LANDIS-II Browse Disturbance v0.4
Extension User Guide

Order just implies people involved.
Patrick Drohan, Penn State University
Susan Stout and Alex Royo, Brian Miranda, Brian Sturtevant, Eric Gustafson USFS Northern Research Station
Nathan De Jager, USGS, Upper Midwest Environmental Sciences Center

Table of Contents

1 Introduction

Herbivory can exert significant control over plant community composition and ecosystem processes (Janzen 1970, Pastor et al. 1988, Rooney and Waller 2003). White-tailed deer (*Odocoileus virginianus*) browsing impacts on forest plant and animal communities derive primarily from defoliation and potential elimination of the shrub and seedling strata (Horsley and Marquis 1983, Liang and Seagle 2002, Horsley et al. 2003, Stout et al. 2014). Given the scale and magnitude of these impacts, white-tailed deer are now often classed as a keystone species in eastern North American forests (McShea and Rappole 1992, McShea and Schwede 1993) and have been suggested to create alternative stable states of woody-plant community composition (Stromayer and Warren 1997, Horsley et al. 2003; Royo et al. 2010). Similar ecosystem impacts have been documented for other forest ungulates, including moose (*Alces alces*) (Pastor et al. 1988, McInnes et al. 1992, Speed et al. 2013) and elk (*Cervus canadensis*) (e.g., Kaye et al. 2005). Such impacts have the potential to feedback and change the density of ungulate populations in dynamic plant-herbivore systems (Coughenour and Singer 1996; Moen et al. 1998,).

This document describes the **Browse Disturbance (v1.0)** extension for the LANDIS-II model. For information about the LANDIS-II model and its core concepts including succession, see the *LANDIS-II Conceptual Model Description*. The Browse Disturbance extension is designed to run with any succession extensions that carry cohort biomass attributes (e.g., Biomass Succession, PnET-Succession, Century Succession). However, this beta version (0.2) is limited to running with a specialized version of Biomass Succession (vBrowse).

The purpose of the Browse Disturbance extension is to reduce the growth and increase the likelihood of mortality for existing established cohorts according to a combination of published food preferences, variable ungulate abundance in time and space with the degree of realism defined by the user, and spatial factors affecting browsing pressure. The general approach to modeling browse disturbance on forests is to define available forage (annual growth of cohorts accessible to browsers) based on species preference and the composition of cohorts on each site (cell), remove some proportion of cohort biomass based on browser abundance and their preference for different species cohorts, and to impact susceptible species cohorts according to their ability to compensate for lost biomass. In addition, the extension provides the option to model reciprocal interactions between browsing populations and landscape distributions of available forage. A conceptual model of the Browse Disturbance extension is outlined in Figures 1 and 2.
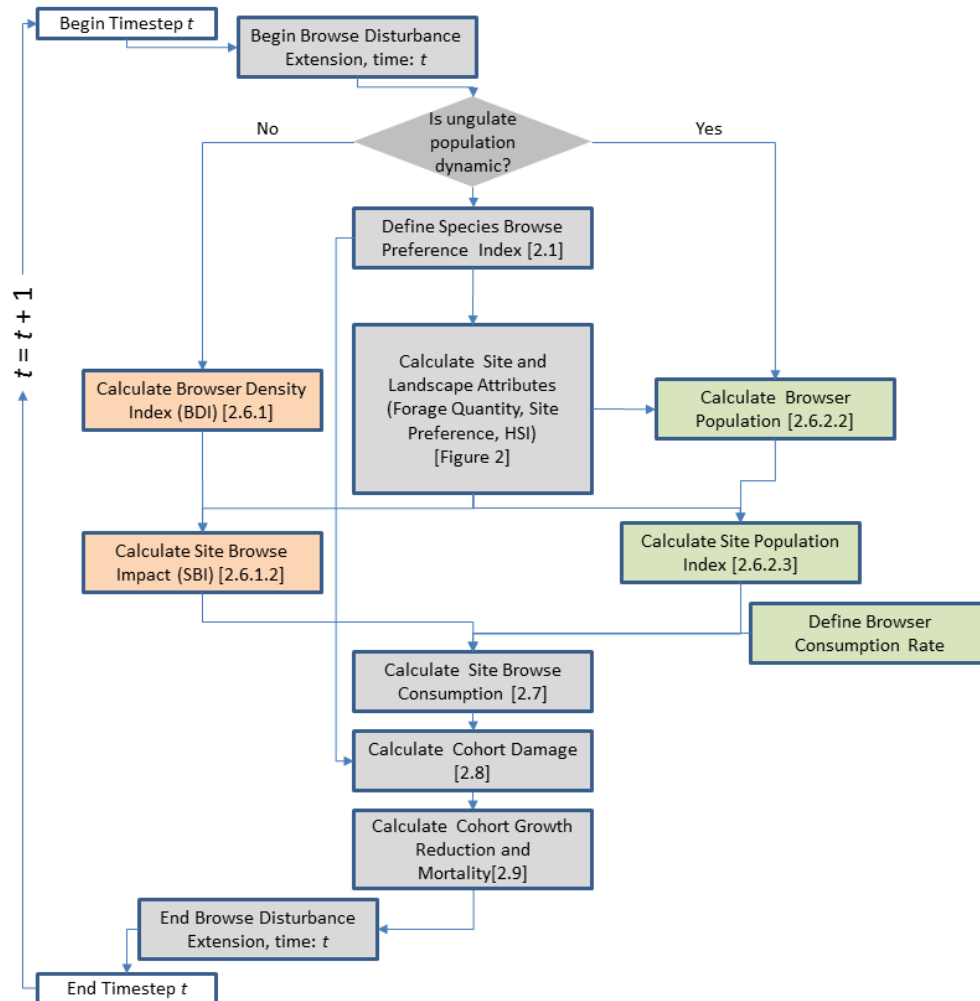
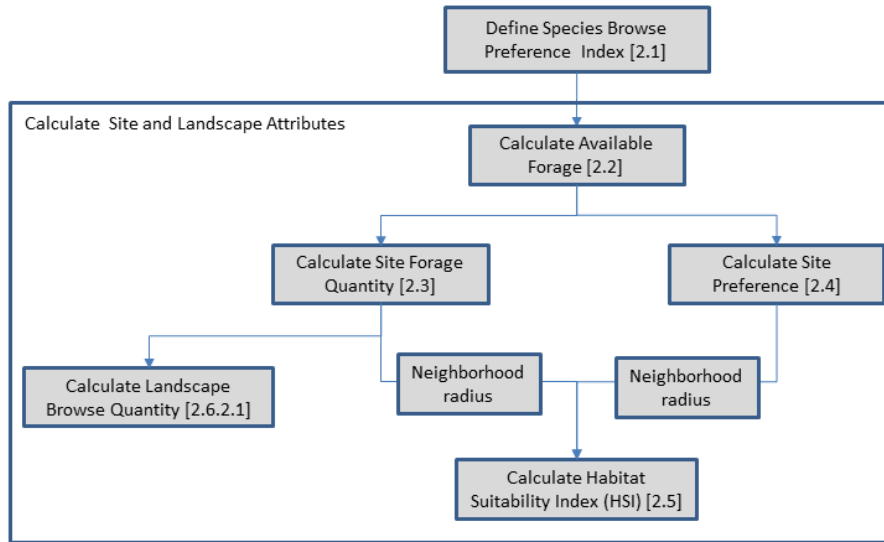**Figure 1. Overall conceptual diagram of Browse Extension.**

