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Neighborhood effects as a plant defense against ungulate herbivory

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Plantans omgivning som ett försvar mot klövviltbetning

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Keywords: winter browsing, plant-animal interactions, associational effects, scale, large herbivores, palatability, Sweden

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Abstract

Neighbourhood effects as a plant defence against ungulate herbivory

For large herbivores patch selection is highly influenced by the presence of plant species and biomass that allows them the highest protein and energy intake. From the plant point of view browsing is seen as damage and loss of fitness and plants evolved different strategies to avoid or tolerate herbivory. Plant defence strategies can be from their own mechanical or chemical properties or can be obtained from neighbouring vegetation. Depending on the foraging strategy of the herbivore, the neighbourhood effect can be divided into 4 strategies: associational defence, associational susceptibility, neighbour contrast defence, or neighbour contrast susceptibility. The aim of this project is to gain a better understanding on the effect of neighbourhood quality (e.g. low or high palatability, habitat type) on browsing intensity of trees of different palatability. Two scales – habitat and tree scale were analyzed for this, using a natural gradient of palatability based on 5 tree species in the boreal zone of Sweden. At the habitat scale I found no evidence for an effect of neighbourhood quality, however at the tree scale there was a strong effect of neighbourhood quality for rowan and spruce. The results of this study suggested associational defence in the case of rowan (palatable species) and contrast defence for spruce (unpalatable species). The more average palatable species showed less effect of neighbourhood, suggesting the importance of the species palatability of the studied individual to which the neighbourhood belongs on the strength of this neighbourhood effect. Concluding, neighbourhood effects differ between foraging scales and tree species and are strongly influenced by the palatability of the focal trees. Due to a shift in palatability ranking along the latitudinal gradient the strength of the neighbourhood effect differs not only between species but also depends on the vegetation zone.

Key words: winter browsing, plant-animal interactions, associational effects, scale, large herbivores, palatability, Sweden

Introduction

Large herbivores make foraging choices at different spatial scales (Senft et al. 1987). At a large scale the dispersal processes and seasonal migrations relate to the choices of the animals (Morris 1987), whereas in the home range or habitat scale shelter, predation risk, forage quality, and forage availability are of high influence (Werner et al. 1983). Migration can be steered by rainfall patterns like in the African savannah (Boone et al. 2006) or on altitudinal gradient in mountains driven by snow cover to permit animals to track the higher palatable food sources (Singh et al. 2012). Some European moose (*Alces alces*) populations migrate between summer and winter homeranges (Sweanor and Sandegren 1988, 1989, Andersen 1991). At a more detailed level, habitat composition and snow depth and quality are influence the migration of moose Ball et al. (2001). At the small feeding patch scale, selection by large herbivores is highly influenced by the presence of plant species and biomass that allows them the highest nutrient and energy intake (Langvatn and Hanley 1993, Wilmshurst and Fryxell 1995). Ungulates show strong preferences for different plant species with higher nutritional values and lower levels of digestibility-reducing compounds (Belovsky 1981, 1984, Palo and Robbins 1991, Stolter et al. 2005). Many herbivores are known to be selective at the tree species level (Danell et al. 1991, Shipley and Spalinger 1995). At a lower level yet, Markgren (1969) shows that many browsing animals select juvenile plants, young shoots and leaves which contain high levels of nitrogen.

From the plant point of view browsing is seen as damage and loss of fitness. Winter browsing has a general negative effect on growth of shoot biomass in the following growing season (Danell et al. 1994). Plants have different strategies to avoid, tolerate or defend themselves against herbivory (Grubb 1992). These plant defence strategies can be from their own mechanical or chemical properties or can be obtained from neighbouring vegetation (Atsatt and O´Dowd 1976, Hjältén 1993, Olff et al. 1999, Milchunas and Noy-Meir 2002, many others). Depending on the foraging strategy of the herbivore, the neighbourhood- or associational- effect can be divided into 4 strategies (Table 1, Bergvall et al. 2006, Rautio et al. 2012).

Table 1: associational effects with different herbivore foraging choices (Bergvall et al. 2006)

	Selective between patches	**Non-selective between patches**	
Selective within patches	Associational defence	Attractant decoy hypothesis	
		Neighbour contrast defence	Neighbour contrast susceptibility
Non-selective within patches	Associational susceptibility	*(no associational effect)*	

When an animal selects between patches a palatable plant gains protection from defended or unpalatable plants in its neighbourhood for the animal will not choose a patch with mainly unpalatable plants. If this is the case we can speak of associational defence/resistance (Figure 1b). If however the animal is unselective within patches an unpalatable plant can be susceptible to foraging if it is surrounded by palatable species. This is named associational susceptibility/palatability (Figure 1a). The attractant decoy hypothesis applies when the animal is unselective between patches but selective within a patch (Atsatt and O'Dowd 1976, Bergvall et al. 2006). This strategy can be subdivided into neighbour contrast defence and neighbour contrast susceptibility. Individual plants are directly contrasted with their neighbours and may obtain a relative higher or lower perception of palatability. When a palatable species is targeted more when located in a neighbourhood with relatively poorly palatable species (Figure 1d) we speak of neighbourhood contrast susceptibility. The opposite, when an unpalatable species is browsed less when it is surrounded by more palatable species (Figure 1c), is called neighbour contrast defence. When animals are unselective both between patch and within patch there is no case of an associational effect (Table 1). One would also expect that the degree of palatability of the focal species, the species of the central tree around which the neighbourhood is determined, is important. If species are exceptionally palatable or poisonous the quality of the neighbourhood will diminish or become redundant (Figure 1e).

Research on associational resistance has been conducted with experimentally manipulated food (Bergvall et al. 2006, Rautio et al. 2008) as well as in natural plant communities in woody pastures (Smit et al. 2005). However, observational research on the relative importance of the 4 associational effects simultaneously and in closed forest habitats is limited. Therefore, non experimental research into the effect of neighbourhood in managed boreal forests of Sweden can help gain better understanding in the subject. The aim of my project is to gain a better understanding on the effect of neighbourhood quality (e.g. low or high palatability, habitat type) on browsing intensity of trees of different palatability. To incorporate the different scales of foraging by large herbivores this study contains two study scales, namely habitat scale (tracts of 1km²) and individual trees scale (feeding patch 1,5m radius). In this thesis I test the overall hypothesis that browsing intensity on a focal tree or in a focal habitat is influenced by its neighbourhood (Figure 1).

Specifically I tested four hypotheses related to neighbourhood effects:

- Low palatability/quality of the neighbourhood decreases the browsing intensity on palatable species (Associational resistance/ defence) if the ungulate is selective between patches.
- High palatability/ quality neighbourhood increases the browsing intensity on lesser palatable species. (Associational susceptibility/palatability) if ungulate is unselective within the patch.
- Low palatability/quality of the neighbourhood increases the browsing intensity on palatable species (neighbourhood contrast susceptibility) if the ungulate is selective within the patches.
- High palatability/quality of the neighbourhood decreases the browsing intensity on lesser palatable species (neighbourhood contrast defence) if the ungulate is selective between patches.

