBH might provide a more meaningful basis for estimating stand ages than median DBH by reducing the influence of large numbers of smaller diameter stems. Smaller trees are less likely to be members of dominant and codominant crown classes and would therefore be less comparable with site trees on FIA plots. Beginning with the species with the highest relative basal area (RBA) in a stand, we used mean DBH and a species-specific regression equation to calculate age and rounded values to the next highest 20-year class (e.g., ages 1–19 assigned to the 20-year age class and ages 21–39 assigned to the 40-year age class). As established by Twery et al. [51], we applied the following general rules for the number of species (SPP) used to estimate age and forest type for each stand:

- (1) Stands where  $SPP1_{RBA} \geq 70\%$ , mean DBH for SPP1 is used to calculate age classes and  $SPP1_{RBA}$  is used to determine forest type
- (2) Stands where  $SPP1_{RBA} \geq 50\%$  and  $<70\%$  and  $SPP2_{RBA} \geq 20\%$ , mean DBH for both species is used to calculate age classes and both species used to define forest type
- (3) Mean DBH for SPP1, SPP2, and SPP3 is used to determine age classes and forest type for all other stands
- (4) Where SPP1 was not considered, a characteristic overstory species (e.g., American hophornbeam), the mean diameter for the second most dominant species was used as a starting point for age calculations

For most stands, we used one or two species that comprised the majority of the basal area to define forest type. When present, we used certain tree species with the lower relative basal area to help define characteristic forest types. For example, eastern hemlock and red maple were dominant species in more than one forest type and often comprised large proportions of the total basal area, but based on the presence of species such as northern white cedar and black ash that are indicative of poorly drained sites, we typed stands as “Wet Forest” instead of “Hemlock” or “Mixed hemlock-hardwood” types. Generally, our forest type classifications followed community descriptions by Erdinger [47]. Using all possible combinations of age classes (7) and species types (9) would have created a very large number of categories to process within LANDIS-II and would not likely improve succession models in any biologically meaningful manner. Therefore, to improve processing time, simplify preparation of parameter files, and maximize interpretability of results from initial simulations, we coded stands into two broad age classes (stand age  $<40$  = “young” stands; stand age  $\geq 40$  = “mature” stands) for each forest type where these age classes occurred.

We derived vegetation types for areas on the installation not covered by the forest inventory using a land cover dataset developed from 1 meter resolution aerial photography in 2006 provided by the natural resources staff at Fort Drum and county soil surveys [42]. These cover types were primarily abandoned agricultural fields comprised of early successional grass-forb and woody shrub species and open grass fields maintained for military training activities. Species were not defined for grass-forb cover types, and subtypes were classified as mesic or xeric based on soil texture and drainage. Shrub cover types were combined into a single class comprised of woody deciduous shrub species such as speckled alder and willow and early successional hardwoods of American elm, gray birch, red maple, and trembling aspen with mesic and xeric subtypes defined by soil texture and drainage. We assigned open fields age class 20 and shrub types contained age classes 20 and 40. Once the stand attribute table was fully coded by type and age classes, we converted stand features (polygons) to a raster format with the 30 meter cell size using an integer value to represent each age-type condition.

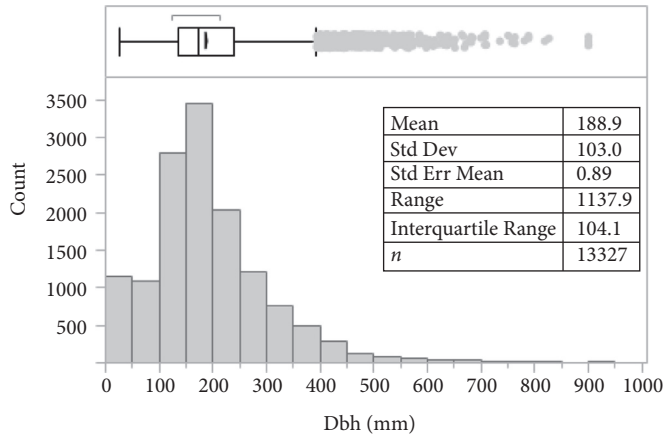
*2.3. Model Parameterization.* The LANDIS-II Age-Only Succession module incorporates life history information on tree species (e.g., longevity, reproductive traits, fire, and shade tolerance), spatial distribution of initial species-age cohorts, and establishment probabilities for each species by site type to model species regeneration, growth, colonization, and mortality for designated time periods [17]. We used silvic information from North America [28] and previous research utilizing LANDIS-II [52, 53] to define species attributes (Table 2). We assigned establishment probabilities for 25 woody species and 2 herbaceous cover types (Table 3) based on known adaptations to site conditions [28], community descriptions [47, 54], and their association with ecological site types derived from soil properties and physiographic variables at Fort Drum [55]. We generated input files using a simple text editor and executed to simulate community succession at Fort Drum over 100 years using a 20-year time step.

