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Resource distribution in disturbed landscapes – the effect of clearcutting on berry abundance and their use by brown bears

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Abstract

To survive winter hibernation, brown bears (*Ursus arctos*) need to store excess energy during late summer and autumn. Scandinavian brown bears usually have an abundance of berries to feed on, but their distribution varies depending on forest structure and age. Especially on newly cut clearcuts, berry distribution is patchy, but berry production in these patches is exceptionally high. My aim was to model fine-scale temporal variation in berry production in the first years after forest cutting and determine whether bears adjust their space according to forage on clearcuts where berries are abundant. Using plot surveys on clearcuts in south-central Sweden, I collected bilberries (*Vaccinium myrtillus*) and lingonberries (*Vaccinium vitis-idea*) from 935 plots and found a nonlinear temporal dynamic of berry presence and abundance following a clearcutting procedure. On young clearcuts, berry production was depressed, it then peaked on clearcuts after around 8 years, and dropped again in later stages of succession. Additionally, bilberry and lingonberry abundance was greater on steeper slopes, with a linear relationship for bilberry and a non-linear relationship for lingonberry, which had a slight decrease at very steep slopes. I found that bears adapted to spatial and temporal dynamics of berry production by selecting for clearcuts of high bilberry presence and especially abundance. This trend was not observed in selection for lingonberry, most likely due to the smaller size of lingonberries and wider availably of bilberries in the year of study. Selection for clearcuts overall was low, with only around 10% of all recorded bear GPS positions being on clearcuts. This is potentially due to perceived hunting risk on open clearcuts and high availability of bilberries also in mature forest. Overall, clearcutting as a method of commercial harvesting of forest landscapes was found to have significant effects on berry production on clearcuts and bears adjusted their space to forage on patches with a high abundance of bilberries.

Keywords: bilberry, lingonberry, forest management, clearcuts, *Ursus arctos*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, resource selection functions, modeling, landscape use.

“All models are wrong, but some are useful.”

- George Box

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Introduction

Forests and forest resources have always been important in Sweden, economically, ecologically and socially (Barklund, 2009; Helander, 2015; Kardell, 1980). With 58 % of the land being productive forest (Nilsson and Cory, 2017), the country has a long history of forest management, which helped Sweden to be one of the wealthiest nations in the world (Helander 2015, UNdata 2018). Sweden now produces around 10% of the sawn timber, pulp and paper of the global market, despite having less than 1% of world's commercial forested areas (Helander, 2015). This efficiency was achieved by strict government regulations on harvest quotas and management, through several laws and acts, most notably the Forestry Act first adopted in 1903 (Barklund, 2009). It has since been revised and updated, but its primary adoption was to address overexploitation of forests, characteristic of the late 19th century (Barklund, 2009; Helander, 2015). Another important feature of Swedish forestry, which arguably contributes to its efficiency, is clearcutting. This controversial practice involves harvesting the majority of the trees in a certain area all at once, thus leaving a large-scale disturbance (Linder and Östlund, 1998). This method creates forest stands where all the trees are of same age, which have shown to have a negative impact on the biodiversity (Angelstam, 1998; Bengtsson et al., 2000; Gamfeldt et al., 2013) and exacerbates habitat fragmentation (Niemelä, 1999), and nutrient loss (Thiffault et al., 2007). One of the main factors favouring this forest management system, from a conservation perspective, is a supposed recreation of natural disturbance regimes, which were historically caused by wildfires (Linder and Östlund, 1998). Natural disturbance regimes through wildfire were characteristic of Scandinavian forests (Barklund, 2009; Helander, 2015), nowadays, however, forest owners try to minimise such loss of profit by interrupting or preventing them (Essen, 2015). Several studies show that clearcutting, even when combined with burning of coarse woody debris, compares poorly to stand-replacing wildfire from a biodiversity perspective (Bengtsson et al., 2000; Gustafsson et al., 2010; Niemelä, 1999), soil chemistry and tree nutrition (Thiffault et al., 2007) as well as reindeer herding (Kivinen et al., 2010). Furthermore, according to new data, disturbance regimes have been found to be of less importance to biodiversity than previously thought (Kuuluvainen, 2009). However, another point to be made in favour of clearcutting is that disturbances are concentrated, thus leaving other areas undisturbed, which is less true for selective cutting (Rosenvald and Lõhmus, 2008).

In this thesis work, I focus on clearcutting as means of creating a mosaic landscape of forest patches in different stages of succession. This gives us an opportunity to study how anthropogenically created forest openings affect regrowth of different plant species. Usually made by natural events, like avalanches, wildfires or windfall, they provide an assortment of important food resources for different species. Generally, young clearcuts are open, with plenty of exposure to sun, but still laden with woody debris and remnants of the clearcut methodology; pools of rain water, timber extraction roads and marks left by machinery (Atlegrim and Sjöberg, 1996a; Kardell, 1979; Kardell and Eriksson, 2011; S. E. Nielsen et al., 2004). With sunlight no longer being a limiting factor for understory plants characteristic of shaded mature forests, there is a burst of growth. Berry-producing shrubs, most of which survive the clearcutting process, have a limited window of growth before being outcompeted by other plants, which readily utilise the change in growing conditions. Among the first are grasses, herbs, and lichens in dry areas (Kardell and Eriksson, 2011; Schoonmaker and McKee, 1988). This period represents the peak of berry presence and abundance on clearcuts, while they are still open areas with little competition for light or resources. This is also the time of peak species biodiversity on clearcuts (Schoonmaker and McKee, 1988). After a few seasons of such abundant growth and berry production, depending on local micro conditions, other aggressive shrubs and grasses start to take over, for example heather (Calluna vulgaris). Being more successful and spreading rapidly, they soon dominate the understory, effectively overgrowing and shading all species of berries (Schoonmaker and McKee, 1988). As a response, berries invest more into vegetative growth instead of berry production, but ultimately cannot compete with the other plants (Kardell and Eriksson, 2011). Slowly, the forest starts to close again and, as trees get higher, they create the shading canopy, thus conditions similar to those in mature forest start to form again (Schoonmaker and McKee, 1988)

Most of the vegetation research in boreal forests tends to focus on the tree component, however there is evidence that understory vegetation might be a forest ecosystem driver (Nilsson and Wardle, 2005). The largest component of the understory in Swedish forests are ericaceous dwarf shrubs, feather mosses, and reindeer lichens (Arnborg, 1990; Kardell, 1980, 1979; Kardell and Eriksson, 2011; Nilsson and Wardle, 2005). Of the berry producing shrubs, the most notable are bilberry (Vaccinium myrtillus), lingonberry (Vaccinium vitis-idea) and crowberry (Empetrum hermaphroditum), with cloudberry (Rubus chamaemorus) and raspberry (Rubus idaeus) having sparser occurrence tied to specific habitats (Arnborg, 1990; Kardell, 1980). Although it has a wide distribution throughout Sweden, bilberries thrive best in open mature evergreen forests, particularly ones dominated by Norway spruce (Picea abies) and Scots pine (Pinus sylvestris) (Kardell, 1980, 1979; Miina et al., 2009). In south-eastern Sweden, the fruiting season for bilberry starts around mid-July and ends by the end of August (Eriksson and Ehrlen, 1991). The situation is different for lingonberries, which can be found on dry, poor soil and prefer evergreen forests dominated by Scots pine (Pinus sylvestris) (Kardell, 1980, 1979). Lingonberry fruits later than bilberry, starting around mid-August and ending towards the end of September (Eriksson and Ehrlen, 1991; Lodberg-Holm, 2015). Crowberry grows well on moist soils and has a fruiting period that spans both bilberry and lingonberry, starting in mid-July and ending in September (Eriksson and Ehrlen, 1991). Further, considering terrain factors, all three berry species are affected by features of the landscape like elevation, slope and habitat type. A study from southwest Canada by Barber et al., (2016) found that terrain factors were the main reason for regional and local variation in both species abundance and berry production. Particularly features that effect the sun exposure, like slope, are thought to be important for describing local variations.

In addition to terrain factors, clearcutting has been shown to have a major impact on berry-producing shrubs. Logging intensity on clearcuts (Bergstedt and Milberg, 2001), method of clearcutting (Nielsen et al., 2004) and clearcutting itself (Atlegrim and Sjöberg, 1996b; Kardell, 1979) have all been shown to influence both the distribution and abundance of berries on clearcuts, but not equally for all species. In several of the studies (Atlegrim and Sjöberg, 1996b; Kardell, 1979; Kardell and Eriksson, 2011), bilberry seemed to be severely reduced by clearcutting, following a time lag period of gradual decrease of berry plants until being outcompeted. This initial decrease has been attributed mainly to mechanical damage during the clearcutting process and coarse woody debris left on site (Atlegrim and Sjöberg, 1996a; Kardell, 1979). Overall, recovery is slow, as it takes 55 years for bilberry plant cover to fully recover after clearcutting (Kardell and Eriksson, 2011). The situation is different for lingonberry which showed less variation, with the highest values of ground cover recorded in mature forests at 7%, dropping down to 5% cover in young forest and clearcuts (Kardell, 1979). Additionally, lingonberry production drops by only about 10% after clearcutting, much less than other berry species (Kardell, 1979). Lower variation and decrease in post-clearcut presence of lingonberry is thought to be explained by the high fertility of lingonberries on open areas with high sun exposure, as opposed to bilberries (Kardell, 1980, 1979; Kardell and Eriksson, 2011).

One of the widely studied omnivores that forages on berries is the brown bear (Ursus arctos). During hibernation, bears experience great energy loss due to the long period of inactivity. This is counteracted by the preceding hyperphagia, during which bears consume and store excess amounts of energy in fat tissue. A study on bear diet in south-central Sweden found that berries accounted for 68% of the estimated dietary energy content (EDEC) in autumn (Stenset et al., 2016). Bears' foraging behavior on berries to satisfy hyperphagia needs in autumn has been well documented by several other studies in Scandinavia (Dahle et al., 1998; Hertel et al., 2016a; Lodberg-Holm, 2015; Persson et al., 2001; Stenset et al., 2016) and accross the range of the brown bear (Carlson, 2017; Ciucci et al., 2014; Nielsen et al., 2004). Another study from south-central Sweden has shown that the bears included in the study prefer bilberries over lingonberries, with crowberries being of minor importance (Hertel et al., 2016a).

As the landscape is not uniform, berry presence and abundance vary spatially across the landscape. This is especially true for young clearcuts, where berry distribution is patchy, although berry production in these patches is exceptionally high (Hertel et al., 2016a). Kotliar and Wiens (1990) provided a framework for dealing with patchiness of forage, which they define as a two-step hierarchy of occurrence and abundance. Both are important for determining bear habitat selection, as bears have shown selection for areas with abundant food resources (Hertel et al., 2016a; Lyons et al., 2003; Servheen, 1983), but also areas with enough cover (Lyons et al., 2003). This can be characterised as a mosaic landscape with a high diversity of available food and habitats, which is thought to be the optimal habitat for bears (Lyons et al., 2003; Nielsen et al., 2004; Servheen, 1983). In this context, clearcuts could provide the disturbances needed to diversify the landscape, because natural disturbances, such as wildfire, have become rare under the current forest management system.

