

LANDIS PRO: a landscape model that predicts forest composition and structure changes at regional scales

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LANDIS PRO predicts forest composition and structure changes incorporating species-, stand-, and landscape-scales processes at regional scales. Species-scale processes include tree growth, establishment, and mortality. Stand-scale processes contain density- and size-related resource competition that regulates self-thinning and seedling establishment. Landscape-scale processes include seed dispersal and disturbances. LANDIS PRO is designed to be compatible with forest inventory data, thus extensive inventory data can be directly utilized to initialize and calibrate model parameters before predicting future forest changes. LANDIS PRO allows for exploring the effects of disturbances, management, climate change, and modeling the spread of invasive species. We demonstrate that LANDIS PRO successfully predicts forest successional trajectories and stand development patterns in the Central Hardwood Forest region in U.S.

Niche- and biogeochemical/ecophysiological process-based models are the primary tools used to predict forest change at regional scales ($> 10^8$ ha) (Morin and Thuiller 2009). Both types of models have limitations in their abilities to incorporate site- and forest landscape-scale processes (but see Engler et al. 2009, Boulangeat et al. 2012). Site-scale processes include growth, mortality, competition, and other stand-scale processes, which are critical in shaping species ranges and influencing biomass predictions at regional scales (Araújo and Luoto 2007, Tylianakis et al. 2008). Forest landscape scale processes are a set of spatial and stochastic processes that include seed dispersal and disturbances (He 2008). They play an important role in shaping forest change at regional scales (Dawson et al. 2011) and may exert greater effects than the direct effects of climate warming (Gustafson et al. 2010). Most niche-based models do not include site- and forest landscape-scale processes (but see Engler et al. 2009), whereas process-based models typically simplify the effects of disturbances as removal of a fixed portion of biomass at specified time (Scheiter and Higgins 2009). Without adequately accounting for the site- and forest landscape-scale processes, regional-scale forest change predictions made by niche- and process-based models may be subject to high uncertainties (Purves and Pacala 2008, McMahon et al. 2011).

Forest landscape models (FLMs) are explicitly designed to incorporate site- and forest landscape-scale processes to predict forest change at landscape scales (He 2008). To date,

FLMs have contributed relatively little to regional-scale forest change predictions due to the immense computational loads required (Supplementary material Appendix 1). The maximum simulation capacity (number of pixels) of FLMs is currently in the range of 10^6 – 10^7 cells (He 2008). Even at such a simulation capacity, site-scale processes are simplified omitting tree density and size metrics, which are key for determining stand-scale competition for resources (e.g. light) (Bohlmann and Pacala 2012). Here we present LANDIS PRO, a variant from LANDIS FLM family designed to overcome these challenges confronting FLMs.

Conceptual design of LANDIS PRO

LANDIS PRO is a raster-based FLM that evolved over 15 yr of development and applications of the original LANDIS model (ver. 6.0 and older) (He and Mladenoff 1999, Mladenoff and He 1999, Yang et al. 2011, Wang et al. 2013a). Within each raster cell, the model records number of trees by species age cohort. It uses a sorted linked list to store trees and age information in a sequential order (Fig. 1a). A lookup table for indexing data value for a given key (hash table) and a new algorithm for compressing data of adjacent raster cells (run-length compression) are used to enhance computational efficiency and memory usage in LANDIS PRO (Yang et al. 2011), thus presenting a computational solution to regional-scale simulation.

