LANDIS-II Browse v0.8 Extension User Guide

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1 Introduction

This document describes the **Browse (v0.8)** 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 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 (0.8) is limited to running with a specialized version of Biomass Succession (vBrowse).

The Browse v0.8 extension is designed to simulate the removal of biomass from tree cohorts by ungulate browsers, the concurrent loss of growth and/or mortality, and optionally the reciprocal feedback between the availability of browse and the population dynamics of the ungulates.

1.1 Acknowledgments

2 Browse Extension

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), elk (*Cervus canadensis*) (e.g., Kaye et al. 2005), and domestic goats (Zamora et al. 2011). Such impacts have the potential to create feedbacks that may potentially change the density of ungulate populations in dynamic plant-herbivore systems (Coughenour and Singer 1996; Moen et al. 1998).

The purpose of the Browse 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 Extension is outlined in Figures 1 and 2.
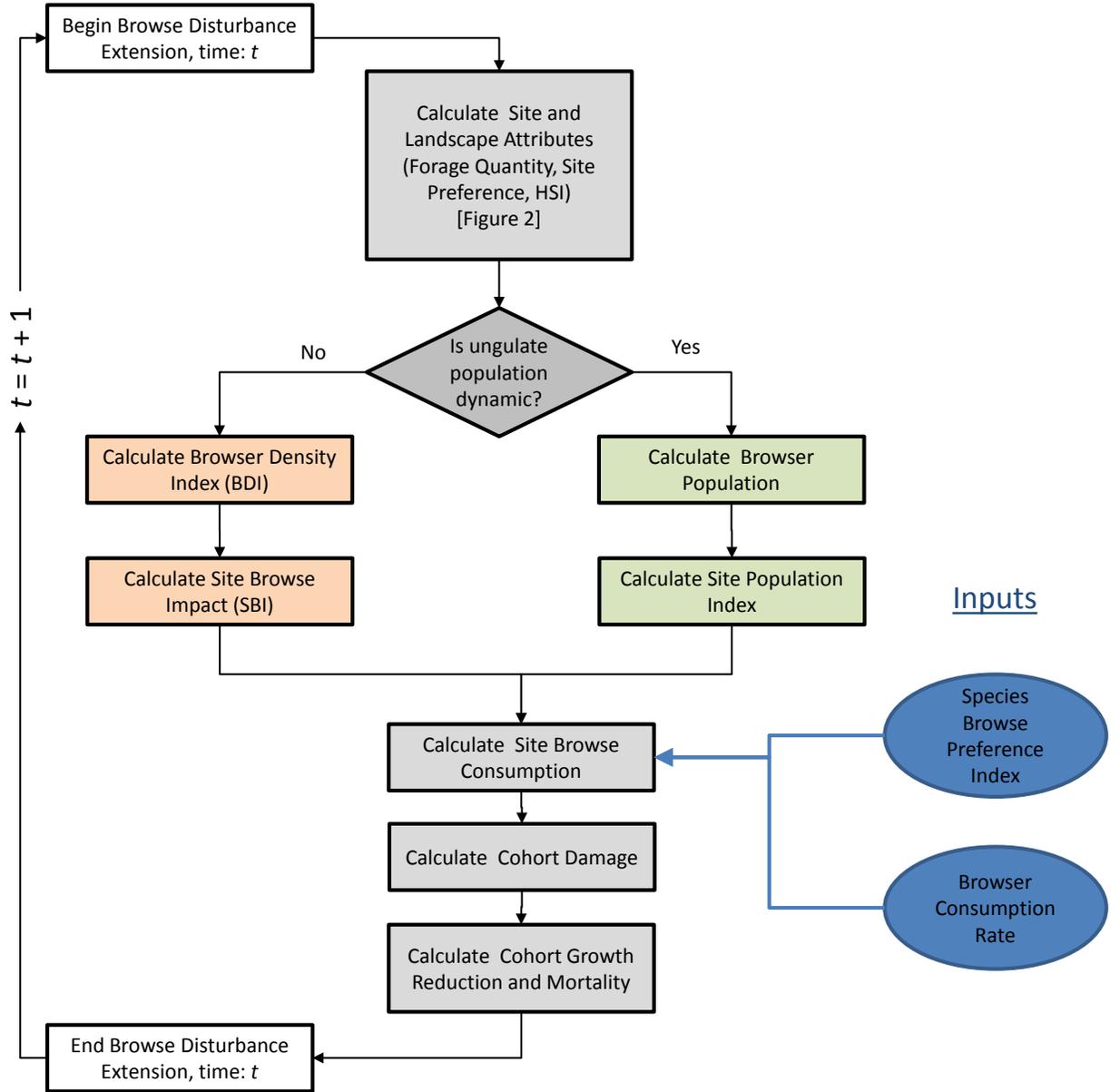
Figure 1. Overall conceptual diagram of Browse Extension.