### 3. Results

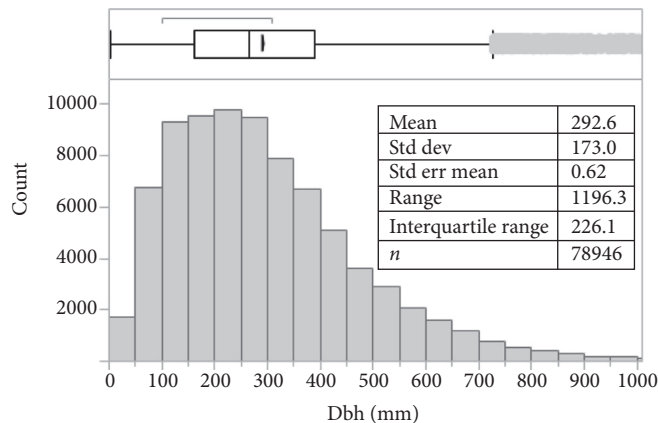
Species composition and relative basal areas were similar for regional FIA site tree plots and Fort Drum forest inventory plots; however, the installation contained a significantly larger proportion of eastern white pine and oak species relative to FIA plots and lower relative basal area in species associated with poorly drained sites such as northern white cedar and black ash (Figure 2(a)). This may be an artifact of under sampling of forested wetlands in the Fort Drum inventory, a larger relative proportion of excessively drained, sandy soils on the installation that favor pine and oak species, or a combination of both. However, relative basal area for the most common northern hardwood species were approximately equivalent. Diameter distributions of trees on FIA versus Fort Drum plots were also similar with both

Tree species	Fort drum relative basal area (percent)	FIA relative basal area (percent)
<b>Pinus strobus</b>	31.4	15.4
Acer rubrum	13.7	13.6
Tsuga canadensis	9.2	9.6
Acer saccharum	9.2	7.8
Prunus serotina	8.9	5.3
<b>Quercus rubra</b>	5.2	1.9
Populus tremuloides	5.0	3.7
<b>Fraxinus americana</b>	1.9	4.3
Populus grandidentata	1.7	1.3
Pinus resinosa	1.7	2.0
Tilia americana	1.6	2.0
<b>Ulmus americana</b>	1.4	4.4
Fagus grandifolia	1.2	2.3
Betula alleghaniensis	1.2	1.6
Quercus alba	1.0	0.2
Thuja occidentalis	0.6	6.4
Betula populifolia	0.6	1.1
Salix spp.	0.4	0.9
Fraxinus nigra	0.3	1.8
Carya cordiformis	0.3	1.0

(a)



(b)



(c)

FIGURE 2: Relative basal area for the twenty most frequent trees at Fort Drum and for the same species on-site tree plots extracted from the New York FIA database (a). Overall, species composition and relative density are similar, but significant differences are highlighted for several species (bold type and gray shading). Diameter distributions (DBH) are shown for all trees for FIA site tree plots (b) and the Fort Drum forest inventory plots (c).

datasets exhibiting an inverse J-shaped distribution, although there was a larger proportion of smaller diameter trees (DBH <300 m) on FIA plots (0.71) than on the installation (0.48) (Figures 2(b) and 2(c)).

Two hundred and twenty-one unique community type-age cohorts (Table 2 for a complete listing of cohorts) were identified at a stand level based on the relative basal area of dominant tree species and age classes derived from age-diameter equations. Linear models of age-diameter

relationships were all statistically significant ( $p < 0.05$ ) with  $r^2$  values ranging from 0.42 for sugar maple to 0.63 for white ash (Table 4). Predicted ages for individual trees ranged from less than 20 (American elm and various poplar species) to over 110 years (white ash and eastern hemlock) with mean ages for all species ranging from 33.8 (SE  $\pm$  2.5) to 69.6 (SE  $\pm$  4.5) years. Age distributions for the most common species were consistent with a priori assumptions that forests at Fort Drum are relatively young (Figure 3). Age-diameter

TABLE 2: Life history traits for species and cover types included in the LANDIS-II Age-Only Succession model.

Species/cover type	Longevity (yr)	Sexual maturity (yr)	Shade tolerance (1–5)	Fire tolerance (1–5)	Effective seeding distance (m)	Max seeding distance (m)	Probability of sprouting (0–1)	Min sprout age (yr)	Max sprout age (yr)	Fire strategy
Mesic meadow/early successional shrub <sup>1</sup>	40	1	1	2	100	1000	0.5	0	40	None
Xeric meadow/early successional shrub <sup>2</sup>	40	1	1	4	200	1000	0.5	0	40	None
<i>Abies balsamea</i>	200	25	5	1	30	160	0	0	0	None
<i>Acer rubrum</i>	150	10	4	1	100	200	0.75	0	100	None
<i>Acer saccharum</i>	300	40	5	1	100	200	0.1	10	60	None
<i>Alnus incana</i>	40	10	1	1	100	500	0.9	0	40	None
<i>Betula alleghaniensis</i>	300	40	3	2	100	400	0.1	10	180	None
<i>Betula populifolia</i>	100	30	2	2	200	5000	0.5	10	70	None
<i>Carya cordiformis</i>	300	30	3	3	30	100	0.75	10	100	None
<i>Fagus grandifolia</i>	300	40	5	1	30	100	0.75	0	100	None
<i>Fraxinus americana</i>	150	20	3	1	100	200	0.75	10	100	None
<i>Fraxinus nigra</i>	150	20	3	1	100	200	0.75	10	100	None
<i>Ostrya virginiana</i>	100	25	5	1	100	500	0.7	0	40	None
<i>Pinus banksiana</i>	100	15	1	3	30	100	0	0	0	Serotiny
<i>Pinus resinosa</i>	200	35	2	4	30	275	0	0	0	None
<i>Pinus strobus</i>	400	40	3	3	60	210	0	0	0	None
<i>Populus deltoides</i>	100	20	1	1	1000	5000	0.9	10	100	None
<i>Populus tremuloides</i>	100	20	1	1	1000	5000	0.9	10	100	None
<i>Populus grandidentata</i>	100	20	1	1	1000	5000	0.9	10	100	None
<i>Prunus serotina</i>	150	20	1	1	30	100	0.75	0	100	None
<i>Quercus alba</i>	300	25	3	2	30	1000	0.75	20	100	None
<i>Quercus rubra</i>	250	25	3	2	30	1000	0.75	20	100	None
<i>Salix</i> spp.	150	20	1	1	200	5000	0.75	10	70	None
<i>Thuja occidentalis</i>	400	20	3	1	30	60	0.1	10	100	None
<i>Tilia americana</i>	250	30	4	1	30	120	0.1	10	200	None
<i>Tsuga canadensis</i>	450	30	5	2	30	100	0	0	0	None
<i>Ulmus americana</i>	200	40	3	1	100	400	0.75	0	100	None