Figure 2. Inset conceptual diagram for calculation of site and landscape attributes.

2 Model Description

2.1 Species Browse Preference Index

Most browsers prefer certain plant species over others. The user must provide a relative preference index to each species. An example of tables bearing categorical values for browse preference by deer in Pennsylvania is provided in addendum 1. Species browse preference is a unit-less index (0-1) that defines the relative selectivity of the browser for certain species. Species with higher values are more preferred than species with lower values. Species with a browse preference of 0 are considered non-forage and therefore do not contribute toward estimates of forage quantity. However, users may include species with browse preference of 0 in calculations of site preference (2.4) if they suspect that non-forage species may influence the palatability of preferred species within the same site. Preference index values should be representative of annual browse preference, taking into account seasonal variability. The relative preference index also defines the target proportion of available browse biomass to remove from species cohorts.

2.2 Forage Availability

Available forage biomass is determined by whether a cohort is susceptible to browsing (i.e., of a size that could be browsed). This determination is based on the assumed height-reach of the herbivore and the assumption that species-cohort biomass is an approximation of cohort height. Forage availability is also determined by the fraction of annual growth that susceptible cohorts allocate to leaf and stem material.

2.2.1 Susceptible Cohorts

Susceptible cohorts are defined as those with total cohort biomass below a user-defined threshold. The user must provide a parameter that represents the proportion of the maximum per-site biomass that equates to a cohort beginning to escape the reach of the herbivore. For example, if an ecoregion has a maximum site-biomass of 10000 g/m^2, then a parameter value of 0.05 means that cohorts above 500 g/m^2 begin to escape browse pressure due to height. Using this biomass threshold, the proportion of each cohort that is within browse reach is estimated. Starting with the cohort with the lowest biomass (regardless of species preference and age), the proportion in browse reach is the ratio of cohort biomass to the biomass threshold, with a maximum value capped at 1.0. If the cohort biomass is less than the biomass threshold, the next cohort in order of increasing biomass is also considered. The first cohort's biomass is subtracted from the threshold, and this new threshold is applied to the second cohort. This sequence is repeated for cohorts until the threshold is met, or until all eligible cohorts have been considered. We assume that apical dominance within low-statured cohorts will drive susceptibility to browsing herbivory, i.e., browsing of lower branches will be compensated by growth beyond the browse line (McLaren and Peterson 1994, Vila et al. 2002). Hence those cohorts that have less than a user-defined proportion (default is 50%; see 3.2.8) of their biomass within browse reach are assumed to have "escaped" browsing herbivory, and are not included in the forage quantity estimate. Cohorts with proportions of biomass in browse reach less than the threshold proportion are considered to contribute to forage quantity at a rate equal to the proportion. For example a cohort with a proportion of 0.75 has 75% of its total forage available within browse reach. Finally, an age threshold as a proportion of longevity is used to prevent senescing mature cohorts from being treated as cohorts within browse reach. Cohorts with ages greater than this age threshold (default is 57% of longevity; see 3.2.10) are not considered as eligible.

2.2.2 Available forage biomass

Available forage biomass is calculated as the annual growth allocated to stems and twigs. Browsing herbivores typically remove leaf material from deciduous trees during summer and remove stem material from deciduous trees during winter. They also tend to avoid browsing conifers during the summer, but remove both stems and the needles attached to them in winter (Persson et al. 2000). Hence, both new leaf and twig material are annually available to foraging herbivores. By default, we assume that 33% of annual growth is allocated to leaves and 33% is allocated to twigs, for a total of 66% of annual growth that is available as forage biomass. These calculations are based on general allocation patterns observed across a wide range of tree species with different life history attributes (Niklas and Enquist 2002). The user can supply a different proportion of ANPP (3.2.7). Users can also apply an option to count 100% of new growth as browseable material during the first year of growth (cohort age = 1).

2.3 Population Zones

Spatial heterogeneity in browsing pressure caused by heterogeneity in either relative or absolute ungulate densities (see Section 2.6 below) can optionally be defined as different population zones within the Browse Disturbance extension. The user may specify spatial zones (termed Population Zones) that represent different regions of the simulated landscape with independent population densities. These zones are defined as an input raster map with map values corresponding to the different Population Zones. If no zone map is provided, the entire simulation area is treated as a single zone.

2.4 Site Forage Quantity

Site forage quantity is a raster map of the total amount of available forage (g/m^2) on each site (cell in the raster). Available forage (as defined in 2.2) is summed for all species-cohorts present on each site. Cohorts with species preference values (as defined in 2.1) of 0 are considered non-forage, and are not included in the calculation of site forage quantity.

