

## Effects of tree species richness and composition on moose winter browsing damage and foraging selectivity: an experimental study

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### Summary

1. The optimal foraging theory, the nutrient balance hypothesis, and the plant association theories predict that foraging decisions and resulting tree damage by large mammalian browsers may be influenced by the species richness and species composition of forest stands. This may lead to either associational susceptibility (increased damage on a focal plant in a mixed stand) or associational resistance (reduced damage in a mixed stand).

2. Better understanding of the mechanisms and the relative importance of tree species richness and composition effects on foraging by mammalian browsers is needed to support sustainable management of forests and mammal populations. However, existing knowledge of forest diversity effects on foraging by large mammalian browsers comes largely from observational studies while experimental evidence is limited.

3. We analysed winter browsing by moose (*Alces alces* L.) in a long-term, large-scale experiment in Finland, which represents a tree species richness gradient from monocultures to 2-, 3- and 5-species mixtures composed of Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L.), Siberian larch (*Larix sibirica* Ledeb.), silver birch (*Betula pendula* Roth.) and black alder (*Alnus glutinosa* L.).

4. The intensity of browsing per plot increased with tree species richness while browsing selectivity decreased with tree species being targeted more equally in species-rich mixtures. Tree species composition of a plot was also an important determinant of intensity of browsing. The greatest browsing occurred in plots containing preferred species (pine and birch) while intermediate preference species (larch and alder) experienced associational susceptibility when growing with pine and birch compared with their monocultures or mixtures without pine and birch. In contrast, we found no evidence of associational resistance; the presence of a least preferred species (spruce) in a mixture had no significant effect on moose browsing on other tree species.

5. We demonstrate that the presence of alternative forage species allows moose to spend longer opportunistically foraging in a plot, resulting in increased level of damage in species-rich stands and stands containing preferred tree species. Our results highlight the limitations of the optimal foraging theory in predicting browsing patterns and demonstrate the importance of associational effects within mixed stands.

**Key-words:** Associational susceptibility, boreal forests, foraging theories, forest diversity, forest experiment, mammalian herbivore, plant associations, plant–animal interactions, resource selection

### Introduction

Plant–animal interactions and herbivore foraging decisions are thought to be shaped by abundance and distribution

of host plants within the landscape (WallisDeVries 1996; Searle, Hobbs & Shipley 2005). Traditionally, herbivory has been viewed as a direct interaction between an individual host plant species and their herbivores (Feeny 1976) with the focus on the quality of the host plant itself, its physical and chemical defences and relative palatability to the herbivore. However, most large mammalian

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herbivores are generalists feeding on several plant species, and there is increasing evidence that their foraging decisions and the degree of resulting plant damage may be influenced not just by quality of the individual host plants but also by the quality, species richness, spatial arrangement and relative abundance of other plants in a community (Atsatt & O'Dowd 1976; Holt & Kotler 1987; Palmer *et al.* 2003; Baraza, Zamora & Hódar 2006; Barbosa *et al.* 2009). The optimal foraging theory, the nutrient balance hypothesis and the plant association theories suggest several mechanisms linking herbivory to plant species richness and composition.

According to the optimal foraging theory (Stephens & Krebs 1986) and the Marginal Value Theorem (MVT) (Charnov 1976), the browsing herbivore should spend longer (and hence consume more resources) in areas of high forage quality to maximize its instantaneous rate of intake. Forage quality, in turn, may be influenced by both plant species richness and species composition of the patch, and patches which are more likely to contain the preferred plant species (species-rich) and/or contain higher proportions of these species should be perceived by mammalian herbivores as high quality. The optimal foraging theory assumes that each plant species has a predetermined value to the foraging herbivore, and that these preferences do not change during a foraging bout. There is mixed and largely qualitative support for this assumption (Vivås & Sæther 1987). The limitations of optimal foraging for predicting foraging by generalist mammalian herbivores have been previously highlighted, including inability to account for hierarchy of foraging decisions (Senft *et al.* 1987) and restrictive assumptions of patch use (Searle, Hobbs & Shipley 2005).

The nutrient balance hypothesis (Westoby 1978) predicts that species-rich plant stands will be preferred by a foraging herbivore such as moose due to the importance of achieving balanced nutrient intake (Edenius, Ericsson & Näslund 2002). Foraging in species-rich stands offers the benefit of diet mixing, allowing greater and complementary intake of nutrients (Wang *et al.* 2010b), as well as buffering against the accumulation of a particular source of digestion-inhibiting or toxic secondary metabolites. Therefore, the availability of multiple plant species growing together leads to reduction in intake of individual plant secondary metabolites (PSMs). Variation in selection of resources at scales from the plant part to habitats may reflect behavioural responses to variation in PSMs (Iason & Villalba 2006). Moreover, plant species richness and composition may be particularly important in influencing this foraging response of browsers in winter when food quality is poor, and costs of travelling to new patches are high due to snow cover (Lundmark & Ball 2008).

Plant association theories emphasize the role of plant species composition within a patch in influencing browsing behaviour, which may lead to increased susceptibility or resistance of some plant species to browsing damage

(Barbosa *et al.* 2009). The associational susceptibility occurs when lower quality plant species experience an increase in detectability and consequent damage by herbivores, for example in the presence of highly preferred species in a patch. The associational resistance describes the opposite situation when a highly preferred plant species gains protection in the presence of a lower preference plant species in a patch (Tahvanainen & Root 1972; Root 1973). Hjältén, Danell & Lundberg (1993) found evidence of associational susceptibility for intermediate preference species (birch), which received more browsing by hares and voles when growing with higher preference species (aspen and rowan), whereas no protection for high preference species was gained when in association with low preference species (alder).