<sup>1</sup>Grass (*Poa pratensis* and *P. compressa*), sedges (*Carex* spp.), and herbs (*Solidago altissima*, *S. nemoralis*, *S. rugosa*, *Sympyotrichum novae-angliae*, *Oenothera biennis*, *Daucus carota*, *Ambrosia artemisiifolia*, and *Cerastium arvense*) communities with scattered clumps of woody shrubs (*Alnus incana*, *Cornus amomum*, *C. racemosa*, *Rhus glabra*, *R. typhina*, and *Rubus* spp.). <sup>2</sup>Grass (*Schizachyrium scoparium* and *Avenella flexuosa*) and sedge (*Carex* spp.) communities with scattered pine (*Pinus strobus* and *P. resinosa*) and oak (*Quercus rubra* and *Q. alba*) regeneration.

TABLE 3: Establishment probabilities for species included in the LANDIS-II Age-Only Succession model listed by ecological site type.

Species	1 Hydric depressional wetland	2 Subhydric alluvial deposit	3 Mesic glaciolacustrine plain	4 Mesic glaciofluvial sand terrace	5 Mesic, acidic glacial till	6 Xeric sand plain	7 Mesic, basic glacial till
Mesic meadow/early successional shrub	0.9	0.9	0.7	0.3	0.2	0.1	0.3
Xeric meadow/early successional shrub	0.1	0.4	0.3	0.3	0.3	0.9	0.5
<i>Abies balsamea</i>	0.9	0.7	0.2	0.1	0.1	0	0.1
<i>Acer rubrum</i>	0.7	0.8	0.9	0.9	0.9	0.5	0.7
<i>Acer saccharum</i>	0.2	0.3	0.9	0.5	0.9	0.5	0.9
<i>Alnus incana</i>	0.9	0.9	0.5	0.1	0.1	0.1	0.1
<i>Betula alleghaniensis</i>	0.9	0.7	0.5	0.7	0.9	0.2	0.5
<i>Betula populifolia</i>	0.3	0.7	0.9	0.3	0.5	0.5	0.5
<i>Carya cordiformis</i>	0.1	0.7	0.6	0.2	0.2	0.1	0.9
<i>Fagus grandifolia</i>	0.3	0.5	0.5	0.6	0.9	0.3	0.4
<i>Fraxinus americana</i>	0.3	0.7	0.9	0.3	0.9	0.3	0.7
<i>Fraxinus nigra</i>	0.9	0.9	0.5	0.2	0.1	0.1	0.1
<i>Ostrya virginiana</i>	0.2	0.5	0.5	0.4	0.8	0.1	0.4
<i>Pinus banksiana</i>	0.1	0.1	0.2	0.3	0.3	0.9	0.2
<i>Pinus resinosa</i>	0.1	0.1	0.2	0.3	0.5	0.9	0.3
<i>Pinus strobus</i>	0.4	0.7	0.5	0.7	0.9	0.9	0.5



TABLE 3: Continued.

Species	1 Hydric depressional wetland	2 Subhydric alluvial deposit	3 Mesic glaciolacustrine plain	4 Mesic glaciofluvial sand terrace	5 Mesic, acidic glacial till	6 Xeric sand plain	7 Mesic, basic glacial till
<i>Populus deltoides</i>	0.3	0.9	0.5	0.2	0.1	0.1	0.4
<i>Populus tremuloides</i>	0.3	0.9	0.9	0.5	0.5	0.5	0.5
<i>Populus grandidentata</i>	0.3	0.7	0.8	0.5	0.7	0.5	0.5
<i>Prunus serotina</i>	0.3	0.9	0.9	0.5	0.9	0.5	0.7
<i>Quercus alba</i>	0.1	0.2	0.4	0.4	0.3	0.8	0.5
<i>Quercus rubra</i>	0.1	0.2	0.5	0.5	0.5	0.9	0.5
<i>Salix</i> spp.	0.9	0.9	0.5	0.1	0.1	0.1	0.1
<i>Thuja occidentalis</i>	0.9	0.5	0.3	0.2	0.1	0.1	0.1
<i>Tilia americana</i>	0.3	0.5	0.9	0.4	0.5	0.2	0.9
<i>Tsuga canadensis</i>	0.9	0.9	0.9	0.9	0.7	0.5	0.4
<i>Ulmus americana</i>	0.3	0.7	0.9	0.2	0.4	0.2	0.7

TABLE 4: Age-diameter relationships developed from site trees ( $n = 395$ ) extracted from the New York FIA database.