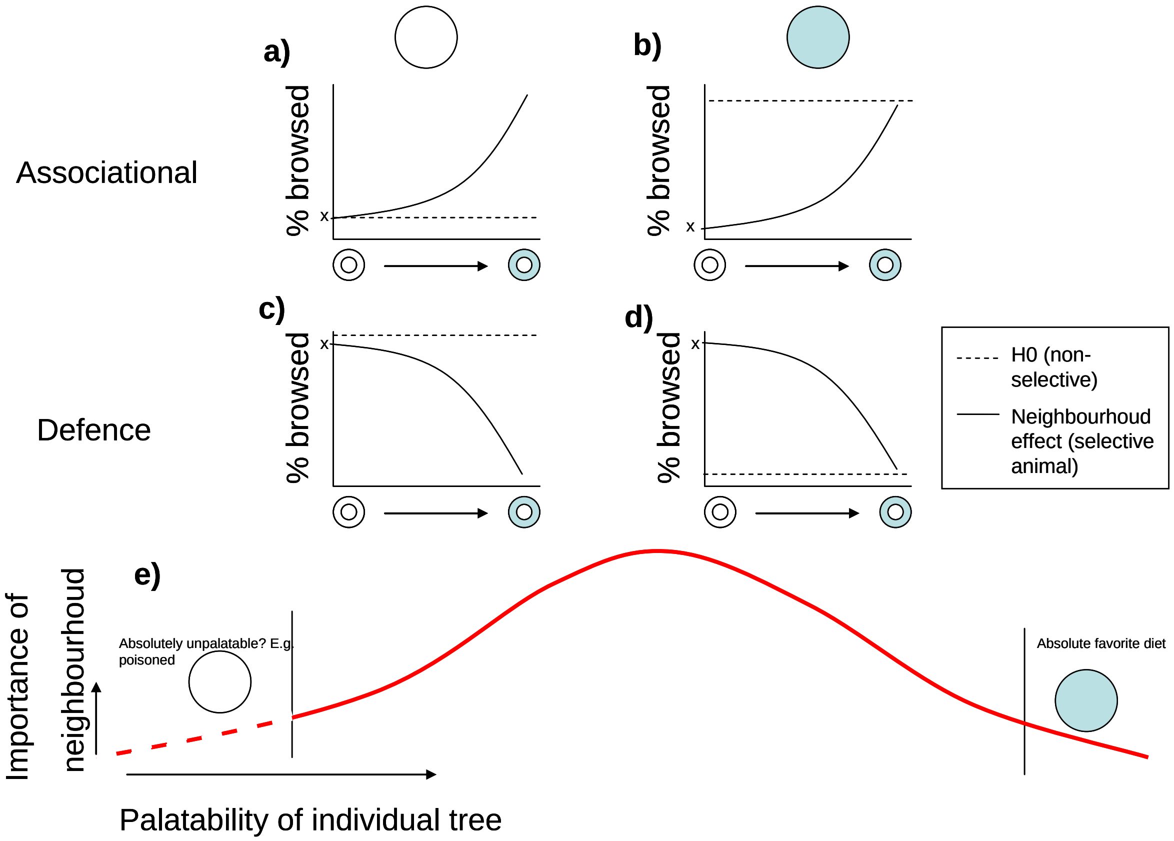


Figure 1: Browsing intensity scenarios depending on palatability (○ unpalatable; ● highly palatable) of both focal tree and the neighbourhood.
With a-b) high palatability neighbourhood increases browsing, c-d) high palatability decreases susceptibility to browsing, e) range in palatability of focal tree influences the importance of neighbourhood quality on browsing.

Material and Methods

Study areas

Habitat scale

For the analysis on habitat scale I used the data of the **Game grazing and forage production project** of the thematic program Wildlife and Forestry. This project is a collaborative effort between Sveaskog, Sveaskog Naturupplevelser, SLU (Swedish University of Agricultural Sciences) and Skogforsk (Edenius et al. 2012). My analysis at the habitat scale, surveys 5 sites spread along the bio- geographical gradient of Sweden (Figure 2). The most northern study site, in the county of Norrbotten, is **Råneå** (66º 12' N – 21º 45'E). This site is situated in the middle boreal vegetation zone bordering the northern boreal vegetation zone (Ahti et al. 1968). These zones are characterized by a dominance of coniferous species with birch (*Betula* spp) and aspen (*Populus tremula*) as the main broad-leaved trees (Dahl 1989). Large ungulate species like Moose and Roe deer are still present up till this latitude. Due to the influence of the Baltic Sea the slightly more southern but inland situated study area **Sorsele** (65º.34' N – 17º 26'E) in the county of Västerbotten, has a colder average climate and a northern boreal vegetation zone (Ahti et al. 1968). During the winter, the migrating moose populations move to Sorsele from the surrounding mountain range (Singh et al 2012) and Roe deer occur in the area as well. **Furudal** (61º.21' N – 15º 13'E), in the county of Dalarna is situated on the border of the middle boreal and north-boreal vegetation zone (Ahti et al. 1968). There are relative high densities of bears (1-2 bears per 100km2, Kindberg et al. 2009) and the study areas are located in wolf territories with 6-7 individuals counted in winters of 2007-8, 2008-9 and 2010-11 (Wabakken et al 2008, 2009, 2011). In this study area both Roe deer and Moose are present. **Malingsbo** (59º57' N – 15 º24'E), a study area on a 3 border point of the counties Dalarnas, Örebro and Västmanlan and a border of south boreal and middle boreal vegetation zone (Ahti et al. 1968). Malingsbo is close to the northern distribution limit of both Red deer and the introduced Fallow deer and is inhabited by the Moose and Roe deer. **Misterhult** (57º32' N – 16º 30'E), the most southern study area is located in Kalmar county. This area is situated in the hemiboreal vegetation zone with a coastal climate (Ahti et al. 1968). It is substantially different, in both forest and presence of mammals, from the other 4 areas. The forest is still dominated by coniferous trees with 57% pine (*Pinus sylvestris*) and 24% spruce (*Picea abies*) but also contains a variety of deciduous trees (Sveaskog 2009). Not only birch (betula spp.), rowan (*Sorbus aucuparia*) and aspen (*Populus tremula*) occur here, this area is also within the northern border of oak (*Quercus robur*). The forest floor is covered with a large number of herbaceous species. Not only Moose, Red deer, Roe deer and Fallow deer are present in this area, also Wild boar (*Sus scrofa*) occurs here (Mansson et al. 2008, Roberge et al. 2009). South Sweden is characterized by relatively dense human populated areas and more abundant infrastructure than the other areas in this study.

Tree scale

The data collection at the tree scale was conducted between April 25th and June 1st 2012 at the small Swedish peninsula **Järnäs** (63º.51' N – 19º 65'E) in the county of Vasterbotten. Considering large herbivores, this peninsula is a diverse system in northern Sweden.

Moose, Red deer, Fallow deer and Roe deer are present in the area. Red and fallow deer form free-ranging breeding populations but were established after release from captivity (Järnäs foresters, personal communication). Järnäs lies within the south boreal vegetation zone with strong coastal influence (Ahti et al. 1968). Small villages, summer cottages and a small road around the peninsula are the main infrastructural influences. Different land use characteristics are primarily managed forest, agriculture, swamps and lakes. A main road cuts the peninsula from the mainland however moose are known to cross over.

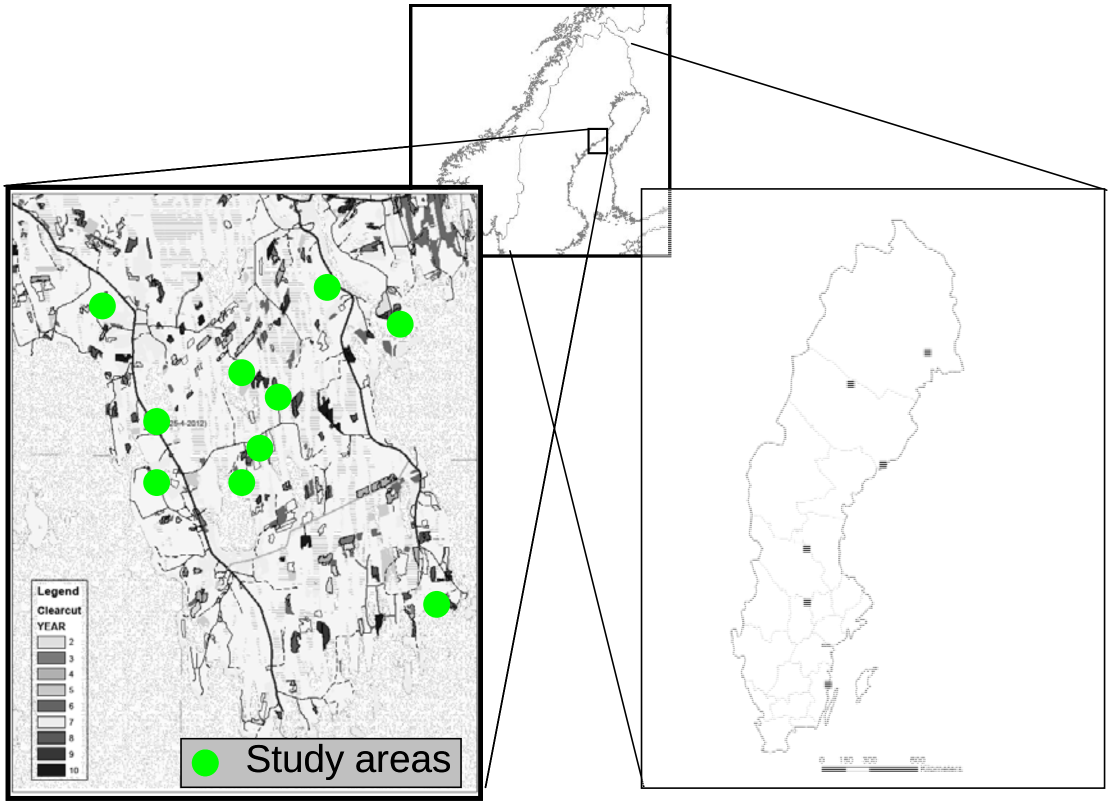


Figure 2: Study site Järnäs with study sites in green and not used clear cuts in grey/black and the habitat scale study areas

Study species

I focus on four large herbivores in the Fenoscandinavian forest. The biggest and most widespread species is the moose which is a browser and selective feeder with different diet between seasons (Bergström and Hjeljord 1987, Cederlund et al. 1980). Along the latitudinal gradient moose also prefer different tree species (Hörnberg 2001). Red deer (*Cervus elaphus*) is classified as an intermediate feeder and has a diverse diet throughout the year (Storms et al. 2008, Clutton-Brock et al. 1982, Gebert and Tixier 2008). Roe deer (*Capreolus capreolus*), a selective feeder and browser feeds on broadleaved trees and *Vaccinium* sp. in spring are found to supplement their winter diet with coniferous species like *Pinus sylverstris* (Storms et al. 2008, Tixier et al. 2009). About the annual diet of the fallow deer (*Dama dama*) in Sweden not much is known, in England their winter diet consists mainly of bramble, billberry and grasses and felled conifers (Jackson 2009). The dominant trees are: pine (*Pinus sylvestris*), spruce (*Picea abies*), downy birch (*Betula pubecens*), and silver birch (*Betula pendula*). Other occurring species are: rowan (*Sorbus* *aucuparia*), alder (*Alnus glutinosa*), aspen (*Populus tremula*) and willow (*Salix sp).* Furthermore, in early spring the vegetation cover in the clear cuts contain *Juniperus, Vaccinum* sp, and moss, grass and *Carex* species.