Inputs

Calculate Site and Landscape Attributes

Calculate Available Forage by Cohort

Species Browse Preference Index

Calculate Average Site Preference

Calculate Total Site Forage Quantity

Site Preference Neighborhood Radius

Calculate Landscape Browse Quantity

Calculate Habitat Suitability Index (HSI)

Forage Quantity Neighborhood Radius
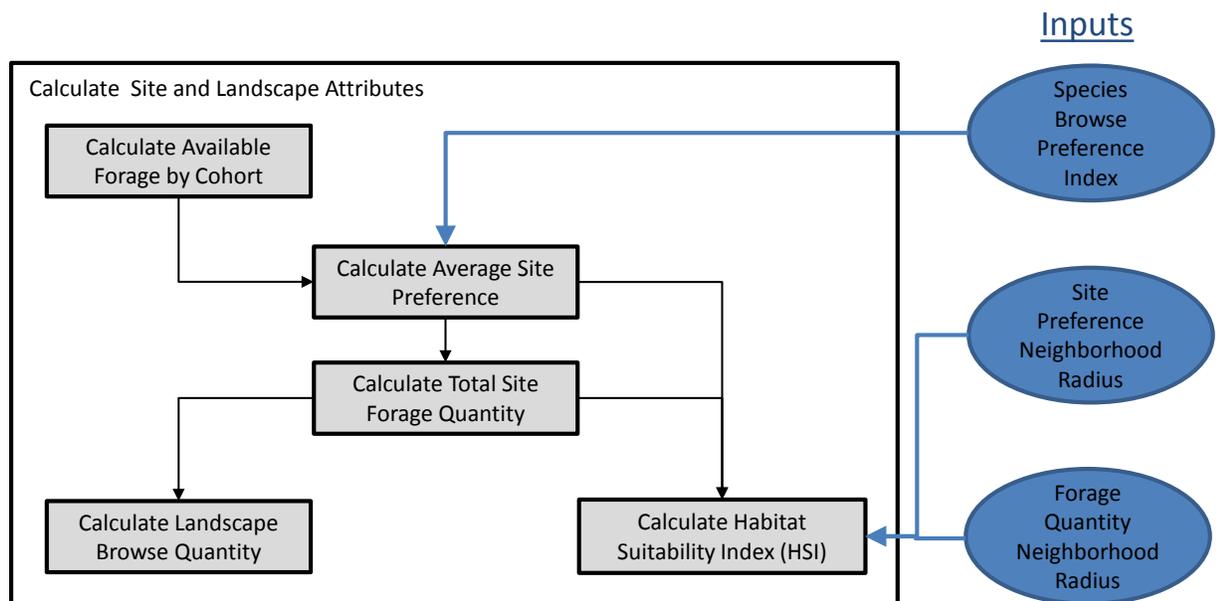
Figure 2. Inset conceptual diagram for calculation of site and landscape attributes.

3 Model Description

3.1 Species Browse Preference Index

Most browsers prefer certain plant species over others. The user must provide a relative preference index for each species. An example of tables bearing categorical values for browse preference by deer in Pennsylvania is provided in Latham et al. (2005). 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 (section 3.5) if they suspect that the presence of 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 (averaging) seasonal variability. The relative preference index also is used to determine the target proportion of the total available browse biomass that is removed from each species cohort (section 3.9).