Plant species richness and species composition may also affect foraging selectivity of generalist mammalian herbivores between and within patches. Generalist herbivores have a preference for the resources in their environment and select plant species disproportionately to availability; however, they also demonstrate the ability to constantly assess the foraging environment on short and long time-scales and adapt foraging behaviours (e.g. changes in selectivity) with changing forage availability and quality (Heller 1980). For example, Wang *et al.* (2010a) have shown that sheep foraging selectivity between patches was significantly reduced when the preferred species coexisted with other plant species. Therefore, both plant species richness and species identity are highly relevant to large herbivores, and individual plant quality should be considered in the context of its neighbours (Palmer *et al.* 2003). However, few studies have examined the relative importance of these plant community characteristics on foraging by mammalian browsers. In this study, we aim to investigate how tree species richness and composition affect the degree of browsing damage and foraging selectivity by moose. The majority of previous work on the effect of plant community characteristics concerning mammal herbivores has been observational or carried out using feeding trials or cut branches planted in arrangement (Danell, Edenius & Lundberg 1991; Hjältén, Danell & Lundberg 1993). Therefore, there is a need to assess the relevance of plant associations and their interactions with mammalian herbivory in more realistic (large-scale and semi-natural) experimental setups. This is particularly important for a large generalist herbivore like moose due to the hierarchical nature of its foraging (Bergman, Iason & Hester 2005), whereby the herbivore selects a foraging environment from the landscape, a foraging patch within this environment and then makes subsequent choices at the tree species and bite level (Senft *et al.* 1987).

The Satakunta forest experiment in south-western Finland offers the opportunity to study natural browsing on established trees in an experimental set up allowing direct comparison of plots with predetermined level of tree species richness and different tree species composition (Scherer-Lorenzen *et al.* 2005, 2007; Vehviläinen & Koricheva

2006). Boreal forests are typically species-poor and therefore the addition of even one more species may have a relatively large effect on plant associations and plant–animal interactions.

The moose is the largest and the most common ungulate herbivore in Finland and Scandinavia and is considered a pest in production forests where intensive browsing causes economic losses (Jalkanen 2001). Moose especially favours young successional stages of trees (Nikula, Heikkinen & Helle 2004) and the majority of browsing on economically important tree species such as Scots pine occurs in winter. Previous results from the Satakunta experiment (Vehviläinen & Koricheva 2006) showed species-rich plots to be more susceptible to damage by moose, supporting the associational susceptibility hypothesis. However, the above study was conducted at very early stages of plot development in the experiment (2- to 4-year-old trees).

In this study, we used the Satakunta experiment to test the following predictions based on the optimal foraging theory, and plant association theories:

- 1 Moose browsing will be higher in species-rich plots than in monocultures and species-poor plots, as predicted by the optimal foraging theory and the nutrient balance hypothesis;
- 2 Tree species composition will affect the degree of browsing damage at the plot level as predicted by the plant association theories. Specifically;
  - a. The presence of preferred tree species in a plot will act as an attractant and will lead to increased browsing on lesser preferred species where they grow in association,
  - b. The presence of least preferred species in a plot will lead to decreased browsing on species of higher preference,
- 3 Moose browsing selectivity for individual tree species will be lower in species-rich plots.

## Materials and methods

### EXPERIMENTAL SITE

The Satakunta experiment is located in south-western Finland and is made up of three separate 1.5–2.0 ha experimental areas (area 1, 61°42' N, 21°58' E; area 2, 61°39' N, 22°09' E; area 3, 61°40' N, 21°42' E) planted with five tree species: Scots pine (*Pinus sylvestris*, P); Norway spruce (*Picea abies*, S); non-native Siberian larch (*Larix sibirica*, L); silver birch (*Betula pendula*, B); and nitrogen-fixing black alder (*Alnus glutinosa*, A). All areas are situated in close proximity to mature coniferous stands dominated by Norway spruce. Snow cover in the Satakunta region occurs from November through to March, and is on average 20 cm deep. The region experienced a greater than average snowfall during the winter of 2010/11 with snow cover exceeding 50 cm in February–March 2011 period (Finnish meteorological institute 2011).

Each area comprises 38 plots (20 m × 20 m), which are randomly allocated to one of 19 different treatments (Data S1, Supporting Information) representing a diversity gradient from monocultures ( $n = 5$ ) to 2-species mixtures ( $n = 7$ ), 3-species mixtures ( $n = 6$ ) and a 5-species mixture (Data S2, Supporting Information). In addition to a species richness gradient, the plots are also designed to represent a gradient from purely coniferous stands, through mixtures of coniferous and deciduous species to purely deciduous stands. Each plot is replicated six times (once at each area). Within each plot, there are 13 rows containing 13 trees (total 169 trees), planted 1.5 m apart. Different tree species are present in equal proportions in mixed stands (50 : 50, 33 : 33 : 33 or 20 : 20 : 20 : 20 : 20), but tree positions within a plot are randomized to mimic natural stands.