Sampling design

Habitat scale

The 5 study areas were all sub-divided into tracts of 1 × 1 km (but 500 × 500 m in Misterhult). The tracts were placed 1000 m apart (500 m in Misterhult) and adjacent in Furudal. 16 points with 200m distance (100m in Misterhult) composed a tract and each point represents a plot location shaped as a 100 m^2 circle. Plot numbering starts in the top-left corner and with a hand held GPS every point was located and sampled. Browsing pressure was measured on pine, downy birch, silver birch and rowan (also oak in Misterhult) for one focal tree per species nearest to the center point and a maximum distance of 5.64 m. All focal trees were in the height range of 0.3-3 meters. The number of total available last year shoots and the number of browsed shoots were measured. Browsing pressure represents the proportion of browsed last year shoots. Data collection took place during spring, in the period between snow melt and growing season (foliation & sprouting). During this period, age determination of fresh bites/browsing is easiest to perform and leaf stripping did not start yet.

Tree scale

In the study area of Järnäs, clear cuts that were felled between 2003 to 2009 were selected based on the harvesting dataset avverkningnya-24 (Skogsstyrelsen) to measure the browsing intensity of individual focal trees and the quality of there neighbourhood. All measured trees had to be within the height range of 0.3 and 3 meters to include the entire foraging scope of the herbivores (Lavsund 1987). To avoid including confusing human damage with herbivore damage), sites with recent forestry measurements like pre-commercial thinning were excluded. A total of 10 sites (Figure 2, Table 3) were selected based on a minimal occurrence of 10 saplings for all 5 focal species and the presence of herbivores (dung, hair, damage, or tracks). Within each site, plots were randomly selected by walking a transect that covered the whole extent of the clear cut and selecting one of the focal species with a minimum distance of 5 meters between measured trees to avoid overlapping neighbourhoods. Although trees were selected randomly, I tried to select trees across the extent of each clear cut and avoid too much spatial clumping of trees. To test neighbourhood effect in a range of focal tree palatability the following 5 species were selected, in order of palatability: rowan, silver birch, downy birch, pine and spruce. For every **focal tree** I recorded: species, height (cm), diameter (mm), canopy cover, number of last year shoots and number of shoots browsed. For each focal tree I defined the neighbourhood as the area with 1.5 meter radius surrounding the focal tree. I took this scale to represent the small scale of feeding patch animals select at (Danell et al. 1991). Animals can feed in this radius of the focal tree without having to move and look for a new patch. **Neighbourhood** quality variables measured in the radius of 1,5 meters around each focal tree include: species, and height (cm) of every sapling between 30 and 300 cm. To approximate the abundance of herbivores, the dung of moose, deer sp., and rodent (hare and vole, *Microtus* spp.) in a radius of 2 meter around the focal tree was recorded. There was a substantial amount of rodent browse and damage, therefore both hare (clean cut branches) and voles (bark consumption) were measured and separated from large herbivore browsing and excluded from the browsing analysis in this thesis.

Statistical analyses habitat scale

Data sources and spatial analysis

I calculated the average browsing intensity of the 16 points per tract per species to index browsing intensity within the habitat. Neighbourhood variables on habitat scale were extracted from the data layer kNN-Sweden 2010 with a resolution of 25×25 m (SLU 2011a) using ArcGIS Desktop 10 (ESRI, Redlands, CA, USA). The kNN layer was constructed by combining data from the National Forest Inventory and satellite images from SPOT 4 and SPOT 5 by means of the k nearest neighbours method (SLU 2011b). A 250 m buffer around each point was created and merged per tract to represent the neighbourhood shape to extracting the average value of the different variables from the kNN layer. Variables exported are Age (years), Height (m), Volume birch (m^3/ha), Volume contorta (m^3/ha), Volume spruce (m^3/ha), Volume pine (m^3/ha), Volume biomass (kg/ha) and Total volume (m^3/ha). Total volume includes species that are not mentioned in individual volume variables in my analysis. The variables above are all average values of the neighbourhood but for simplification and easier display in the report the variable names are shortened.

Data exploration

To test the data for normality I used the Kolmogorov-Smirnov (KS) test for large data sets. Furthermore, arcsin, sqrt and sqrt(arcsin) transformations were tested with the KS goodness of fit test but the transformations did not improved the normality of the dataset. Therefore non parametric tests were used for further analysis. Explanatory variables were tested for correlation with the Spearman rank test to prevent including strongly correlated (correlation coefficient > 0.6) variables in the modelling procedure (Appendix Table 1).

Model selection

To analyze differences in preference of focal trees and the effects of habitat neighbourhood quality, I used Generalized Linear Mixed Models (GLMMs) with the assumption of a binomial distributed response variable for proportion data (Bolker et al. 2009). To take the effect of difference among study areas into account, “Site” was set as random effect in the GLMMs. For GLMMs the lme4 package was used (Bates et al. 2011). GLLMs were fitted by maximum likelihood assuming a Laplace approximation. All the modelling and computing was conducted with the statistical software R 2.15.0 (R Core Development Team 2012). At the habitat scale, 4 different species were measured within one neighbourhood resulting in repetitions of neighbourhoods in the data. Therefore at habitat scale the models were run separately for each species. For the habitat scale stepwise deletion was used to determine the minimum adequate models for each species. Variables with the weakest significance in the model are excluded based on chi square test until models were significantly different or all variables were significant (Bolker 2007, Crawley 2007). The models were selected and compared with Akaike (AIC) values (Akaike 1974, Shibata 1981).

Statistical analyses tree scale

Data exploration

Similarly to the habitat scale analysis, the Kolmogorov-Smirnov (KS) test was used to test for normality. Transformations did not result in normality, so non-parametric tests were used. The results of the Spearman rank test can be found in Appendix Table 2. Descriptive results and graphs were conducted partially with Windows Excel 2003.

Model selection

To analyze differences in preference of focal trees at tree scale and the effects of neighbourhood palatability, I used Generalized Linear Mixed Models (GLMMs) with the assumption of a binomial distributed response variable for proportion data (Bolker et al. 2009). To take the effect of difference among clear cuts into account, “Area” was set as a random effect in the GLMMs. For the method used I refer to model selection of habitat scale. At the tree scale every individual tree had a unique neighbourhood (because no trees closer than twice the 1.5 m radius were sampled) and all species were included as a categorical factor in one model.

Ranking of neighbourhood quality

To determine focal species palatability ranking and influence of focal tree variables a GLMM was used, followed by a Tukey multiple comparison to determine the differences between the focal tree species. For the multiple comparison the packages multcomp (Hothorn et al. 2012) and ez (Lawrence 2012) were used. Based on the multiple comparison results from difference between proportion browsed shoots per species I assigned palatability weights to the different species in neighbourhood to create a relative difference between the species contribution to neighbourhood quality. Weights are calculated by starting at 1 with the least palatable species (zero is reserved for focal trees without neighbouring trees), and adding the difference in posthoc coefficient values to end up with the highest score for the most palatable and preferred species. A priori and based on ranking in literature, the other neighbourhood species were assigned weights by estimating there palatability ranking compared to the already calculated species (Shipley et al. 1998, Hörnberg 2001). For example, in palatability and preference studies willow was mainly ranked between rowan (6.3) and silver birch (5.0) and was therefore given the average weight value of these two species resulting in the weight of 5.7 (see Table 7). An estimation of weight was given by averaging the weight of the lower and higher palatable species from the multiple comparison. The sum of all species weight values multiplied by the number of this species occurring in the neighbourhood and corrected for total number of trees in the neighbourhood was used as a neighbourhood quality value (Q).

$$Q = \frac{\sum (W_{(s)} \times n_{(s)})}{\Sigma n_{(s)}},$$

where *W* is the weight assigned to species (s), n is number of individual trees of species (s).

