LANDIS-II Browse Disturbance v2~~1~~.0 Extension User Guide

Brian Miranda, Brian Sturtevant, Eric Gustafson
USFS Northern Research Station

Nathan De Jager, USGS
Upper Midwest Environmental Sciences Center

Patrick Drohan
Penn State University

Samuel Flake, Robert Scheller
North Carolina State University

Commented [SWF1]: Add Rob?

Last revised: July 15, 2024

Table of Contents

1 Introduction

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, NECN Succession), though it has currently been tested only with Biomass Succession and NECN Succession.~~.~~

The Browse Disturbance ~~v1.0~~v2.0 extension is designed to simulate the removal of biomass from tree cohorts by ungulate browsers, and the concurrent loss of growth and/or mortality.

1.1 Major Releases

1.1.1 2.0 (May 2022)

Several modifications were made to the input and outputs of the extension to enhance the usability of the extension.

1.1.1.1 *Added "LinearEachCohort" method to calculate forage in reach*

A second option for calculating forage in reach was added. This option depends only upon the attributes of the cohort, without reference to site conditions. This makes for simpler calibration of forage production. The previous model behavior is still available, under the "Ordered cohort" method. See section 3.2.1.

1.1.1.2 *Added Calibrate Log*

Additional cohort-level information is available in a calibrate log, to facilitate calibration of forage production and removals by browsers.

1.1.1.3 *Added metadata to output files*

Metadata has been added to output files to facilitate interpretation.

1.1.1.4 *Added defined population mode to input observed populations*

The extension now accepts an input that gives a list of observed population sizes, in order to test historical or hypothetical populations.

1.1.2 1.0 (September 2021)

Now compatible with Core v7 and does not require a special version of succession extensions. Previously, the Browse extension required ecoregion-level Maximum Biomass values for each species, which it received from Biomass Succession. To make the Biomass Browse extension compatible with more succession extensions, Biomass Browse now requires a Maximum Biomass value to be given for each species. ANPP is also calculated internally to Biomass Browse, rather than obtained from the succession extension. Currently, ANPP is hard-coded as 0.04 times the cohort biomass.

1.2 Minor Releases

1.2.1 1.1 (December 27, 2021)

Now compatible with NECN Succession. ~~Previously, the Browse extension required ecoregion-level Maximum Biomass values for each species, which it received from Biomass Succession. To make the Biomass Browse extension compatible with more succession extensions, Biomass Browse now requires a Maximum Biomass value to be given for each species.~~

1.2.2 Beta 0.8 (July 30, 2015)

- Bug fix in the neighborhood calculation of SitePreference for HSI calculation.
- Multiplied HSI values by 100 for map output.

1.2.3 Beta 0.7 (July 28, 2015)

- Defined EffectivePopulation as the minimum of zone population and zone carrying capacity (K).
- Added fields to log file, including TotalForage(kg), K, EffectivePopulation, BiomassRemoved(g/m2) and BiomassMortality(g/m2). The last 2 columns used to be lumped into one value labeled BiomassRemoved. The following columns of BiomassRemoved by species still represent a combination of browsing consumption and mortality.
- Changed units of the population output map to #/km2 * 100. To convert this to a per cell population (given 100x100m cell) you would divide by 10000. Summing the cell values and converting the units should result in the same value as the EffectivePopulation reported in the log file (give or take small rounding errors).
- Bug fixes to the accounting of browse removal. There were some inconsistencies that mostly affected sites when browse levels were high (second pass removals), and resulted in less removal than should have been applied.

1.2.4 Beta 0.6 (May 27, 2015)

Bug fix related to the implementation of the "UseInitBiomassAsForage". This option was not functioning previously and behaved as if always set to TRUE.

1.3 Acknowledgments

Funding for the development of the Browse Disturbance Extension has been provided by the Northern Research Station (Irvine, PA) of the U.S. Forest Service and the USGS ecosystems program. Valuable contributions to the development of the model and extensions were made by Patrick Drohan (Penn State University), Susan Stout, Alex Royo, Brian Miranda, Brian Sturtevant, Eric Gustafson (USFS Northern Research Station), Nathan De Jager (USGS Upper Midwest Environmental Sciences Center), Sam Flake (NC State University), and Robert Scheller (NC State University).

Funding for the development of LANDIS-II was provided by the Northern Research Station (Rhinelander, Wisconsin) of the U.S. Forest Service. Valuable contributions to the development of LANDIS-II were made by Robert M. Scheller, Brian R. Sturtevant, Eric J. Gustafson, and David J. Mladenoff.

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

Formatted: Font: 12 pt

Formatted: Normal

Formatted: Font: 12 pt

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.