Species	Dbh (mm)		Age (yrs)		$r^2$	RMSE	Linear regression model	
	$N$	$\bar{x}$ (SE)	$\bar{x}$ (SE)	Range			$P$	Equation
<i>Fraxinus americana</i>	35	249.7 (12.2)	47.7 (3.9)	21–118	0.63	14.1	<0.001	$A = -14.77259 + 0.250115 D$
<i>Tilia americana</i> **	35	299.5 (13.6)	50.5 (3.3)	24–102	0.56	13.1	<0.001	$A = -4.309491 + 0.1830496 D$
<i>Prunus serotina</i> *	15	273.6 (19.9)	46.9 (5.1)	23–77	0.54	13.8	0.002	$A = -4.579108 + 0.1880035 D$
<i>Ulmus americana</i> **	62	243.0 (10.2)	33.8 (2.5)	17–120	0.52	13.6	<0.001	$A = -9.319295 + 0.1774207 D$
<i>Acer rubrum</i>	81	255.0 (6.9)	52.0 (1.8)	20–87	0.50	11.7	<0.001	$A = 5.018457 + 0.1840787 D$
<i>Betula alleghaniensis</i>	10	230.6 (29.4)	57.6 (6.0)	26–88	0.48	14.4	0.025	$A = 24.976281 + 0.1414536 D$
<i>Quercus rubra</i> *	13	282.3 (21.0)	52.2 (4.4)	27–77	0.48	11.9	0.009	$A = 11.665456 + 0.1434076 D$
<i>Populus tremuloides</i> , <i>P. grandidentata</i>	17	256.5 (21.1)	35.1 (3.1)	19–67	0.45	9.8	0.003	$A = 9.7495765 + 0.0986561 D$
<i>Tsuga canadensis</i> *	22	313.1 (17.8)	69.6 (4.5)	33–115	0.44	16.3	0.001	$A = 16.623835 + 0.1693081 D$
<i>Pinus strobus</i> , <i>P. resinosa</i>	44	292.9 (9.6)	42.2 (2.2)	19–74	0.42	11.2	<0.001	$A = -0.836716 + 0.1473024 D$
<i>Acer saccharum</i>	61	288.4 (8.2)	61.3 (2.1)	27–95	0.42	12.6	<0.001	$A = 11.430045 + 0.1734929 D$

\*Additional data from FIA plots <500 m elevation located in Clinton, Franklin, Oneida, and Oswego counties included to increase the sample size.

\*\*Additional data from FIA plots <500 m elevation in all New York counties included to increase the sample size.

curves for sugar maple (Figure 4) and northern red oak (Figure 5) compared reasonably well with previous research in terms of growth rates (slope of best fit lines), although stands represented by FIA site trees appeared to be younger than those described in the literature.

Changes in forest types and individual species over time largely followed expected successional trends (Figure 6). Early successional species such as quaking aspen and black cherry increased substantially (13% and 8%, respectively) over the first 40–60 years and then declined as more shade-tolerant species (sugar maple and red maple) increased in the landscape. The impacts of Dutch elm disease were not simulated in initial succession models, and therefore, American elm appeared to increase substantially in importance by colonizing many of the grass-forb and shrub communities on mesic sites with fine-textured and relatively base-rich soils. The young red maple-American elm forest type, which also included significant components of quaking aspen and big-tooth aspen, gray birch, and black cherry, increased more than any other community type on the installation (>400%) and continued its expansion throughout the 100-year simulation. Much of the increase in

the aforementioned types occurred in postagricultural, old-field communities that declined substantially in the first 20–40 years and were almost entirely absent by year 60 of the simulation. Oak species and eastern hemlock did not increase substantially (+3%) but were able to maintain their relative abundance in the landscape despite increasing competition from sugar maple and red maple on all but the most xeric sites. However, in lieu of disturbance, oak woodland, oak-maple, and oak-pine forest types all declined substantially as composition shifted to more shade-tolerant maple species. Forested wetlands remained relatively constant over time in terms areal extent. Species changes in this type covered a very small proportion of the landscape and showed some loss of shade-intolerant species such as yellow birch and black ash while maintaining an overstory comprised of eastern hemlock, northern white cedar, and red maple. Despite its current dominant position in the landscape (>30% relative basal area), the relative abundance of eastern white pine remained constant over the duration of the simulation at a landscape level, but pine dominance in mixed stands declined at a stand level as more shade-tolerant hardwoods increased in younger age classes (Figure 7).