Results

Habitat scale

Descriptive statistics

Browsing intensity differs among the different areas along the latitude gradient (Figure 3). In the most northern area Råneå the species with the highest browsing proportion is the silver birch where as in the most southern area silver birch is the least browsed species. Rowan followed by silver birch are the two species with the overall highest browsing intensity. Misterhult is somewhat of an anomaly compared to the other areas because of the presence of oak, high browsing on pine, and low browsing intensity on both birch species compared to the other 4 areas.

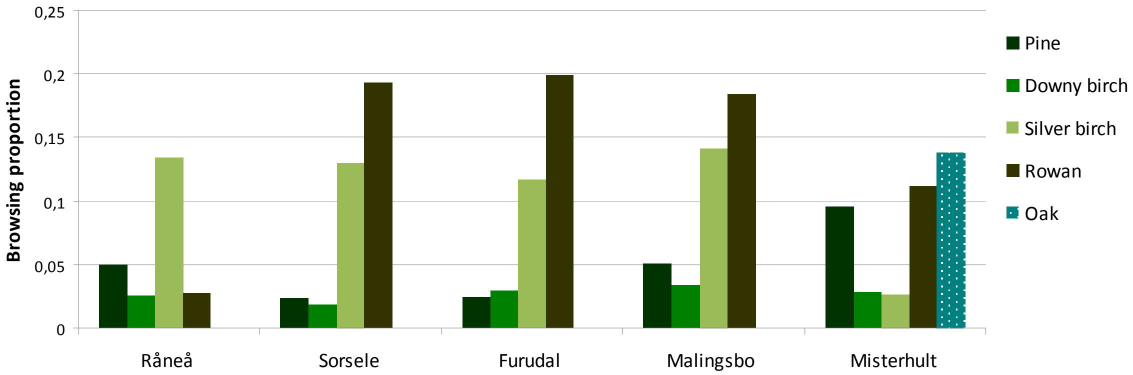


Figure 3: Average browsing intensity of different species from 2008

The majority of browsing intensity for all 4 species is below 20% with a high frequency of zero values (Figure 3-4). Only rowan and silver birch had 100% browsed available shoots in some places.

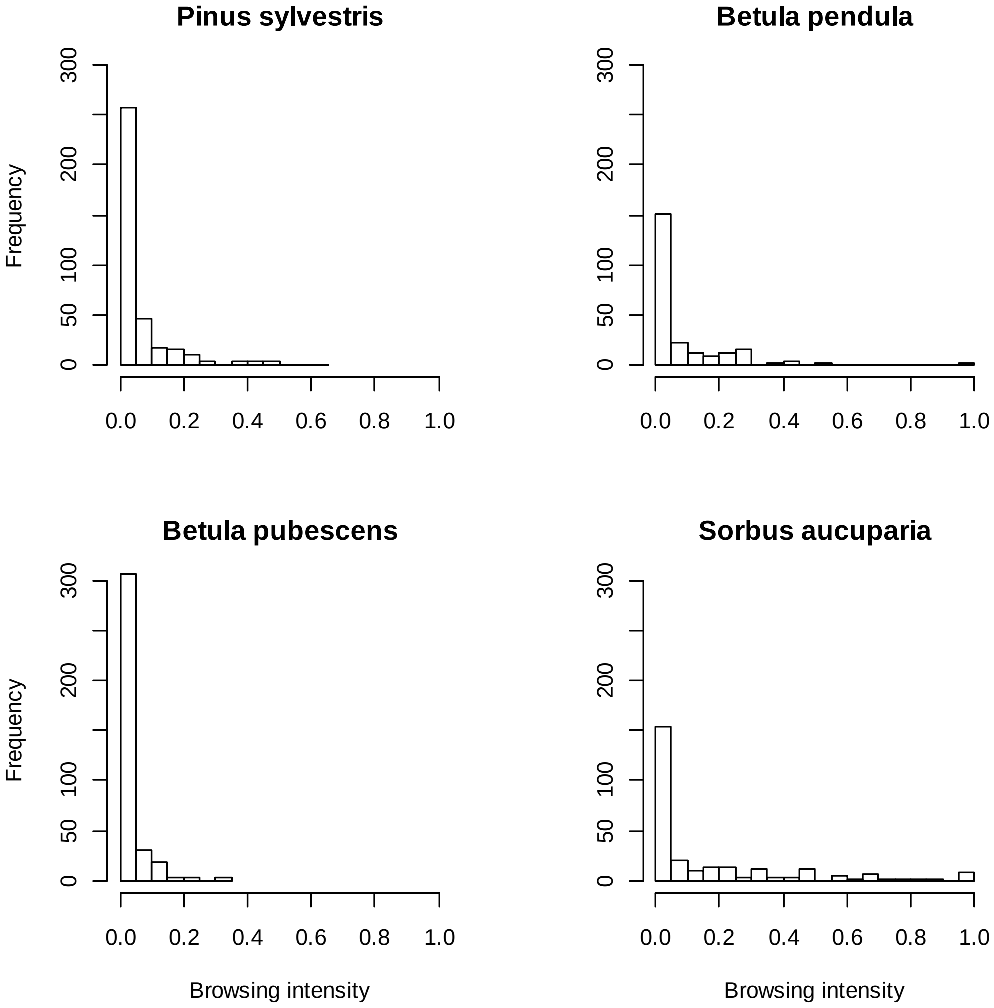


Figure 4: Data distribution of browsing intensity per species

In total 372 habitats remained as complete and sampled tracts. Not all of these habitats contain all 4 species. 361 habitats contained 1 or more pine trees, downy birch, silver birch, rowan and oak occur in respectively 366, 240, 271 and 67 habitats. Because oak is restricted to Misterhult the browsing intensity of this species is not included in further analysis. Based on the correlation matrix (Appendix Table 1) the variables height and total volume are excluded from the modelling because of there high correlation (>0.6) with biomass, spruce volume and pine volume. The differences between areas for the remaining habitat neighbourhood variables are displayed in Figure 5.

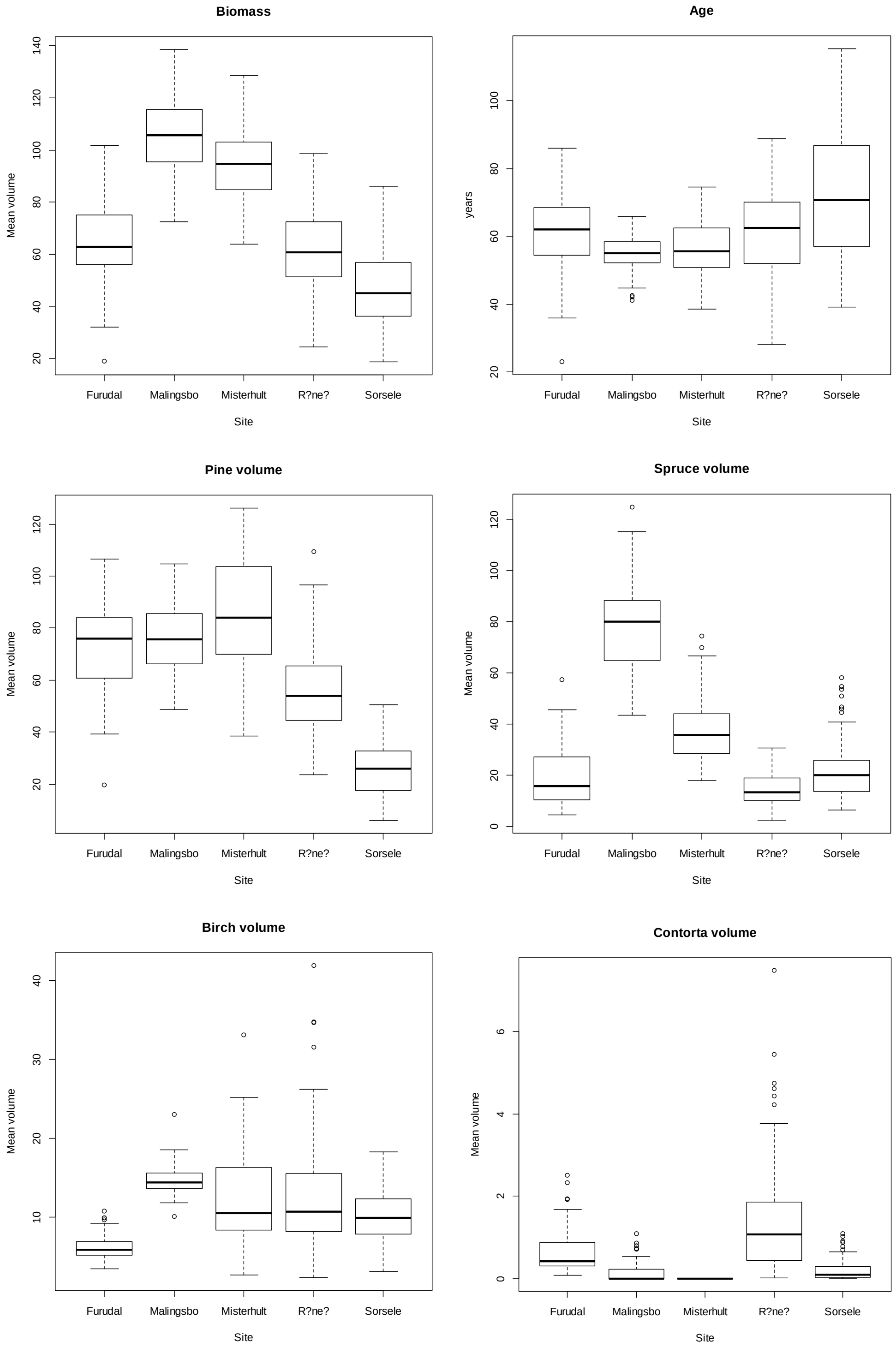


Figure 5: Data distribution of habitat neighbourhood variables (included in models). With median, shoulders representing upper 75th percentile and 25th percentile, and whiskers showing the min and max y excluding outliers (dots).