The Satakunta experiment was planted in spring 1999 and all dead saplings were replaced in 2000. In 2001, saplings were replanted only in plots where mortality exceeded 10% and no replanting has been done since. In spring 2010, plots were cleaned from naturally regenerating woody vegetation. At the time of browsing assessment, trees were 12 years old with an average height of 4.92 m (J. Koricheva, unpublished data). Trees of this age and size are particularly vulnerable to moose browsing (Jalkanen 2001). Average tree survival per plot at area 1 in May 2011 was 72.98% ( $n = 38$ ); at area 2 61.43% ( $n = 34$ ); and at area 3 65.91% ( $n = 38$ ). Four plots at area 2 had suffered severe mortality and poor establishment as a result of moose damage and were excluded from sampling and data analysis (a LBA 3-species mixture; a BA 2-species mixture; an A monoculture; and an L monoculture). Despite tree mortality, the remaining 110 plots retained the intended tree species richness and composition at the time of monitoring as indicated by the average evenness (E) values per plot, which were 0.98, 0.93 and 0.98 for areas 1, 2 and 3 respectively ( $E = H/\ln R$ , where H is Shannon–Wiener diversity index and R is species richness).

The most prevalent large mammal herbivore species in the study area is moose. For the winter of 2010/11, the moose population for the Satakunta region is estimated at 3,353 individuals, resulting in a population density of 2.75 individuals per 10 km<sup>2</sup> (Riistaweb 2012), although these numbers may vary locally and seasonally. Other cervids in the region include introduced white-tailed deer (*Odocoileus virginianus* Zimmerman) and fallow deer (*Dama dama* L.), as well as native roe deer (*Capreolus capreolus* L.). While it is difficult to distinguish the damage caused by moose from damage caused by smaller deer species (Jalkanen 2001), faecal pellet counting revealed that moose densities in our study area were much higher relative to deer densities with all other deer species faecal pellet groups accounting for only 3% of cervid pellets recorded (50 of 1635 pellet groups for the entire experiment). Damage by other mammalian herbivores such as voles and hare usually occurs at sapling stage, and is restricted to the base of the trunk and lower branches. Furthermore, feeding marks are distinct from those left by moose (Bang & Dahlström 2006). We are confident, therefore, that moose caused the vast majority of damage recorded.

### MONITORING METHOD: HERBIVORY

Moose herbivory assessment was carried out in the first two weeks of May 2011 following snowmelt and before the start of active plant growth. Browsing damage was assessed on every live tree in every plot and intensity of browsing was classified into

three predetermined categories: minor browsing (up to 25% of available twigs browsed), moderate browsing (26–75% of available twigs browsed) and severe browsing (more than 75% of available twigs browsed).

In addition to browsing damage, bark damage was also recorded when seen and was classified into three categories: minor (wounds up to 25% stem circumference and/or length of the stem), moderate (26–50% stem circumference and/or length) and severe (more than 50% stem circumference and/or length).

Moose is known to return to the same winter ranges year after year (Sweaner & Sandgren 1989) and to browse the same trees repeatedly (Bergqvist, Bergström & Edenius 2003). As moose damage remains visible for several years, we have recorded total damage, which included both recent (winter 2010/11) and older moose browsing in the Satakunta experiment, thus accounting for cumulative damage over several years. Therefore, even though the monitoring was conducted only once, our data reflect the cumulative impact of moose damage on tree stands for several years.

#### MONITORING METHOD: HABITAT USE

To assess the relative density of, and the habitat use by, mammalian herbivores across the three experimental areas, and between different plots, faecal pellet group counts were made at each plot. A faecal pellet group was considered as a group of five or more individual pellets located within one pellet distance of one another, a method previously shown to correspond with estimated moose density calculations (Harkonen & Heikkilä 1999). The number of pellet groups per plot indicates the amount of time moose spent in the plot and compares with other measures of habitat use (Månsson *et al.* 2012). Moose and deer faecal pellets were distinguished and recorded. Counts were made concurrently with herbivory sampling.

#### ANALYSIS

To obtain an estimate of the available biomass removed, the number of trees in each of the three browsing categories (minor, moderate, severe) was multiplied by the category midpoint (12.5%, 50%, 87.5% respectively), and divided by the total number of trees present per plot or species level, then the three values were summed to give an estimate of the degree of moose browsing (%MB) (Vehviläinen & Koricheva 2006). Total moose browsing (%TB) was assessed as the percentage of live trees in a plot that suffered damage regardless of the amount of twigs browsed per tree. At the species level, linear mixed models were used to compare both indices for each species along the richness gradient and to compare total browsing between species. At the plot level, both indices of damage were compared along the richness gradient and between treatments using linear mixed models. Area was selected as a random effect, and species identity, plot species richness or plot species composition as fixed factors. Polynomial contrasts were conducted to identify trends. Data were log-transformed where necessary to improve normality. All analyses were carried out in SPSS 19.0.

To investigate the degree of moose selectivity for forage within plots of different composition and diversity, an overall selectivity index (OSI) was calculated for each plot. The index assesses selectivity based on a comparison of the consumed diet and diet offered in a particular plot, with a value of 0 resulting from equal

consumption of all options offered, and a value of 1 resulting from complete selection, i.e. consumption of only one option in a mixture (Wang *et al.* 2010a). The OSI per plot was determined by the following equation:

$$OSI = \frac{\sum_{i=1}^n (q_i - p_i)^2}{\max \{1 - 2q_i + \sum_{i=1}^n q_i^2\}}$$

where  $p_i$  represents the proportions of each tree species options browsed (%TB as proportion),  $q_i$  is the proportion of each tree species present in the plot (options offered, e.g. c. 0.5 for each species in 2-species plot), and  $n$  is the number of tree species in the plot (i.e. number of options offered).