Formatted: Font: 12 pt

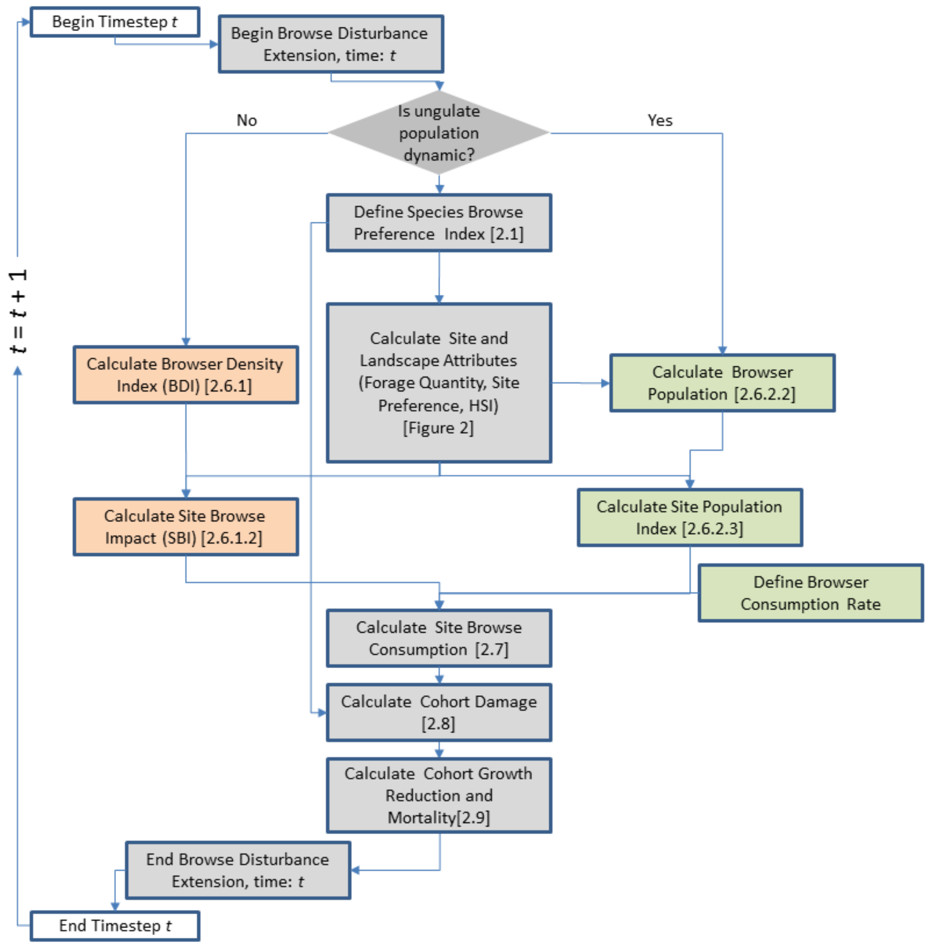
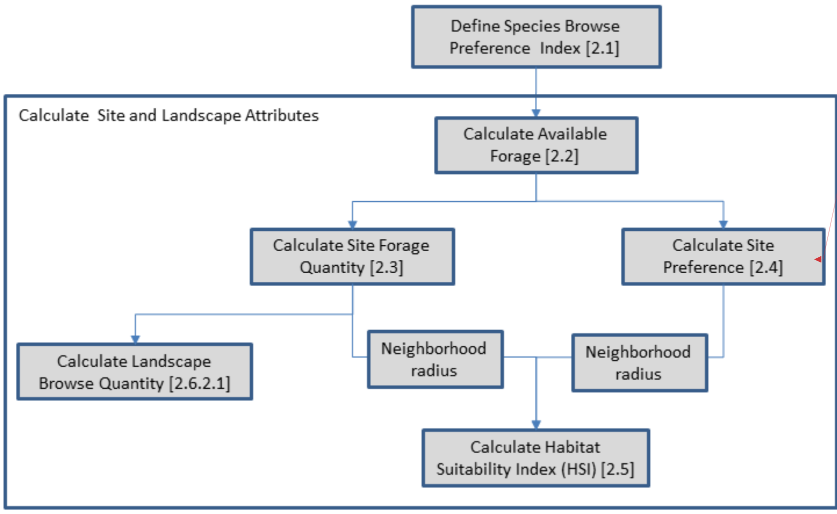


Figure 1. Overall conceptual diagram of Browse Extension.

Commented [EJG2]: There is some unconventional notation here. E.g., multiple exits from boxes, with no Boolean rule for deciding which exit is used. The convention is to use diamonds for multiple exits. It is therefore confusing.



Formatted: Keep with next

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

Formatted: Caption

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

Commented [EJG3]: Same issues with this diagram.

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 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 (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 seasonal variability. The relative preference index also is used to determine the proportion of the total available browse biomass that is removed from each species cohort.