3.2 Forage Availability

In nature, the amount of forage available to browsers is determined by the amount of browseable biomass (i.e., leaves, buds, small twigs) within the vertical reach of the ungulate. LANDIS-II does not track the height of cohorts, but because an assumption of LANDIS-II that established cohorts are "fully stocked" with respect to the available growing space in a cell, the Browse Extension uses cohort biomass as a surrogate for height. User-specified parameters are used to define three thresholds used to calculate forage availability. The first threshold specifies an amount of cohort biomass below which the entire cohort is available as forage and above which a portion of the cohort biomass can "escape" browsing because it is assumed that portion is above the reach of the herbivores. The second threshold is the proportion of available forage below which the entire cohort has "escaped" the reach of the herbivores and is not available as forage biomass. This assumes that apical dominance within low-statured cohorts will cause the browsing of lower branches to be compensated by growth beyond the browse line (McLaren and Peterson 1994, Vila et al. 2002), allowing cohorts to gradually escape herbivory. The third threshold is the proportion of longevity at which cohorts are no longer eligible to be forage. This threshold is intended to prevent old cohorts with declining biomass from being treated as forage the same way a young cohort of equal biomass would. Actual biomass available as forage is calculated according to the fraction of annual growth that susceptible cohorts allocate to leaf and stem material (See 3.2.2 below).

3.2.1 Susceptible Cohorts

The BrowseBiomassThreshold parameter specifies the first forage threshold, which is the proportion of the maximum possible-site biomass (calculated by the succession extension) below which cohorts are susceptible to browsing. For example, if a site has a maximum possible biomass of 10,000 g/m^2, then a BrowseBiomassThreshold value of 0.05 means that all cohorts up to a site total

of 500 g/m^2 are fully available as forage. As site biomass exceeds this threshold, a proportion of cohorts' biomass may be available.

Because sites often contain a mixture of species and cohort sizes, these calculations are not made by individual cohorts, but for all cohorts taken together. In some cases, all cohorts may be susceptible, in other cases parts of cohorts may be susceptible, and in others (e.g., only large cohorts on the site), no cohorts may be susceptible. Starting with the cohort with the **lowest biomass** (regardless of species preference and age), and an empty (0) AvailableForage pool, the proportion of the cohort available as forage ("in reach") is computed as:

$$PropInReach = \frac{(BrowseBiomassLimit - AvailableForage)}{CohortBiomass}$$

where *BrowseBiomassLimit* is the maximum biomass for the site multiplied by *BrowseBiomassThreshold*, and *PropInReach* has a maximum value of 1. The computed biomass available as forage (*PropInReach * CohortBiomass*) is added to the *AvailableForage* pool. This sequence is iterated for cohorts (from lowest to highest biomass) until all cohorts have been considered.

The second forage threshold (MinBrowseProp) is a minimum threshold for PropInReach, below which a cohort is assumed to be completely out of reach and has escaped browsing. If the calculated PropInReach is less than the MinBrowseProp, then no biomass is considered as available browse for that species.

The third threshold (MaxBrowseAge), which is a proportion of longevity, is used to prevent old senescing cohorts from being treated as cohorts within browse reach. Cohorts with ages greater than MaxBrowseAge (default is 57% of longevity; see 4.2.10) are not considered as eligible for forage.

3.2.2 Available forage biomass

Available forage biomass is calculated as the proportion of annual aboveground net primary productivity (ANPP) 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, the extension assumes that 33% of ANPP is allocated to leaves and 33% is allocated to twigs, for a total of 66% of ANPP that is available as forage biomass. This assumption is 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 (4.2.7). Users can also apply an option (4.2.14) to count 100% of new growth as browseable material during the first year of growth (cohort age = 1).

3.3 Population Zones

Spatial heterogeneity in browsing pressure caused by heterogeneity in either relative or absolute ungulate densities (see Section 3.7below) can optionally be defined as different population zones within the Browse 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.

3.4 Site Forage Quantity

Site forage quantity is an output raster map of the total amount of available forage (g/m^2) on each site (cell in the raster). Available forage (as defined in 3.2) is summed for all species-cohorts present on each site. Cohorts with species preference values (as defined in 3.1) of 0 are considered non-forage, and are not included in the calculation of site forage quantity.