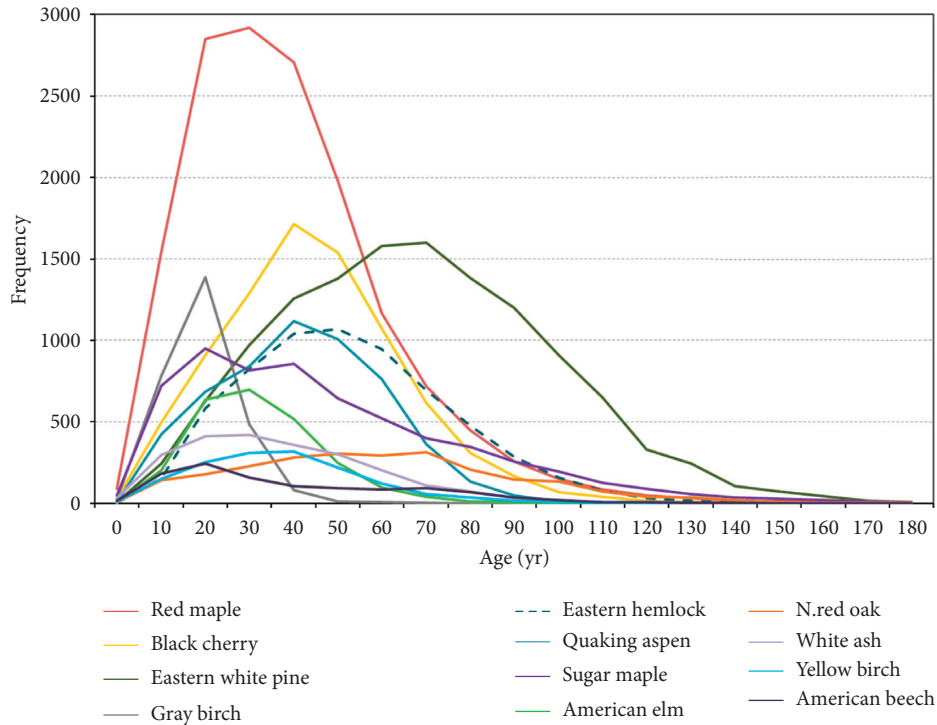


FIGURE 3: Age distributions for the 12 most common tree species at Fort Drum, New York, USA, based on age-diameter equations developed from FIA site trees: red maple (*Acer rubrum*), black cherry (*Prunus serotina*), eastern white pine (*Pinus strobus*), gray birch (*Betula populifolia*), eastern hemlock (*Tsuga canadensis*), quaking aspen (*Populus tremuloides*), sugar maple (*Acer saccharum*), American elm (*Ulmus americana*), northern red oak (*Quercus rubra*), white ash (*Fraxinus americana*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*).

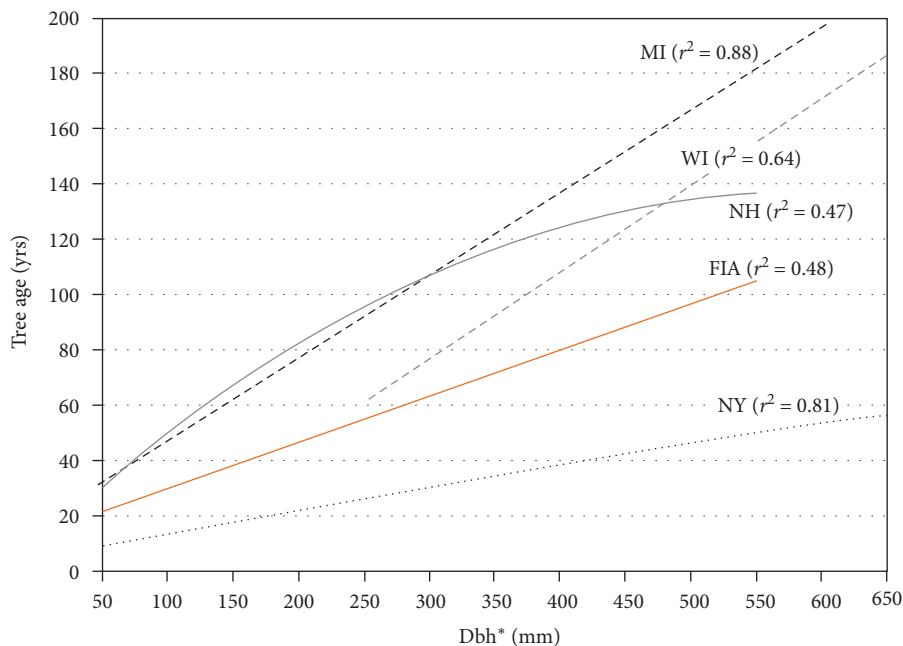


FIGURE 4: Age-diameter relationships for sugar maple (*Acer saccharum*) derived from previous studies and analysis of FIA site trees in North America: Michigan (MI), managed stand with several selection harvests ([24], Table 1); Wisconsin (WI), managed stands, selectively harvested ([25], Figure 1, \*diameter measured from top of cut stump); New Hampshire (NH), old-growth stand ([26], Table 1, \*diameter measured at top of root swell); FIA, site trees from New York FIA database (this study); New York (NY), uneven-aged managed stand, Allegheny Plateau ([27], Figure 2).

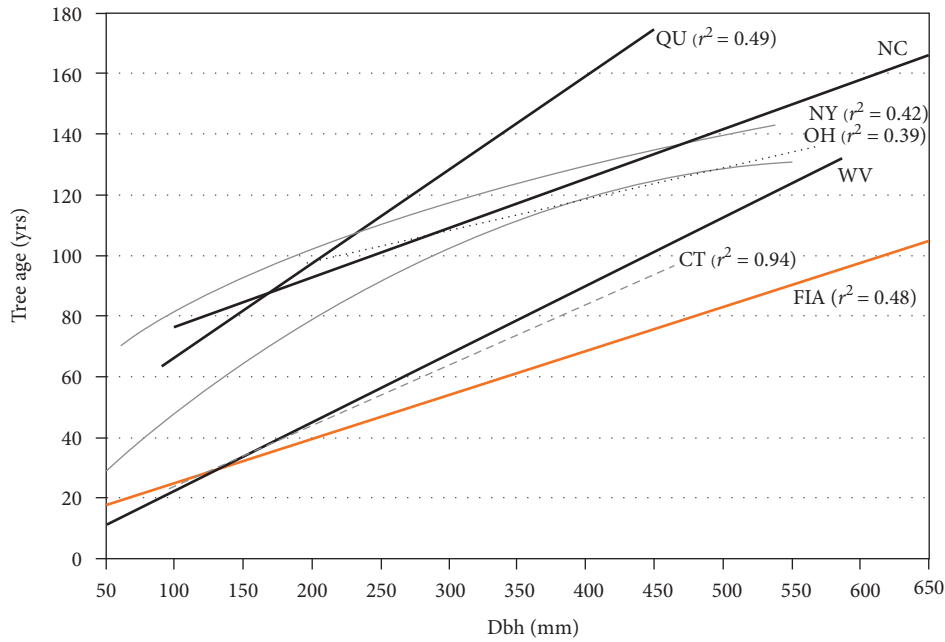


FIGURE 5: Age-diameter relationships for northern red oak (*Quercus rubra*) derived from previous studies and analysis of FIA site trees in North America: Quebec (QU), based on mean radial growth averages for 12 stands in southern Canada ([35], Table 2); North Carolina (NC), old-growth stand, southern Appalachian Mountains ([36], Figure 3); New York (NY), Black Rock Forest ([34], Ohio (OH), old-growth stands (5), Allegheny Plateau ([32], Figure 4.7); West Virginia (WV), average for 16, 55, and 80 year old managed stands, Monongahela National Forest ([37], Table 5); Connecticut (CT), average diameter and age for 7 managed stands ([33], Table 1); FIA, site trees from New York FIA database (this study).