Commented [NDJ4]: I have a bunch of information like this as well. Should we figure out a way to present it in publication that introduces the extension? Then leave the user guide as-is, with no suggested parameters?

Commented [EJG5]: Averaging?

3.2 Forage Availability

In nature, the accessibility of biomass to browsers is primarily a function of the height of the biomass above the ground. LANDIS-II does not track the height of cohorts, but because an assumption of LANDIS-II is that sites are fully stocked, the Browse extension uses cohort biomass as a surrogate for height. The Biomass Browse extension provides two methods to estimate the proportion of a cohort's forage biomass that is available to be consumed (i.e., in reach of browsers). While previous versions of Biomass Browse used ANPP values estimated from the succession extension, the current version estimates total forage biomass as 0.04 times the current biomass (adjusted for growth reduction, see section 3.10).

Commented [SWF6]: Future versions could use ANPP as a Biomass Cohort attribute, and thus communicate with the succession extension.

I'd also like to make the proportion of biomass as ANPP, as a user-provided parameter. Right now it's hard-coded at 0.04.

User-specified parameters are used to define two 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 that biomass is above the reach of the herbivores. The second threshold is the amount of biomass above which the entire cohort has "escaped" the reach of the herbivores and is not available as forage biomass. ~~Actual biomass available as forage is calculated according to the fraction of annual growth that susceptible cohorts allocate to leaf and stem material (**section reference here**).~~

Commented [SWF7]: revise

3.2.1 Susceptible Cohorts

Biomass Browse implements two ways to calculate which cohorts are susceptible to browse.

3.2.1.1 "Ordered cohort" method

This is the original behavior of the model from version 0.8. In the ordered cohort method, the biomass at which a cohort escapes browse depends upon the site's total biomass. A threshold of browsable biomass is calculated based on site biomass, and cohorts are browsed entirely in order of preference and age until the threshold is met.

The MinEscapeThreshold parameter specifies the first threshold, which is the proportion of the maximum possible-site biomass (calculated by the succession extension) below which cohorts having less than that biomass cannot escape browsing. For example, if site has a maximum possible biomass of 10000 g/m^2, then a MinEscapeThreshold value of 0.05 means that cohorts with biomass ≤500 g/m^2 are fully available as forage. As site biomass exceeds this threshold, the MaxEscapeThreshold parameter specifies how high a cohort's biomass much be to fully "escape" herbivory. To continue the example, if site has a maximum possible biomass of 10,000 g/m^2, then a Max~~in~~EscapeThreshold value of 0.1 means that cohorts with biomass ≥1000 g/m^2 have escaped herbivory and none of their biomass would be available as forage.

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 (only small cohorts are on the site), 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), the proportion of the cohort available as forage is computed as 1-(cohort biomass – minimum biomass threshold), with a minimum of 0.0, and the computed biomass available as forage is added to an available forage pool. If the size of the pool is less than the biomass threshold computed from the Max~~in~~EscapeThreshold, the next cohort in order of increasing biomass is then considered. The difference between the size of the pool and the original ~~biomass~~ MaxEscape~~t~~Threshold is used as a new threshold for the second cohort. This sequence is iterated for cohorts until the size of the pool is equal to the original biomass threshold, or until all cohorts have been considered.

Once the available forage pool has reached the minimum biomass threshold, increasingly large cohorts are processed in a similar way, except that the proportion of biomass available as forage decreases linearly as the available forage pool approaches the maximum biomass threshold computed using MaxEscapeThreshold. 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. Here the proportion of the cohort available as forage is computed as 1-(cohort biomass – maximum biomass threshold), with a minimum of 0.0, and the computed biomass available as forage is added to an available forage pool. This process is iterated until the size of the available forage pool is equal to the maximum biomass threshold, or until all cohorts have been considered.~~).~~

Commented [EJG8]: This seemed backwards as written. Smaller cohorts have most of their biomass unavailable as forage, but relatively larger cohorts have it all available as forage. Why?

Commented [EJG9]: I have re-written this, but I may have it all wrong.

Commented [EJG10]: This seems backwards. Smaller cohorts have most of their biomass unavailable as forage, but relatively larger cohorts have it all available as forage. Why?

Commented [SWF11]: Revise for clarity

Note that 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 4.2.13) are not considered as eligible for forage.

3.2.1.2 "Linear each cohort" method

In the Linear each cohort method, cohorts escape browse depending solely upon species-level parameters describing the relationship between forage-in-reach and cohort biomass (Fig. 3). The site biomass does not contribute to the calculation, and there is no cap on the amount of forage that a site could contain. Cohorts are foraged in order of preference to meet the browse demand, but they are not ranked by age.