2.4.1 Zone Forage Quantity

The total forage quantity for each population zone (Z, see 2.3) is summed from the site forage quantity values.

$$ForageQuantity_Z = \sum ForageQuantity_{site}$$

Zone forage quantity is used in the calculation of zone carrying capacity (when using the Dynamic Browser Population [2.6.2]) and to rescale the site forage quantity (2.4.2)

2.4.2 Rescaled Forage Quantity

A rescaled site forage quantity value is calculated so that the sum of the rescaled values sums to 1.0 in each zone (Z, see 2.3).

$$Quantity\_rescale_{site} = \frac{ForageQuantity_{site}}{ForageQuantity_Z}$$

The rescaled site quantity is used calculate site browse impacts (2.6.1.2) or site population density (2.6.2.3), and serves as a component in downscaling the zone population to the site-scale.

2.5 Site Preference

Site preference is a raster map of the average preference value for available forage on each site (cell), and is an indicator of forage "quality". The value is calculated as a weighted average of either:

    A) the preference values for all species-cohorts present in a cell, or

    B) the preference values for species-cohorts with >0 preference,

where the weighting is based on the cohorts' available forage (as defined in 2.2). Users should choose option A if they suspect that the presence of non-forage species at a site could reduce the susceptibility of preferred species-cohorts to browsing. The default behavior is option B, but users can choose option A with the optional "CountNonForageSitePref" parameter (3.2.13).

2.6 Habitat Suitability Index

To account for the spatial pattern of available browse and how it might influence whether any one site (cell) is browsed, a Habitat Suitability Index (HSI) raster is calculated. Users have the option to calculate the HSI using a moving window of a specific size if they assume that the quantity and/or quality of available browse in the surrounding neighborhood of sites will impact the susceptibility of sites to browsing. Options for calculating HSI include:

    A) neighborhood average of site forage quantity (2.2),

    B) neighborhood average of site preference (2.4),

    C) the product of A and B.

If the user does not choose to implement the moving window algorithm (neighborhood radius = 0), then HSI will be based on site-specific A, B or C.

2.6.1 *Rescaled HSI*

A rescaled HSI value is calculated so that the sum of the rescaled values sums to 1.0 in each zone (*Z*, see 2.3).

$$HSIrescale_{site} = HSI_{site} \div \sum HSI_{site}$$

The rescaled HSI values are used as a component a component in downscaling the zone population to the site-scale.

2.7 Browser Population Density

The browse disturbance extension provides users with two alternative options to defining browsing pressure related to ungulate density. The first (elaborated in Section 2.7.1) implements a user-defined browser density across the landscape or within different spatial zones (defined below). Under this option, the user defines how browser densities vary in time and space as a modeling scenario (i.e., they are pre-determined by the user). This option will be most applicable where browser density is primarily defined by external factors such as hunting activities. The second option (elaborated in Section 2.7.2) explicitly models browser population dynamics as a function of forage availability and user-supplied mortality rates. Regardless of the browser density option used, the user may specify population zones (2.3) that represent different regions of the simulated landscape with independent browser densities. If no zone map is provided, the entire simulation area is treated as a single zone and single population.

2.7.1 Density Option 1: Browser Density Index (BDI)

The Browser Density Index is a user-supplied value between 0 and 1 that represents the population density relative to its capacity for browsing impacts. For example, a BDI value of 0.50 represents a density which would, on average, consume 50% of available forage. A value of 1.0 would be an extreme case where 100% of available forage would be consumed, representing densities at (or above) the

carrying capacity. Values are provided by the user for each Population Zone (2.3). When multiple population zones exist within the simulation area the user has the option to 'smooth' the distribution of BDI using a moving window average of the BDI values. After smoothing, each site has its own BDI value (BDI$_{site}$).

2.7.1.1 Site Browse Impact (SBI)

The site browse impact raster uses the zone total browse impact, the rescaled local HSI (2.6.1) values and the rescaled site forage quantity (2.4.2) to estimate local browse impacts, as a rate of browse removal. The total browse impact (TBI$_Z$) for zone (Z) is calculated by summing the BDI values of all sites in the zone.

$$TBI_Z = \sum BDI_{site}$$

As the browse density index (BDI) approaches 1.0, the HSI value has less influence on the distribution of impacts (SBI). In the extreme case of BDI of 1.0, where all available forage will be consumed, impacts must be distributed in proportion to the quantity of available forage on each site. Therefore, the site browse impact is the product of total zone impact TBI$_Z$ and a weighted average of [HSIrescale] (2.6.1) and [Quantity_rescale] (2.4.2), where BDI (2.7.1) provides the weighting.

$$SBI_{site} = TBI_Z \times [(Quantity\_resacle_{site} \times BDIsite) + (HSIresacle_{site} \times (BDIsite - 1))]$$

In essence, this is the BDI value downscaled to the site-level using the HSI and forage quantity values. It is possible for this calculation to result in a SBI value greater than one, which would indicate a removal of more than 100% of the available forage. To account for this artifact, SBI values are capped at 1.0, and the remainder beyond 1 is recorded and summed across sites within a zone. The total remainder is then allocated equally (not biased by HSI or forage quantity) to sites with initial SBI values less than 1. This approach will maintain an average SBI value equal to the zone BDI, with a spatial bias determined by HSI values and forage quantity.

2.7.2 Density Option 2: Dynamic Browser Population (DBP)

Ungulate populations are influenced by density-dependent growth and mortality, along with other factors that may reduce population density (e.g. hunting, predation, disease outbreaks). Under the DBP option, density-dependent changes in the ungulate populations are modeled according to the discrete-time quadratic model (May 1975), which models population increases or decreases in relation to a population carrying capacity. When the animal population exceeds its carrying capacity, animal mortality exceeds recruitment and the population declines. When the animal population is less than carrying capacity, recruitment of new animals exceeds mortality and the population increases. The carrying capacity of the animal population is estimated by the annual forage requirements for individual animals in the population in relation to the forage biomass available across the landscape. Additional factors also reduce ungulate populations and will be modeled accordingly (e.g. harvest, stochastic mortality, and predation). Stochasticity is incorporated by parameter estimates for population growth and mortality factors ~~using mean estimates and normal distributions.~~ by drawing a value between provided minimum and maximum values.

2.7.2.1 Calculate Zone Carrying Capacity

We define the carrying capacity of the browser population as the forage quantity available across the landscape in relation to the annual intake rate of the population. The total available forage in the population zone is calculated as the sum of site forage quantity across all sites in the zone (2.4.1). Zone carrying capacity is determined by dividing the total forage quantity by the annual consumption rate for the browser population, which is supplied by the user.