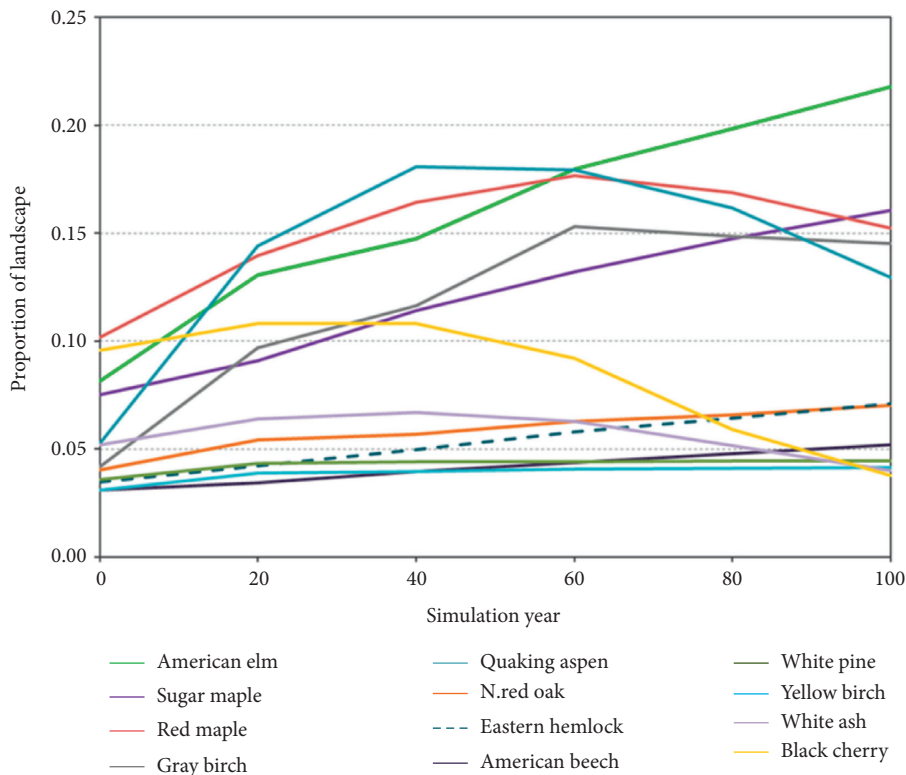
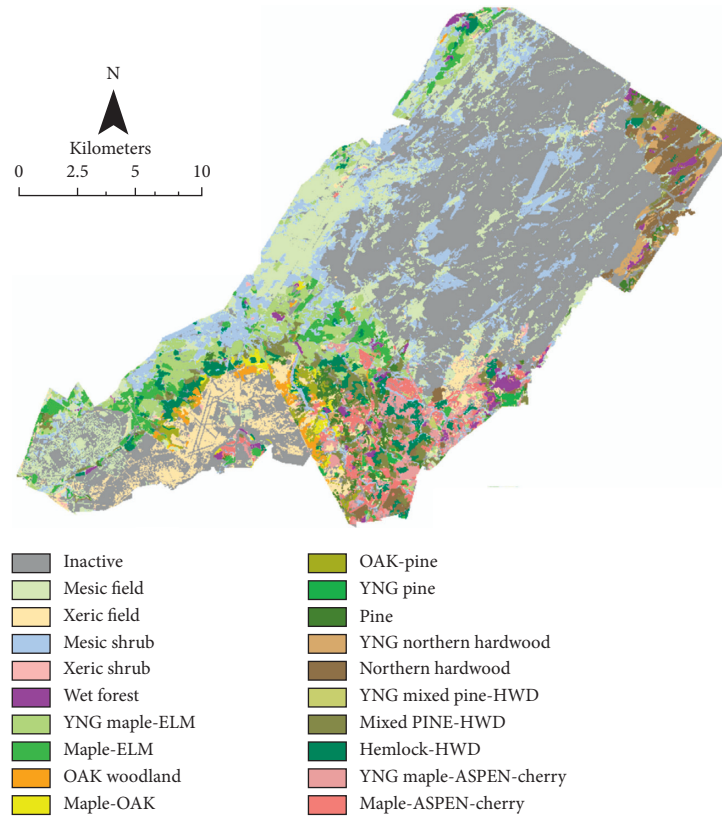
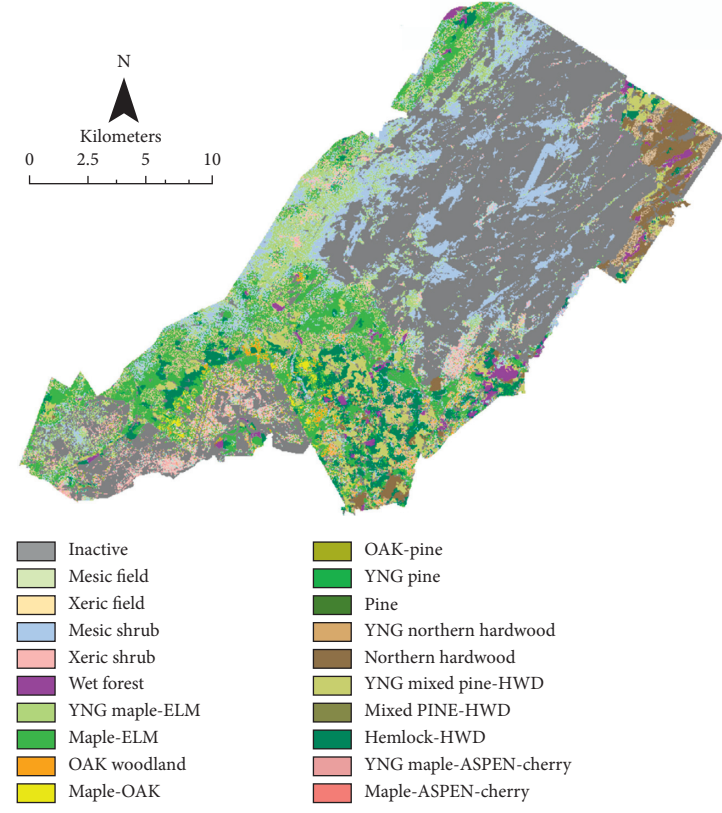