Formatted: Normal

Formatted: Keep with next

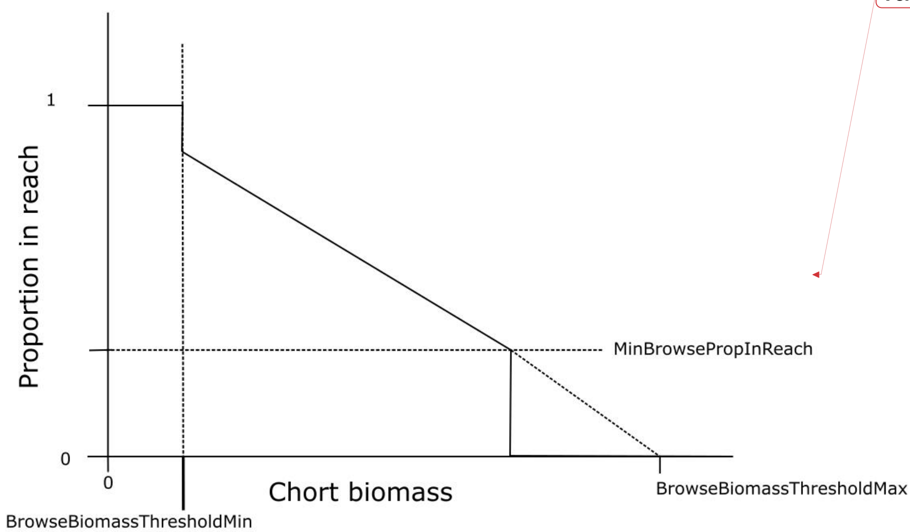


Figure 3 Relationship between cohort biomass and proportion forage in reach, when using the "LinearEachCohort" method. BrowseBiomassThresholdMin controls the range of biomass below which PropInReach is always 1. BrowseBiomassThresholdMax controls the slope of the line of declining PropInreach with cohort biomass. MinBrowsePropInReach controls the maximum cohort biomass which is browsable, together with BrowseBiomassthresholdMax. For example, larger cohorts could be set to be more browsable by either increasing BrowseBiomassThresholdMax (creating a shallower slope), or by decreasing MinBrowsePropInReach (allowing cohorts nearer to BrowseBiomassThresholdMax to be browsed).

Formatted: Caption

~~3.2.1~~3.2.2 Available forage biomass

Available forage biomass is calculated as the annual growth (ANPP) allocated to stems and twigs. ANPP is estimates as 0.04 times the cohort biomass (citation). 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 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. 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 (4.2.8). Users can also apply an option to count 100% of new growth as browseable material during the first year of growth (cohort age = 1) by specifying the input parameter Use Initial Biomass as Forage (4.2.14).

Commented [EJG12]: This term is without precedent in the section. Is this referring to the allocation percentages?

Commented [SWF13]: revise

3.3 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.

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.

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

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)

3.4.2 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 3.3).

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

The rescaled site quantity is used calculate site browse impacts (3.8) or site population density (3.8.1.3), and serves as a component in downscaling the zone population to the site-scale.

3.5 Site Preference

Site preference is an output 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 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 (4.2.17).

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 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 (3.5),

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.

Commented [EJG14]: Would it be clearer to call this site quality instead of site preference? That would be consistent with the forage quantity terminology.

Commented [SWF15]: Is this implemented?

3.6.1 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.

3.7 Browser Population Density

The browse disturbance 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 (defined above). 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. A second option allows the user to provide a population size. This is best used in cases where historical observations of population sizes are known, or the user wishes to test the effects of a given population size. The ~~second~~ third option (elaborated in Section 1.1.1) 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 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}).

Commented [NDJ16]: Is there any interest in having some stochasticity , or temporal variability in the BDI?

Formatted: Normal

Commented [BRM17]: This has not been implemented yet.

Formatted: Font: 12 pt

3.7.2 Density Option 2: User-specified population

Population size may also be provided for one or more timesteps. In this configuration, the population size remains static until a new value is provided. This method allows the user to replicate observed population sizes, or to test hypothetical stocking rates. If the population exceeds the carrying capacity, the population will be capped to the carrying capacity for the purposes of determining browse impacts (i.e., the maximum BDI is 1). This mode is similar to the BDI mode, as BDI is internally converted to population size (population = carrying capacity * BDI), but BDI scales directly with forage amount.

3.7.3 Density Option 3: 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 accordingly (e.g. harvest, stochastic mortality, and predation).

Stochasticity is incorporated by parameter estimates for population growth and mortality factors assuming a uniform distribution of potential values between minimum and maximum.

~~3.7.2~~3.8 Site Browse Impact (SBI)

The site browse impact temporary raster uses the total browse impact for a zone, the rescaled local HSI (2.6.1) values and the rescaled site forage quantity (2.4.2) to estimate local browse impacts, computed as a rate of browse removal for each site. 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 site browse impact (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.