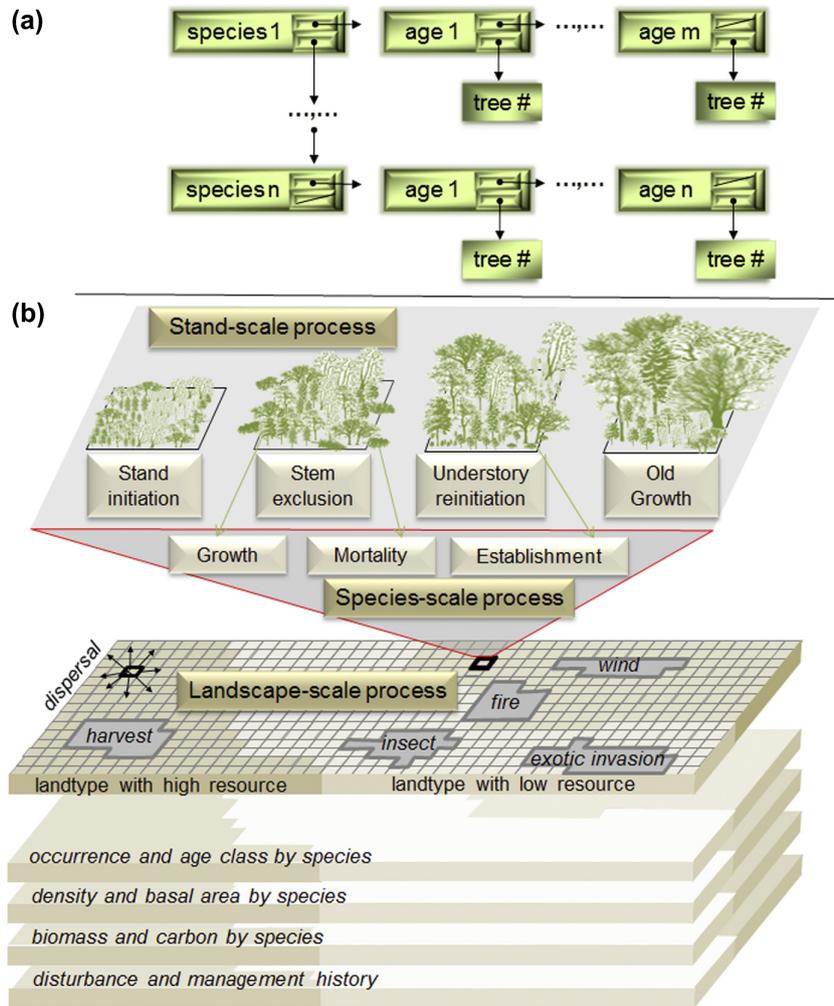


Figure 1. (a) LANDIS PRO uses a sorted linked list to store number of trees occurring by species age cohort in sequential order in each raster cell; (b) the conceptual design of LANDIS PRO that simulates forest change incorporating species-, stand-, and landscape-scale processes.

Size (diameter at breast height or DBH) for each species age cohort is derived from empirical age-DBH relationships. With both tree density and size information, LANDIS PRO derives key stand parameters including density, basal area, stocking, and biomass by species for each raster cell. LANDIS PRO simulation results allow for straightforward comparisons with forest inventory data, thus making it possible to fully utilize such data to construct the initial forest conditions and calibrate model parameters.

LANDIS PRO simulates forest composition and structure changes incorporating species-, stand-, and landscape-scale processes at regional scales (Fig. 1b). Species-scale processes include tree growth, establishment, resprouting, and mortality and are simulated using species' vital attributes as in previous versions of LANDIS (He and Mladenoff 1999) and LANDIS II (Scheller et al. 2007), but with new functionalities. For example, tree growth is simulated as DBH increment (species growth curves) in addition to age increment. DBH increment is simulated using empirical log-normal relationships of DBH to age or calibrated locally using forest inventory data by landtype, which accounts for the effects of varying resource availabilities and species establishment.

Stand-scale processes contain density- and size-related resource competition that regulates self-thinning and seedling establishment. The competition intensity is quantified by growing space occupied (GSO), which is estimated by summing the total growing space required to support all trees within each raster cell. The growing space is derived from the stand density index (Reineke 1933) using tree density and size information. Stand development patterns are governed by GSO and simulated to follow stand initiation, stem exclusion, understory reinitiation, and old-growth stages (Oliver and Larson 1996) (Fig. 2). Four GSO thresholds are defined to regulate seedling establishment in the stand initiation stage, where seedlings can only become established before stands reach fully occupied: 1) open grown (0-GSO_1), 2) partially occupied ($\text{GSO}_1\text{-GSO}_2$), 3) crown closure ($\text{GSO}_2\text{-GSO}_3$), 4) fully occupied ($\text{GSO}_3\text{-MGSO}$) (maximum growing space occupied) (Fig. 3). These GSO thresholds can vary by ecological section and can be modeled outside LANDIS PRO platform to incorporate the effects of varying MGSO resulting from nitrogen or CO_2 fertilization under climate change that is similar to the concept of maximum above-ground net primary productivity (ANPP) in LANDIS II