2.7.2.2 Calculate Browser Population

Changes in the browser population are modeled according to the discrete-time quadratic model (May 1975):

$$\Delta N_{t,Z} = R_Z N_{t,Z} \left(1 - \frac{N_{t,Z}}{K_Z}\right) - \sum M_Z N_{t,Z}$$

Where $\Delta N_{t,Z}$ is the change in browser population density N at time t and in Population Zone Z, R_Z is a user-supplied population growth rate for zone Z and $\sum M_Z N_{t,Z}$ is the sum of all reductions in the population due to mortality factors. Users can supply mortality rates for A) generic mortality (any factor that might reduce population density), B) harvesting (population management), and C: predation. K_Z is the carrying capacity for the browser population (2.7.2.1).

2.7.2.3 Calculate Site Population Index

The site population index raster combines the zone population (2.7.2.2), the rescaled local HSI (2.6.1) values and the rescaled site forage quantity (2.4.2) to estimate local populations of browsers. This process distributes the zone population to sites as a function of the HSI values and forage quantity in a manner directly analogous to the spatial distribution of BDI to local SBI values (2.7.1.2). Here the spatial distribution of population is influenced by the population proximity to carrying capacity (K, 2.7.2.1). As a population approaches K, the distribution must more closely match the distribution of available forage and HSI has less influence on population distribution. In the extreme case of the population at (or above) K, then the distribution of the population must be distributed in proportion to the quantity of available forage on each site. Therefore, the site population (Pop$_{site}$) is the product of total zone population (Pop$_Z$) and a weighted average of [HSIrescale] (2.6.1) and [Quantity_rescale] (2.4.2), where the ratio of Pop$_Z$ to K provides the weighting.

$$Pop_{site} = Pop_Z \times \left[\left(Quantity\_resacle_{site} \times \frac{Pop_Z}{K}\right) + \left(HSIresacle_{site} \times \left(\frac{Pop_Z}{K} - 1\right)\right)\right]$$

2.8 Site Browse Consumption

If using defined browser densities (2.6.1), the SBI (2.6.1.3) determines the overall browse rate for a site. The total amount of forage to be removed on a site is the product of the SBI and the Site Forage Quantity (2.3). If using the dynamic browser densities (2.6.2), the defined browser consumption rate is multiplied by the site population index (2.6.2.3) to calculate the total amount of forage to be removed.

2.9 Cohort Damage

Within a site, biomass is removed from cohorts (i.e., they are damaged) preferentially according to species preferences. The total amount of forage to be removed from a site is first calculated (2.7). Then, species-cohorts are rank-ordered by their preference values (2.1). These values not only rank species, but define a target removal percentage (i.e., a 0.8 preference equates to 80% consumption of that species). Forage biomass is first removed from species with the highest browse preference (all species with the same rank are treated equivalently), up to the target removal rate for the species-cohort. If more biomass needs to be removed to reach the calculated total amount of forage for the site, then biomass is removed from the next most preferred species-cohort, again up to the species-cohort's target removal rate. This

procedure is repeated for all species until the biomass to be removed is satisfied, or all cohorts have been browsed at their target removal rates. If browse removal using the defined target removal rates does not meet the required total amount of forage, then additional biomass is removed again starting with the most preferred species. The biomass removal needed to meet the target is removed from the most preferred species until all available biomass has been removed from that species (i.e., now ignoring the target removal rate for the species). Any remaining biomass to be removed comes from the next most preferred species, and continues down the preference list until either the demand for removed biomass is met, or all available biomass is removed from the site.

Example: A site has a SBI of 0.45 and 100 g/m^2 available forage, translating to a total forage removal of 45 g/m^2. There are 2 cohorts on the site, one high preference (0.85) and one low preference (0.165). Assume the high preference cohort has 30 g/m^2 available forage, which get browsed at a rate equal to its species preference (0.835). Therefore, 25 g/m^2 is removed from this cohort. The second cohort is low preference with 70 g/m^2 available forage. This cohort will be browsed at its removal rate (0.165) to have 12 g/m^2 forage removed. The total forage consumed (37 g/m^2) is less than the total target removal for the site (45 g/m^2). The remaining forage to remove (8 g/m^2) comes from the most preferred species first, up to its total available forage. In this case, and additional 5 g/m^2 can be removed from the highly preferred cohort for a total removal of all 30 g/m^2. The remaining 3 g/m^2 is removed from the less preferred cohort for a total of 15 g/m^2.

2.10 Browse Effect on Cohort Growth and Mortality

The browse disturbance extension models the effects of biomass removal on subsequent cohort growth and survival via separate user-defined threshold proportions of annual growth removed (see Figure 3). Browse rates above these thresholds (a) lead to growth reduction in the following year, and/or increased probability of mortality prior to the following year. Beyond the threshold removal proportions, effects on growth reduction and mortality increase linearly to maximums (b) set by the user.
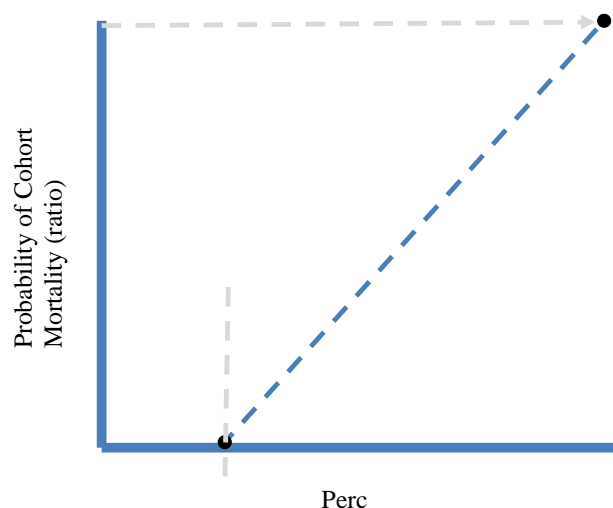
Figure 3. Effects of browse on cohort mortality and growth reduction. A user-defined threshold (a) determines the minimum amount of browse for any effect, and a second user-defined threshold (b) determines the maximum effect when browse is 100%.