Neighbourhood models

Table 2 Model summaries for all four focal species in the year 2008

Focal Species	Model*	Dropped variable	Df	AIC	ΔAIC	Pr(>Chisq)
Pine	0	None	9	55,994		
n (obs.) = 361	1	Count	8	54,012	1,982	0,8934
	2	BirchVol	7	52,027	3,967	0,9039
	3	ContortaVol	6	50,983	5,011	0,3281
	4	PineVol	5	50,662	5,332	0,1951
	5	SpruceVol	4	49,053	6,941	0,5316
	6	Age	3	48,994	7	0,1636
Rowan	0	None	9	129,82		
n (obs.) = 271	1	ContortaVol	8	127,92	1,9	0,7591
	2	BirchVol	7	126,19	3,63	0,6023
	3	PineVol	6	124,36	5,46	0,6793
	4	Age	5	122,63	7,19	0,6009
	5	SpruceVol	4	121,06	8,76	0,5121
	6	Biomass	3	119,25	10,57	0,6645
Downy birch	0	None	9	41,58		
n (obs.) = 366	1	ContortaVol	8	39,661	1,919	0,7754
	2	BirchVol	7	37,705	3,875	0,8339
	3	PineVol	6	35,782	5,798	0,7821
	4	SpruceVol	5	33,814	7,766	0,8566
	5	Biomass	4	31,850	9,730	0,8504
	6	Count	3	30,105	11,475	0,6137
Silver birch	0	None	9	70,134		
n (obs.) = 240	1	ContortaVol	8	68,177	1,957	0,8363
	2	Count	7	66,478	3,656	0,5835
	3	Age	6	66,142	3,992	0,197

*** Full model, Fixed term: BrowsingIntensity08 ~PineVolume +SpruceVolume+BirchVolume +Age+Biomass+ContortaVolume+CountFocalsp, Random term: (1|Site)**

Stepwise deletion resulted for 3 out of the 4 species in exclusion of all variables. Stepwise deletion in the 4th model (silver birch) resulted in least significant value for the intercept. Thus, the variables I tested in this analysis do not significantly contribute to the understanding of the variation in the dependent variable browsing intensity. Looking at the ΔAIC values there is weak indication of improving models because no model was improved by more than 2 ΔAIC (Richards 2005). Variable age and biomass are among the later variables to be removed. With silver birch I stopped the stepwise deletion because the weakest significant variable was the intercept.

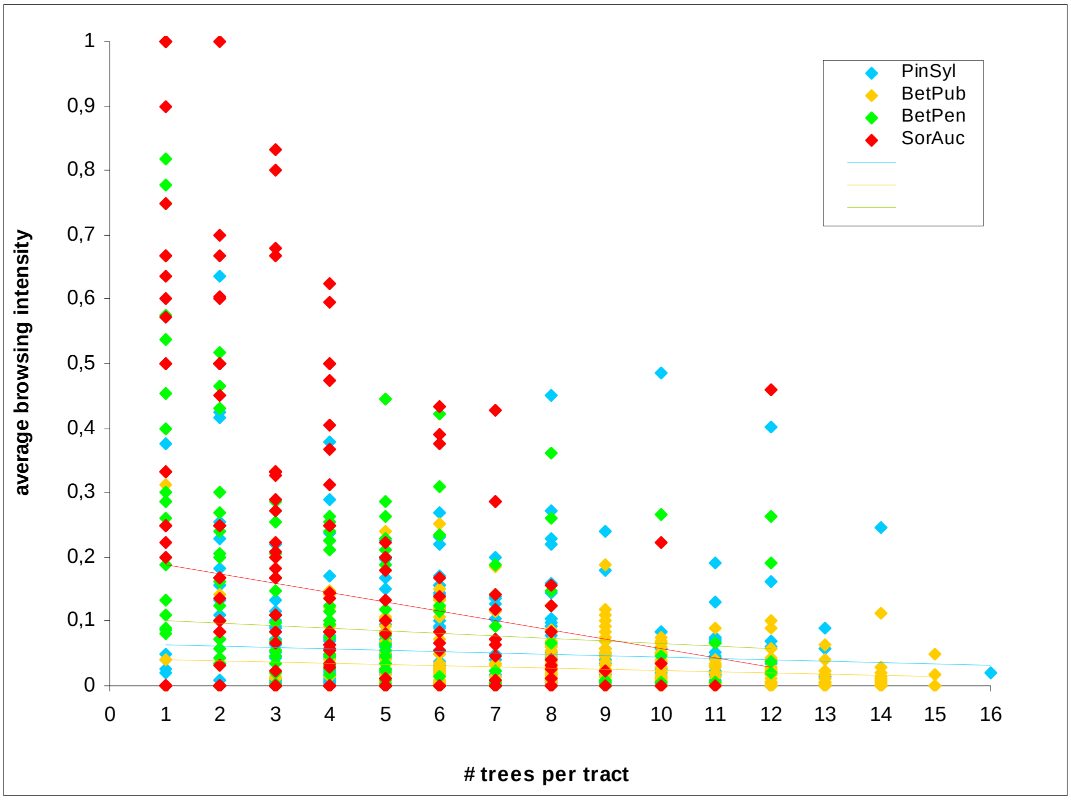


Figure 6: Average browsing intensity and number of trees per tract.

Browsing intensity is based on an average of different number of trees per tract because not all tracts contained 16 trees of each species (Figure 6). In fact only one tract contained 16 pine trees. From Figure 6 it is visible that there is a preference ranking. Rowan and silver birch are the highest and pine is higher than downy birch.

Tree scale

Descriptive statistics

A total of 500 focal trees with neighbourhood were measured with 175 browsed and 325 unbrowsed focal trees and an average of 15 ± 12 (mean ± SD) trees in the neighbourhood. From the 100 focal trees per species, 49 silver birch, 36 downy birch, 70 Rowan, 14 pine and 6 spruce were browsed. The area of the clear cuts varied, however all sites were sampled equally with a sum of 353.43 m^2 from all the neighbourhoods resulting in a total measured surface of 0.353429 ha (Table 3). Figure 8 shows the distribution of the 5 focal species and the 4 other species occurring in the neighbourhood. The most dominant species over all the measured sites was downy birch (40%) followed by the both coniferous species pine and spruce (resp 17% , 17%). Clear cut sites in Järnäs differed in sapling/tree density and species distribution (Table 3, Figure 9).

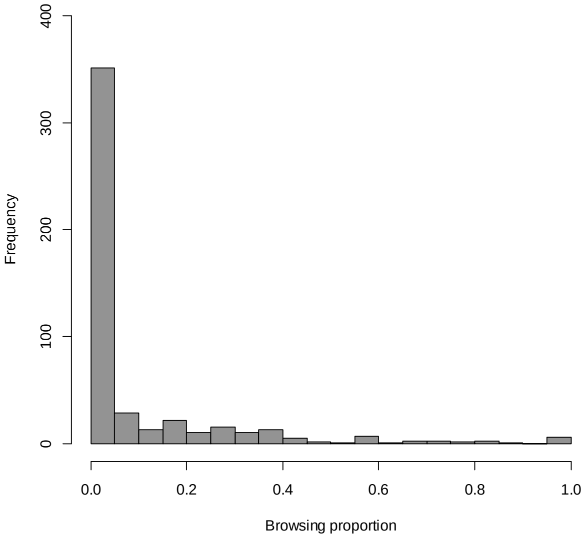


Figure 7: Frequency of proportion browsed.

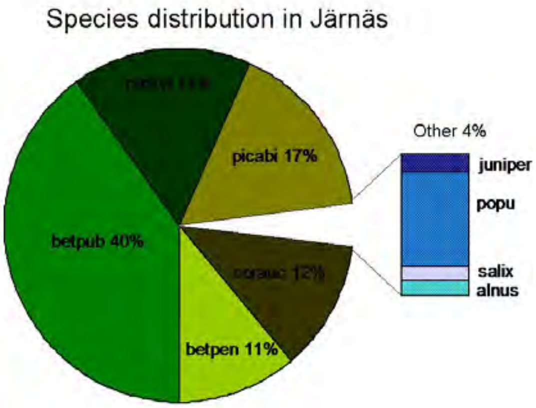


Figure 8 Average distribution of tree species in shoots of focal saplings the study area of Jarnas. Focal species and asubset of the other occurring species (others).