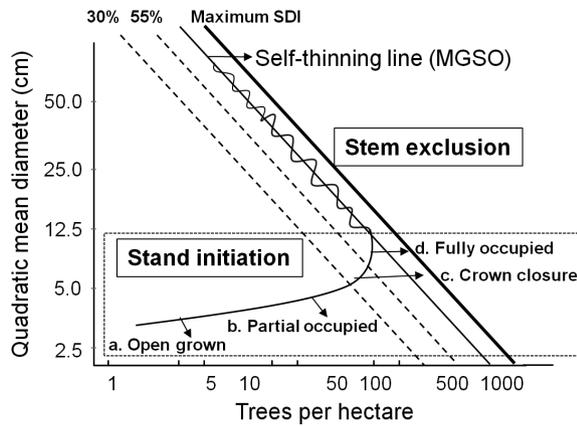


Figure 2. The Reineke density diagrams (Reineke 1933) and Yoda's $-3/2$ self-thinning rule (Yoda et al. 1963) are combined to display the stand development patterns governed by GSO. Reineke density diagrams plots the log of quadratic mean diameter against log of stem density (trees per hectare). The maximum size density lines represents 100% growing space and other size-density combinations express as a percentage of the maximum resource availability at different stand development stages: 1) stand initiation stage, 2) stem exclusion stage, 3) understory reinitiation stage, and 4) old-growth stage (Oliver and Larson 1996). In four sub-stages are defined based on GSO to regulate seedling establishment in stand initiation stage: open grown, partially occupied, crown closure, fully occupied. Seedling can only become established before stands reach fully occupied depending on species shade tolerance and SEPs. Once stands exceed MGSO, stands are presumed to reach stem exclusion stage, meanwhile, self-thinning is initiated and continues to the following understory reinitiation and old-growth stages. Self-thinning associated tree mortality is characterized by a decrease in the number of trees with increasing average tree size in the stand and follows the $-3/2$ rule. Stand development trajectories converge with the self-thinning line and moved along the self-thinning line from lower right to upper left.

(Scheller et al. 2012). They can also be defined for a variety of ecosystems. For example, a woodland system may never reach the crown closure stage and have low GSO_1 and GSO_2 values. Once stands exceed MGSO, stands reach stem exclusion stage; meanwhile, self-thinning is initiated and continues to the following understory reinitiation and old-growth stages (Oliver and Larson 1996) (Fig. 2). LANDIS PRO implements self-thinning, where tree mortality is characterized by a decrease in the number of trees with increasing average tree size in the stand and follows the $-3/2$ Yoda's self-thinning line (Yoda et al. 1963). Trees that are small, shade intolerant, or approaching their longevity can be out-competed first via self-thinning. Such design enables stand development trajectories to converge with the self-thinning line and move along the line from lower right to upper left (Fig. 2). During the understory reinitiation stage, seedlings with higher shade tolerance can establish. Continued tree growth and mortality in the absence of exogenous disturbance moves the stand into the old-growth stage, where old trees die as they reach their longevity, creating large canopy gaps that promote tree regeneration and move the stand into uneven-aged condition.

LANDIS PRO simulates landscape-scale processes including seed dispersal (exotic species invasion), fire, wind, insects and diseases, forest harvesting, and fuel treatments

in independent modules (Fig. 1b). Seed dispersal is simulated using a dispersal kernel determined by species-specific maximum dispersal distances, where the probability of seed dispersal to every cell is calculated using a negative exponential decay function (Mladenoff and He 1999). The total number of potential germination seeds (NPGS) for each species reaching a given raster cell are accumulated from all available mature trees within the dispersal kernel. The NPGS can be derived from Burns and Honkala (1990) and calibrated to ensure the predicted species density and basal area are consistent with forest inventory data. Thus, LANDIS PRO accounts for dispersal limitation and seed availability that can constrain species distributions under rapidly changing environment. Further information on the disturbance modules can be found elsewhere (Fraser et al. 2013, Wang et al. 2013b).

A heterogeneous landscape is stratified into landtypes in LANDIS PRO (also called ecoregions for broad-scale studies), which capture the coarse-level (coarse grain) spatial heterogeneity in resource availabilities (MGSO) and species assemblages (species establishment probability). Seed dispersal and disturbances result in the intermediate-level (fine grain, within or between landtype) heterogeneity in forest composition and structure. Finally, site-scale processes (e.g. competition, establishment) result in the fine-level (within raster cell) heterogeneity in forest composition and structure.

LANDIS PRO is a 32- or 64-bit computer model that runs on Windows XP and Windows 7, whose software package and a detailed user's guide can be downloaded from <http://landis.missouri.edu>.