Since energy acquisition from berries is so critical for brown bears in Scandinavia, we need to understand how they optimise their intake rate of berries. Hertel et al. (2016) has shown that bears actively select good foraging areas on clearcuts, but in their study, clearcuts were treated as one category. Similarly, although studies have been conducted on berry presence and abundance following a clearcutting procedure (Atlegrim and Sjöberg, 1996b; Bergstedt and Milberg, 2001; Kardell, 1979), they, with the exception of Kardell and Eriksson (2011), focused either on the immediate short-term (0-4 years after final cutting) or long–term effects (10 year intervals) of berry growth dynamics. Here, my aim is to evaluate berry availability on newly cut clearcuts along an age gradient from 1 to 15 years and identify at which age clearcuts present good opportunities for brown bears to forage on berries. Next, I will test whether brown bears adjust their space use according to the profitability of a clearcut, using resource selection functions (Boyce et al., 2002; Ciarniello et al., 2007; Manly et al., 1993). With this thesis, I will contribute to the knowledge of how brown bears adapt their space use to anthropogenically altered resource availability.

To achieve a more systematic approach I have developed several hypotheses that will serve as a framework for the study process:

H1 Berry presence and abundance are affected by clearcut age since final cutting

H2 Production of berries is higher on steeper south-facing slopes

H3 Bears select for clearcuts with a high probability of berry occurrence and high berry abundances

Associated predictions:

P1 In the first few years following clearcutting, berry occurrence and abundance will be low, due to the presence of coarse woody debris and mechanical damage. After initial partial recovery, berry production will peak, followed by a gradual decrease again, due to competition for space and resources from other plant species.

P2 Steep south-facing slopes receive a higher amount of solar radiation, which should benefit berries in the short time window of growth.

P3 Bears balance risk versus profitability and will focus mostly on the clearcuts with good foraging opportunities, such as those with high berry production.

Methods, analysis and study area

Study area

The study area comprised approximately 1,500 km² located in south-central Sweden (Figure 1). The topography is mostly gently rolling hills with elevations between 175 m and 725 m above sea level (Dahle and Swenson, 2003; Martin et al., 2010). Mean daily temperatures are -7°C in January and 15°C in June with 350-450 mm of rain in the vegetation period (150-180 days) and snow cover generally between November and April (Elfström et al., 2008). Coniferous Norway spruce and Scots pine are the predominant trees, with deciduous birch (*Betula pubescens* and *B. pendula*), aspen (*Populus tremula*) and grey alder (*Alnus incana*) found occasionally on clearcuts and open forest areas. The ground layer is comprised mostly of heather (*Calluna vulgaris*) and the three berry species, bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*) and crowberry (*Empetrum hermaphroditum*), along with lichens and mosses (Elfström et al., 2008). Although over 80% of the area is covered with forests, there is an extensive network of gravel roads (0.7-1.5 km per km²), used mostly for harvesting forests and outdoor activities (Martin et al., 2010; Ordiz et al., 2014). The human population in the area is sparse, with 4-7 habitants per km² in 2011, which makes it the lowest human density area in the brown bear range of Western Europe (Nellemann et al., 2007; Ordiz et al., 2014, 2012). With up to 80% of the coniferous forests in the area under intense harvest management (Frank et al., 2015), 40% of the forests are younger than 35 years (Swenson et al., 1999). Harvest rotation age in the area is reported at 80-120 years (Kardell and Eriksson, 2011; Ordiz et al., 2014).

Bear density in the study area has been estimated at 30 bears/1000 km^2 (Solberg et al., 2006), with the combined bear population of both counties of Dalarna and Gävleborg estimated at 793 in 2013 and in decline (Kindberg and Swenson, 2014).

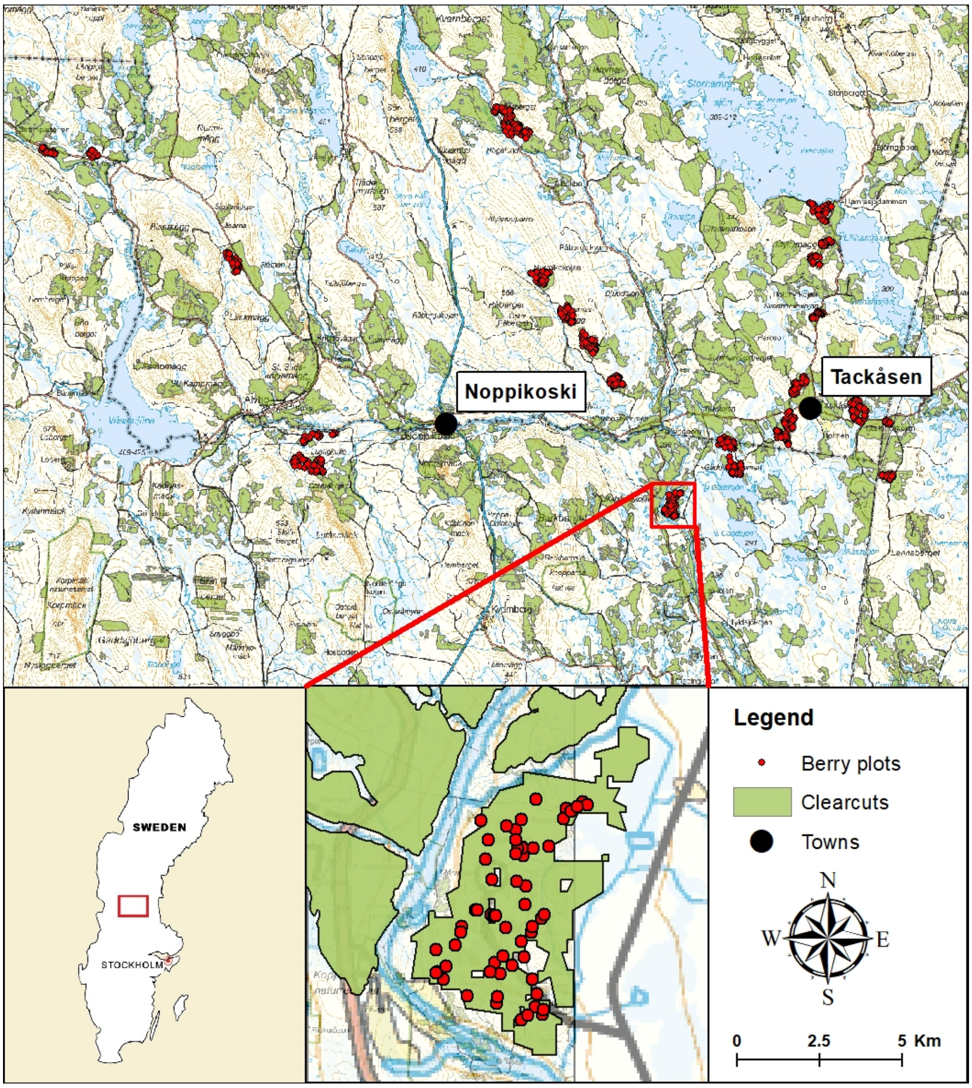


Figure 1 Top: Detail map of the study area with clearcuts <15 yrs of age (green polygons) and sample locations visited in this study (red dots). The project's field station is located in Tackåsen. Bottom left: Location of the study area in Sweden. Bottom centre: Closeup of a sample clearcut and random berry plots. Note that the scale in the bottom right only applies to the top map.

Data collection and analysis

Extraction of spatial covariates

A high-resolution digital elevation model (DEM, 2x2 m per pixel size) and soil maps (1:25 000 - 1:100 000 vector) were obtained from Lantmäteriet (Swedish mapping, cadastral and land registration authority) and Geological Survey of Sweden (Sveriges geologiska undersökning, SGU), respectively (© Lantmäteriet, 2017). Using ArcGIS and QGIS software (ESRI 2017, Quantum GIS Development Team 2017), I extracted several spatial covariates for all plots based on DEM; slope, aspect of the slope, TRI (terrain ruggedness index), and HLI (heat load index), as suggested by previous studies on berry modelling (Barber et al., 2016; Hertel et al., 2016a; Lodberg-Holm, 2015). Slope is the basic derivative of DEM and represents the rate of change in elevation between each cell in the DEM (Skidmore, 1989). Aspect identifies the direction the slope is facing by comparing the change between neighbouring cells (Skidmore, 1989). Terrain ruggedness index is a method to quantify topographic heterogeneity by assigning values to cells, based on the change in elevation and slope (Nellemann and Fry, 1995). Heat load index uses potential direct incident radiation on every cell in the DEM model and refines it with slope, aspect and latitude, to estimate the amount of heat load it receives from the sun (Mccune, 2007; McCune and Keon, 2002). The latter was calculated using the “Geomorphometry and Gradient Metrics” tool in ArcGIS (Evans 2017). Additionally, all plots were assigned the age of the clearcut in which they occurred and Euclidian distance of the sample plot to the clearcut perimeter was determined.

Berry data collection

Data collection was conducted on commercially harvested clearcuts between the ages of 0 and 15 years, located around the SBBRP research station in Tackåsen (Figure 1), from 24 July to 30 August 2017 (38 days), which roughly corresponds with the fruiting period of bilberry (*Vaccinium myrtillus*) (Eriksson and Ehrlen, 1991; Kardell and Eriksson, 2011).

I obtained information about the year of harvest and the spatial configuration of harvested areas and their respective year of harvest from the local forest cooperative Orsa Besparingsskog and the Swedish Forestry Agency (Skogsstyrelsen). I generated random points with R (R Development Core Team 2017) for all clearcuts aged 1-15 years in my study area, with a density of 1.5 points per hectare. Clearcuts ranged from 6.9 ha (10 points) to 42 ha (63 points), with an average of 21 ha (32 points). During fieldwork, points were found with a hand-held GPS device. The last number of the Y coordinate served as a direction pointer (0, 1 and 2 would point north, 3, 4 east, 5, 6, 7 south and 8, 9 west). After one step in the appropriate direction, determined with a compass, a 1 m^2 frame was dropped on the ground, directly in front of the observer's feet (Appendix, Picture 1). If this location proved to be unsuitable for berry plant growth (e.g. water, large stones, road, cliff) the point was abandoned and another randomly generated point was chosen. If the obstacle was small (e.g. a rock, small tree or a stump), the plot was moved to the right of the obstacle. I recorded berry plant cover and number of berries inside the plot; branches leaning in were recorded, branches leaning out were not. I also recorded percentage of plant cover, mean height of five plants, number and weight of the berries of each of the three berry species present; bilberry, lingonberry and crowberry. Environmental variables were collected at the plot level: soil moisture, stems per hectare and habitat type classification according to NILS - Nationell Inventering av Landskapet i Sverige (Esseen et al. 2004). Soil moisture was separated into three classes, dry, mesic and wet, determined by testing the soil by hand. Presence of characteristic plants was used to help the determination, moisture-loving plants and lichen, for wet and dry environment respectively. Stems per hectare were recorded for each plot according to method used in NILS (Esseen et al. 2004), which differentiates between trees of up to 0.5 m high and above, then assigns a circle radius for counting (1.78 m and 5.64 m) and a multiplication factor (1000 and 100). I sampled 935 plots in total during the study.

All berries inside the plot were collected in separated plastic bags according to species and ripeness (ripe/unripe) and stored in cooler boxes to be counted and weighed later at the field station (Appendix, Picture 2). Berries were considered ripe if they had a round shape, were of the appropriate colour (dark blue for bilberries, red for lingonberries, black for crowberries) and juice came out when squeezed.

Berry data analysis

Here I analysed the effect of spatial covariates on the probability of berry presence and the number of berries (abundance). Number and weight of berries were positively, linearly correlated; therefore, I limited the analysis to the number of berries.