~~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 accordingly (e.g. harvest, stochastic mortality, and predation).~~

Commented [BRM18]: This is not implemented. We need to define the standard deviation of these normal distributions in order to use them for stochasticity.

Commented [SWF19]: Is this provided as an output file at all? How does SBI relate to BDI at a site?

Formatted: Heading 2

Formatted: Normal

~~Stochasticity is incorporated by parameter estimates for population growth and mortality factors using mean estimates and normal distributions.~~

Commented [BRM20]: This is not implemented. We need to define the standard deviation of these normal distributions in order to use them for stochasticity.

~~3.7.3.1~~3.8.1.1 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 (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.

~~3.7.3.2~~3.8.1.2 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 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). The estimated population ($\Delta N_{t,Z} + N_{t-1,Z}$) is recorded in the log file as the population, but the effective population (N_{Eff}) is the minimum of the population and K_Z. N_{Eff} is used for all subsequent calculations including browse impacts and population growth the following year.

Commented [NDJ21]: Here is another place where I have a whole bunch of detail that I'd like to add to the publication, but not the user guide.

~~3.7.3.3~~3.8.1.3 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.

$$Pop_{site} = Pop_Z \times \left[\left(Quantity\_resca\cancel{ac}le_{site} \times \frac{Pop_Z}{K}\right) + \left(HSIrescal\cancel{acl}e_{site} \times \left(\frac{Pop_Z}{K} - 1\right)\right)\right]$$

~~3.8~~3.9 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.

~~3.9~~3.10 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 iterated 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). If the high preference cohort has 30 g/m^2 available forage, which gets browsed at a rate equal to its species preference (0.835), then 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 be removed (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.

Commented [EJG22]: Define "available" again. I'm assuming that escaped biomass is not available.

Commented [UFS23]: BRS – I found this a little hard to follow, and wonder if it is defendable.

Commented [UFS24]: We could try adding a graphical representation that might make it more clear.

Commented [EJG25]: I had no trouble following this, FYI.

~~3.10~~3.11 Browse Effect on Cohort Growth and Mortality

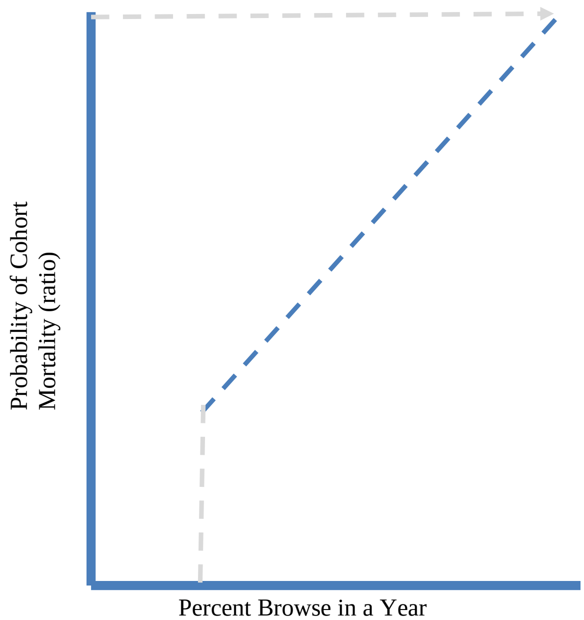


Figure 4 Effects of browse on cohort mortality and growth reduction. A user-defined threshold (a) determines the minimum amount of browse for any effect, and a second user-defined threshold (b) determines the maximum effect when browse is 100%.

Formatted: Font: 9 pt

Formatted: Caption, Space After: 0 pt, Line spacing: single

The browse disturbance extension also models the effects of biomass removal on subsequent cohort growth and survival via separate user-defined threshold proportions of annual growth lost (see Figure ~~3~~4). 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 4~~3~~) , n growth losses and mortality increase linearly to maximums (b, Figure 4~~3~~) set by the user.

3.12 Areas for additional development

~~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~~

3.12.1 Stochasticity –where and how.

3.12.2 Seed predation

Formatted: Heading 2

Formatted: Heading 3

Commented [NDJ26]: 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.

~~3.11~~3.13 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.

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.

4 Input Files

Commented [SF27]: TODO check that these are all accurate!