## Results

### TREE SPECIES PREFERENCE BY MOOSE

Moose preference for the tree species in the experiment was found to be pine > birch > alder > larch > spruce, and this preference was seen at all tree species richness levels (Fig. 1; Table 1). Browsing (%MB and %TB) differed significantly between the individual tree species (Species ID, Table 1), with all pairwise comparisons significant ( $P \leq 0.039$ ), apart from birch and alder ( $P = 0.184$ ).

### EFFECT OF TREE SPECIES RICHNESS ON MOOSE BROWSING

At the individual species level, tree species richness did not significantly affect %MB on any of the five tree species ( $P \geq 0.321$ ) or %TB of pine, spruce, birch or alder ( $P \geq 0.403$ ). For larch, %TB increased in more species-rich plots ( $F_{3,40} = 3.09$ ,  $P = 0.038$ ), with greater

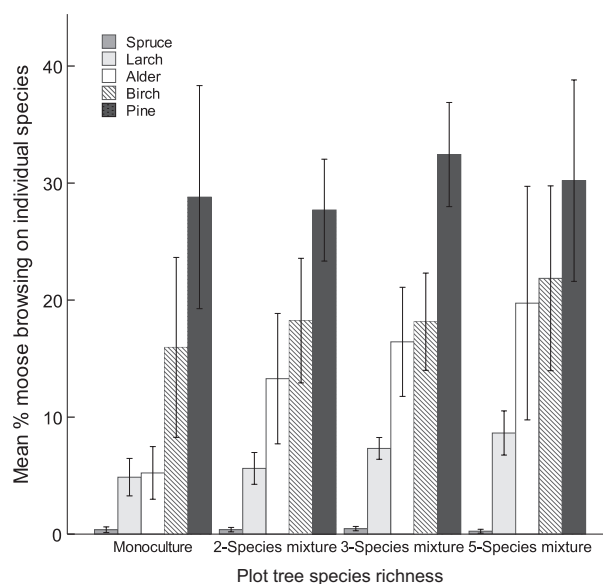


Fig. 1. The degree of moose browsing (%MB) on individual tree species in monocultures and mixed plots. Error bars are  $\pm 1$  SE.



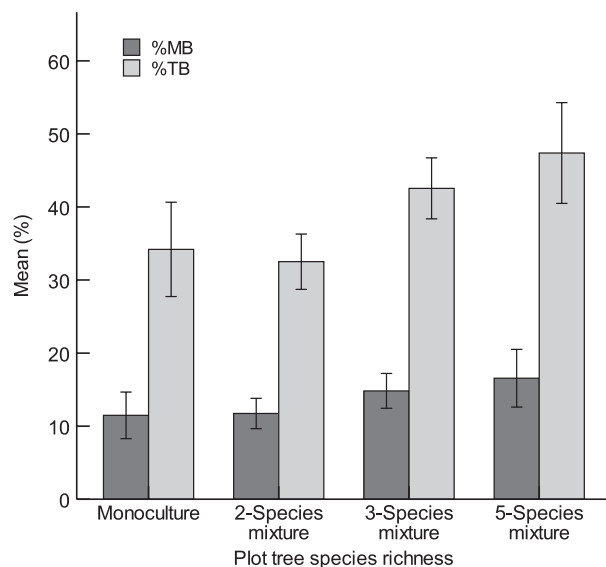
**Table 1.** Results from linear mixed models testing the effects of tree species identity, species richness and species composition on degree of moose browsing (%MB), and percentage total trees browsed (%TB).

Analysis	Variable	Factor	F(df)
<i>Species identity</i>	%MB	Species ID	19.089 <sub>(4,225-000)</sub> ***
		Richness	0.741 <sub>(3,225-000)</sub>
		SpeciesID (Richness)	0.196 <sub>(12,225-000)</sub>
	%TB	Species ID	27.978 <sub>(4,225-000)</sub> ***
		Richness	1.553 <sub>(3,225-000)</sub>
		SpeciesID (Richness)	0.245 <sub>(12,225-000)</sub>
<i>Species richness</i>	%MB (Log10)	Richness	3.438 <sub>(3,104-002)</sub> *
	%TB (Log10)	Richness	4.801 <sub>(3,104-002)</sub> **
<i>Species composition (treatment)</i>			
2-species mixture	%MB	Plot composition	4.077 <sub>(6,32-004)</sub> **
	%TB	Plot composition	7.525 <sub>(6,2-004)</sub> ***
3-species mixture	%MB	Plot composition	5.302 <sub>(5,27-006)</sub> **
	%TB	Plot composition	7.768 <sub>(5,27-006)</sub> **

\*( $P < 0.05$ ), \*\*( $P < 0.01$ ), \*\*\*( $P < 0.001$ ).

percentage of trees browsed in 3- and 5-species mixtures than in 2-species mixtures ( $P = 0.027$  and  $P = 0.011$ , respectively; LSD). In agreement with our prediction, at the plot level both %MB and %TB increased along the species richness gradient (Table 1, Fig. 2) and the relationship between browsing damage and tree species richness was linear, as indicated by significant linear contrasts ( $P \leq 0.017$ ).