I performed initial data exploration using a protocol developed by Zuur et al. (2010) and found that the dataset suffered from several statistical problems common in ecological data. Numbers of berries were left skewed (i.e. many plots with few berries and fewer plots with many berries), highly overdispersed, and zero inflated (many plots with no berries), including outliers of particularly high berry abundance. To counter the zero inflation, I used zero-altered negative binomial models, also called hurdle models (Zuur and Ieno, 2009). These work in two steps: first, the data is separated into zero and non-zero values, then a binomial model is used to model the probability of observing berries (regardless of how many); second, a truncated negative binomial model is used to model the non-zero values i.e. number of berries >0. This process eliminates the impact of zero inflation, but gives us results in two separate categories, presence and abundance.

Crowberry was found in very low numbers and widely dispersed (only 12.7% of the plots contained crowberries). Of all the berries collected, less than 8% were crowberry. This is in line with other recent studies on the study area (Hertel et al., 2016a; Lodberg-Holm, 2015), which found that crowberries occurred rarely. Because of the low sample size, I was not able to formally analyse the drivers of crowberry occurrence and abundance on clearcuts. Additionally, twenty-four of the 935 sample plots had to be removed from the analysis. Alignment problems in the two clearcut datasets (Orsa Besparingskog and Skogstyrelsen) caused 10 of the berry plots to have miscalculated distance to the edge values. They were removed from the analysis. Similarly, one clearcut suspected of recent fire management yielded no berries of any species (CC 6991, 8 years old, 14 plots, Picture A6 & A7) and was also excluded from the analysis.

I used logistic regression (a GLM with argument family set to binomial) to analyse occurrence and negative binomial GLMs to analyse abundance. The full model included the explanatory variables of age, slope, aspect, TRI, heat load, edge and soil. I tested for non-linear effects of age and slope on berry occurrence and production by including them as second-order polynomials. Also called quadratic polynomials, they go up to the degree of 2 (i.e., x^2) and plot a function with one peak. I used the backward stepwise selection procedure, removing non-significant covariates one at a time. I compared the reduced model with the previous, more complex model and the model with the lowest AICc value was considered to have the most explanatory power. When values different by less than a ΔAICc of 2, the model with fewer degrees of freedom was selected. I selected the best models explaining bilberry occurrence, bilberry abundance, lingonberry occurrence, and lingonberry abundance in this way (Table 2).

I could have fitted a mixed effects model including a random effect for clearcut ID to control for clearcut specific variation, but this would not have allowed the extrapolation of predictions to other clearcuts that were not sampled. To test the effect of clearcut ID, I fit a GLM to explain probability of berry occurrence on different clearcuts, using no spatial covariates, only clearcut ID and predicted the probability of berry presence for each clearcut.

Lastly, I extracted all variables that were important for predicting berries (Table 2) on the bear positions. Based on that, I was able to predict the expected probability of berry occurrence and abundance for all positions of bears.

Bear data collection

Bear positions were provided by the SBBRP, as part of the base project of long-term individually-based monitoring of bears (Swenson and Kindberg, 2015). In 2017, 43 bears were followed with GSM-GPS collars (Vectronic Aerospace GmBh, Berlin, Germany). All bear captures in the SBBRP follow a standard protocol, where radio-marked bears are darted from a helicopter using a remote drug delivery system (Dan-Inject, Børkop, Denmark). This is done on clearcuts or other open areas in mid-April, shortly after bears exit dens, to prevent overheating the animals during the chase or accidental drowning (Ordiz et al., 2012; Zedrosser et al., 2007). Tiletamine, zolazepam and medetomidine are the drugs used for immobilization, with the dose adjusted to bear body mass and oxygen administered when necessary (Fahlman et al., 2011). See Arnemo et al. (2012) for further details on capture and handling. All animal captures and handling were approved by the Ethical Committee on Animal Experiments in Uppsala, Sweden and the Swedish Environmental Protection Agency.

I used bear relocations during two separate periods in fall, the bilberry period from 19 July to 31 August (43 days) and the lingonberry period from 1- 30 September (30 days). GPS relocation intervals were set to 1 hr, yielding optimally 24 bear GPS positions per day (equals 1032 positions for the bilberry and crowberry period and 720 positions for the lingonberry period). This kind of data density was unavailable for most of the bears followed by the SBBRP in 2017. This is due to sampling frequency of the collars, limited by the GPS and GSM signal quality, which varied over the study area. Therefore, I only used bears whose positions overlapped with my study area and had at least 700 and 400 successful relocations during the bilberry and lingonberry period, respectively. This left me with 19 (bilberry period) and 17 (lingonberry period) bears that had sufficient position fixes (see Table 1). All positions of the individual bears included in the study were used to construct 100% minimum convex polygons – MCP (Gillies et al., 2006; Moe et al., 2007) to generate home ranges.

During the 2017 hunting season, one adult male bear was harvested legally. Prior to its death on 21 August 2017, it still generated enough points to be included in bilberry period (>700 GPS positions) but was excluded from the lingonberry period. Similarly, another adult male dropped its collar around 11 September 2017 and was excluded from the lingonberry period but included in the bilberry period.

Table 1: List of Swedish brown bears included in the analysis with their sex, status in winter and cub status if applicable. In period section, B equals bilberry, L equals lingonberry, B+L equals both. COO – mother with cubs older than a year, COY – mother with cubs of the year, SHM – subadult hibernated with mother, NA – not available.

BearID	Name	Sex	Status in winter	Cubs	Cub age 2017	Period
W0605	Sälga	F	COO	2	2	B+L
W0720	Rådika	F	COO	2	1	B+L
W1011	Lillunn	F	COO	2	1	B+L
W1205	Klummy	F	COO	2	1	B+L
W1418	Hässja	F	COO	2	1	B+L
W0104	Abborrgina	F	COY	NA		B+L
W0716	Spjuta	F	COY	NA		B+L
W1017	Pässan	F	COY	2	0	B+L
W1203	Pengel	F	COY	NA		B+L
W1417	Brunna	F	COY	NA		B+L
W1505	Gymåsa	F	COY	2	0	B
W1319	Snygga	F	NA	NA		B+L
W1408	Misan	F	NA	3	0	B+L
W1416	Lutane	M	NA	-	-	B
W1512	Latola	F	NA	NA		B+L
W1509	Väsa	F	SHM			L
W1110	Strandas	F	Solitary			B+L
W1204	Kil-kalle	M	Solitary	-	-	B
W1304	Bergsloga	F	Solitary			B+L
W1608	Majko	F	Solitary			B+L

Bear data analysis

Bear GPS data was postprocessed and prepared. Movements between two points that had spatial and temporal mismatch were removed and positions of dead bears and dropped collars were truncated to the day prior to the events (N=1 for dead bears, N=1 for dropped collars). Only active positions were retained, characterized by a movement distance of more than 25 m between consecutive locations (Hertel et al., 2017). Bear locations were separated into the bilberry and lingonberry periods. Using R (R Development Core Team 2017), general habitat and, in the case of clearcuts, clearcut age was extracted for every bear location using a reclassified SMD map (Svensk Marktäckedata - habitat map of Sweden) and clearcut maps obtained from Skogssyrelsen and Orsa Besparingsskog. Spatial covariates identified during berry analysis that affected bilberry and lingonberry occurrence and abundance were extracted for all bear locations to predict berry occurrence and abundance using the best berry models.

To quantify bear habitat selection, I used third-order resource selection functions (RSFs), which are a widely used method to explore habitat selection of animals (Boyce, 2006; Hertel et al., 2016a; Manly et al., 1993). RSFs start with a generalized linear model, which includes the variable of interest versus a response. A prediction of selection response is then made along the gradient of the variable, showing preference or avoidance, usually displayed with a graph. To calculate RSFs, random points must be generated, serving as available positions and matching the number of used positions. This was done within the individual bears' minimum convex polygon (MCP) home ranges (Gillies et al., 2006; Moe et al., 2007). Next, spatial covariate data for the points that were on clearcuts was extracted; slope, distance to the edge and clearcut age. Berry occurrence and abundance was predicted for all used and random positions on clearcuts for each period. Thus, bilberry data was predicted for bear positions recorded during the bilberry period and lingonberry data was predicted for bear positions recorded during lingonberry period.

I fitted RSF's using logistic regression, again with locations used by bears and random locations as the binary response variable. I tested whether the probability of clearcut use was affected by age of the clearcut and presence and abundance of bilberries and lingonberries, in their respective periods.

Results

Berries

The distribution of berries I collected was heavily skewed, with 13,223 collected bilberries (23.0 %), 40,044 lingonberries (69.7 %) and 4,152 crowberries (7.3%). Another important thing to note is that 87% of lingonberries were collected unripe, as the fieldwork preceded the main fruiting period of lingonberries. Figure 2. shows proportion of ripe to unripe berries over time, showing disparity in the timing of fruit ripening between bilberry and lingonberry. For further details on numbers, weight, height and ripeness of collected berries see Appendix, Table 3.

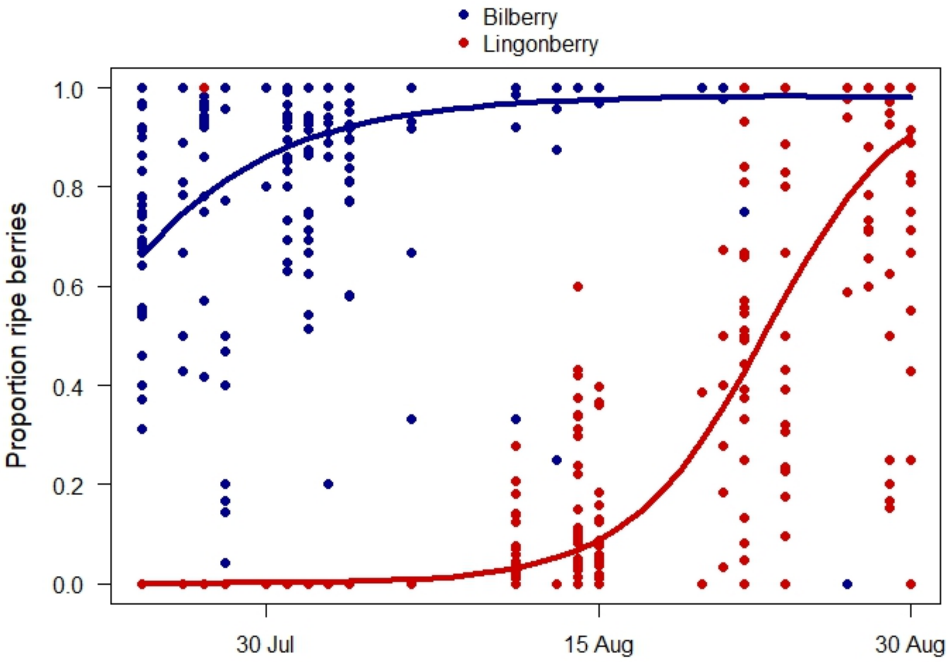


Figure 2: Proportion of ripe berries on plots during the fieldwork in south-central Sweden (24 July – 30 August 2017). For reference, the bilberry period was from 19 July to 31 August, whereas the lingonberry period was defined as the whole month of September, based on data collected earlier (Lodberg-Holm, 2015).

Soil moisture affected the berry occurrence of both species (Figure 3A&B) but was rejected from the final analysis. This was due to heavily biased sample size and subjective methodology. First, of 935 plots sampled, 83% (785) were labelled as mesic, resulting in a skewed sample size. Secondly, the sampling method for soil moisture (testing by hand) was considered too subjective to be used in the analysis. Third, no accurate soil moisture maps were available for the area, which made extrapolation beyond the sampled points impossible.