Case study

To demonstrate the capabilities of LANDIS PRO, we applied the model to the Central Hardwood Forest Region (CHFR) in U.S. covering 98 million ha (Fig. 3a). The area was dominated by broadleaf deciduous hardwood forests. Forests in CHFR regenerated following extensive timber harvesting in the early 1900s and at or near maturity and thus self-thinning was a key process in driving stand development. We restricted our analyses to the most prominent 16 tree species, which included oaks (*Quercus* spp.), hickories (*Carya* spp.), and maples (*Acer* spp.) and accounted for 95% of the total forest biomass.

The initial forest species compositions map (Fig. 3b₁) included the number of trees by species age cohort for each raster cell for the entire CHFR and was directly derived from U.S. Forest Service Inventory and Analysis (FIA) data for 1980. All the input maps were gridded to 90 m resolution, which yielded about 100 million cells. We iteratively adjusted species growth curves and NPGS following 30 yr (1980 to 2010) of simulation by statistically comparing the simulated species density and basal area with the observed values of FIA data in the same period for each ecological section until the calibrated results passed chi-square test. Finally, we used the constrained initial forest conditions and calibrated parameters to project forest changes from 1980 to 2130 at five-year time steps without any disturbance. To evaluate the model projections, we compared the projected forest succession trajectories with characteristics of old-growth forests from field