The browsed proportion of focal trees (Figure 7) had a high frequency of zero values and a binomial distribution was assumed. However, 100% browsed available shoots also occurred.

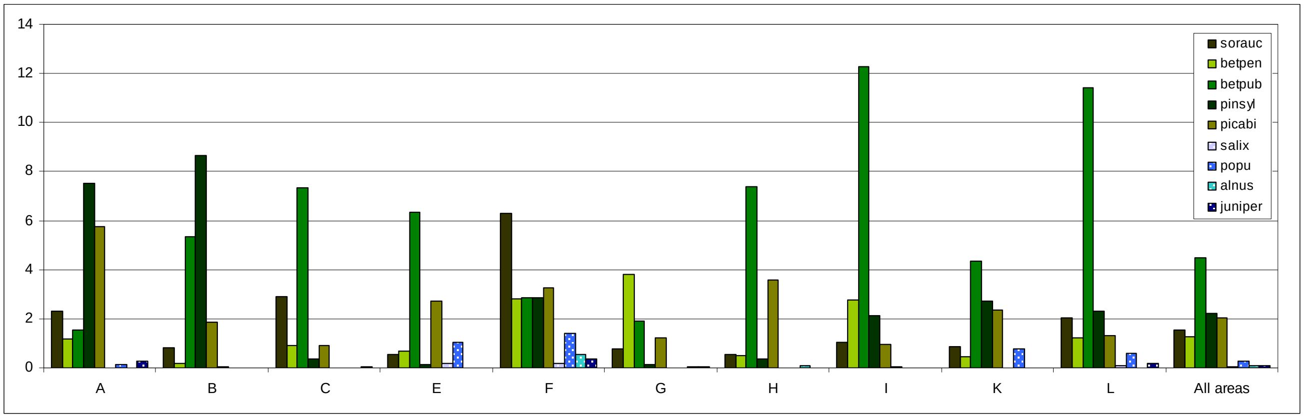


Figure 9: Number of neighbourhood trees per species in the different clear cut sites

Category “All areas” represents an average of sites A-L.

There is a big difference in dung counts of moose with the highest count of 13 in the area with the highest proportion of rowan and the highest mean tree height of 103 ±54 cm (mean ± SD). Based on the dung count, all areas where visited by both moose and deer species. The site with the highest total large herbivore dung count was the youngest clear cut with the second highest rowan proportion and low coniferous densities.

Table 3 : Characteristics of clear-cut sites

sapling height	SD	42	47	14	17	54	31	33	23	42	33
	Mean height (cm)	80	99	42	42	103	61	57	55	76	79
sapling species proportion	Alder	0.0	0.0	0.0	0.0	2.8	0.4	0.7	0.0	0.0	0.1
	Willow	0.0	0.3	0.1	1.4	0.9	0.0	0.1	0.2	0.0	0.5
	Aspen	0.7	0.0	0.0	8.3	6.3	0.0	0.0	0.0	6.8	3.1
	Juniper	1.5	0.0	0.3	0.0	1.8	0.4	0.0	0.0	0.0	0.9
	Spruce	30.2	11.1	8.2	23.1	15.9	15.7	28.0	5.6	20.3	6.8
	Pine	40.1	49.8	4.0	2.5	14.2	3.5	4.0	11.5	23.6	12.1
	Downy birch	8.8	31.1	56.0	52.1	14.1	23.2	56.1	61.7	37.6	59.5
	Silver birch	6.5	2.0	8.3	6.8	13.9	44.2	5.3	14.7	4.0	6.5
	Rowan	11.9	5.7	23.0	5.7	30.1	11.5	5.6	6.2	7.6	10.5
Density (trees/ m^2)		2.7	2.6	1.9	1.8	3.1	1.3	1.9	2.9	1.6	2.7
Dung	Rodent	5	0	20	6	14	38	14	34	12	9
	Deer sp	35	9	65	29	38	40	54	48	24	18
	Moose	2	5	5	5	13	2	5	1	7	8
Size (m^2)		6984	38666	16407	19899	21206	66739	30348	20406	43605	60231
Clearing Year		2005	2003	2009	2008	2005	2008	2008	2006	2005	2004
Site		A	B	C	E	F	G	H	I	K	L

Density is calculated per total sampled area of 353.43 m^2 for all trees measured (both focal and neighbouring)

Focal tree Palatability ranking

Browsing differed significantly (Tukey test, p <0.001) among focal species. This ranking is used for further analyses and modelling of neighbourhood quality. The ranking I found based on the browsing difference in Järnäs is different for the intermediate species, but out of the 5 focal species rowan is still the most palatable and spruce is least preferred.

Table 4: Pair-wise difference test on focal species (Multiple Comparisons of Means Tukey Contrasts)

Linear Hypotheses:	Coefficient	Standard Error	Z value	P value
betpub - betpen == 0	**-0.767**	0.093	-8.263	< 0.0001
picabi - betpen == 0	**-4.035**	0.209	-19.329	< 0.0001
pinsyl - betpen == 0	**-1.403**	0.127	-11.091	< 0.0001
sorauc - betpen == 0	**1.359**	0.087	15.626	< 0.0001
picabi - betpub == 0	**-3.268**	0.213	-15.309	< 0.0001
pinsyl - betpub == 0	**-0.636**	0.134	-4.733	< 0.0001
sorauc - betpub == 0	**2.126**	0.098	21.773	< 0.0001
pinsyl - picabi == 0	**2.632**	0.230	11.453	< 0.0001
sorauc - picabi == 0	**5.394**	0.211	25.594	< 0.0001
sorauc - pinsyl == 0	**2.762**	0.130	21.324	< 0.0001

General Linear Hypotheses were tested simultaneously, adjusted p values by single-step method. Coefficients are presented at model scale (logit-link) and significant coefficients are in bold font.

Table 5: Ranking (for models) based on posthoc

without height		Palatability scale	
Species	Δcoef	Jarnas	Literature
Rowan	-	H	H
Silver birch	1.3	M	M
Downy birch	0.8	M	L
Pine	0.6	M	M
Spruce	2.6	L	L

Including the interaction of the focal tree height in the browsing model improved the model AIC value considerably (see Table 6). In general height has a negative effect on proportion browsed shoots, but this effect was different between species. Spruce (Figure 10b) shows a strong increase in browsing at low heights while this effect of height was less strong for the other species.

Table 6: Akaike information criterion (AIC) for focal tree variables

Model	df	AIC	ΔAIC	Pr(>Chisq)
Fixed term: Proportion browsed ~ Species * **Height**	11	2000.9	0.0	< 0.0001
Fixed term: Proportion browsed ~ Species + **Height**	7	2094.5	94.5	<0.0001
Fixed term: Proportion browsed ~ Species	6	2114.9	114	

Including the Random effect (1|Area)

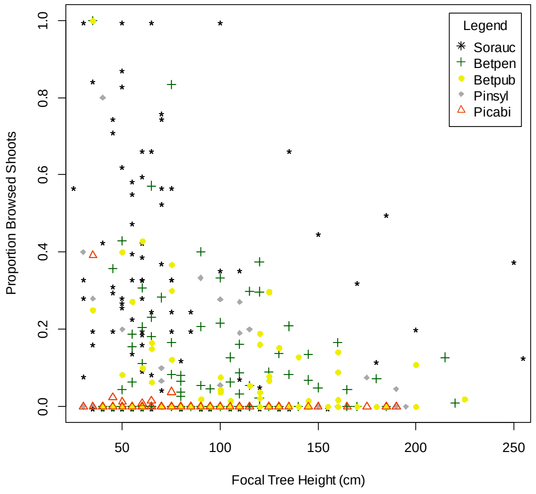


Figure 10a: Proportion browsed shoots for the 5 species at different heights

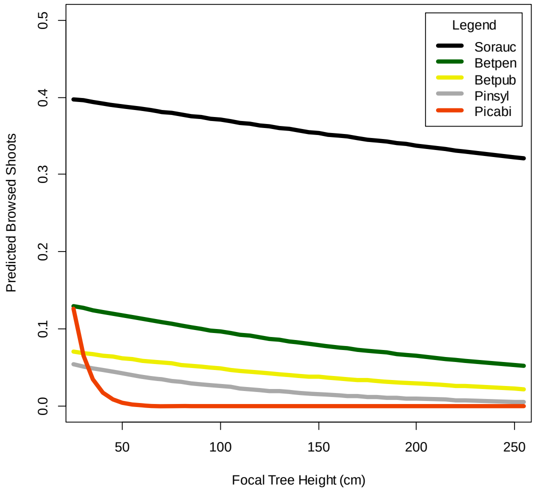


Figure 10b: Predicted browsing curves based on GLMMs of Focal Species and Height

Neighbourhood quality

The most occurring neighbourhood qualities are between 3 and 5 and can be considered middle quality. High and low quality are less frequent. A fourth category can be included, no neighbours where quality is zero.