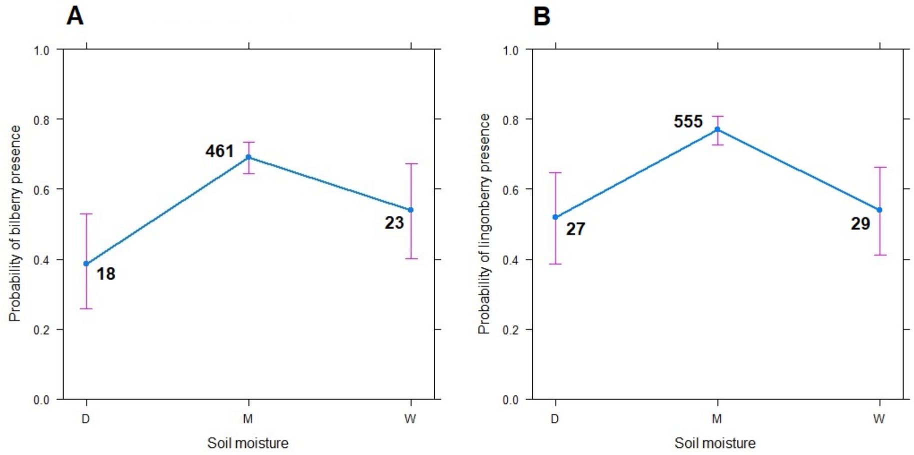


Figure 3A & 3B: Berry presence in different soil moisture classes on the study area in south-central Sweden. Numbers in the plot indicate sample size and labels stand for: D = dry, M = mesic, W = wet.

Clearcut age, slope and distance from the edge were the only variables that showed a significant effect on berries. Clearcut age and slope showed non-linear relationships, but not for both species equally (see Table 2). Distance from the edge of the clearcut had a linear relationship for both berry species. The four best models with the most explanatory power for presence and abundance of berries are shown in Table 2 below.

Table 2: Final models with the most explanatory power for presence and abundance of bilberry and lingonberry on the study area in south-central Sweden. Edge is used to abbreviate "distance from the edge of the clearcut" and NL indicates a non-linear relationship.

Stage\Berry species	**Bilberry**	**Lingonberry**
Presence (GLM)	age + NL age + slope + edge	age + NL age + slope + NL slope + edge
Abundance (NBGLM)	age + NL age + slope	age + NL age + slope

Probability of berry presence

Both bilberry and lingonberry showed a non-linear effect of age of the clearcut on the probability of berry presence (Table 2, Figure 4 A&B). This effect was stronger for bilberry than for lingonberry (see 95% confidence interval Figure 4 A). The probability that bilberries are present was highest around a clearcut age of 8 years (67.2%); the same holds true for lingonberry (74.4%). See Appendix, Picture A4 for an example of an 8-year-old clearcut. The probability to find bilberries was much lower on young and newly cut clearcuts (1 year: 34.1 %), with the probability for lingonberries also dropping (1 year: 61.7%) (Picture A3). The probability of berry presence became low again as succession progressed and the vegetation was closing (15 year: 30.3% for bilberry and 58.9% for lingonberry) (Picture A5).

Slope was found to affect berry presence for both species (Table 2, Figure 4 C&D). Steeper slopes led to higher probabilities of berry presence. For lingonberry occurrence, there was a decrease in berry probability on very steep slopes, however, the wide confidence intervals indicated high variability (Table 2, Figure 4 D). Peak lingonberry presence on slopes was observed at around 8-10 degrees, but, due to low sampling effort at steeper slopes, this result was unreliable. The two variables related to slope, aspect of the slope and heat load, had no effect on the presence of any berry species (p= 0.18 and p= 0.67 for bilberry and lingonberry, respectively).

Both berries showed a significant relationship with distance from the edge of the clearcut, with the probability of berry occurrence increasing with increasing distance from the edge. Wide confidence intervals were observed, especially at higher distances, which again was probably due to lower sampling effort at higher distances. The average size of the sampled clearcut was 21.4 ha, which, in a perfect situation of a circle, yielded a radius of 216.2 m. Clearcuts, however, have very varied shapes with undulating edges (see Figure 1), so even an average radius distance was rarely achieved.

Table 3: Model estimates, standard errors and *p* values for variables included in the best explanatory model for presence of bilberries and lingonberries on clearcuts in south-central Sweden.

Explanatory variables	Bilberry presence		Lingonberry presence	
	β ± SE	*P*	β ± SE	*p*
Age	0.419 ± 0.076	> 0.001	0.187 ± 0.076	0.014
Non-linear age	-0.029 ± 0.004	> 0.001	-0.012 ± 0.004	0.003
Slope	0.233 ± 0.03	> 0.001	0.449 ± 0.08	> 0.001
Non-linear slope			-0.023 ± 0.006	> 0.001
Distance from the edge	0.005 ± 0.001	0.001	0.003 ± 0.001	0.045

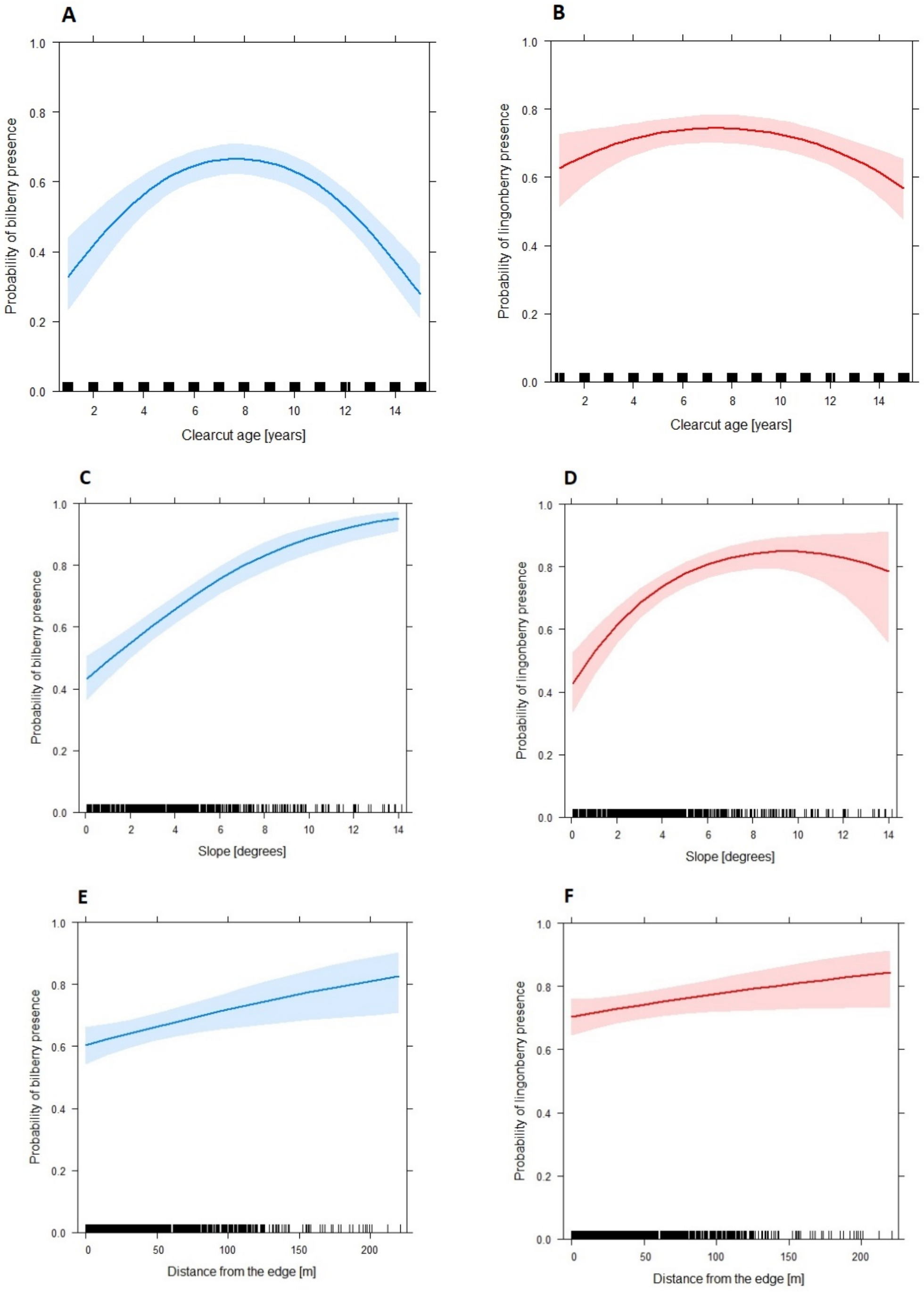

A
B
C
D
E
F
Probability of bilberry presence
Probability of lingonberry presence
Clearcut age [years]
Slope [degrees]
Distance from the edge [m]
0.0
0.2
0.4
0.6
0.8
1.0
2
4
6
8
10
12
14
0
50
100
150
200

Figure 4 A-F: Panel A shows the effect plot of bilberry presence on clearcuts depending on the age of the clearcuts and panel B shows effect plot of lingonberry presence on clearcuts depending on the age of the clearcuts. Panels C and D show effect plots of berry abundance on clearcuts depending on the slope for bilberry and lingonberry, respectively. Panels E and F show effect plots of berry presence on clearcuts depending on the distance from the edge for bilberry and lingonberry, respectively. Figures are coloured blue for bilberry and red for lingonberry. Shaded bands represent 95% confidence intervals.

The overall explanatory power of the best fitting models was relatively low (McFadden’s pseudo r-squared: 0.105 for bilberry and 0.059 for lingonberry), indicating that other variables that we did not control for, some of which may be clearcut specific, affected berry presence. By ordering the clearcuts by age, the non-linear effect that peaks around clearcuts of 7 years old (CC2114, CC3136), can still be observed (Appendix, Figure A1). Thus, the predictions of berry occurrence were similar for clearcuts of the same age, which corroborates the results above. The same was found for berry abundance (Appendix, Figure A2).

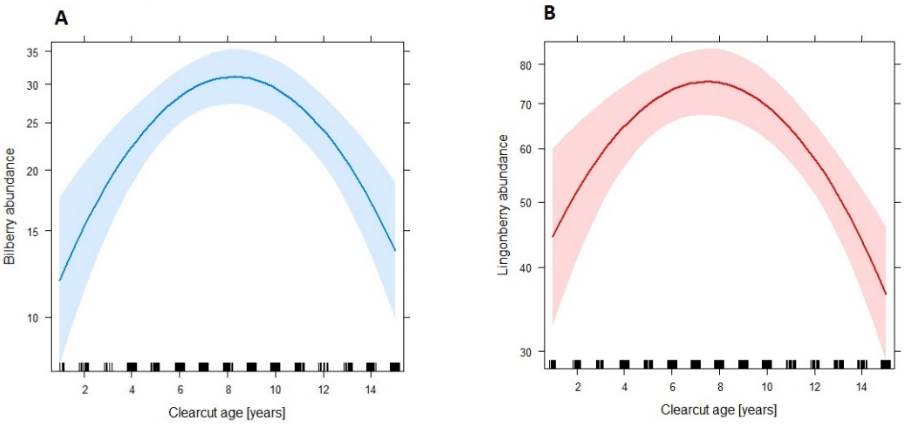
Predicted berry abundance

Clearcut age and slope were the only variables retained in the final models explaining both bilberry and lingonberry abundance (Table 4). Clearcut age had a significant non-linear effect on berry abundance that was similar for both bilberry and lingonberry, like the effect found for berry occurrence. Berry abundance was lower at very young (1 year: 12.7 for bilberry and 44.1 for lingonberry) and older clearcuts (15 year: 14 for bilberry and 37.5 for lingonberry) and peaked at around 8 years old (31.3 for bilberry and 74.9 for lingonberry).