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

Commented [UFS28]: To be determined

4.2.1 Extension title, time step

The first parameter is the title of the input file:

```
LandisData  "Dynamic UngulateBiomass 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.- This value (unless preference == 0) indirectly affects the amount that a species is foraged. While total site forage is determined by cohort ANPP, age, and biomass, species' forage preferences and the rank-order of preferences determine how site-level browsing is distributed among species. Site-level browsing is initially assigned using the ratios of preferences for species at a given site. If forage demand still exists after this first calculation, the rest of the forage demand is satisfied in rank order of preference. 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 4~~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 4~~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 4~~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 4~~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%.

4.2.2.7 Biomass Maximum

The sixth column in the SpeciesTable is the maximum biomass attainable by each species (in g m^{-2}). This value should match the maximum biomass used for the chosen succession extension (Biomass Succession or NECN Succession). Biomass Maximum no longer varies at the ecoregion level; rather, it is constant for each species across the entire landscape.

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 BrowseMethod

The keyword “BrowseMethod” is followed by either “Population” or “BDI” to indicate which type of population calculations and input format will be used. Using “Population,” either a defined population or dynamic population may be used, depending on the value for DynamicPopulationFile (see 4.2.6).

~~4.2.4~~4.2.5 Defined Population File

The keyword "DefinedPopulationFile" is followed by a file name pointing to a text input file that defines the initial populations/browser density index for each zone. Values may be provided for additional timesteps, for example to mimic observed population sizes (for "BrowseMethod Population") or observed BDI ("BrowseMethod BDI"), or to simulate changes in population or BDI over time. If a population size is provided, the provided population will be used instead of the calculated Dynamic Population size (see 4.2.6). The initial population or BDI must be provided, even when using Dynamic Population calculations.

Commented [SWF29]: update

~~4.2.5~~4.2.6 Dynamic Population File (Optional)

Commented [SWF30]: update

~~4.2.5.1 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.~~ The keyword "DynamicPopulation" is used to indicate that the Dynamic Population calculations should be used (see 3.7.4). Dynamic Population calculations will only function if BrowseMethod is set to "Population" – that is, the Defined Population File must provide initial population sizes, rather than BDI values, for the browse regions. If DynamicPopulation is specified, then the following rows in the input file must be as follows (user note: these values are now provided in the main Browse input file, and replace the separate DynamicPopulationFile used in previous versions):

4.2.6.1 RMin

The minimum intrinsic growth rate for the population.

Formatted: Normal

4.2.6.2 RMax

The maximum intrinsic growth rate for the population. Each timestep, *R* is randomly selected from a uniform distribution between *RMin* and *Rmax*.

Formatted: Normal

Formatted: Font: Italic

4.2.6.3 MortalityMin

The minimum intrinsic mortality rate for the population.

Formatted: Normal

4.2.6.4 MortalityMax

The maximum intrinsic mortality rate for the population. Each timestep, *Mortality* is randomly selected from a uniform distribution between *MortalityMin* and *MortalityMax.*

4.2.6.5 PredationMin

The minimum rate of predation for the population.

4.2.6.6 PredationMax

The maximum rate of predation for the population.

4.2.6.7 HarvestMin

4.2.6.8 HarvestMax

~~4.2.6~~4.2.7 Consumption Rate

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

~~4.2.7~~4.2.8 ANPP Forage Proportion

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

4.2.9 MinBrowsePropInReach

The keyword "MinBrowsePropinReach" is followed by a decimal value between 0 and 1 representing a minimum threshold for PropInReach, below which a cohort is assumed to have entirely escaped browsing even if the cohort has not attained BrowseBiomassThresholdMax.

~~4.2.8~~4.2.10 Minimum Biomass Threshold for Escape~~Minimum Browse in Reach Proportion~~

The keyword "BrowseBiomassThresholdMin ~~MinBrowsePropinReach~~" is followed by a decimal value between 0 and 1 representing the proportion of maximum biomass below which a cohort is entirely susceptible to browse~~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)~~. This threshold (BrowseBiomassThresholdMin times Maximum Biomass) represents juvenile trees that are entirely reachable by browsers. Cohorts with browse in reach proportions ~~less~~ greater than this biomass threshold ~~are considered~~are able to partially escape browse, as described in section 3.9. ~~"escaped"~~ ~~from the browse reach, and none of their forage is available to the browser.~~ (Figure 3)

Formatted: Normal

Formatted: Normal

Formatted: Normal

Formatted: Heading 4

Commented [SWF31]: Really need a figure to explain this

Commented [SWF32]: Revise

Commented [SWF33R32]: These parameters have slightly different meanings when using the LinearEachCohort method or Ordered method; Sam TODO

Commented [EJG34]: "Less than" means escaped?????

4.2.11 Maximum Biomass Threshold for Escape

The keyword "BrowseBiomassThresholdMax" is followed by a decimal value between 0 and 1 representing the proportion of maximum biomass above which a cohort is entirely escaped browse. For cohorts with biomass less than BrowseBiomassThresholdMax and greater than BrowseBiomassThresholdMin, the proportion of browse is calculated as one minus the ratio of cohort biomass to BrowseBiomassThresholdMax. This functional relationship is a linear decrease in the proportion of the cohort biomass in reach, until the cohort totally escapes browse. (Figure 3)

Commented [SWF35]: Need to make a figure to illustrate this