Table 7: palatability weights for neighbourhood trees

Species	Palatibility weight*	Species	Palatibility weight
Rowan	6.3	Willow**	5.7
Silver birch	5.0	Aspen**	5.3
Downy birch	4.2	Alder**	4.6
Pine	3.6	Juniper**	2.3
Spruce	1.0		

***Weights represent multiplication values based on posthoc coefficient differences from Table 4.**

**** These species were not included in the ranking analysis and the weights are therefore based on literature (Shipley et al. 1998, Hörnberg 2001).**

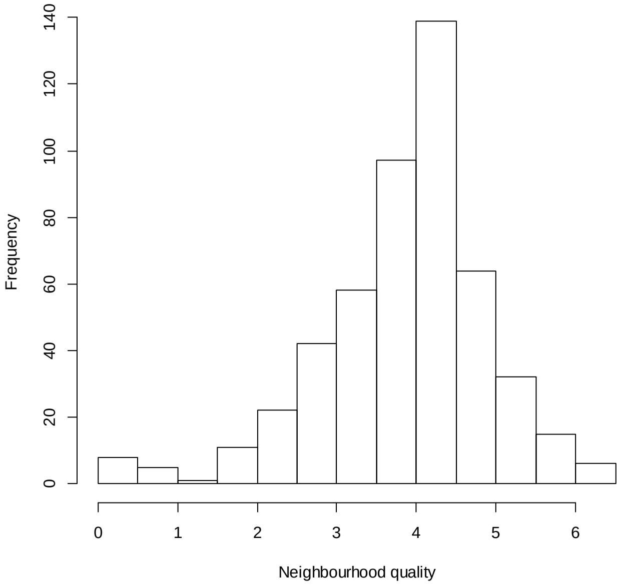
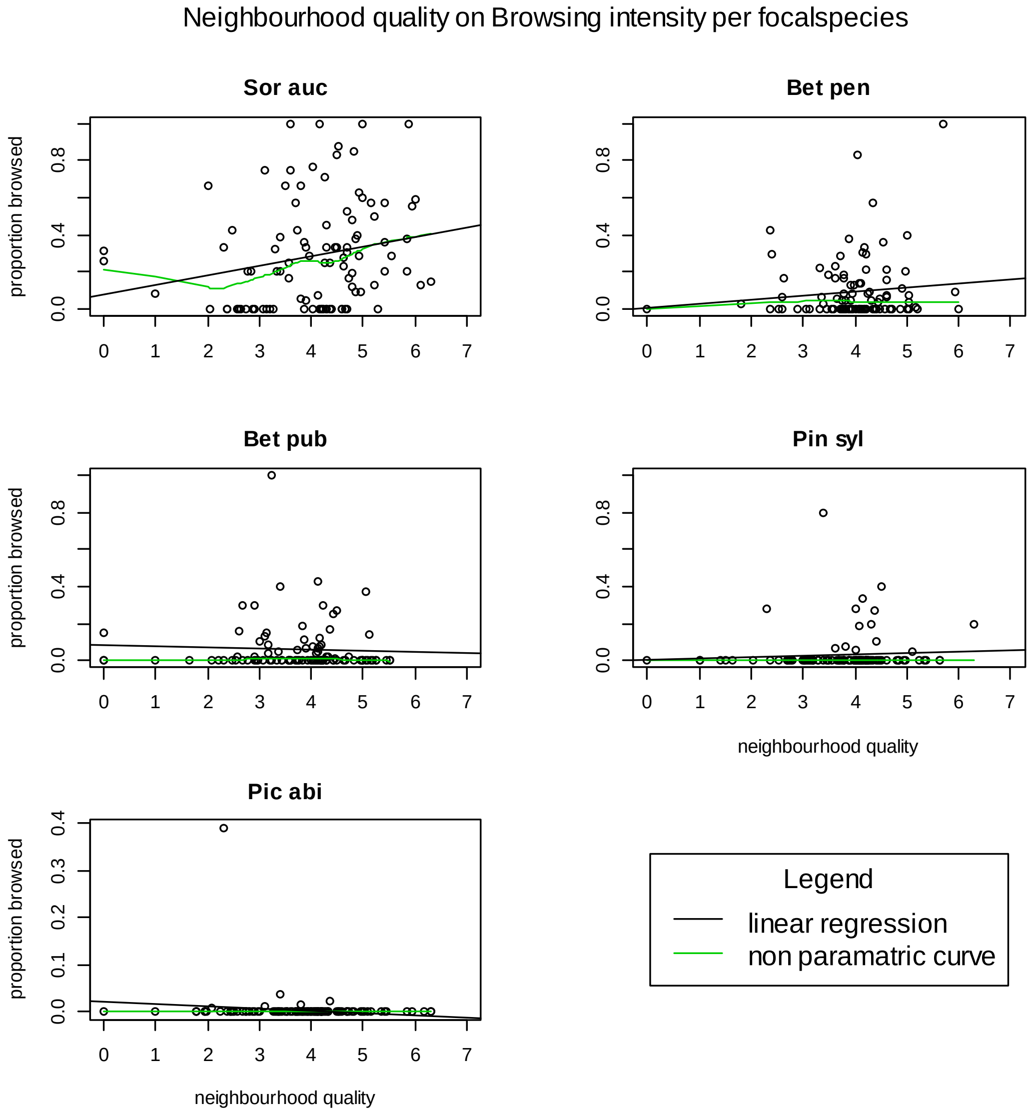


Figure 11: Neighbourhood quality distribution

The effect of neighbourhood was strongest with rowan (Figure 12) Browsing intensity is lower in low quality neighbourhoods. Silver birch browsing intensity showed a similar interaction with the neighbourhood quality although weaker. Spruce showed a very weak trend for increased browsing intensity in lower quality neighbourhoods.


Neighbourhood quality on Browsing intensity per focalspecies

Sor auc

Bet pen

Bet pub

Pin syl

Pic abi

Figure 12: effect of neighbourhood quality 0-7 (resp. low to high) on proportion of browse on focal tree per species. 0 represents focal trees without neighbourhood trees.

Neighbourhood modelling

Only the variables downy birch and number of neighbourhood trees had a higher correlation than 0.6 (Appendix Table 2). However the other focal tree species do not correlate therefore I decided to still include species and number of neighbourhood trees in the modelling.

Table 8 Akaike information criterion (AIC) for neighbourhood variables.

Fixed term: Proportion browsed ~ Species Model variables	df	AIC	ΔAIC
Species * FHeight + NeighbTrees	12	**2002.6**	0.0
Species * NeighbTrees	11	2122.9	120.3
Species * Fheight + H+L	13	**1999.4**	0.0
Species * Fheight + H	12	1999.8	0.4
Species * Fheight + H+M+L	14	2001.3	1.9
Species * Fheight + Coniferous + AvrNeighbHeight	13	**1947.3**	0.0
Species * Fheight + Coniferous + NeighbTrees	13	1994.6	47.3
Species * Fheight + Coniferous+ Deciduous+NeighbTrees	14	1996.6	49.3
Species * Fheight + NeighbQuality+AvrNeighbHeight	13	**1926.6**	0.0
Species * Fheight + NeighbQuality	12	2002.8	76.2

Random: (1|Area)
(H (height) = P_sorauc+P_popu+P_salix; M (middle) = P_betpub+P_betpen+P_alnus+P_pinsyl; and L(low) P_picabi+P_juniper)

The model with the lowest AIC values includes height of focal, height of neighbourhood trees and neighbourhood species. The later is integrated as the neighbourhood quality values given to the neighbourhoods. Not only palatability is thus of importance but these models also show that height explains part of the difference in browsing intensity.

Discussion

Browsing preference ranking

Browsing proportion and preference differed among species and there was a high variation in preference ranking among sites. This shift seems to follow the latitudinal vegetation gradient with an extreme shift in palatability ranking in the hemi-boreal vegetation zone. In the most southern site Misterhult, oak had the highest browsing intensity followed by rowan. Rowan was a highly preferred species in all study areas including Misterhult where due to the presence of oak it was the second highest. A shift in preference that is not related to addition of a species appears in the far north of Sweden in the study area Råneå where rowan is clearly preferred less. A similar shift occurs in pine and birch preference. In the north of Sweden there is an apparent preference for silver birch which has a significantly higher browsing intensity (Tukey test, $P < 0{,}001$) than downy birch in Järnäs. Also in the habitat scale it is visible that in the middle and northern boreal vegetation silver birch is browsed more intense than downy birch. In Misterhult this preference shifts to a lower browsing intensity for both birch species with a slightly higher browsing intensity for downy birch. Spruce was not included in the measurements on habitat scale but, in Järnäs, spruce was the least preferred species and browsing intensity was strongly influenced by the height of the focal tree.