Tree species richness had no significant effect on bark damage by moose (Kruskal-Wallis,  $H = 6.9$ ,  $df = 3$ ,  $P > 0.05$ ); however, there was a significant positive correlation between bark damage and browsing damage (%



**Fig. 2.** Effects of tree species richness on moose browsing (%MB and %TB) per plot. Error bars are  $\pm 1$  SE.

MB or %TB) per plot ( $r_s = 0.24$ ,  $P = 0.014$ ,  $n = 110$ ; and  $r_s = 0.22$ ,  $P = 0.021$ ,  $n = 110$  respectively).

#### EFFECT OF TREE SPECIES COMPOSITION ON MOOSE BROWSING

The effects of plot tree species composition were examined at the 2- and 3-species richness levels. We found significant differences in %MB and %TB between different 2-species mixtures and 3-species mixtures (Table 1, Fig. 3), confirming our prediction. In general, mixtures containing both pine and birch (most preferred tree species) suffered more damage than those that contained only one of the preferred species or the less preferred species (larch, alder and spruce; Table 2). In area 2, moose browsed more on birch than in areas 1 and 3, resulting in higher browsing scores for all birch containing mixtures (Fig. 3).

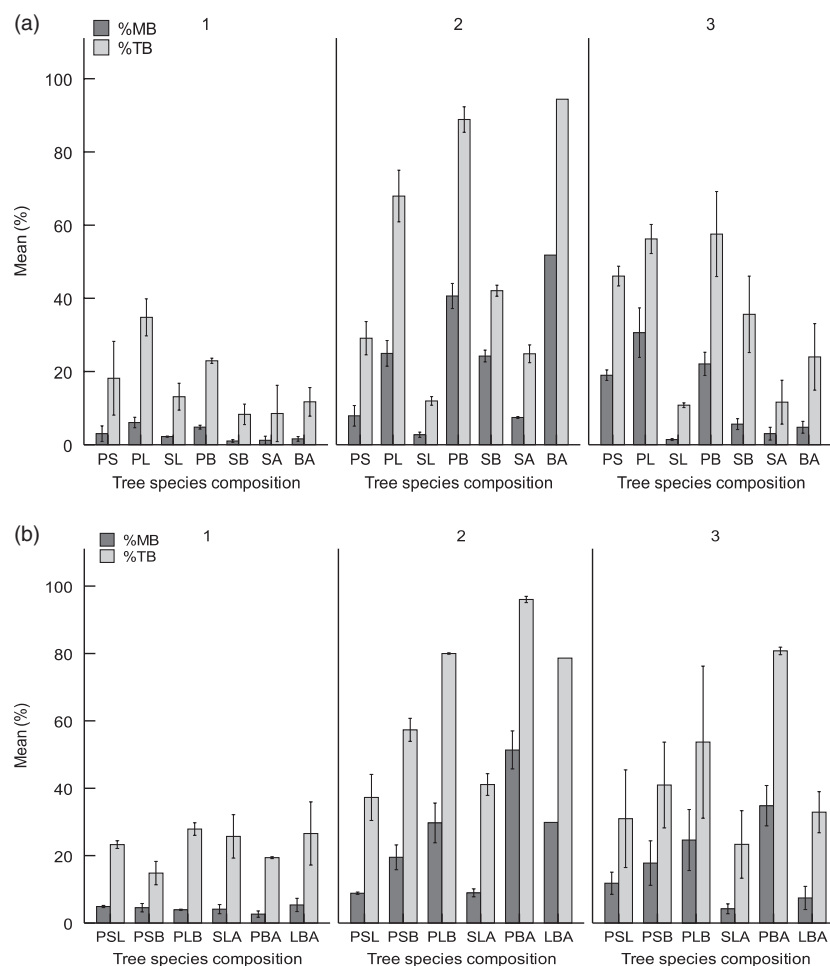
By assigning each tree species a preference ranking from one (least preferred) to five (most preferred) and calculating the overall species preference score for each plot based on its tree species composition, we showed that the degree of moose browsing per plot follows the expected trend relative to average preference of all species found in the plot ( $F_{9,100} = 6.14$ ,  $P < 0.001$ ; Fig. 4). Regression analysis indicates that, as predicted, increased relative density of preferred species (pine and birch) in a plot leads to an increase in browsing on less preferred species (spruce, larch, alder) growing in association ( $P = 0.01$ ; Fig. 5). Associational susceptibility is strongest in plots with both pine and birch, i.e. in species-rich plots. However, contrary to our prediction, reduced browsing on preferred species due to the presence of spruce (the least preferred species) in a plot was not observed ( $R = 0.001$ ,  $P > 0.05$ ).

#### FORAGER SELECTIVITY

As predicted, OSI calculations reveal that moose selectivity for tree species within plots decreased with increasing tree species richness (Kruskal-Wallis,  $H = 12.7$ ,  $df = 2$ ,  $P = 0.002$ , Fig. 6A). Selectivity in 2-species mixtures was significantly higher than selectivity in either 3-species or 5-species mixtures (Mann-Whitney U, Fig. 6A). OSI varied significantly among the 2-species mixtures (Kruskal-Wallis,  $H = 6.0$ ,  $df = 6$ ,  $P = 0.002$ ; Fig. 6B), and doubled when spruce was present in a plot at both the 2-, and 3-species diversity level ( $t$ -test,  $t = 6.34$ ,  $df = 39$ ,  $P < 0.001$ ;  $t = 2.57$ ,  $df = 33$ ,  $P = 0.015$ , respectively; Fig. 6B), corresponding to a reduction in plot %TB and %MB in both 2- and 3-species mixtures.