~~4.2.9~~4.2.12 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~~ site ceases to be browsed ~~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.

Commented [EJG36]: This needs to be revised depending on the description in Section 3.

~~4.2.10~~4.2.13 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.

4.2.14 Calibrate Mode (Optional)

The keyword CalibrateMode is followed by "ON" or "OFF" to turn on detailed reporting of browse in the Calibrate Log (see 5.7). This option should only be used for single-site model runs, because of the volume of outputs generated.

~~4.2.11~~4.2.15 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 (3.11). This is an optional parameter. The default is "ON", and excluding this parameter will include simulation of growth reductions.

~~4.2.12~~4.2.16 Mortality Option (Optional)

The keyword "Mortality" is followed by "ON" or "OFF" to turn the browse impacts on cohort mortality on or off (3.11). This is an optional parameter. The default is "ON", and excluding this parameter will include simulation of cohort mortality.

~~4.2.13~~4.2.17 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~~4.2.18 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 (4.2.8) to the initial biomass when determining the forage of a new cohort.

4.2.19 Forage in reach method (Optional)

The keyword "ForageInReachMethod" is followed by either "Ordered" or "LinearEachCohort" to select between two methods of calculating forage in reach. The default is "Ordered" (same behavior as in previous releases).

~~4.2.15~~4.2.20 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.

Commented [EJG37]: The example file should include examples of each.

~~4.2.15.1~~4.2.20.1 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 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~~4.2.20.2 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 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~~4.2.21 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.

Commented [EJG38]: Are there any map formats that cannot be chosen? E.g., .gis.

~~4.2.16.1~~4.2.21.1 *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 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.

Commented [EJG39]: I think an example or 2 would be appropriate here.

~~4.2.16.2~~4.2.21.2 *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.

~~4.2.16.3~~4.2.21.3 *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 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.

~~4.2.16.4~~4.2.21.4 *Site Population Output Maps (Optional)*

The keyword "SitePopulationMapNames" is followed by a path and filename template for output maps of site population (3.8, 3.8.1.3). 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.

~~4.2.16.5~~4.2.21.5 *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 (3.9) as well as biomass lost to mortality caused by browsing (3.11).

~~4.2.17~~4.2.22 Output Log

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

5 Output Files

Commented [EJG40]: Can this be combined with the previous page to reduce redundancy?

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. Values are in units of 100 individuals per square km; divide these values by 100 to get real population density. Population density maps are now identical for both static and dynamic browse (as of v2.0). ~~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.

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 (3.9) as well as biomass lost to mortality caused by browsing (3.11). Non-active cells always have a biomass removed of 0.

5.6 Output Log

Commented [SWF41]: TODO: update this

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.

5.6.4 Total Forage (kg)

The total zone/landscape forage quantity. Units: kg biomass.

5.6.5 Carrying Capacity (K)

The maximum number of browsers that could be supported in the zone/landscape based on the total forage available. Units: # of individuals.

5.6.6 Effective Population

The minimum of Population and K, used in subsequent browse impact calculations. Units: # of individuals.

5.6.7 Damaged Sites

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

5.6.8 Biomass Removed (g/m^2)

Total biomass removed from the zone/landscape by the browser due to direct browsing. Units: g/m^2.

5.6.9 Biomass Mortality (g/m^2)

Total biomass removed from the zone/landscape by the browser due to browse-induced mortality. Units: g/m^2.

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.

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.

5.7 Calibrate log

5.7.1 Year

Simulation year.

5.7.2 CohortEstYear

The year in which the cohort was established. The value will be negative for trees in the initial communities which established before timestep 0. This column allows a particular cohort to be tracked over time (a combination of species and CohortAge should uniquely identify a cohort).

5.7.3 CohortCode

Species index of the cohort.

5.7.4 CohortName

Species name of the cohort.

5.7.5 GrowthReduction

Proportion by which ANPP was reduced due to browsing.

5.7.6 NewForageInReach

Quantity of forage available for browsing. This is calculated even for unpalatable species.

5.7.7 FirstPassRemoval

How much biomass is removed in the “first removal” step. This step depends upon the site-level browse demand and the absolute value of the browse preference for the species.

5.7.8 SecondPassRemoval

How much biomass is removed in the “second removal” step. This step depends on the unmet demand for forage after the first removal pass, and the rank order of browse preference compared to other species at the site.

5.7.9 FinalRemoval

How much biomass was removed by foraging? Sum of FirstPassRemoval and SecondPassRemoval.

5.7.10 NewForage

Total available forage, whether it is within reach of browsers or not. Calculated as (cohort biomass * 0.04) * ANPPForageProp * (1-growthReduction)

5.7.11 LastBrowseProportion

The ProportionBrowsed from the preceding timestep. Used to calculate current-year GrowthReduction.

5.7.12 ProportionBrowsed

Proportion of total forage that was removed by browsing.

5.7.13 ProbabilityMortality

Probability of cohort mortality due to browsing.

6 Example Input Files

6.1 Biomass Browse input file (with Dynamic Population parameters)