Slope had a significant positive effect on berry production of both species (bilberry: 0.042 ± 0.018, p=0.024; lingonberry: 0.099 ± 0.016, p> 0.001). Both species showed a linear relationship and produced more berries on steeper slopes (Table 4, Figure 6 C&D). However, the wide confidence intervals in bilberry especially at steeper slopes indicated a large amount of uncertainty around the slope effect (Table 4).

Table 4: Model estimates, standard errors and *p* values for variables used in modelling of abundance of bilberries and lingonberries on clearcuts.

Explanatory variables	Bilberry abundance		Lingonberry abundance	
	β± SE	*p*	β± SE	*p*
Age	0.292 ± 0.061	> 0.001	0.189 ± 0.048	> 0.001
Non-linear age	-0.019 ± 0.003	> 0.001	-0.012 ± 0.002	> 0.001
Slope	0.042 ± 0.018	0.024	0.099 ± 0.016	> 0.001



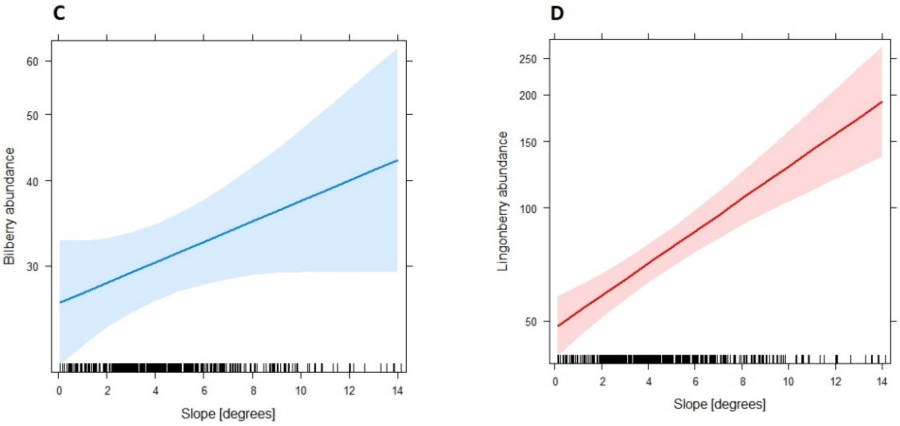


Figure 6 A-D: Panel A shows the effect plot of bilberry abundance on clearcuts depending on the age of the clearcuts and panel B shows the effect plot of lingonberry abundance on clearcuts depending on the age of the clearcuts. Panels C and D show the effect plots of berry abundance on clearcuts depending on the slope for bilberry and lingonberry, respectively. Figures are coloured blue for bilberry and red for lingonberry. Shaded bands represent 95% confidence intervals.

Bears

In total, 20 individual bears were included in the study (Table 1). Together they generated 17,987 GPS positions for the bilberry period and 10,987 GPS positions for the lingonberry period, however not all of the positions were on clearcuts. Only 10% (1889) of positions during the bilberry period and 12,5% (1318) during the lingonberry period were on clearcuts. The sex ratio of instrumented bears was heavily biased in the bilberry period, with 17 females and 2 males, whereas in the lingonberry period both males were excluded and only 17 females remained. The reproduction status in winter, cub presence and age can be seen in Table 1.

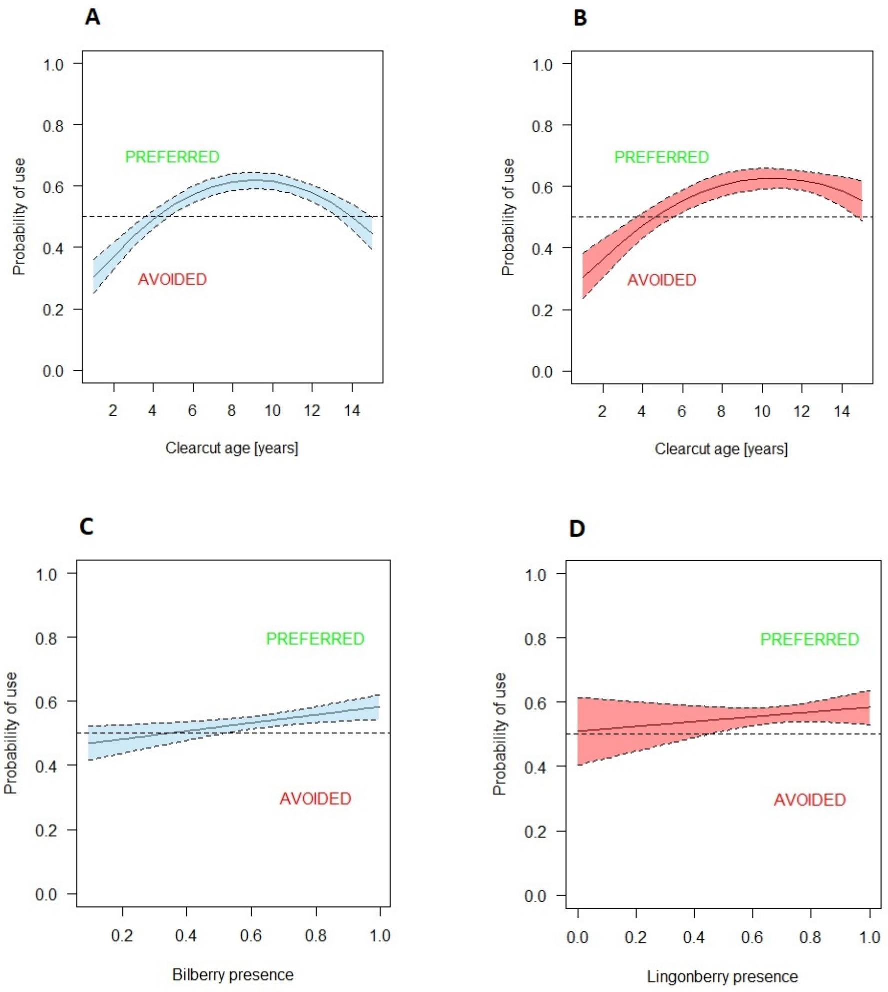
Age of the clearcut was found to be an important factor for bear selection of both berry species (Figure 7 A&B). We observed a non-linear trend for bilberries, with a peak around clearcut age 9, where selection for clearcut was highest (0.366 ± 0.045, z = 5.42, p= >0.001). Bears showed the highest selection for lingonberry on clearcuts of around 10 years old (0.312 ± 0.061, z = 5.8, p= >0.001).

Bears selected for locations with a high probability of bilberry occurrence and avoided locations with a low probability of bilberry occurrence (0.51 ± 0.191, z value= 2.3, p=0.007), which can also be seen in Figure 7 C. The strength of selection was weak, as indicated by confidence intervals close to the value of 0.5, which indicates use close to that of random, but still significant. Bears also selected for lingonberry presence during the lingonberry period (Figure 7 D), where bears selected for clearcut locations when they had a 50% or higher probability of having lingonberries. However, the results of the lingonberry presence model were not significant (0.302 ± 0.311, z = 5.42, p= 0.333).

Bears selected locations with a bilberry abundance of more than 30 berries per m^2 (0.022 ± 0.004, z = 5.67, p= > 0.001, Figure 7 E). This was not observed with lingonberries, because both models for abundance (-0.0003 ± 0.0003, z = 0.55, p= 0.341) and presence (0.302 ± 0.311, z = 1.63, p= 0.333) were not significant.

Table 5: Brown bear selection for bilberry and lingonberry presence and abundance of both berry species depending on clearcut age in south-central Sweden.

Explanatory variables	Bilberry		Lingonberry	
	β± SE	*p*	β± SE	*p*
Age	0.366 ± 0.045	> 0.001	0.312 ± 0.061	> 0.001
Non-linear age	-0.02 ± 0.002	> 0.001	-0.014 ± 0.003	> 0.001
Presence	0.51 ± 0.191	0.007	0.302 ± 0.311	0.333
Abundance	0.022 ± 0.004	> 0.001	-0.0003 ± 0.0003	0.341


A
B
C
D
Probability of use
1.0
0.8
0.6
0.4
0.2
0.0
PREFERRED
AVOIDED
2
4
6
8
10
12
14
Clearcut age [years]
0.2
0.4
0.6
0.8
1.0
Bilberry presence
0.0
Lingonberry presence

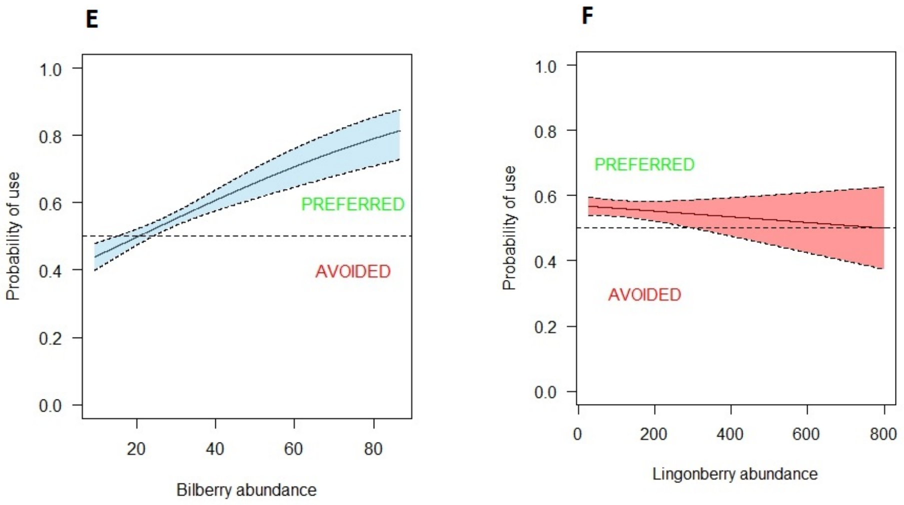


Figure 7 A-F: Panel A shows probability of use of clearcuts for bilberry by bears based on age of the clearcuts; similarly, panel B shows probability of use of clearcuts for lingonberry by bears based on age of the clearcuts. Panels C and D show probability of use of clearcuts, based on berry presence for bilberry and lingonberry, respectively. Panels E and F show probability of use of clearcuts based on berry abundance for bilberry and lingonberry, respectively. The shaded areas and broken lines represent 95% confidence intervals. Values above 0.5 expected use by random indicated that the clearcuts are selected for, if below, they are avoided. Blue shading represents bilberry and red, lingonberry.

Discussion

I found a non-linear temporal relationship of berry presence and abundance on clearcuts. Both bilberry and lingonberry presence and abundance were depressed immediately after final cutting. This is in line with several other studies showing that berry production, especially bilberry, decreases following clearcutting (Atlegrim and Sjöberg, 1996b; Kardell, 1979; Kardell and Eriksson, 2011). After several years of growth, both berry species showed peak predicted presence and abundance on clearcuts aged around 8 years old. During this time, both berries were abundant on clearcuts and could present good foraging opportunities for brown bears. However, this peak was short (2-3 years), as there was soon a decline in both presence and abundance. This largely reflected clearcut dynamics where berry producing shrubs have a limited time to grow until succession takes over and they become outcompeted by other plants (Schoonmaker and McKee, 1988). My data also confirmed the differences in response of berry species to the clearcutting described by Kardell (1979), who showed that bilberry presence was affected more by the clearcutting than was lingonberry. There was a steep decrease in bilberry presence and abundance following the first few years after clearcutting, whereas this variation was less pronounced in lingonberry. It seems that lingonberries were less affected by the clearcutting process, possibly owing to the physiological characteristics of the plants, such as height of the plants and resiliency, but this was not confirmed. Overall my results showed support for H1, in that berries were affected by age since the clearcutting procedure was performed and in the direction of P1, in that there was a non-linear relationship.