#### HABITAT USE

The number of moose faecal pellet groups recorded per plot tended to increase with increasing tree species richness; however, this trend was not significant (Kruskal-Wallis,  $H = 4.3$ ,  $df = 3$ ,  $P = 0.23$ ). A significant positive correlation was found between the number of faecal pellet

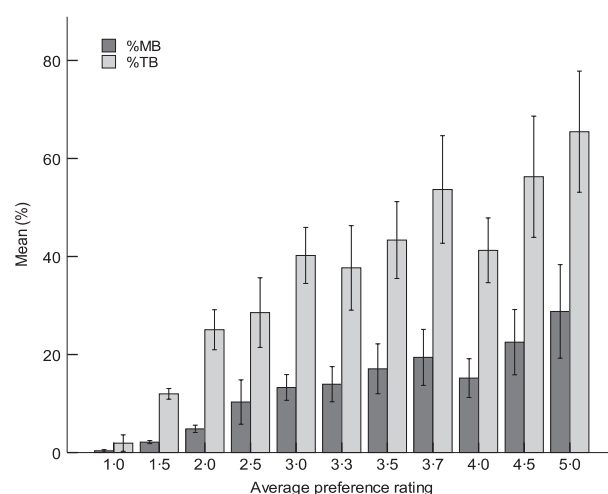


**Fig. 3.** Effects of tree species composition on moose browsing (%MB and %TB) in 2-species (A) and 3-species (B) mixtures at different experimental areas (1, 2, 3). Error bars are  $\pm 1$  SE.

**Table 2.** Least significant difference post-hoc test results from analysis of differences in %MB, %TB between the 2- and 3-species treatments.

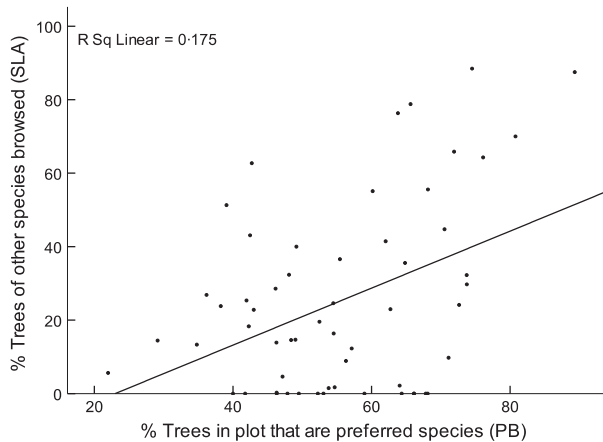
Analysis	Direction	Mean difference (%MB)	Mean difference (%TB)
Species composition (2-species)	PS > SL		19.14*
	PL > PS		21.86*
	PL > SL	18.43**	41.00***
	PL > SB		24.30**
	PL > SA	16.65**	37.96***
	PB > PS	12.54*	25.33**
	PB > SL	20.38***	44.47***
	PB > SB	12.21*	27.76**
	PB > SA	18.61**	41.43***
	PB > BA		20.48*
	BA > SL	12.40*	23.98*
	BA > SA		20.94*
Species composition (3-species)	PLB > PSL	10.91*	23.36*
	PLB > SLA	13.67*	23.81*
	PBA > PSL	21.09***	34.90**
	PBA > PSB	15.67**	27.70**
	PBA > SLA	23.85***	35.35**
	PBA > LBA	16.52**	22.03*

\*( $P < 0.05$ ), \*\*( $P < 0.01$ ), \*\*\*( $P < 0.001$ ).

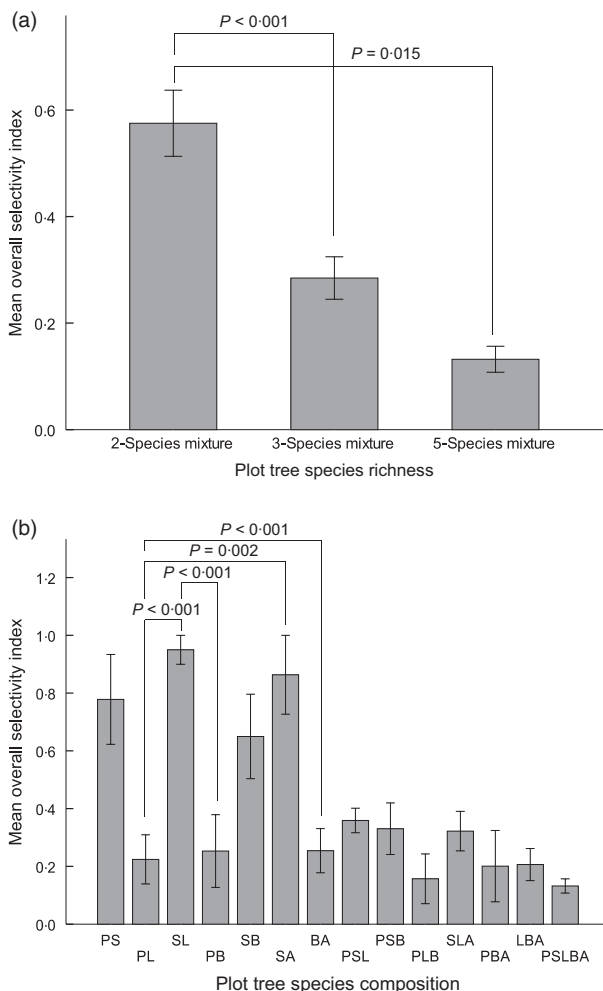


**Fig. 4.** Effects of plot's average preference rating on moose browsing (%MB and %TB). Plot's preference ratings are based on plot's species composition; preference values for each species are: pine = 5; birch = 4; alder = 3; larch = 2; spruce = 1. Error bars are  $\pm 1$  SE.