3.4.1 Zone Forage Quantity

The total forage quantity for each population zone (Z, see 3.3) is summed from the site forage quantity values.

$$ForageQuantity_Z = \sum ForageQuantity_S$$

Zone forage quantity is used in the calculation of zone carrying capacity (when using the Dynamic Browser Population [3.7.3]) and to calculate local browse impacts (3.7.2, 3.7.3.3).

3.5 Site Preference

Site preference is an optional output raster map (4.2.16.1) 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 3.2). 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 (4.2.13).

3.6 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 (i.e., preference) 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 (3.2),

B) neighborhood average of site preference (3.4),

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.

3.7 Browser Population Density

The Browse Extension provides users with two alternative options to define browse pressure related to ungulate density. The first (elaborated in Section 3.7.1) implements a user-defined browser density across the landscape or within different spatial zones (3.3). 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 3.7.3) 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 (3.3) 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.

3.7.1 Density Option 1: Browser Density Index (BDI)

The Browser Density Index (BDI) is a user-supplied value between 0 and 1 that represents the population density relative to the capacity of the landscape to support it.   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 (3.3), and each site (S) in the zone is assigned the same BDI value (BDI_S).

3.7.2 Site Browse Impact (SBI)

The site browse impact temporary raster uses the total browse impact for a zone, the local HSI (3.6) values and the site forage quantity (3.4) to estimate local browse impacts, computed as a target rate of browse removal for each site. The total browse impact (BDI_Z) for zone (Z) is calculated by summing the BDI values of all sites in the zone.

$$BDI_Z = \sum BDI_S$$

As the browse density index (BDI_Z) approaches 1.0, the HSI value has less influence on the distribution of site browse impact (SBI_S). In the extreme case of BDI_Z 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 the total zone BDI_Z and a weighted average of HSI(3.6) and Forage Quantity(3.4), where BDI (3.7.1) provides the weighting.

$$SBI_S = \sum BDI_Z \times \left[\left(\frac{\text{ForageQuantity}_S}{\text{ForageQuantity}_Z} \times BDI_Z \right) + \left(\frac{HSI_S}{HSI_Z} \times (BDI_Z - 1) \right) \right]$$

Where SBI_S is the site-level browse removal rate, BDI_Z is the browser density index for zone Z, $ForageQuantity_S$ is the site-level forage quantity, $ForageQuantity_Z$ is the total forage quantity summed within a zone, HSI_S

is the site-level habitat suitability index, and *HSI*~Z~ is the sum of habitat suitability indices within a zone. In essence, this is the zone 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.

3.7.3 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 are modeled as mortality rates (e.g., harvest, stochastic mortality, and predation). Stochasticity is incorporated by defining minimum and maximum parameter estimates for population growth and mortality factors and by randomly selecting the parameter value within this range.

3.7.3.1   Calculate Zone Carrying Capacity

The carrying capacity of the browser population is defined 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 (3.4.1). Zone carrying capacity (K_Z) is determined by dividing the total forage quantity by the annual consumption rate for the browser population (4.2.6), which is supplied by the user.

3.7.3.2   Calculate Browser Population

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

$$\Delta N_Z = R \ \ N_Z \left(1 - \frac{N_Z}{K_Z}\right) - \sum M \ \ N_Z$$

Where ΔN_Z is the change in browser population density *N* in Population Zone *Z*, R is a user-supplied population growth rate and $\sum M \ \ N_Z$ 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 (3.7.3.1).

3.7.3.3   Calculate Site Population Index

The site population index raster combines the zone population (3.7.3.2), the local HSI (3.6) values and the site forage quantity (3.4) 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 (3.7.2). Here, the spatial distribution of population is influenced by the population proximity to carrying capacity for the zone (K_Z, 3.7.3.1). As a population approaches K_Z, 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_Z, then the distribution of the population must be distributed in proportion to the quantity of available forage on each site. Therefore, the site population (N_S) is the product of total zone population (N_Z) and a weighted average of HSI (3.6) and Forage Quantity (3.4), where the ratio of N_Z to K_Z provides the weighting.

$$N_S = N_Z \times \left[\left(\frac{\text{ForageQuantity}_S}{\text{ForageQuantity}_Z} \times \frac{N_Z}{K_Z} \right) + \left(\frac{HSI_S}{HSI_Z} \times \left(\frac{N_Z}{K_Z} - 1 \right) \right) \right]$$

3.8 Site Browse Consumption

If using defined browser densities (3.7.1), the SBI (3.7.2) 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 (3.4). If using the dynamic browser densities (3.7.3), the defined browser consumption rate (4.2.6) is multiplied by the site population index (N_S, 3.7.3.3) to calculate the total amount of forage to be removed.