Areas for additional development
  Stochasticity –where and how.
  Seed predation

2.12 Literature Cited
Coughenour, M.B., Singer, F.J. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecological Applications 6: 573-593.

Horsley, S.B., Marquis, D.A., 1983. Interference by weeds and deer with Allegheny (Pennsylvania, USA) hardwood reproduction. Canadian Journal of Forest Research 13, 61–69.

Horsley, S.B., Stout, S.L., deCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications 13, 98–118.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501–528.

Latham, R. E., J. Beyea, M. Benner, C. A. Dunn, M. A. Fajvan, R. R. Freed, M. Grund, S. B. Horsley, A. F. Rhoads and B. P. Shissler. 2005. Managing White-tailed Deer in Forest Habitat From an Ecosystem Perspective: Pennsylvania Case Study. Report by the Deer Management Forum for Audubon Pennsylvania and Pennsylvania Habitat Alliance, Harrisburg. xix + 340 pp

Liang, S. Y., and Seagle, S. W. 2002. Browsing and microhabitat effects on riparian forest woody seedling demography. Ecology, 83, 212-227.

Kaye, M. W., Binkley, D., & Stohlgren, T. J. 2005. Effects of conifers and elk browsing on quaking aspen forests in the Rocky Mountains, USA. Ecological Applications, 15, 1284-1295

Marquis, David A. 1987. Silvicultural techniques for circumventing deer browsing. In: Cochran, Roe S., chair. Proc. Symp.; Deer, Forestry and Agriculture: Interactions and strategies for management. 1987 June 15-17. Warren, PA. Erie, PA: Plateau & North. Hardwood Chap., Allegheny Soc. Amer. For. p. 125-136. 183p.

May, R.M. 1975. Biological populations obeying difference equations: stable points, stable cycles, and chaos. J. Theor. Biol. 51:511-524

McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 73:2059–2075.

McLaren, B.E., Peterson, R.O. 1994. Wolves, moose, and tree rings on Isle Royale. Science 266:1555-1558.

McShea, W. J., and J. H. Rappole. 1992. White-tailed deer as a keystone species within forest habitats of Virginia. Virginia Journal of Science 43:177–186.

McShea, W. J., and G. Schwede. 1993. Variable acorn crops: responses of white-tailed deer and other mast consumers. Journal of Mammalogy 74:999–1006.

Moen, R., Cohen, Y., Pastor, J. 1998. Linking moose population and plant growth models with a moose energetics model. Ecosystems 1: 52-63.

Niklas, K.J., Enquist, B.J. 2002. Canonical rules for plant organ biomass partitioning and annual allocation. American Journal of Botany 89:812-819.

Comment [NDJ9]: See other version for more details. If we can get sections 2.2 and 2.9 to 'calibrate' available browse than I think these two issues are our next topics of discussion.

Pastor, J., R. J. Naiman, B. Dewey, and P. McInnes. 1988. Moose, microbes, and the boreal forest. BioScience 38: 770–776.

Persson, I-L., Danell, K., Bergström, R. 2000. Disturbance by large herbivores in boreal forests with special reference to moose. Ann. Zool. Fennici 37: 251-263/

Rooney, T.P. and Waller, D.M. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181: 165-176.

Royo, A.A., Stout, S.L., deCalesta, D.S., and T.G. Pierson. 2010. Restoring forest herb communities through landscape-level deer herd reductions: Is recovery limited by legacy effects? Biological Conservation, 43: 2425–2434

Speed, J. D. M., Austrheim, G., Hester, A. J., Solberg, E. J., & Tremblay, J.-P. 2013. Regional-scale alteration of clear-cut forest regeneration caused by moose browsing. Forest Ecology and Management, 289, 289-299.

Stromayer, K. A. K., and R. J. Warren. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? Wildlife Society Bulletin 25:227–234.

Stout, S. L., Royo, A. A., deCalesta, D. S., McAleese, K., and J.C. Finley. 2013. The Kinzua Quality Deer Cooperative: can adaptive management and local stakeholder engagement sustain reduced impact of ungulate browsers in forest systems? Boreal Environment Research, 18(Suppl. A), 50-64.

Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. J. Wildl. Manage. 53(3):524-532.

Vila, B, Vourc'h, G., Gillon, D., Martin, J-L., Guibal, F. 2002. Is escaping deer browse just a matter of time in Picea sitchensis? A chemical and dendroecological approach. Trees 16: 488-496.

3 Input Files

3.1 Input File Rules

The input rules for the Dynamic Browse Extension are identical to those of the LANDIS-II Core Model. Please see the LANDIS-II Core User's Guide for further instruction.

3.2 Input File Parameters

3.2.1 Extension title, time step

The first parameter is the title of the input file:

```
LandisData  "Dynamic Ungulate Browse"
```

The second parameter is the time step in years, which should always be 1. For example:

```
Timestep    1
```

3.2.2 Species Inputs

The keyword "SpeciesTable" denotes the section of the input file for providing species-specific parameters. The table consists of 6 columns of values, with each row corresponding to a species. Species need not be listed and may appear in any order. If a species is listed, all 6 parameter values must be provided.

3.2.2.1 Species Name

The first column in the SpeciesTable is the species name. The names must match the species names in the simulation's main species input file.

3.2.2.2 Preference

The second column in the SpeciesTable is the species preference. This value must range between 0 and 1, and represents the relative rate of consumption of the browser for this species. Species with a preference of 0 are not considered forage for the browser, and will never be damaged by the browser. Any species not listed in the SpeciesTable will have a default preference of 0.

3.2.2.3 Growth Reduction Threshold

The third column in the SpeciesTable is the threshold of browse proportion at which growth reduction begins (*a* in Figure 3). Threshold values should generally range between 0 and 1, but values outside this range are acceptable to achieve greater than 0 growth reduction at very low browse proportions. In all cases, 0% browse results in no growth reduction.

3.2.2.4   Growth Reduction Maximum

The fourth column in the SpeciesTable is the maximum growth reduction caused by 100% browse (*b* in Figure 3). Threshold values should generally range between 0 and 1, but values outside this range are acceptable to achieve 100% growth reduction at a browse proportion less than 1. In all cases, growth reduction is capped at 100%.