There are several ways in which my models on berry dynamics on clearcuts could be improved. First, my analysis lacked an inclusion of climate data, such as temperature and precipitation, which is thought to play a major role in determining berry dynamics (Barber et al., 2016; Eriksson and Ehrlen, 1991). Unfortunately, climate data on such a precise plot scale was not available for my study area. Second, the depression of soil during the harvesting process and destruction of plants during harvest is another important source of variation of berry presence within clearcuts. Studies from North America indicate the importance of different clearcut methods on the distribution of berries, as well as clearcut selection by brown bears (Nielsen et al., 2004; Nielsen et al., 2004). In their study area, bears showed a preference for specific methods, but it is unclear how these methods can be compared to Swedish forestry. I was unable to obtain any such data from the forestry company Orsa Besparingsskog or Swedish Forestry Agency – Skogsstyrelsen, which supplied data used in this study.

Another factor to consider is fire management of clearcuts, which has a strong effect on the berry presence (McRae et al., 2001; Nilsson and Wardle, 2005). Fire management is done to emulate the effect of wildfires, found to be important in preserving the biodiversity of Scandinavian forests (Barklund, 2009; Helander, 2015; McRae et al., 2001). The material burned is usually coarse woody debris left on the clearcut after the harvest of commercially viable stems. Some of the clearcuts I visited had obviously been burned, based on charred standing woody debris and stumps and ash mixed in the soil (see Appendix, Picture A6 & A7), whereas others had just a few small fire scars. This could indicate the age since last performed burning, but there is no method to accurately assess this, so I was not able to include this variable in my models. In this study, I had no means of quantifying the effects of fire management, because Sweden does not maintain an updated national database of performed fire management[1]. Furthermore, field work was done entirely during the bilberry period, which is another source of bias. Most of the collected lingonberries (87%) were unripe, under the assumption that they would all become ripe if given enough time. This is probably not the case and by using this assumption the number of lingonberries was overestimated. The fact remains that plant growth dynamics are governed by multitude of factors, which result in variations within the data, berry-producing shrubs being no exception. Capturing this variation is challenging and the methodology I used in this thesis faced certain trade-offs, notably between sampling for higher precision within clearcuts or capturing more of the variation between differently aged clearcuts; either I would sample more plots per hectare for precision, or I would sample more clearcuts. Capturing the variation of berries on clearcuts proved to be even more challenging as it is thought that mechanical damage from the clearcutting process largely influences plant growth (S. E. Nielsen et al., 2004). Quantifying such effects is very challenging on young clearcuts and nearly impossible on old ones, due to succession.

Most of the spatial covariates I was able to collect for all the plots proved to be not significant for berry presence or abundance, with the only exception being slope and edge (Euclidian distance of the sample plot to the clearcut perimeter). Although soil moisture was found to be an important factor in berry presence, lack

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[1] Personal communication; Andreas Wedman - fire manager of Länsstyrelsen in Gävleborg, 2017.

of reliable soil moisture maps prevented me from extrapolating soil moisture data on the entire study area and problems in methodology prevented me from including it in the analysis. Suprisingly, aspect of the slope did not have an effect on either the presence or abundance of berries. I had expected that berries would grow best on south-facing slopes, with a higher degree of solar exposure. I consider H2 to be partially confirmed, becasue slope did positively influence presence and abundance of berries in most cases, showing a slight decrease only at higer slopes for lingonberry presence. The study area was defined as a landscape of gently rolling hills (Lodberg-Holm, 2015; Ordiz et al., 2012) and, consequently, there were not many steep slopes to sample. This can partially explain the high uncertainty of predictions in the models, particularly at higher slopes. Further, whereas there were variations within clearcuts, such as large rocks, puddles of water, and depressions, overall the clearcuts were quite uniform, as they were usually cut over a short time span and with the same method of harvest. Interestingly Euclidian distance from the edge of the clearcut was significant in the models for berry presence of both species. The trend shows a slightly higher presence of both species of berries farther away from the edge of the clearcut. One explanation could be shading from the surrounding forest.

When foraging, bears are constrained by a series of factors that ultimately guide their behaviour. Factors pertaining to bears include intake rate (function of bite rate and bite size), the physiological capacity of the gastrointestinal system and the efficiency of metabolism (Welch et al. 1997) and external factors are hunting risk, human encroachement, and thermoregulation (Hertel et al., 2016b; Pigeon et al., 2016). In order to gain the maximum amount of weight, bears need to maximize food intake, thus they should select for areas of high berry abundance while avoiding risk. Considering the patchy distribution of berries, each area has a different profitability, and thus a different rate of selection. In my study the treshold of selection was determined to be around 40 bilberries per m^2, which is in line with studies from Sweden (Hertel et al., 2016a) and North America, where they report a threshold of 44-50 berries per m^2 (Pelchat and Ruff 1986, Welch et al. 1997). This shows support for H3, as bears selected for clearcuts with a high probability of berry occurrence and abundance. However, across all 19 bears included in the bilberry period, the general selection for clearcuts was not strong, with only 10 % of all positions being on clearcuts. This can be partially be explained by the fact that bilberry, the food most selected for, was readily available in abundance in mature forests as well (Hertel et al., 2016a; Kardell, 1980, 1979). Another reason for low selection of clearcuts might be the bear hunting season, which starts on 21 August in Sweden (Swenson et al., 2017). This directly coincides with the fruiting period of bilberry and the start of fruiting period of lingonberry (Figure 2) which presents a challenge for bears. Effects of hunting on foraging behaviour of bears in my study area has been studied by Hertel et al. (2016b), who found that bears do indeed reduce foraging when hunting risk is high. Because clearcuts are characterized as open, bears might not select for them due to perceived hunting risk.

Perhaps fortunately for the bears, berries do not all ripen at the same time, with bilberry ripeness peaking around 15 August, when lingonberry only started to rippen. By the end of August, many bilberries found on clearcuts were starting to become overripe, becoming soft and falling off the bushes. Berries that have fallen off the bush are no longer available as a food resource for bears, suggesting that bears need to forage on alternative food resources, like lingonberry. Suprisingly this was not supported by my data, as bears showed low selection, or a selection close to random, for clearcuts high in lingonberry abundance. This might be due to the size of lingonberries, which are about a third of the size of bilberries (Hertel et al., 2016a). Thus bears would need to eat three times more to gain the same amount of energy. Additionally, lingonberry bushes are consistently shorter than bilberry bushes. If intake rate is reduced by bears having to bend lower, even the most profitable lingonberry patches might not be selected for. In a previous study in my study area, Hertel et al. (2016a) concluded that bears concentrate foraging on bilberries, rather than lingonberries, primarily because of their wide availability. This is further supported by the fact that bilberries have no significant advantage over lingonberries in terms of nutrition or energy gain (Coogan et al., 2014). Thus, I have rejected H3, that bears select for clearcuts of high berry presence and abundance, when considering lingonberries. Interestingly, both lingonberries and crowberries are more strongly attached to the bush and often stay on the bushes until after the winter, when they become an important food resource for bears after emerging from hibernation in the following spring (Dahle and Swenson, 2003; Stenset et al., 2016).

A potential source of bias in capturing the selection of clearcuts could be the frequency of recording GPS positions of bears, because the collars were set to take a position every hour. During two recordings of position, the bear could have gone on to the clearcut and back, thus falsely under- or overreporting the use of clearcuts.

Future studies could look at differences in clearcut use between sexes or solitary and nursing animals. This was unfeasible in my study, due to the heavily biased sex ratio and a low sample size of bears. Some other aspects to consider would be the effect of shape, size and time of the day on the use of clearcuts, as particularly shape has been shown to have an impact on clearcut use in North America (Scott E. Nielsen et al., 2004)

Conclusions

In this study I have found a nonlinear temporal relationship of berry presence and abundance following clearcutting. On young clearcuts, berry production is depressed, but steadily increases until it peaks on clearcuts around 8 years old. Afterwards, with the forest closing, berries probably become outcompeted by other plants, where heather is thought to have major impact, and berry production drops. Berry growth dynamics were found to be variable and could not be entirely explained by the methods used in this study. Another factor found to affect berry growth dynamics was slope, which had a positive linear effect on bilberries and a positive non-linear effect on lingonberries, with a slight decrease at higher slopes.

Bears adapt to these spatial and temporal dynamics by selecting for clearcuts of high bilberry presence and especially abundance. This trend was not observed in selection for lingonberry, perhaps because of the smaller size of lingonberries compared to bilberries. Selection for clearcuts was overall low, with only around 10% of all recorded locations being on clearcuts. This is thought to be due to the bear’s perceived risk of hunting on open clearcuts and the high availability of bilberries in mature forests.

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References

Angelstam, P.K., 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. J. Veg. Sci. 9, 593–602. https://doi.org/10.2307/3237275

Arnborg, T., 1990. Forest types of northern Sweden. Vegetatio 90, 1–13. https://doi.org/10.1007/BF00045585

Arnemo, J., Evans, A., Fahlman, Å., 2012. Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx, Hedmark University College. Evenstad. https://doi.org/10.13140/RG.2.1.2717.7120

Atlegrim, O., Sjöberg, K., 1996a. Effects of clear-cutting and single-tree selection harvests on herbivorous insect larvae feeding on bilberry (Vaccinium myrtillus) in uneven-aged boreal Picea abies forests. For. Ecol. Manage. 87, 139–148. https://doi.org/10.1016/S0378-1127(96)03830-3

Atlegrim, O., Sjöberg, K., 1996b. Response of bilberry (Vaccinium myrtillus) to clear-cutting and single-tree selection harvests in uneven-aged boreal Picea abies forests. For. Ecol. Manage. 86, 39–50. https://doi.org/10.1016/S0378-1127(96)03794-2

Barber, Q.E., Bater, C.W., Braid, A.C.R., Coops, N.C., Tompalski, P., Nielsen, S.E., 2016. Airborne laser scanning for modelling understory shrub abundance and productivity. For. Ecol. Manage. 377, 46–54. https://doi.org/10.1016/j.foreco.2016.06.037

Barklund, Å., 2009. The Swedish Forestry Model. Stockholm.