Neighbourhood effects

I observed a clear difference in influence of neighbourhood between the two study scales. The neighbourhood variables I tested at habitat scale failed to explain variation in browsing intensity. However, during the stepwise deletion process tree species showed the weakest significance and the quantitative based variables as biomass, count and age were last to be removed. This suggests at habitat scale, the availability of browse might play a stronger role than palatability and quality of browse. At the tree scale, neighbourhood quality and average height of neighbourhood trees did explain variation in the browsing intensity. The neighbourhood quality has the strongest effect on the most palatable species rowan and showed an increased browsing intensity with increasing neighbourhood quality. This suggests that for very palatable species it is more beneficial to be surrounded by less palatable species supporting associational defence. Both pine and silver birch, which are palatable species show a weaker but similar effect. In conclusion, for palatable species it is beneficial to be surrounded by less palatable neighbours, but this effect is stronger for more palatable focal tree species. For the relatively unpalatable species spruce the opposite trend seems to occur. Spruce was browsed more strongly in neighbourhoods with low quality or no neighbours at all. For a non palatable species it can be considered to be beneficial to be compared to a higher palatable neighbourhood because it could lead to a contrasting defence mechanism. The results from spruce support that neighbour contrast defence can explain the effect of the contrasting better neighbourhood decreasing browsing intensity.

As predicted (Figure 1), the degree of palatability of the focal tree seems to determine the importance of the neighbourhood palatability in browsing intensity. This also results in different associational effects for different levels of palatability.

Shifts in palatability ranking

The strong ranking in palatability and preference found in this study is not supported by all studies. For example Bergström and Hjeljord (1987) gives a different palatability preference ranking namely: rowan, willow, aspen, juniper, birch, pine, alder, spruce (resp high-low). I chose not to give juniper such a high ranking because during my data collection juniper was often still covered with snow (<30 cm) and I never found it browsed. Grouping birch species occurs in more studies (Hörnberg 2001, Wam and Hjeljord 2010). However from this study and other studies it is clear that by grouping these species valuable information about preference is lost (Shipley et al. 1998). Furthermore, my ranking is based on browsing intensity observed from the field. There is however an effect due to combination of abundance and palatability (Bergström and Hjeljord 1987, Shipley et al. 1998) that can make pine and birch the most browsed species like in the study of Bergström and Hjeljord (1987). Browsing intensity at tree scale is based on equal numbers of focal trees per species. Influence of abundance of species is accounted for by means of neighbourhood, in fact the chance of being browsed depending on abundance of similar and other species is what I was interested in.

In Sweden (Hörnberg 2001) and Norway (Wam and Hjeljord 2010) studies show the difference in preference along the latitudinal gradient. In my study, differences between browsing intensity on the focal species were detected within each study area, but also between study areas. Along the latitudinal gradient a shift between species preference was visible. This difference can be due to difference in tree species composition in the forest as well as difference in herbivore abundance and occurrence which can lead to shifts in niche and or competition (Bergström and Hjeljord 1987, Shipley et al. 1998). The study of Hörnberg (2001) shows similar shifts between species which could be connected to availability of species but also a difference in herbivore species. In this study there was no differentiation between browsing of moose or one of the deer species and the large herbivores do not occur in the same species compositions and abundance between the areas. It is known that herbivore species have different preferences (e.g. Hörnberg 2001, Storms et al. 2008) and dung count alone is not enough to determine the species of the actual browser on a given tree. DNA analysis on saliva found on browsed shoots can help to differentiate between browsing preference for species and height among the different herbivore species (Nichols et al. 2012).

Importance of neighbourhood effects

In this study I tested the neighbourhood quality effects in a natural gradient, whereas previous studies applied mainly experimental designs, controlling for neighbourhood quality (Bergvall et al. 2006, Rautio et al. 2008). Therefore, the most frequent neighbourhood value in my study sites was of middle quality and results are therefore not based on extreme unpalatable or palatable neighbourhoods. However one can wonder if testing these extreme neighbourhoods is reasonable if in reality these scenarios are very infrequent. However additional experimental neighbourhoods with extreme low or high quality can contribute to a stronger visible effect and for complete testing of the associational theories and this would be a recommended addition to future studies. Rowan and downy birch have high browsing intensities at the zero quality values compared to the relative trend. Zero neighbourhood quality represents neighbourhoods with only the focal tree and no neighbours since the minimum value for a tree in the neighbourhood was 1. This suggests a third category, next to the palatable and non palatable neighbourhoods, of a non/low biomass neighbourhood. Therefore, solitary focal trees should be separated from the palatable and unpalatable neighbourhoods (Rautio et al. 2012).

The results of this study suggested associational defence in the case of rowan (palatable species) and contrast defence for spruce (unpalatable species) in the natural gradient. Rautio et al. (2008) found associational susceptibility to be the defence mechanism explaining browsing intensity of fallow deer. In fact, susceptibility and defence are closely related in the sense that with opposite palatability but similar trends these terms are interchangeable. Meaning that, with the experimental research of Rautio et al. (2008) a stronger contrast for neighbourhood qualities was possible. Bergvall et al. (2006) on the other hand, found that deer were unselective between patches but selective within patches indicating neighbourhood contrast susceptibility as a defence. This corresponds with my results on the effects of neighbourhood quality on spruce browsing as an attractant decoy defence. Research that focused more on the combination of unpalatable neighbours and physical protection by neighbours (Smit et al. 2006, 2011) indicate associational resistance. In this study however, the importance of physical structures was not examined.

Possible pitfalls in data collection

It is difficult to compare the two studies (the 1km2 vs. the 1.5m radius patch scale) in this report not just because of the scale. Although the browsing data is collected at similar ways for the neighbourhood quality variables at habitat scale I was dependent on digital data sources. These sources are not measured at the same time as browsing actually occurred and due to averaging and different accuracy scales I was dealing with estimations of neighbourhoods at habitat scale versus individual trees at the small scale.

At the tree scale, neighbourhood was a fixed diameter regardless of the size and shape of the patch. Size and density of a browse patch can also influence the time spend foraging within the area (Shipley and Spalinger 1995). I regard this effect as rather small in my study because of the structural cultivation characteristics in the clear cuts. In this study height was a significant factor in browsing intensity. Species like moose might benefit from the protection higher trees might bring. Excluded study sites, due of the upper age restriction, still showed moose browsing (personal observations). Omitting clear cuts of older age, by selecting on tree height and not stand age, could therefore help to expand to the optimal range for testing neighbourhood effect on browsing intensity. Finally, I suggest including previous years of browsing as a value in neighbourhood quality. If herbivores browse a tree it influences this individuals browsing intensity for the following years (Danell et al. 1994).

In conclusion, my analysis revealed that neighbourhood effects differed among foraging scales and tree species and were influenced by the palatability of the focal trees. Due to a shift in palatability ranking along the latitudinal gradient, the strength of the neighbourhood effect differed not only among species but also with the vegetation zone.

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Appendix I

Appendix Table 1: Spearman correlation matrix of habitat scale factors.

	PineVol	SpruceVol	BirchVol	Height	Age	BiomassVol	ContVol	TotalVol
PineVol	x							
SpruceVol	0.34	x						
BirchVol	-0.11	0.43	x					
Height	**0.79**	**0.72**	0.35	x				
Age	0.05	-0.07	0.02	0.25	x			
BiomassVol	**0.74**	**0.83**	0.41	**0.96**	0.06	x		
ContVol	-0.17	-0.23	0.46	-0.15	0.03	-0.14	x	
TotalVol	**0.79**	**0.83**	0.33	**0.94**	-0.02	**0.99**	-0.18	x

Appendix Table 2: Spearman correlation matrix of tree scale factors.

	FHeight	NeighbTrees	alnus	betpen	betpub	juniper	picabi	pinsyl	popu	salix	sorauc	AvrHeight
FHeight	x											
NeighbTrees	0.17	x										
alnus	0.09	0.07	x									
betpen	0.03	0.45	0.09	x								
betpub	-0.03	**0.69**	-0.02	0.25	x							
juniper	0.18	0.02	-0.02	-0.04	-0.10	x						
picabi	0.06	0.43	0.15	0.05	-0.02	0.03	x					
pinsyl	0.21	0.43	-0.05	-0.02	-0.05	0.08	0.22	x				
popu	0.13	0.17	-0.03	0.02	0.01	0.03	0.03	-0.07	x			
salix	-0.02	0.10	0.22	0.01	0.06	-0.03	0.03	-0.02	0.02	x		
sorauc	0.14	0.22	-0.05	0.01	-0.10	0.04	-0.01	-0.04	0.07	0.05	x	
AvrHeight	0.54	0.16	0.18	0.00	-0.07	0.05	0.10	0.23	0.13	0.03	0.13	x

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