3.2.2.5   Mortality Threshold

The fifth column in the SpeciesTable is the threshold of browse proportion at which cohort mortality begins (*a* in Figure 3). Threshold values should generally range between 0 and 1, but values outside this range are acceptable to achieve greater than 0 mortality probability at very low browse proportions. In all cases, 0% browse results in no mortality.

3.2.2.6   Mortality Maximum

The sixth column in the SpeciesTable is the maximum mortality probability caused by 100% browse (*b* in Figure 3). Threshold values should generally range between 0 and 1, but values outside this range are acceptable to achieve 100% mortality at a browse proportion less than 1. In all cases, mortality is capped at 100%.

3.2.3 Zone Map

The keyword "ZoneMap" is followed by a raster map file name that defines the population zones within the landscape (2.3). Zones are assumed to have independent browser populations.

3.2.4 Population File

The keyword "PopulationFile" is followed by a file name pointing to a text input file that defines the initial populations/browser density index for each zone.

3.2.5 Dynamic Population File (Optional)

The keyword "DynamicPopulationFile" is followed by a file name pointing to a text input file that defines the additional population parameters required when modeling a dynamic population (2.7.2). This parameter should be excluded when using defined populations (2.7.1). The presence of this parameter and associated file trigger the extension to model dynamic populations and to treat the values in the PopulationFile (3.2.4) as initial populations instead of browser density indices.

3.2.6 Consumption Rate

The keyword "ConsumptionRate" is followed by an integer value representing the annual forage requirements (kg) for an individual browser.

3.2.7 ANPP Forage Proportion

The keyword "ANPPForageProp" is followed by a decimal value representing the proportion of annual growth that is assumed to be available as forage. The default value for this parameter is 0.66 (see 2.2.2).

3.2.8 Minimum Browse in Reach Proportion

The keyword "MinBrowsePropinReach" is followed by a decimal value representing the minimum proportion of a cohort's available forage that must be considered within browser reach in order for the cohort to be susceptible to browsing (2.2.1). Cohorts with browse in reach proportions less than this threshold are considered "escaped" from the browse reach, and none of their forage is available to the browser.

3.2.9 Browse Biomass Threshold

The keyword "BrowseBiomassThreshold" is followed by a decimal value representing the proportion of the ecoregion maximum potential biomass when a cohort begins to escape browse (2.2.1). This proportion (multiplied by the ecoregion maximum potential biomass) defines the threshold at which cumulative biomass represents cohorts above the reach of browsers.

3.2.10   Proportion of Longevity to Escape Browse

The keyword "EscapeBrowsePropLong" is followed by a decimal value representing the proportion of longevity at which cohorts are considered escaped from browse (2.2.1). This age threshold is used to prevent senescing mature cohorts from being treated as cohorts within browse reach as their biomass declines.

3.2.11   Growth Reduction Option (Optional)

The keyword "GrowthReduction" is followed by "ON" or "OFF" to turn the browse impacts on the following year's growth on or off (2.10). This is an optional parameter. The default is "ON", and excluding this parameter will include simulation of growth reductions.

3.2.12   Mortality Option (Optional)

The keyword "Mortality" is followed by "ON" or "OFF" to turn the browse impacts on cohort mortality on or off (2.10). This is an optional parameter. The default is "ON", and excluding this parameter will include simulation of cohort mortality.

3.2.13 Count Non-Forage in Site Preference Option (Optional)

The keyword "CountNonForageinSitePref" is followed by "TRUE" or "FALSE" to set whether cohorts with preference values of 0 should be used in the calculation of average site preference (2.5). This is an optional parameter. The default is "FALSE", and excluding this parameter will follow option B as described in 2.5.

3.2.14 Use Initial Biomass as Forage Option (Optional)

The keyword "UseInitBiomassAsForage" is followed by "TRUE" or "FALSE" to set whether the forage of new cohorts (age = 1) includes all of the initial biomass. This is an optional parameter. The default is "FALSE", and excluding this parameter will apply the ANPPForageProp (3.2.7) to the initial biomass when determining the forage of a new cohort.

3.2.15 HSI Inputs

The HSI inputs list the components (ForageQuantity and/or SitePreference) that should be included in the HSI calculation along with any neighborhood window that should be used for each component. The HSI Inputs table can include one or two rows depending on the user's choice of HSI components (2.6). If both ForageQuantity and SitePreference are included, ForageQuantity should be listed first, and the resulting HSI is the product of the forage quantity and site preference values.

3.2.15.1 Forage Quantity (Optional)

The keyword "ForageQuantity" is followed by an integer value defining a neighborhood radius. When the radius is > 0, then the site forage quantity used in the HSI calculation is the average forage quantity of all sites within the defined neighborhood. If this parameter is excluded, forage quantity will not be used to calculate HSI. Either ForageQuantity or SitePreference (or both) must be listed in the HSI Inputs.

3.2.15.2 Site Preference (Optional)

The keyword "SitePreference" is followed by an integer value defining a neighborhood radius. When the radius is > 0, then the site preference used in the HSI calculation is the average site preference of all sites within the defined neighborhood. If this parameter is excluded, site preference will not be used to calculate HSI. Either ForageQuantity or SitePreference (or both) must be listed in the HSI Inputs.

3.2.16 Output Maps (Optional)

Five potential output maps have been defined for this extension. The generation of any of the output maps can be turned on or off by including or excluding it from the parameter file.

3.2.16.1 Site Preference Output Maps (Optional)

The keyword "SitePrefMapNames" is followed by a path and filename template for output maps of site preference (2.5). The filename should include the key "{timestep}" to indicate where the value of the timestep should be included in the file name. This output map is optional.

3.2.16.2 Site Forage Output Maps (Optional)

The keyword "SiteForageMapNames" is followed by a path and filename template for output maps of site forage quantity (2.4). The filename should include the key "{timestep}" to indicate where the value of the timestep should be included in the file name. This output map is optional.

3.2.16.3 Site HSI Output Maps (Optional)

The keyword "SiteHSIMapNames" is followed by a path and filename template for output maps of site habitat suitability (2.6). The filename should include the key "{timestep}" to indicate where the value of the timestep should be included in the file name. This output map is optional.