FIGURE 6: Landscape level change in the 12 most common overstory tree species at Fort Drum, New York, USA, over a 100-year simulation of forest succession under a no disturbance scenario: American elm (*Ulmus americana*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), gray birch (*Betula populifolia*), quaking aspen (*Populus tremuloides*), northern red oak (*Quercus rubra*), eastern hemlock (*Tsuga canadensis*), American beech (*Fagus grandifolia*), eastern white pine (*Pinus strobus*), yellow birch (*Betula alleghaniensis*), white ash (*Fraxinus americana*), and black cherry (*Prunus serotina*).



(a)



(b)

FIGURE 7: Current (a) and simulated (b) community type-age cohorts at Fort Drum, New York, USA. Maple-dominated stands in maple-elm (bright green) and northern hardwood (dark brown) types increased substantially over the 100-year simulation, while open grass-forb communities, oak woodlands (orange), and mixed pine (dark olive) stands declined. Forest stand data were not available for “INACTIVE” (gray) areas. In the map legend, “YNG” denotes stands less than 40 years of age and “HWD” denotes northern hardwood species. (a) 2015. (b) 2115.

#### 4. Discussion

Simulation of forest succession over 100 years on a landscape in northern New York State produced results largely consistent with our general understanding of how tree species composition changes over time in this ecoregion [52, 56–58]. In the absence of major disturbances and/or a full accounting for potential future forest pathogen impact, i.e., balsam woolly adelgid (*Adelges tsugae*), emerald ash borer (*Agrilus planipennis*), and beech-bark disease (*Neonectria* spp.), shade-tolerant mesophytic broadleaved species such as sugar maple, red maple, and American beech increased in importance in established forest stands. Sugar maple and red maple are abundant and widespread at Fort Drum and appear to be able to rapidly colonize all but the most xeric sites. Sugar maple increased 200% in terms of its relative frequency in the landscape and maintained a constant rate of increase of 2% per year throughout the simulation period. Red maple increased at a similar rate until year 60 and then showed a modest decline of 3% over the last 40 years of the simulation, presumably due to increased competition from more shade-tolerant species. American beech is a relatively minor component in the landscape as a whole (relative abundance and relative basal area <2%), which may reflect an inability to compete on the relatively fertile sites that comprise much of the installation, impacts of beech bark disease that is prevalent in the region [59], or simply inadequate time for populations to recover from past land use disturbance [58].

Large areas on Fort Drum remain in early successional grass-forb and shrub communities resulting from conversion of agricultural lands 50–60 years ago. Early successional tree species such as gray birch, quaking aspen, and American elm appear to be slowly colonizing these areas and increased substantially over the first 60 years of the simulation. Gray birch and quaking aspen declined slightly during latter stages of the simulation, whereas American elm continued to increase at a rapid rate. The latter may be attributable to American elm being slightly more shade tolerant than other early successional species and more competitive on the fertile and moderately poorly drained soils that characterize much of the former agricultural lands at Fort Drum. It is unclear why black cherry, an important component of early successional stands and the second most common species in terms of relative frequency and abundance on the installation, declined precipitously after year 40 of the simulation (from 10% to less than 4% of the total landscape). Other early successional species have more abundant, wind-dispersed seeds and substantially larger effective seed dispersal distances that may account for the inability of black cherry to maintain a dominant position in the landscape in some settings. Old field community types (24% of the current landscape) were almost completely absent by the end of the simulation as they were overtaken by woody shrub and early successional tree species.

The proportion of the installation covered by mature stands of important conifer species such as eastern hemlock and eastern white pine remained fairly constant throughout the simulation, although mixed pine-hardwood stands

tended to shift towards hardwood dominance as shade-tolerant deciduous species, primarily sugar maple and red maple, increased in abundance. Young pine and mixed pine-hardwood types decreased by 83% and 74%, respectively, during the 100-year simulation. Oak woodlands that occur almost exclusively on excessively drained, coarse-textured soils declined almost 99%. Establishment probabilities for the various maple species were almost half of those for oak and pine species on these sites, but high relative abundance, greater regeneration potential, and shade tolerance apparently combined to overcome any potential adaptations to relatively low soil fertility and moisture. It may be that despite the low stand densities (mean basal area <17.5 m<sup>2</sup>/ha) and concomitant high light levels that would appear to favor oak reproduction, the cold wet climate at Fort Drum may limit acorn production and increase seedling mortality for oaks relative to the more prolific and cold-adapted maple and aspen species [28, 60, 61]. Currently, oak dominance is maintained in these stands by mechanical mowing and low-intensity wildfires emanating from military training exercises. Accordingly, it seems evident that some form of disturbance will be required in the future if northern red oak and white oaks are to remain as even minor components of the forest landscape at Fort Drum.