groups per plot and %MB (Pearson's  $r = 0.614$ ,  $n = 38$ ,  $P < 0.001$ ). The greatest number of moose faecal pellet groups was found at area 3 ( $n = 1,006$ ) and the lowest at area 1 ( $n = 11$ ).



**Fig. 5.** Relationship between percentage of trees of most preferred species (pine and/or birch) per plot and the percentage browsing on trees of less preferred species (spruce, larch, alder).



**Fig. 6.** The mean within-plot 'overall selectivity index' (OSI) at the 2-, 3- and 5-species richness levels (A) and in the different 2- and 3-species mixtures (B). The OSI is a comparison of the consumed diet and offered diet per plot. *P*-values show significant pairwise differences based on Mann-Whitney U tests. Error bars are  $\pm 1$  SE.

## Discussion

### EFFECTS OF TREE SPECIES RICHNESS ON MOOSE BROWSING

We found that species-rich plots receive more browsing damage compared with species-poor plots, confirming our prediction. As all plots had the same number of trees and plots were clustered together, differential browsing among plots reflects selection for quality of, rather than quantity of resources (van Beest *et al.* 2010). Therefore, greater browsing in species-rich plots suggests that these plots are more vulnerable to large herbivores that perceive them as high-quality resources. These results support the predictions based on the optimal foraging theory. The increase in species number and presence of preferred species in a plot increases the marginal value of that plot relative to the entire foraging environment and retains the herbivore for longer (Charnov 1976). Accordingly, the herbivore should leave a plot once the plot's value equals the average for the foraging environment and thus, time spent foraging will be higher in higher preference plots (Krebs, Ryan & Charnov 1974) and lower preference species growing in association are utilized as well as high preference species. At Satakunta, species-rich plots (3-, and 5-species mixtures) contain high relative densities of the preferred tree species (pine and birch). As a result, 3-species and 5-species mixtures (species-rich) retain moose for longer than monocultures and 2-species mixtures (species-poor) due to the increase in processing time required with increased number of food items added to the diet (MacArthur & Pianka 1966). Consequently, when a moose visits a species-rich plot, the outcome is a greater degree of browsing (%MB, %TB) because it is profitable to expand the diet.

Species-rich plots may also provide nutritional benefits for generalist mammalian herbivores such as moose (Westoby 1978), which cannot be met by species-poor plots. Large bodied herbivores, such as moose, are able to tolerate low nutrient content of forage, but require a greater abundance of plants to maintain energy requirements (Belovsky 1997). Furthermore, diet switching is important for large generalist herbivores, as nutrient requirements often cannot be met by a single plant species (Westoby 1978; Wiggins, McArthur & Davies 2006). Wang *et al.* (2010b) conducted cafeteria and field experiments using one, two, four, six, eight and 11 species mixtures and found an asymptotic relationship between plant species richness and intake by sheep. Daily nutrient intake increased, not just from selection of the most palatable species in the patch, but also from complementary effects of plant species richness.

In addition to nutritional content benefits, a mixed diet including several tree species may be beneficial for large herbivores as a mechanism of behavioural avoidance of plant secondary metabolites (PSMs). It has been suggested that mammalian herbivores might be able to overcome

the toxic effects of different PSMs by simultaneously consuming several types of them (Tilman 1982; Bryant 2003; Alm Bergvall *et al.* 2006). This may result in a higher consumption of food containing a mixture of different classes of PSMs as compared with consumption of food containing only one type of PSMs. Therefore, differences in nutrients and secondary metabolites between plant species may also lead to associational effects, with species-rich plots offering opportunity to regulate intake without expending energy in search and travel, which is the case in species-poor plots.