3.2.16.4 Site Population Output Maps (Optional)

The keyword "SitePopulationMapNames" is followed by a path and filename template for output maps of site population (2.7.1.1, 2.7.2.3). The filename should include the key "{timestep}" to indicate where the value of the timestep should be included in the file name. This output map is optional.

3.2.16.5 Biomass Removed Output Maps (Optional)

The keyword "BiomassRemovedMapNames" is followed by a path and filename template for output maps of biomass removed. The filename should include the key "{timestep}" to indicate where the value of the timestep should be included in the file name. This output map is optional. Biomass removed includes biomass consumed by the browser (2.8) as well as biomass lost to mortality caused by browsing (2.10).

3.2.17 Output Log

The keyword "LogFile" is followed by a path and filename for the output log to be written.

4 Output Files

4.1 Site Preference Output Maps (Optional)

The inclusion of "SitePrefMapNames" in the parameter file generates output maps of Site Preference values. Map values are site preference values multiplied by 100, for a range of 0 to 100. Non-active cells always have a site preference of 0.

4.2 Site Forage Output Maps (Optional)

The inclusion of "SiteForageMapNames" in the parameter file generates output maps of site Forage Quantity values. Map values are forage quantity in g/m^2. Non-active cells always have a forage quantity of 0.

4.3 Site HSI Output Maps (Optional)

The inclusion of "SiteHSIMapNames" in the parameter file generates output maps of site Habitat Suitability Index values. Map values depend on the components (site preference and/or forage quantity) used in the HSI calculation. Non-active cells always have HSI values of 0.

4.4 Site Population Output Maps (Optional)

The inclusion of "SitePopulationMapNames" in the parameter file generates output maps of site population. Map values depend on whether the option of dynamic populations was used. With non-dynamic populations, the map values represent the Site Browse Index (2.7.1.1) value multiplied by 100, for a range of 0 to 100. With dynamic populations, the map values represent the Site Population Index (2.7.2.3). Non-active cells always have population values of 0.

4.5 Biomass Removed Output Maps (Optional)

The inclusion of "BiomassRemovedMapNames" in the parameter file generates output maps of site biomass removed values. Map values are biomass in g/m^2. Biomass removed includes biomass consumed by the browser (2.8) as well as biomass lost to mortality caused by browsing (2.10). Non-active cells always have a biomass removed of 0.

4.6 Output Log

The output log is a text file that contains information about the browse events over the course of a simulation. For each timestep, the log includes separate records for each population zone (2.3) and for the landscape as a whole.

4.6.1 Timestep

The simulation timestep.

4.6.2 Zone

The population zone map code. Records representing the full landscape have a Zone value of -1.

4.6.3 Population

The total zone/landscape population (dynamic population) or browser density index (non-dynamic population).

4.6.4 Damaged Sites

Number of sites in the zone/landscape damaged by the browser.

4.6.5 Biomass Removed

Total biomass removed from the zone/landscape by the browser due to direct browsing and mortality.

4.6.6 Cohorts Killed

Number of cohorts killed in the zone/landscape by the browser.

4.6.7 Biomass Removed by species

Total species biomass removed from the zone/landscape by the browser due to direct browsing and mortality. A column is included for each species.

4.6.8 Cohorts Killed by species

Total cohorts killed for each species within the zone/landscape by the browser. A column is included for each species.

5 Example Input Files

5.1 Dynamic Ungulate Browse

```
LandisData  "Dynamic Ungulate Browse"
Timestep 1

<< Species Inputs >>
SpeciesTable
>>                        -GrowthReduction-  ---Mortality---
>> Name      Preference  Threshold   Max   Threshold   Max
>> --------  ----------  ---------   ---   ---------   ---
   abiebals   0.0         0.5         0.4   0.5         0.1
   acerrubr   0.3         0.5         0.4   0.5         0.1
   acersacc   0.5         0.5         0.4   0.5         0.1
   betualle   0.3         0.5         0.4   0.5         0.1
   betupapy   0.6         0.5         0.4   0.5         0.1
   fraxamer   0.6         0.5         0.4   0.5         0.1
   piceglau   0.0         0.5         0.4   0.5         0.1
   pinubank   0.0         0.5         0.4   0.5         0.1
   pinuresi   0.0         0.5         0.4   0.5         0.1
   pinustro   0.0         0.5         0.4   0.5         0.1
   poputrem   0.4         0.5         0.4   0.5         0.1
   querelli   0.0         0.5         0.4   0.5         0.1
   querrubr   0.0         0.5         0.4   0.5         0.1
   thujocci   0.5         0.5         0.4   0.5         0.1
   tiliamer   0.4         0.5         0.4   0.5         0.1
   tsugcana   0.5         0.5         0.4   0.5         0.1

<< Browser population Inputs >>
ZoneMap   ecoregions.gis
PopulationFile DefinedUngulatePopulation.txt
DynamicPopulationFile  DynamicUngulatePopulation.txt  <<Optional
ConsumptionRate  745  << kg/yr/individual

<< Forage Inputs >>
ANPPForageProp       0.66  <<Prop of ANPP that counts as forage
```

```
MinBrowsePropinReach 0.50  <<Min prop of browse within reach for a
cohort to be browsed

BrowseBiomassThreshold     0.05  <<Proportion of ecoregion max
biomass when cohort begins to escape browse

EscapeBrowsePropLong 0.57  <<Prop of longevity when browse is
escaped


<< Options >>
<<GrowthReduction    OFF               << Default is ON
<<Mortality    OFF                << Default is ON
<<CountNonForageinSitePref TRUE       << Default is FALSE
<<UseInitBiomassAsForage         TRUE  << Default is FALSE


<< HSI Inputs >>
<< Component         Neighborhood >>
<< ---------         ------------
<<ForageQuantity     0     << ForageQuantity and/or SitePreference
SitePreference       500   << ForageQuantity and/or SitePreference



<< Output Maps >>
SitePrefMapNames          browse/SitePref_{timestep}.gis
SiteForageMapNames        browse/SiteForage_{timestep}.gis
SiteHSIMapNames           browse/HSI_{timestep}.gis
SitePopulationMapNames    browse/Pop_{timestep}.gis
BiomassRemovedMapNames    browse/BioRemoved_{timestep}.gis


<< Output Logs >>
LogFile  browse/browse_log.csv
```

5.2 Defined Ungulate Population

```
LandisData "Defined Ungulate Population"


>>Year   Zone   Browser Density Index
>>----   ----   ---------------------
   0       1      0.5
   0       2      0
```

5.3 Dynamic Ungulate Population

```
LandisData "Dynamic Ungulate Population"


R
<<Min    Max
<<---    ---
  0.3    0.4


Mortality
<<Min    Max
<<---    ---
  0.0    0.0


Predation
<<Min    Max
<<---    ---
  0.0    0.0


Harvest
<<Min    Max
<<---    ---
  0.0    0.0
```

6 Addendum 1

Tables containing categorical values of browse preference for forest species in Pennsylvania are from Table 4 of the Latham et al. (2005) report.