The full accuracy of age classes derived from FIA site trees was impossible to determine without undertaking a significant effort to collect and analyze tree increment cores or without input from technologies such as airborne laser scanning [21]. However, age-diameter curves developed for two species, sugar maple and northern red oak, were consistent with relationships derived from published data in terms of growth rates and stand ages (Figures 4 and 5). Most of the stands in previous studies were described as old growth or mature and age-diameter curves developed from FIA site trees and applied to stands at Fort Drum consistently predicted younger age classes in comparison to stands analyzed in these studies. However, Kenefic and Nyland [27] provided an exception for sugar maple in southcentral New York on the Allegheny Plateau that had a similar diameter distribution but was apparently younger and growing faster in comparison to sugar maple stands at Fort Drum. This stand had a much higher percentage of sugar maple in comparison to most stands at Fort Drum and was selectively harvested in 1973 and 1993 with the specific intent of modifying the diameter distribution, including the removal of poor quality and noncommercial stems. Trees in this study were approximately half the age of trees at Fort Drum for the same diameter. Timber harvests have also occurred over the past 10 years in stands with a sugar maple component at Fort Drum but were likely not carried out with the express intention of creating balanced diameter distributions and increasing radial growth of remaining sugar maple trees as in Kenefic and Nyland [27].

Typically, age-diameter relationships from previous research were based on single, mature stands with known cutting histories. Mature sugar maple-dominated stands do occur at Fort Drum and in the surrounding landscape, but most of the installation is characterized by relatively younger stands with smaller mean DBH than the stands described

from other works. In addition, site conditions in any single stand should be less variable than the range of conditions in hundreds of northern hardwood stands at Fort Drum, which may mean that growth rates (and therefore age-diameter relationships) may be applicable to some stands, but not others. Overall, age-diameter curves for sugar maple and northern red oak showed a high degree of variability across the studies reviewed with diameter explaining as little as 39% to as much as 94% of the variation in age. Age-diameter relationships based on published studies may be more representative of older northern hardwood stands on upland sites at Fort Drum but may not reflect growth rates for lower elevation species on mesic (maple-basswood type) and xeric (pine and pine-oak types) sites at Fort Drum.

Although the accuracy of age classes developed for forest stands at Fort Drum was not quantified, ages represented by 20-year classes should account for some level of variation in age-diameter relationships and have been used elsewhere to model successional trajectories at a landscape scale. Zhang et al. [62] used FIA site trees to develop age-diameter equations and species-age cohorts for oak (*Quercus* spp.) and hickory (*Carya* spp.) forests in the Missouri Ozarks. Details of their regression analyses were not presented, but  $r^2$  for age-diameter correlations was fairly low, ranging from 0.15 (red maple) to 0.35 for white oak. Duveneck et al. [52] calculated tree ages using FIA plot data and site index curves to develop 5-year age classes to parameterize a LANDIS-II model for a landscape in Michigan. Other research has referenced FIA data as the source of species-age cohorts used to parameterize LANDIS-II models [63–65], but these studies often do not clearly describe how age data were derived, do not provide an accuracy assessment of age cohort estimates, nor include sensitivity analyses that might help to understand how variability in age cohorts might affect modeling results. Indeed, if only a few trees on FIA plots are used to assign stand ages within the FIA database, estimates of stand age would be subject to a high degree of variation since each FIA plot represents approximately 2,362 ha of forest [38], which could contain hundreds of stands with varying histories, species compositions, and site conditions.

## 5. Conclusions

Developing broad age cohorts from species-specific age-diameter equations derived from FIA site trees is a relatively straightforward process and provides a means of minimizing site variability to some degree by selecting FIA plots and site trees from similar ecoregions as those being modeled. However, unknown stand histories and variability in growth rates, both within a species at different life stages and among species with different shade tolerances in mixed northern hardwood stands, create a substantial level of uncertainty concerning the accuracy of FIA-based age cohorts used in LANDIS-II simulations. Over long simulation timeframes (>100 years), inaccuracies in cohort ages may become somewhat unimportant since, in lieu of major disturbance, shade-tolerant species should eventually dominate most northern hardwood stands regardless of whether stand simulations begin at age 20 or 40. However, as exogenous

disturbances are introduced to models to simulate more realistic future landscape conditions, especially over shorter time periods, the accuracy of cohort ages would appear to be a significant issue because response to various disturbances can be highly age-dependent. Therefore, it would seem additional assessments of tree or stand ages for landscapes being modeled, including sensitivity analysis to more accurately assess how inaccuracies in cohort ages might influence model results are needed. As managers go forward, these kinds of data will be critical for understanding potential outcomes relative to climate change or changes in forest utilization.

## Data Availability

The datasets used and/or analyzed during the current study are available from the corresponding author upon request.

## Disclosure

The use of any trade, product, or firm names does not imply endorsement by the U.S. government.

## Conflicts of Interest

The authors declare that they have no conflicts of interest.

## Authors' Contributions

RHO and WMF conceived the study. WMF obtained funding and provided study oversight. RHO performed the analyses. RHO and WMF interpreted the data. RHO prepared the manuscript. WMF edited and prepared the manuscript for submission.

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