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of european forests. For. Ecol. Manage. 132, 39–50. https://doi.org/10.1016/S0378-1127(00)00378-9

Bergstedt, J., Milberg, P., 2001. The impact of logging intensity on field-layer vegetation in swedish boreal forests. For. Ecol. Manage. 154, 105–115. https://doi.org/10.1016/S0378-1127(00)00642-3

Boyce, M.S., 2006. Scale for resource selection functions. Divers. Distrib. 12, 269–276. https://doi.org/10.1111/j.1366-9516.2006.00243.x

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecol. Modell. 157, 281–300. https://doi.org/10.1016/S0304-3800(02)00200-4

Carlson, S.M., 2017. Synchronous timing of food resources triggers bears to switch from salmon to berries. Proc. Natl. Acad. Sci. 114, 201713968. https://doi.org/10.1073/pnas.1713968114

Ciarniello, L.M., Boyce, M.S., Seip, D.R., Heard, D.C., 2007. Grizzly bear habitat selection is scale dependent. Ecol. Appl. 17, 1424–1440. https://doi.org/10.1890/06-1100.1

Ciucci, P., Tosoni, E., Di Domenico, G., Quattrociocchi, F., Boitani, L., 2014. Seasonal and annual variation in the food habits of Apennine brown bears, central Italy. J. Mammal. 95, 572–586. https://doi.org/10.1644/13-MAMM-A-218

Coogan, S.C.P., Raubenheimer, D., Stenhouse, G.B., Nielsen, S.E., 2014. Macronutrient optimization and seasonal diet mixing in a large omnivore, the grizzly bear: A geometric analysis. PLoS One 9. https://doi.org/10.1371/journal.pone.0097968

Dahle, B., Sørensen, O.J., E.H., W., Swenson, J.E., Sandegren, F., 1998. The diet of brown bears Ursus arctos in central Scandinavia: Effect of access to free-ranging domestic sheep Ovis aries. Wildlife Biol. 4, 147–158.

Dahle, B., Swenson, J.E., 2003. Home ranges in adult Scandinavian brown bears (Ursus arctos): effect of mass, sex, reproductive category, population density and habitat type. J. Zool. 260, 329–335. https://doi.org/10.1017/S0952836903003753

Elfström, M., Swenson, J.E., Ball, J.P., 2008. Selection of denning habitats by

Scandinavian brown bears Ursus arctos. Wildlife Biol. 14, 176–187. https://doi.org/10.2981/0909-6396(2008)14[176:SODHBS]2.0.CO;2

Eriksson, O., Ehrlen, J., 1991. Phenological Variation in Fruit Characteristics in Vertebrate- Dispersed Plants. Oecologia 86, 463–470.

Fahlman, Å., Arnemo, J.M., Swenson, J.E., Pringle, J., Brunberg, S., Nyman, G., 2011. Physiologic evaluation of capture and anesthesia with medetomidine-zolazepam-tiletamine in brown bears (Ursus arctos). J. Zoo Wildl. Med. 42, 1–11. https://doi.org/10.1638/2008-0117.1

Frank, S.C., Steyaert, S.M.J.G., Swenson, J.E., Storch, I., Kindberg, J., Barck, H., Zedrosser, A., 2015. A “clearcut” case? Brown bear selection of coarse woody debris and carpenter ants on clearcuts. For. Ecol. Manage. 348, 164–173. https://doi.org/10.1016/j.foreco.2015.03.051

Gamfeldt, L., Snall, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Froberg, M., Stendahl, J., Philipson, C.D., Mikusinski, G., Andersson, E., Westerlund, B., Andren, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nat. Commun. 4, 1340. https://doi.org/10.1038/ncomms2328

Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Saher, D.J., Stevens, C.E., Jerde, C.L., 2006. Application of random effects to the study of resource selection by animals. J. Anim. Ecol. 75, 887–898. https://doi.org/10.1111/j.1365-2656.2006.01106.x

Gustafsson, L., Kouki, J., Sverdrup-Thygeson, A., 2010. Tree retention as a conservation measure in clear-cut forests of northern Europe: A review of ecological consequences. Scand. J. For. Res. 25, 295–308. https://doi.org/10.1080/02827581.2010.497495

Helander, C.-A., 2015. Forests and forestry in Sweden. Stockholm. https://doi.org/10.1007/BF00578267

Hertel, A.G., Steyaert, S.M.J.G., Zedrosser, A., Mysterud, A., Lodberg-Holm, H.K., Gelink, H.W., Kindberg, J., Swenson, J.E., 2016a. Bears and berries: species-specific selective foraging on a patchily distributed food resource in a human-altered landscape. Behav. Ecol. Sociobiol. 70, 831–842. https://doi.org/10.1007/s00265-016-2106-2

Hertel, A.G., Swenson, J.E., Bischof, R., 2017. A case for considering individual variation in diel activity patterns. Behav. Ecol. 28, 1524–1531. https://doi.org/10.1093/beheco/arx122

Hertel, A.G., Zedrosser, A., Mysterud, A., Stöen, O.G., Steyaert, S.M.J.G., Swenson, J.E., 2016b. Temporal effects of hunting on foraging behavior of an apex predator: Do bears forego foraging when risk is high? Oecologia 182, 1019–1029. https://doi.org/10.1007/s00442-016-3729-8

Kardell, L., 1980. Forest Berries and Mushrooms: An Endangered Resource? Ambio 9, 241–247.

Kardell, L., 1979. Occurrence and production of bilberry, lingonberry and raspberry in Sweden's forests. For. Ecol. Manage. 2, 285–298. https://doi.org/10.1016/0378-1127(79)90055-0

Kardell, L., Eriksson, L., 2011. Blåbärs- och lingonrisets återhämtning 30 år efter kalavverkning och markberedning 1977-2010. Umeå.

Kindberg, J., Swenson, J.E., 2014. Björnstammens storlek i Sverige 2013 – länsvisa uppskattningar och trender.

Kivinen, S., Moen, J., Berg, A., Eriksson, Å., 2010. Effects of modern forest management on winter grazing resources for reindeer in Sweden. Ambio 39, 269–278. https://doi.org/10.1007/s13280-010-0044-1

Kotliar, N.B., Wiens, J.A., 1990. Multiple Scales of Patchiness and Patch Structure: A Hierarchical Framework for the Study of Heterogeneity. Oikos 59, 253–260.

Kuuluvainen, T., 2009. Forest Management and Biodiversity Conservation Based on Natural Ecosystem Dynamics in Northern Europe: The Complexity Challenge. Ambio 38, 309–315.

Linder, P., Östlund, L., 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. Biol. Conserv. 85, 9–19. https://doi.org/10.1016/S0006-3207(97)00168-7

Lodberg-Holm, H.K., 2015. When the Hunter Becomes the Hunted: Impacts of Hunting on the Foraging Behavior of the Brown Bear (Ursus arctos) in Sweden. MSc Thesis, Nor. Univ. Life Sci. Norwegian University of Life Sciences.

Lyons, A.L., Gaines, W.L., Servheen, C., 2003. Black bear resource selection in the northeast Cascades, Washington. Biol. Conserv. 113, 55–62. https://doi.org/10.1016/S0006-3207(02)00349-X

Manly, B., McDonaldd, L., Thomas, D., 1993. Examples of the use of resource selection functions, in: Resource Selection by Animals: Statistical Design and Analysis for Field Studies. pp. 27–45.

Martin, J., Basille, M., Van Moorter, B., Kindberg, J., Allainé, D., Swenson, J.E., 2010. Coping with human disturbance: spatial and temporal tactics of the brown bear (Ursus arctos). Can. J. Zool. 88, 875–883. https://doi.org/10.1139/Z10-053

Mccune, B., 2007. Improved estimates of incident radiation and heat load using non-parametric regression against topographic variables. J. Veg. Sci. 18, 751–754. https://doi.org/10.1658/1100-9233(2007)18%5B751:IEOIRA%5D2.0.CO;2

McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. 13, 603–606. https://doi.org/10.1111/j.1654-1103.2002.tb02087.x

McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J., Woodley, S., 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. Environ. Rev. 9, 223–260. https://doi.org/10.1139/er-9-4-223

Miina, J., Hotanen, J.P., Salo, K., 2009. Modelling the abundance and temporal variation in the production of bilberry (Vaccinium myrtillus L.) in Finnish mineral soil forests. Silva Fenn. 43, 577–593. https://doi.org/10.14214/sf.181

Moe, T.F., Kindberg, J., Jansson, I., Swenson, J.E., 2007. Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (Ursus arctos). Can. J. Zool. 85, 518–525. https://doi.org/10.1139/Z07-034

Nellemann, C., Fry, G., 1995. Quantitative analysis of terrain ruggedness in reindeer winter grounds. Arctic 48, 172–176. https://doi.org/10.14430/arctic1239

Nellemann, C., Støen, O.G., Kindberg, J., Swenson, J.E., Vistnes, I., Ericsson, G., Katajisto, J., Kaltenborn, B.P., Martin, J., Ordiz, A., 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. Biol. Conserv. 138, 157–165. https://doi.org/10.1016/j.biocon.2007.04.011

Nielsen, S.E., Boyce, M.S., Stenhouse, G.B., 2004. Grizzly bears and forestry: I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. For. Ecol. Manage. 199, 51–65. https://doi.org/10.1016/j.foreco.2004.04.014

Nielsen, S.E., Munro, R.H.M., Bainbridge, E.L., Stenhouse, G.B., Boyce, M.S., 2004. Grizzly bears and forestry: II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. For. Ecol. Manage. 199, 67–82. https://doi.org/10.1016/j.foreco.2004.04.015

Niemelä, J., 1999. Management in relation to disturbance in the boreal forest. For. Ecol. Manage. 115, 127–134. https://doi.org/10.1016/S0378-1127(98)00393-4

Nilsson, M.C., Wardle, D.A., 2005. Understory vegetation as a forest ecosystem driver: Evidence from the northern Swedish boreal forest. Front. Ecol. Environ. 3, 421–428. https://doi.org/10.2307/3868658

Nilsson, P., Cory, N., 2017. Forest statistics 2017. Umeå.

Ordiz, A., Kindberg, J., Sæbø, S., Swenson, J.E., Støen, O.G., 2014. Brown bear circadian behavior reveals human environmental encroachment. Biol. Conserv. 173, 1–9. https://doi.org/10.1016/j.biocon.2014.03.006

Ordiz, A., Støen, O.G., Sæbø, S., Kindberg, J., Delibes, M., Swenson, J.E., 2012. Do bears know they are being hunted? Biol. Conserv. 152, 21–28. https://doi.org/10.1016/j.biocon.2012.04.006

Persson, I., Wikan, S., Swenson, J.E., Mysterud, I., 2001. The diet of the brown bear Ursus arctos in the Pasvik Valley, northeastern Norway. Wildlife Biol. 7, 27–37.

Pigeon, K.E., Cardinal, E., Stenhouse, G.B., Côté, S.D., 2016. Staying cool in a changing landscape: the influence of maximum daily ambient temperature on grizzly bear habitat selection. Oecologia 181, 1101–1116. https://doi.org/10.1007/s00442-016-3630-5

Rosenvald, R., Lõhmus, A., 2008. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. For.

Ecol. Manage. 255, 1–15. https://doi.org/10.1016/j.foreco.2007.09.016

Schoonmaker, P., McKee, A., 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. For. Sci. 34, 960–979.

Servheen, C., 1983. Grizzly bear food habits, movements, and habitat selection in the Mission Mountains, Montana. J. Wildl. Manage. 47, 1026–1035. https://doi.org/10.2307/3808161

Skidmore, A.K., 1989. A comparison of techniques for calculating gradient and aspect from a gridded digital elevation model. Int. J. Geogr. Inf. Syst. 3, 323–334. https://doi.org/10.1080/02693798908941519

Solberg, K.H., Bellemain, E., Drageset, O.-M., Taberlet, P., Swenson, J.E., 2006. An evaluation of field and non-invasive genetic methods to estimate brown bear (Ursus arctos) population size. Biol. Conserv. 128, 158–168. https://doi.org/10.1016/j.biocon.2005.09.025

Stenset, N.E., Lutnæs, P.N., Bjarnadóttir, V., Dahle, B., Fossum, K.H., Jigsved, P., Johansen, T., Neumann, W., Opseth, O., Rønning, O., Steyaert, S.M.J.G., Zedrosser, A., Brunberg, S., Swenson, J.E., 2016. Seasonal and annual variation in the diet of brown bears *Ursus arctos* in the boreal forest of southcentral Sweden. Wildlife Biol. 22, 107–116. https://doi.org/10.2981/wlb.00194

Swenson, J.E., Jansson, A., Riig, R., Sandegren, F., 1999. Bears and ants: myrmecophagy by brown bears in central Scandinavia. Can. J. Zool. 77, 551–561. https://doi.org/10.1139/z99-004

Swenson, J.E., Kindberg, J., 2015. The Scandinavian Brown Bear Research Project Report 2015.