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
Abies balsamea	balsam fir		
Acer negundo	boxelder	not preferred	not preferred
Acer nigrum	black maple	low/moderate	high
Acer pensylvanicum	striped maple	low	low
Acer rubrum	red maple*	low/moderate	high
Acer saccharinum	silver maple	low/moderate	moderate
Acer saccharum	sugar maple*	low/moderate	moderate
Aesculus flava	yellow buckeye	(unknown, but toxic to cattle)	(unknown, but toxic to cattle)
Aesculus glabra	Ohio buckeye	(unknown, but toxic to cattle)	(unknown, but toxic to cattle)
Amelanchier arborea	downy serviceberry	(is browsed)	(is browsed)
Amelanchier laevis	Allegheny serviceberry	(is browsed)	(is browsed)
Aralia spinosa	devils-walkingstick	not preferred	not preferred
Asimina triloba	pawpaw	not preferred	not preferred
Betula alleghaniensis	yellow birch*	low/moderate	high (late autumn)
Betula lenta	sweet birch*	low/moderate	high (late fall)
Betula nigra	river birch	low	moderate

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
Betula papyrifera	paper birch	low/moderate	high (late fall)
Betula populifolia	gray birch	low/moderate	moderate
Carpinus caroliniana	American hornbeam		
Carya cordiformis	bitternut hickory*	low	low
Carya glabra	pignut hickory	low	low
Carya laciniosa	shellbark hickory	low	low
Carya ovalis	sweet pignut hickory (red hickory)	low	low
Carya ovata	shagbark hickory*	low	low
Carya tomentosa	mockernut hickory*	low	low
Castanea dentata	American chestnut		
Castanea pumila	Allegheny chinkapin		
Celtis occidentalis	hackberry	low	low
Celtis tenuifolia	Georgia hackberry (dwarf hackberry)	low	low
Cercis canadensis	eastern redbud		
Chamaecyparis thyoides	Atlantic white-cedar	low	moderate
Chionanthus virginicus	fringetree	low	low
Cornus alternifolia	alternate-leaf dogwood	moderate	high
Cornus florida	flowering dogwood	moderate	high
Crataegus brainerdii	Brainerd hawthorn	low	high
Crataegus calpodendron	pear hawthorn	low	high
Crataegus coccinea	scarlet hawthorn	low	high
Crataegus crus-galli	cockspur hawthorn	low	high

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
Crataegus dilatata	broadleaf hawthorn	low	high
Crataegus flabellata	fanleaf hawthorn	low	high
Crataegus intricata	Biltmore hawthorn	low	high
Crataegus mollis	downy hawthorn	low	high
Crataegus pruinosa	frosted hawthorn	low	high
Crataegus punctata	dotted hawthorn	low	high
Crataegus rotundifolia	fireberry hawthorn	low	high
Crataegus succulenta	fleshy hawthorn	low	high
Diospyros virginiana	common persimmon		
Fagus grandifolia	American beech	low	high
Fraxinus americana	white ash*	low/moderate	high
Fraxinus nigra	black ash	low/moderate	high
Fraxinus pennsylvanica	green ash	low/moderate	high
Fraxinus profunda	pumpkin ash	not preferred	not preferred
Gleditsia triacanthos	honeylocust	(is browsed)	(is browsed)
Gymnocladus dioicus	Kentucky coffeetree		
Ilex opaca	American holly	low	low
Juglans cinerea	butternut		
Juglans nigra	black walnut	(is browsed)	(is browsed)

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
Magnolia acuminata	cucumbertree	low	moderate
Magnolia tripetala	umbrella magnolia	low	low
Magnolia virginiana	sweetbay		
Malus coronaria	sweet crab apple		
Morus rubra	red mulberry		
Nyssa sylvatica	blackgum (black tupelo)*	high	high
Ostrya virginiana	eastern hophornbeam	low	low
Oxydendrum arboreum	sourwood		
Picea mariana	black spruce	not preferred	low
Picea rubens	red spruce	not preferred	low
Pinus echinata	shortleaf pine		

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
Prunus angustifolia	Chickasaw plum		
Prunus pensylvanica	pin cherry	high	high
Prunus serotina	black cherry*	low	low
Prunus virginiana	common chokecherry		
Quercus alba	white oak*	moderate	high
Quercus bicolor	swamp white oak	moderate	high
Quercus coccinea	scarlet oak*	moderate	high
Quercus falcata	southern red oak	moderate	high
Quercus imbricaria	shingle oak	moderate	high
Quercus macrocarpa	bur oak	moderate	high
Quercus marilandica	blackjack oak	moderate	high
Quercus montana	chestnut oak*	moderate	high
Quercus muhlenbergii	chinkapin oak (yellow oak)	moderate	high
Quercus palustris	pin oak	moderate	high
Quercus phellos	willow oak	moderate	high
Quercus rubra	northern red oak*	moderate	high
Quercus shumardii	Shumard oak	moderate	high
Quercus stellata	post oak	moderate	high
Quercus velutina	black oak*	moderate	high
Robinia pseudoacacia	black locust	low	low

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
Sorbus decora	showy mountain-ash		
Tilia americana	American basswood*	(is browsed)	(is browsed)
Toxicodendron vernix	poison-sumac		
Tsuga canadensis	eastern hemlock	low	high
Ulmus americana	American elm	(is browsed)	(is browsed)
Ulmus rubra	slippery elm	(is browsed)	(is browsed)
Viburnum prunifolium	blackhaw	moderate	high