3.9 Cohort Damage

Within a site, biomass is removed from cohorts (i.e., they are damaged) according to species preferences. The total amount of forage to be removed from a site is first calculated (3.8). Then, species-cohorts are rank-ordered by their preference values (3.1). These values not only rank species, but define a target removal proportion (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 proportion for the species-cohort. If more biomass needs to be removed to reach the calculated total browse consumption for the site, then biomass is removed from the next most preferred species-cohort, again up to the species-cohort's target removal proportion. This procedure is iterated for all species-cohorts until the total browse consumption is achieved, or all cohorts have been browsed at their target removal proprotions. If browse removal using the defined target removal proportions does not meet the total browse consumption, then additional biomass is removed, again starting with the most preferred species-cohorts. The biomass removal needed to meet the target is removed from the most preferred species-cohorts until all available forage biomass (3.2.2) has been removed from those cohorts (i.e., now ignoring the

target removal proprotions for the species). Any remaining biomass to be
removed comes from the next most preferred species-cohorts, and continues
down the preference list until either the demand for browse consumption is met,
or all available forage biomass is removed from the site.

Example: A site has a SBI of 0.45 and 100 g/m^2 of available forage biomass,
translating to a total browse consumption of 45 g/m^2. There are two cohorts on
the site, one high preference (0.85) and one low preference (0.15). If the high
preference cohort has 30 g/m^2 available forage, which gets browsed at a
proprotion equal to its species preference (0.85), then 25.5 g/m^2 is initially
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 proprotion (0.15) to
have 10.5 g/m^2 forage removed. The total forage consumed so far (36 g/m^2) is
less than the total browse consumption for the site (45 g/m^2). The remaining
forage to be removed (9 g/m^2) comes from the most preferred species first, up to
its total available forage. In this case, and additional 4.5 g/m^2 can be removed
from the highly preferred cohort for a total removal of all 30 g/m^2. The
remaining 4.5 g/m^2 is removed from the less preferred cohort for a total of 15
g/m^2.

3.10 Browse Effect on Cohort Growth and Mortality

The Browse Extension also models the effects of biomass removal on subsequent
cohort growth and survival via separate user-defined threshold proportions of
ANPP lost (see Figure 3). Browse rates above these thresholds (a) lead to growth
reduction (losses) in the following year, and/or increased probability of mortality
prior to the following year. When browse rates are above the minimum threshold
(a, Figure 3; 4.2.2.3, 4.2.2.5), growth losses and mortality increase linearly to
maximums (b, Figure 3; 4.2.2.4, 4.2.2.6) set by the user. The growth reduction
and mortality thresholds do not need to be the same, but the relationship is
similar in application.
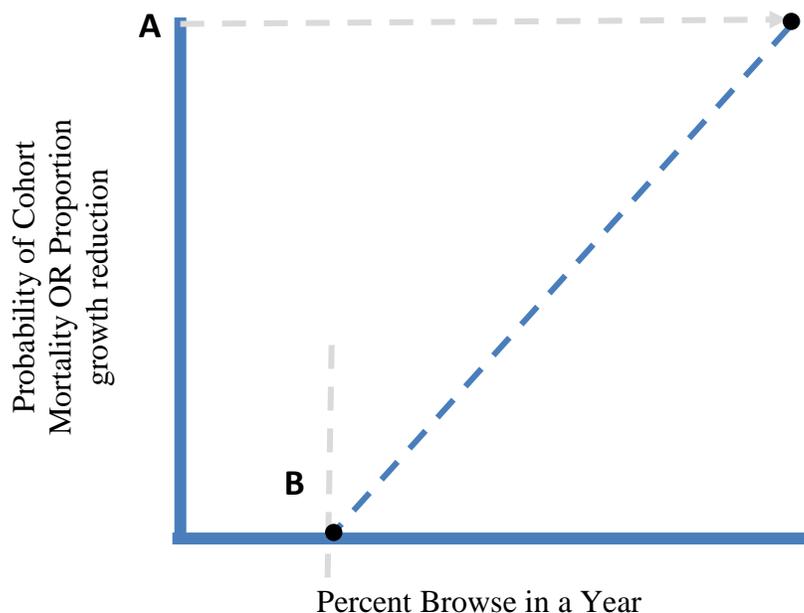
Figure 3. Effects of browse on cohort mortality and growth reduction. A user-defined threshold (a) determines the minimum amount of browse for any effect, and a second user-defined threshold (b) determines the maximum effect when browse is 100%.