#### EFFECTS OF TREE SPECIES COMPOSITION: ROLE OF PLANT ASSOCIATIONS

At the 2- and 3-species richness levels tree species composition of a plot had a significant effect on moose browsing (%MB and %TB; Table 1). The greatest degree of browsing across the experiment was on pine and birch, both of which are known to be of high preference to moose, especially as winter forage (Hörnberg 2001). Moose showed intermediate preference for Siberian larch and black alder, and Norway spruce was the least preferred species. The consumption of the most preferred species, pine, and least preferred, spruce, did not vary with tree species richness, whereas intermediate preference species experienced differing degrees of associational susceptibility in mixed stands. This suggests that moose were consistent in ranking forage species at the experimental areas, but browsing on intermediate species was influenced by variation in plot characteristics, such as tree species composition as predicted. Therefore, our results show some disagreement with traditional optimal foraging theory, which assumes that each tree species has a predetermined value to the foraging mammal, that intake should be maximized from preferred species only, and that these do not change during a foraging bout. Instead, our results can best be explained by plant association theory, which takes into account relative palatability of the different tree species and the perceived quality of patches containing different combinations of tree species. Lower preference species receive more browsing in plots containing high abundances of preferred species, supporting the associational susceptibility hypothesis. In our study, these plant–herbivore interactions are driven by the proportion of preferred species growing in association with larch and alder; there is a significant positive relationship between the proportion of pine and birch in a plot and the degree of browsing on larch and/or alder in the same plot. These results are consistent with previous studies that have found that intermediate or low preference species receive more browsing when mixed with a highly preferred species (Hjältén, Danell & Lundberg 1993; Rautio *et al.* 2008; Bee *et al.* 2009). In contrast, our results refute the argument that plants gain protection when associated with plants of higher quality, the attractant-decoy hypothesis (Atsatt & O'Dowd 1976). Moreover, contrary to our prediction, we

found that spruce does not deter moose browsing and therefore preferred species do not gain from growing in association with lower preference species, refuting the repellent-plant hypothesis (McNaughton 1978).

While our results show that associational susceptibility operates at the plot level (20 m<sup>2</sup> in our experiment), it may also be relevant at smaller spatial scales such as neighbourhood effects for an individual tree (Miller, McArthur & Smethurst 2006) or at larger spatial scales such as moose home range. For instance, Pusenius, Pritinen & Roininen (2003) found that birch seedlings may be protected from herbivory if there is an alternative food source to be exploited first, but when seedlings are in close proximity to herbs, the seedling may actually receive more intense herbivory. Therefore, depending on the spatial scale, either optimal foraging theory or plant associational effects can explain the observed browsing, reiterating the point that different mechanisms apply at different scales.

#### BROWSING SELECTIVITY

We found support for our predictions that moose selectivity will be lower in species-rich plots as compared with species-poor plots. Even though moose preference for individual tree species remained the same across the richness gradient, at the plot level preferences were more variable. The OSI indicates that species richness affects the way browsing mammals select resources, and their degree of preference. Tree species are targeted more equally in species-rich plots (lower within-plot selectivity) compared with species-poor plots where the moose predominantly target the preferred species such as pine. MacArthur & Pianka (1966) proposed that items (in this case tree species) are added to the diet sequentially in order of preference ranking; therefore, a strategy of high selectivity in 2-species plots and those plots with the lowest ranked species spruce is optimal, and moose are likely to move through these patches more quickly in search of patches with a preferred species or with more species (greater net energy gain). This hypothesis is supported by the OSI and preference score results.

The ability of a browsing herbivore to adapt its foraging behaviour to changing forage availability and quality in this way has previously been described as an 'expanding specialist diet' (Heller 1980). Therefore, the occurrence and strength of associational susceptibility may increase in stands with multiple tree species, such as the species-rich plots at Satakunta, as a result of more opportunistic (less selective) foraging behaviours in such stands. This may be linked to the mechanism of nutrient balance discussed above, whereby moose actively adjust selectivity in response to their environment. Alternatively, species-rich plots may represent a complex spatial environment, which makes highly selective browsing within plots more costly and moose passively reduce selectivity (Wang *et al.* 2010a) leading to associational susceptibility for less preferred species and less targeted browsing on highly preferred species.



## Conclusions

The results from our study on tree–moose interactions in a boreal experimental forest provide evidence of the relative role of tree species richness and species composition in shaping mammalian herbivore foraging behaviour as well as shed light on the possible mechanisms linking moose browsing to forest diversity.

Large mammalian herbivores experience ecosystem heterogeneity at several different spatial scales (Senft *et al.* 1987), and therefore their functional responses to differences in richness and composition are also likely to vary at different scales. At the plot scale, which was studied here, results indicate that moose foraging is responsive to characteristics of the local plant community. We have shown that foraging is not only driven by diet preferences for tree species but also by the context in which tree species are found (plot species richness and species composition), and associational effects operating. This has consequences for browsing intensity on individual tree species, and can lead to shifts in the tree community due to differences in selectivity.

Our study suggests that the optimal foraging theory is not sufficient in explaining browsing patterns or predicting damage to tree species or mixtures of trees, and that associational effects of trees growing in a mixture help explain the difficulty in applying optimal foraging rules to large herbivores. We found little support for attractant-decoy or repellent-plant hypotheses, which have previously been the focus of studies on large herbivore spatial foraging (Hjältén, Danell & Lundberg 1993; Bergman, Iason & Hester 2005; Bee *et al.* 2009). However, species richness and presence of preferred species increase the susceptibility to browsing for lower preference tree species, and for the plot as a whole. The strategy of flexible selectivity could be attributed to opportunistic foraging and an expanding diet, high costs of being selective in complex environments, or a strategy to increase diversity of nutrients and limit plant secondary metabolites (diet mixing).

The importance of mammal foraging in shaping plant community composition and diversity in a variety of contexts is widely acknowledged. Associational effects within mixed stands and shared herbivore-mediated competition between plant species is an important component of ecosystem functioning and can explain how herbivore foraging can lead to shifts in abundance and spatial distribution of species. Understanding how associational effects in a patch or environment shape behaviour of browsers and consequent browsing damage can help to regulate the impact of large mammal herbivores in forests.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Data S1.** Example of plot layout and random allocation of treatment.

**Data S2.** Each of the 19 plot treatments, with abbreviations.