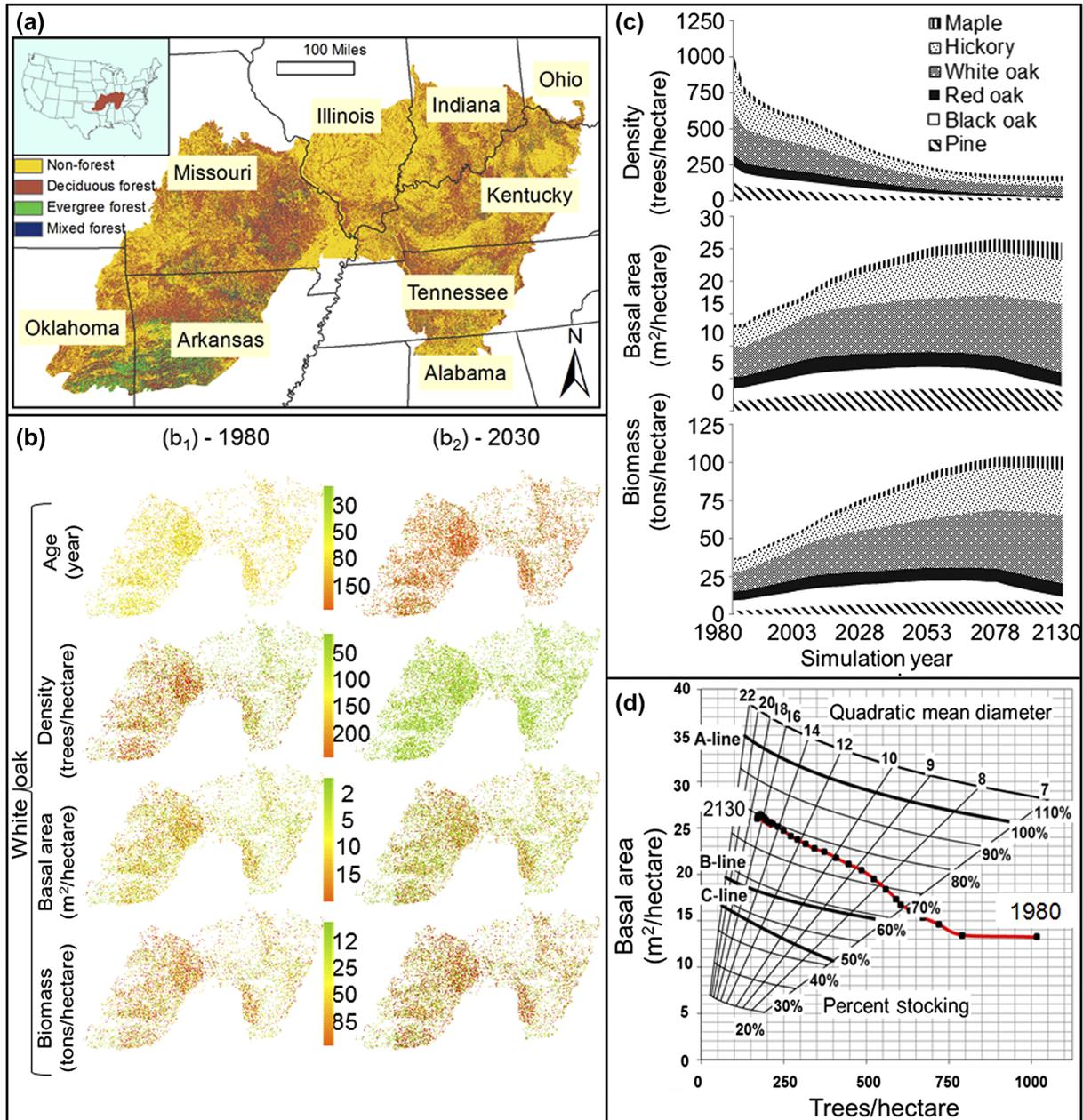


Figure 3. (a) The study area is U.S. Central Hardwood Forest Region (CHFR) covering 98 million ha; (b) the projected age, density, basal area, and biomass for white oak at 1980 and 2130 for the entire CHFR and show decrease in density, increase in age, basal area and biomass, and white oak range expansion; (c) the projected density, basal area, and biomass summarized by six species group and total carbon for the Ozark Highlands ecological section; and (d) the evaluation of stand development trajectories for mean stand conditions using Gingrich (1967) stocking charts from 1980 to 2130 for the Ozark Highlands ecological section.

studies, because our model was meant to project the potential natural succession in the time frame we simulated.

We presented white oak projections for the entire CHFR to illustrate model results (Fig. 3b). White oak decreased in density and increased in basal area, biomass, and age due to self-thinning and tree growth. White oak range expanded due to seed dispersal. Because of space restrictions, we only presented results from one of ecological sections – Ozark Highlands ecological section to illustrate the model calibration and evaluation processes (Fig. 3c, d). Overall, the initial forest composition of the Ozark Highlands for 1980 captured the historical conditions in 1980 reasonably well (density: $\chi^2 = 1.93$, DF = 5,

$p = 0.86$; basal area: $\chi^2 = 1.40$, DF = 5, $p = 0.92$). There were also no significant differences in density and basal area by species between the simulated and FIA data for 2010 (density: $\chi^2 = 1.85$, DF = 5, $p = 0.87$, basal area: $\chi^2 = 2.61$, DF = 5, $p = 0.76$). Thus, the calibrated model parameters predicted reasonable outcomes for the Ozark Highlands ecological section. The projected density of oaks, hickories, and pines in the Ozark Highlands decreased while the projected basal area increased over the 150 simulation years. The projected density and basal area of maples gradually increased over the next 150 yr, because a lack of disturbances favored the establishment of shade tolerant species. These projected successional trajectories

were consistent with studies of oak-dominated forest: oak forests typically transition to a greater proportion of longer-lived white oak species and shade-tolerant species such as maple in absence of disturbance (Johnson et al. 2009). We plotted the increases in mean stocking percentage and mean diameter and decreases in density as results of tree growth and mortality on Gingrich (1967) stocking charts (Fig. 2d). These resultant stocking percentages were consistent with the 75–90% stocking percentages reported for mature and old-growth oak forests in CHFR (Johnson et al. 2009). Therefore, LANDIS PRO projected the credible stand development patterns from 1980 to 2130.

Conclusions

LANDIS PRO achieves the regional-scale predictions while incorporating site- and forest landscape-scale processes. Such regional-scale predictions allow for comparisons with predictions made from niche- and process-based models to reveal the effects of forest landscape scale processes, thus reducing the prediction uncertainties. Since LANDIS PRO is designed to be compatible with field inventory data, it enables the model to fully utilize these data for model initialization, calibration, and evaluation. With number of trees and DBH by species age cohort, LANDIS PRO is able to simulate tree-based mortality and more realistically simulate forest disturbances and management. With the design of stand-scale processes, LANDIS PRO predictions can be directly linked to stand density management diagrams, thus making model predictions more relevant to forest management and planning. LANDIS PRO has the potential to explore the effects the spread of invasive species and climate change on species' range shift, forest composition, structure, and biomass at regional scales.

To cite LANDIS PRO or acknowledge its use, cite this Software note as follows, substituting the version of the application that you used for 'version 0':

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Supplementary material (Appendix ECOG-00495 at <www.oikosoffice.lu.se/appendix>). Appendix 1.