3.11 Areas for Additional Development

3.11.1   Zone-specific population parameters

Currently, all zones use the same parameter values for R, Mortality, Predation and Harvest. Each population zone could be assumed to be independent populations with their own specific reproductive and mortality rates. The model design can accommodate zone-specific population parameters, but this has not been implemented.

3.11.2   Habitat Suitability criteria

The model design can support additional options for determining habitat suitability besides just neighborhood averages of browse quantity and quality. Other habitat metrics could include distance to certain features, cover values and landscape configuration metrics.

3.11.3   Smoothing zone boundaries (BDI)

When multiple population zones exist within the simulation area the user could have the option to 'smooth' the distribution of BDI using a moving window average of the BDI values. After smoothing, each site would have its own BDI value (BDI_S), which would then be summed by zone to give an adjusted BDI_Z value.

3.11.4 Seed Predation

Ungulate browsers can often be consumers of seeds (mast) as well as foliage and twigs. The net result of seed consumption could be modeled as reductions in establishment probability for species with highly preferred seeds.

3.12 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.

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

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.

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.

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.

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.

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.

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.

Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., García, D., 2001. Effects of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: consequences for forest regeneration. Forest Ecology and Management 144, 33-42.

4 Input Files

4.1 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.

4.2 Input File Parameters

4.2.1 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
```

4.2.2 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 tree species. All species do not have to be listed and they may appear in any order. If a species is listed, all 6 parameter values must be provided.

4.2.2.1   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.

4.2.2.2   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.

4.2.2.3   Growth Reduction Threshold

The third column in the SpeciesTable is the threshold of proportion browsed 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 > 0 growth reduction at very low browse proportions. In all cases, 0% browsed results in no growth reduction.

4.2.2.4   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 proportion browsed <1. In all cases, growth reduction is capped at 100%.

4.2.2.5   Mortality Threshold

The fifth column in the SpeciesTable is the threshold of proportion browsed 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 > 0 mortality probability at very low browse proportions. In all cases, 0% browse results in no mortality.

4.2.2.6   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 <1. In all cases, mortality is capped at 100%.

4.2.3 Zone Map

The keyword "ZoneMap" is followed by a raster map file name that defines the population zones within the landscape (3.3).

4.2.4 Population File

The keyword "PopulationFile" is followed by a file name pointing to a text input file that defines the initial populations or browser density index for each zone (see 4.3).

4.2.5 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 (3.7.3; see 4.4). This parameter should be excluded when using defined populations (3.7.1). The presence of this parameter and associated file trigger the extension to model dynamic populations and to treat the values in the PopulationFile (4.2.4) as initial populations instead of browser density indices.

4.2.6 Consumption Rate

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

4.2.7 ANPP Forage Proportion

The keyword "ANPPForageProp" is followed by a decimal value between 0 and 1 representing the proportion of annual tree growth (ANPP) that is assumed to be available as forage. The default value for this parameter is 0.66 (see 3.2.2).

4.2.8 Minimum Browse in Reach Proportion

The keyword "MinBrowsePropinReach" is followed by a decimal value between 0 and 1 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 (3.2.1). 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.

4.2.9 Browse Biomass Threshold

The keyword "BrowseBiomassThreshold" is followed by a decimal value between 0 and 1 representing the proportion of the ecoregion maximum potential biomass when a cohort begins to escape browse (3.2.1). This proportion (multiplied by the ecoregion maximum potential biomass) defines the threshold at which cumulative biomass represents cohorts above the reach of browsers.

4.2.10   Proportion of Longevity to Escape Browse

The keyword "EscapeBrowsePropLong" is followed by a decimal value between 0 and 1 representing the proportion of longevity at which cohorts are considered to have escaped from browse (3.2.1). This age threshold is used to prevent senescing mature cohorts from being treated as cohorts within browse reach as their biomass declines.

4.2.11   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 (3.10). This is an optional parameter. The default is "ON", and excluding this parameter will include simulation of growth reductions.

4.2.12   Mortality Option (Optional)

The keyword "Mortality" is followed by "ON" or "OFF" to turn the browse impacts on cohort mortality on or off (3.10). This is an optional parameter. The default is "ON", and excluding this parameter will include simulation of cohort mortality.

4.2.13   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 (3.5). This is an optional parameter. The default is "FALSE", and excluding this parameter will follow option B as described in 3.5.

4.2.14   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 (4.2.7) to the initial biomass when determining the forage of a new cohort.

4.2.15   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 (3.6). 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.

4.2.15.1   Forage Quantity (Optional)

The keyword "ForageQuantity" is followed by a positive 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 keyword 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.

4.2.15.2   Site Preference (Optional)

The keyword "SitePreference" is followed by a positive 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 keyword 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.

4.2.16   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. All output map filenames should specify the raster file format, such as .img or .gis.

4.2.16.1   Site Preference Output Maps (Optional)

The keyword "SitePrefMapNames" is followed by a path and filename template for output maps of site preference (3.5). The site preference values in the output map have been multiplied by 100 for display as integer value. 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. Example:

```
SitePrefMapNames            browse/SitePref_{timestep}.gis
```

4.2.16.2   Site Forage Output Maps (Optional)

The keyword "SiteForageMapNames" is followed by a path and filename template for output maps of site forage quantity (3.4). 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. Example:

```
SiteForageMapNames          browse/SiteForage_{timestep}.gis
```

4.2.16.3   Site HSI Output Maps (Optional)

The keyword "SiteHSIMapNames" is followed by a path and filename template for output maps of site habitat suitability (3.6). The HSI values in the output map have been multiplied by 100 for display as integer values. 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. Example:

```
SiteHSIMapNames                 browse/HSI_{timestep}.gis
```

4.2.16.4   Site Population Output Maps (Optional)

The keyword "SitePopulationMapNames" is followed by a path and filename template for output maps of site population (3.7.2, 3.7.3.3). The units for population density are #/km^2, but the values in the output map have been multiplied by 100 for display as integer values. 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. Example:

```
SitePopulationMapNames          browse/Pop_{timestep}.gis
```

4.2.16.5   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 (3.8) as well as biomass lost to mortality caused by browsing (3.10). Example:

```
BiomassRemovedMapNames      browse/BioRemoved_{timestep}.img
```

4.2.17 Output Log

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

4.3 Population File Parameters

4.3.1 LandisData label

The first parameter is the title of the input file:

```
LandisData  "Defined Ungulate Population"
```

4.3.2 Input table

An input table with three columns provides the population information for each zone through time.

4.3.2.1 Year

An integer value ≥ 0 that defines at what simulation year (simulations start at Year 0) the population data applies.   The input table should always include rows for Year 0 for all zones. If modeling a dynamic population (3.7.3) then only Year 0 should be included in this table; all other years will calculated from the initial population.

4.3.2.2 Zone

An integer value that matches a mapcode in the population zone input map (3.3, 4.2.3). Mapcodes that are not include in the input table will have a density/population value of 0.

4.3.2.3 BrowserDensityIdex/InitialPopulation

When using static populations (BDI, 3.7.1) the values in this column should be decimals ranging between 0 and 1. The values represent the average proportion of available forage that the ungulate population will consume in each timestep. It can also be thought of as an index of the population relative to carrying capacity. A value of 1.0 means the population is at carrying capacity, and will consume all available forage. The browser density index can vary across population zones, and through time by providing multiple values with different years. When a BDI value is changed at a new timestep, the new value will be used for all subsequent years, unless another value is provided to replace it at a later simulation year.

When using a dynamic population (DBP, 3.7.3) the values in this column should represent actual population numbers for each zone in the table. These values represent initial populations at Year 0 (and the Year column should be 0), which is used for the calculations of population in all subsequent years.

4.4 Dynamic Population File Parameters

4.4.1 LandisData label

The first parameter is the title of the input file:

```
LandisData  "Dynamic Ungulate Population"
```

4.4.2 R

The keyword "R" is followed (on the next line) by two values represent the minimum and maximum values for the population growth rate (R, 3.7.3.2). At each timestep, a value will be selected from a uniform distribution between the minimum and maximum values.

4.4.3 Mortality

The keyword "Mortality" is followed (on the next line) by two values represent the minimum and maximum values for the population mortality rate (R, 3.7.3.2). This is background mortality that is due to causes other than predation and harvest. At each timestep, a value will be selected from a uniform distribution between the minimum and maximum values.

4.4.4 Predation

The keyword "Predation" is followed (on the next line) by two values represent the minimum and maximum values for the population predation rate (R, 3.7.3.2). This is specific mortality that is due to predation. At each timestep, a value will be selected from a uniform distribution between the minimum and maximum values.

4.4.5 Harvest

The keyword "Harvest" is followed (on the next line) by two values represent the minimum and maximum values for the population harvest rate (R, 3.7.3.2). This is specific mortality that is due to management (e.g., hunting). At each timestep, a value will be selected from a uniform distribution between the minimum and maximum values.

5 Output Files

5.1 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.

5.2 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.

5.3 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.

5.4 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 (3.7.2) value multiplied by 100, for a range of 0 to 100. With dynamic populations, the map values represent the Site Population Index (3.7.3.3) with units of $\#/km^2$, multiplied by 100. Non-active cells always have population values of 0.

5.5 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 (3.8) as well as biomass lost to mortality caused by browsing (3.10). Non-active cells always have a biomass removed of 0.

5.6 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 (3.3) and for the landscape as a whole.

5.6.1 Timestep

The simulation timestep.

5.6.2 Zone

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

5.6.3 Population

The total zone/landscape population (dynamic population) or browser density index (non-dynamic population). Units: # of individuals or BDI (0-1 index).

5.6.4 Total Forage

The total zone forage quantity. Units: kg (summed across all sites in the zone).

5.6.5 Carrying Capacity (K)

The total carrying capacity for the zone, given the total forage and consumption rate. Units: # of individuals

5.6.6 Effective Population (EffectivePop)

The effective population of the zone, which is the minimum of the actual population and carrying capacity (K). The effective population is used for calculation of browse removal, which effectively assumes that the population is reduced to K due to inadequate forage whenever the population exceeds K. Units: # of individuals

5.6.7 Damaged Sites

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

5.6.8 Biomass Removed

Total biomass removed from the zone/landscape by the browser due to direct browsing (i.e., biomass actually consumed). Units: g/m^2 (summed across sites impacted by browse).

5.6.9 Biomass Mortality

Total biomass lost due to cohort mortality. Forage biomass consumed is not counted in biomass mortality. Units: g/m^2 (summed across sites with browse mortality).

5.6.10   Cohorts Killed

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

5.6.11   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. Units: g/m^2 (summed across site impacted by browse).

5.6.12   Cohorts Killed by species

Total number of cohorts killed for each species within the zone/landscape by the browser. A column is included for each species. Units: # of cohorts.

6 Example Input Files

6.1 Dynamic Ungulate Browse

See section 4.2.

```
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
```

6.2 Population File

See section 4.3.

6.2.1 Browser Density Index (BDI) option

```
LandisData "Defined Ungulate Population"
```

```
>>Year Zone Browser Density Index
>>---- ---- --------------------
   0   1     0.5
   0   2     0
  50   1   0.3
```

6.2.2 Browser Density Index (BDI) option

```
LandisData "Defined Ungulate Population"


>>Year Zone Initial Population
>>---- ---- --------------------
   0   1     500
   0   2     425
```

6.3 Dynamic Population File

See section 4.4

```
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
```