Swenson, J.E., Schneider, M., Zedrosser, A., Söderberg, A., Franzén, R., Kindberg, J., 2017. Challenges of managing a European brown bear population; lessons from Sweden, 1943–2013. Wildlife Biol. 1, wlb.00251. https://doi.org/10.2981/wlb.00251

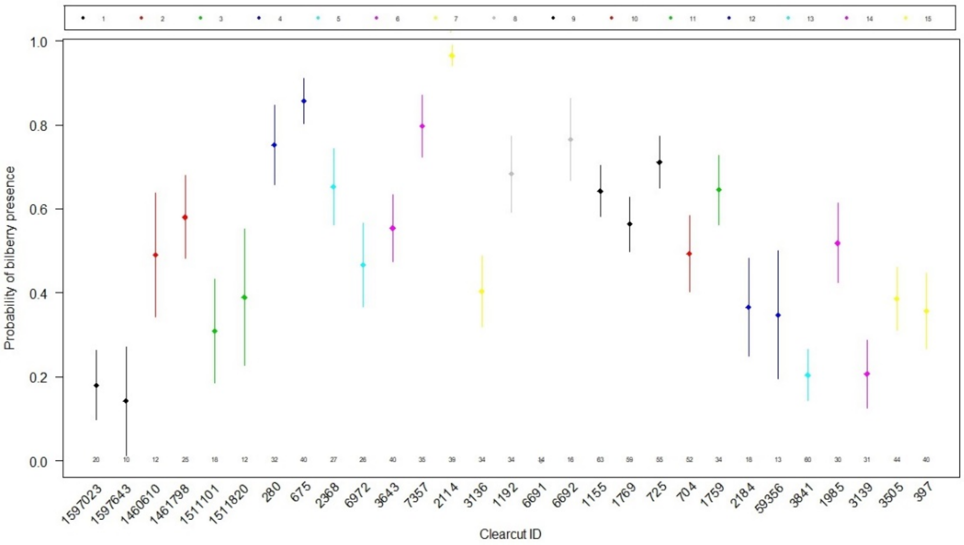
Thiffault, E., Bélanger, N., Paré, D., Munson, A.D., 2007. How do forest harvesting methods compare with wildfire? A case study of soil chemistry and tree nutrition in the boreal forest. Can. J. For. Res. 37, 1658–1668. https://doi.org/10.1139/X07-031

Zedrosser, A., Støen, O.G., Sæbø, S., Swenson, J.E., 2007. Should I stay or should I go? Natal dispersal in the brown bear. Anim. Behav. 74, 369–376. https://doi.org/10.1016/j.anbehav.2006.09.015

Zuur, A.F., Ieno, E.N., 2009. Mixed Effects Models and Extensions in Ecology with R, 1st ed. Springer Science+Business Media LLC, New York. https://doi.org/10.1017/CBO9781107415324.004

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Appendix



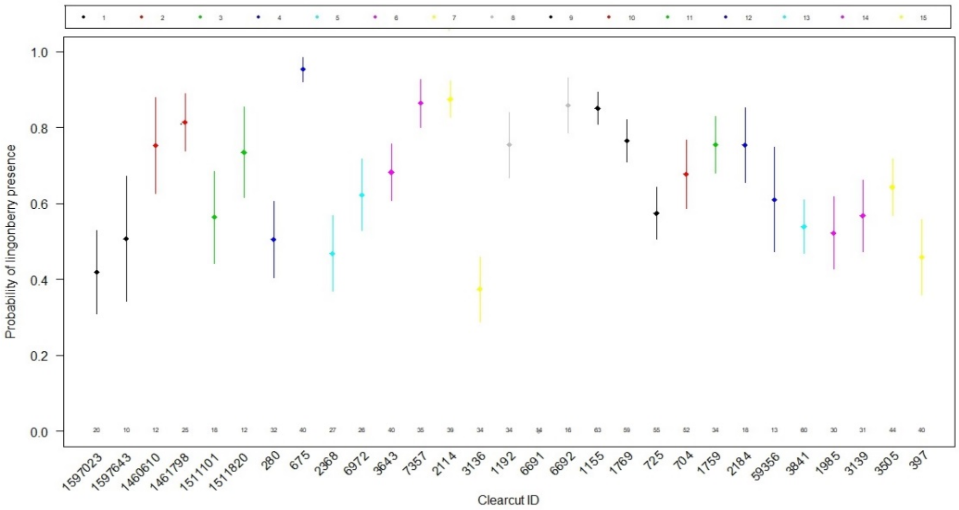
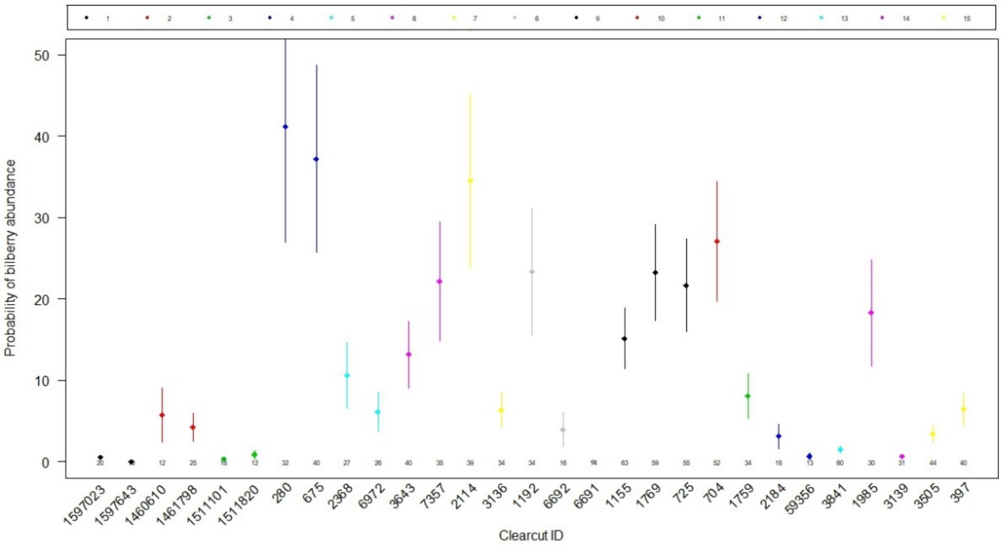


Figure A1: Probability of bilberry and lingonberry presence on clearcuts on the study area in south-central Sweden using only clearcut ID, ordered and coloured by age. Numbers below the X axis represent unique clearcut IDs and numbers above the X axis represent number of plots of those same clearcuts. Vertical lines from the data points are 95% confidence intervals.



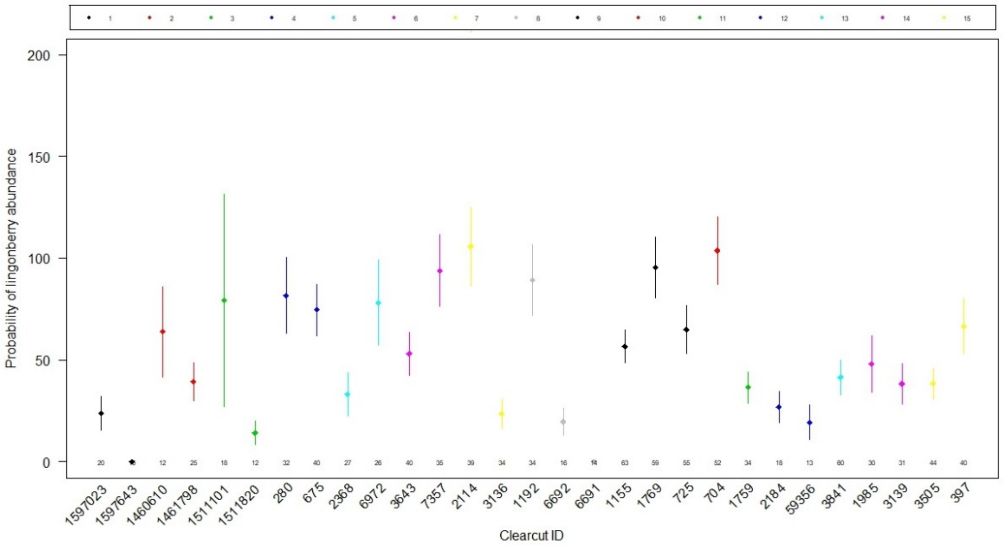


Figure A2: Predicted bilberry and lingonberry abundance per square meter on clearcuts on the study area in south-central Sweden using only clearcut ID, ordered and coloured by age. Numbers below the X axis represent unique clearcut IDs and numbers above the X axis represent number of plots of those same clearcuts. The non-linear trend is still visible, although less pronounced then with berry presence.

Picture A1: Collection of berries in the field using a 1x1m plot. (Matej Domevscik, 2017)

Picture A2: Counting and weighing berries at the field station. (Matej Domevscik, 2017)

Picture A3: A two-year-old clearcut, still barren with a lot of woody debris on the ground. (Matej Domevscik, 2017)

Picture A4: An eight-year-old clearcut in early stages of succession. Spruce and birch are starting to grow and heather slowly takes over the understory. (Matej Domevscik, 2017)

Picture A5: A 14-year-old clearcut with dense vegetation starting to close in. (Matej Domevscik, 2017)

Picture A6: Charred wood and ash. This clearcut was recorded as 8 years old, but obvious fire management was performed sometime after that. (Matej Domevscik, 2017)

Picture A7: Fire scar on a standing woody debris. This clearcut was recorded as 8 years old, but obvious fire management was performed sometime after that. (Matej Domevscik, 2017)

Table A1: Number, weight, ripeness and height distribution of three berry species collected during 24 July to 30 August 2017 in south-central Sweden.

	Bilberry	**Lingonberry**	**Crowberry**
Number/berry species	13,223	40,044	4,152
% total number	0.23	0.69	0.07
Total number of berries	57,419	57,419	57,419
Number of ripe	11,938	5,207	3,975
% number ripe	0.90	0.13	0.96
Number of unripe	1,285	34,837	177
% number unripe	0.10	0.87	0.04
Ripe weight/berry species [g]	4,164	1,308	1,026
% total ripe weight	0.64	0.20	0.16
Total ripe weight of berries [g]	6,498	6,498	6,498
Unripe weight/berry species [g]	320	4,375	18
% total unripe weight	0.06	0.92	0.004
Total unripe weight of berries [g]	4,713	4,713	4,713
Total weight of all berries [g]	11,211	11,211	11,211
Average height/berry species [cm]	19.37	9.97	13.69
Maximum height/berry species [cm]	44	25	31
Minimum height/berry species [cm]	4	3	3

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2017:15	Analysing the seal-fishery conflict in the Baltic Sea and exploring new ways of looking at marine mammal movement data Författare: Ornella Jogi
2017:16	Importance of sampling design using an eDNA monitoring approach for pond-living amphibians Författare: Sabrina Mittl
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