```
LandisData  "Biomass Browse"

Timestep 1

<< Species Inputs >>
SpeciesTable
>>                    --GrowthReduction--   --Mortality-    Biomass
>> Name    Preference   Threshold   Max   Threshold   Max      Max
>> -------- ----------  ---------   ---   ---------   ---    -------
ABBA        0.15        0.3         0.4   0.8         0.01   5000
ACSA3       0.15        0.3         0.4   0.8         0.01   5000
BEAL2       0.15        0.3         0.4   0.8         0.01   5000
BEPA        0.25        0.4         0.3   0.9         0.01   5000
PIGL        0           0           1     0.8         0.01   5000
PIBA2       0           0           1     0.8         0.01   5000
POTR5       0.30        0.4         0.3   0.9         0.01   5000
THOC2       0.05        0.3         0.4   0.8         0.01   5000
FRNI        0           0           1     0.8         0.01   5000
PIMA        0           0           1     0.8         0.01   5000
PIST        0.05        0.3         0.4   0.8         0.01   5000
QURU        0.05        0.3         0.4   0.8         0.01   5000
SFTWD       0.15        0.3         0.4   0.8         0.01   5000
HRDWD       0.15        0.3         0.4   0.8         0.01   5000

<< Browser population Inputs >>
ZoneMap  "./rasters/single3.tif" <<same as ecoregions right now;
every active cell can be browsed. sf 2021-12-20
BrowseMethod "Population" <<must be either "Population" or "BDI"
DefinedPopulationFile   "DefinedUngulatePopulation.txt"  << File with
user-defined population or BDI; must contain year-0 data
DynamicPopulation  << Optional.  If exists, then the next 8
parameters must be input
RMin 0.15
RMax 0.25
```

```
MortalityMin 0.15
MortalityMax 0.25
PredationMin 0.0
PredationMax 0.0
HarvestMin 0.0
HarvestMax 0.0

<< Forage Inputs >>
ConsumptionRate  2738  << kg/yr/individual
ANPPForageProp          0.66  <<Prop of ANPP that counts as forage
MinBrowsePropinReach    0.2   <<Min prop of browse within reach for a
cohort to be browsed. Prevents larger cohorts from being browsed. Not
needed for Ordered forage in reach method
BrowseBiomassThresholdMin     0.05  <<Proportion of ecoregion max
biomass when cohort begins to escape browse; cohorts smaller than
this threshold are completely reachable as forage
BrowseBiomassThresholdMax     0.1   <<Proportion of ecoregion max
biomass above which cohorts completely escape browse; also controls
maximum forage possible per cell
EscapeBrowsePropLong    0.57  <<Prop of longevity when browse is
escaped

<< Options >>
CalibrateMode OFF <<Default is OFF
GrowthReduction   ON  << Default is ON
Mortality   ON  << Default is ON
CountNonForageinSitePref      TRUE  << Default is FALSE
UseInitBiomassAsForage        TRUE  << Default is FALSE
ForageInReachMethod     "LinearEachCohort"

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


<< 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 Defined Population file

```
   LandisData "Defined Population"

   >>Year   Zone  Zone total population
   >>----   ----  ---------------------
     0      3       10
     1      3       5
     2      3       20
     3      3       5
     4      3       20
     5      3       5
```

7 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)
Juniperus virginiana	eastern redcedar	moderate	moderate
Larix laricina	tamarack		
Liquidambar styraciflua	sweetgum	low	low
Liriodendron tulipifera	yellow-poplar (tuliptree)*	high	high

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		
Pinus pungens	Table-Mountain pine		
Pinus resinosa	red pine		
Pinus rigida	pitch pine		
Pinus strobus	eastern white pine*	low	moderate
Pinus virginiana	Virginia pine		
Platanus occidentalis	American sycamore	(is browsed)	(is browsed)
Populus balsamifera	balsam poplar		
Populus deltoides	eastern cottonwood		
Populus grandidentata	bigtooth aspen	(is browsed)	low
Populus tremuloides	quaking aspen	(is browsed)	low
Prunus alleghaniensis	Allegheny plum		
Prunus americana	American plum		

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
Salix amygdaloides	peachleaf willow		
Salix caroliniana	coastal plain willow		
Salix nigra	black willow	low	moderate
Sassafras albidum	sassafras	moderate	high
Sorbus americana	American mountain-ash		

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