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Hotspots of fear: Effects of wolves on tree recruitment in the Białowieża Primeval Forest

by

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Declaration

"I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person nor material which to a substantial extent has been accepted for the award of any other degree or diploma of the university or other institute of higher learning, except where due acknowledgment has been made in the text".

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Abstract

The landscape of fear concept has been extensively studied in different large scale ecosystems such as the North American Yellowstone National Park. In this area, elk (*Cervus elaphus)* have been shown to change large scale movement and foraging patterns to avoid predation by wolves (*Canis lupus*). After reintroduction of wolves and consequent effects on elk occurrence and distribution, several tree species have recovered due to decreased elk browsing pressure. In an European temperate forest system, the Białowieża Primeval Forest, a recent study suggests small scale shifts (<1km) of ungulate behaviour caused by the presence of wolf. Woodland habitat characteristics such as coarse woody debris (CWD) were considered to act as escape impediments for red deer (*C. elaphus*) that resulted in reduced local browsing pressure. However, the effect of this lower browsing pressure on tree recruitment in the vicinity of CWD has not yet been verified. In this study, I compared tree seedling numbers and tree recruitment effects of presence of CWD combined with a wolf core area and a gradient of wolf activity in the strict reserve in the Białowieża Primeval Forest. I sampled seedling number, seedling species and seedling height (<2m) in plots with CWD paired with control plots without CWD in areas of deciduous forest. Additionally, I recorded features of CWD (e.g. height, length, presence of branches), as well as potential confounding factors such as the canopy openness. Successful recruitment of a tree was defined as seedling tree height exceeding ungulate browsing reach (>2m). The data I gathered required to be controlled for zero truncation, overdispersion, and zero inflation issues, and eventually were modeled using zero truncated generalized models and negative binomial mixed effects zero inflated models. In regard to the occurrence of seedlings, their numbers were not facilitated by the presence of CWD neither by wolf occurrence. Indeed, I only found a quadratic effect of canopy openness on seedling occurrence, with an optimum at 20% of canopy closure. However, tree recruitment (e.g., increased likelihood of seedlings reaching 2 meters of height) was facilitated in direct vicinity of CWD (Kaplan Meier Survival Analysis, $\rho 1<0.0001$). Within control plots (no-CWD), tree recruitment was significant lower due to higher mortality or overbrowsing pressure, leading plants to remain short. Interestingly, higher numbers of seedlings were associated with increasing CWD height ($p=0.048$), irrespective to the probability of encountering the wolf. Other characteristics (presence of branches, uprooted tree, CWD length, CWD species, CWD age class and CWD volume) were not significantly contributing to the model. This study is the first one that indicated an effect of a certain CWD feature on tree recruitment. My results included a first comprehension of the underlying behavioral mechanism. Red deer avoided browsing close to high CWD, which is likely, a result of reduced visibility and higher escape impediments. The avoidance of this habitat characteristic appears important for tree recruitment close to CWD in this small scale European forest situation. High CWD seems perceived by red deer as a ‘hotspot of fear’ throughout the whole area of the strict reserve.

Introduction

The direct and indirect effects of large carnivore presence on prey populations have been investigated in several studies of large scale ecosystems such as the Yellowstone National Park, Wyoming (Hayward et al. 2005; Brown 1999; Li et al. 2009; Laundré et al. 2009). Trophic cascade patterns used to be explained by density- mediated top down control of predators (Ripple & Beschta 2005). Recently, several studies indicate increasing consent for behaviorally- mediated trophic cascades (Beckerman et al. 1997; Beyer et al. 2007). However, the debate is still ongoing, whether behaviorally mediated effects are the main driver for trophic cascade effects or just a factor of minor importance (Kauffman et al. 2010; Winnie 2012). Trophic cascades alter community structures and energy fluxes (Ripple & Beschta 2012a; Ripple et al. 2014; Painter et al. 2014b). In the Yellowstone system, after reintroduction of wolves (*Canis lupus*) in 1995, several tree species, such as aspen and cottonwood could recover from elk (*Cervus elaphus)* related browsing (Figure 1) (Ripple & Beschta 2012b; Painter et al. 2014a).

The underlying mechanism of the landscape of fear concept includes changes of large scale movement and foraging patterns, habitat selection as well as group size of ungulates to reduce predation risk (Fortin et al. 2005; Creel & Winnie 2005; Middleton et al. 2013). Several studies on North American systems confirm that this antipredator behavior results in decreasing browsing pressures and facilitation of seedling recruitment (Figure 2) (Ripple et al. 2001; Ripple & Beschta 2003; Beschta & Ripple 2013).

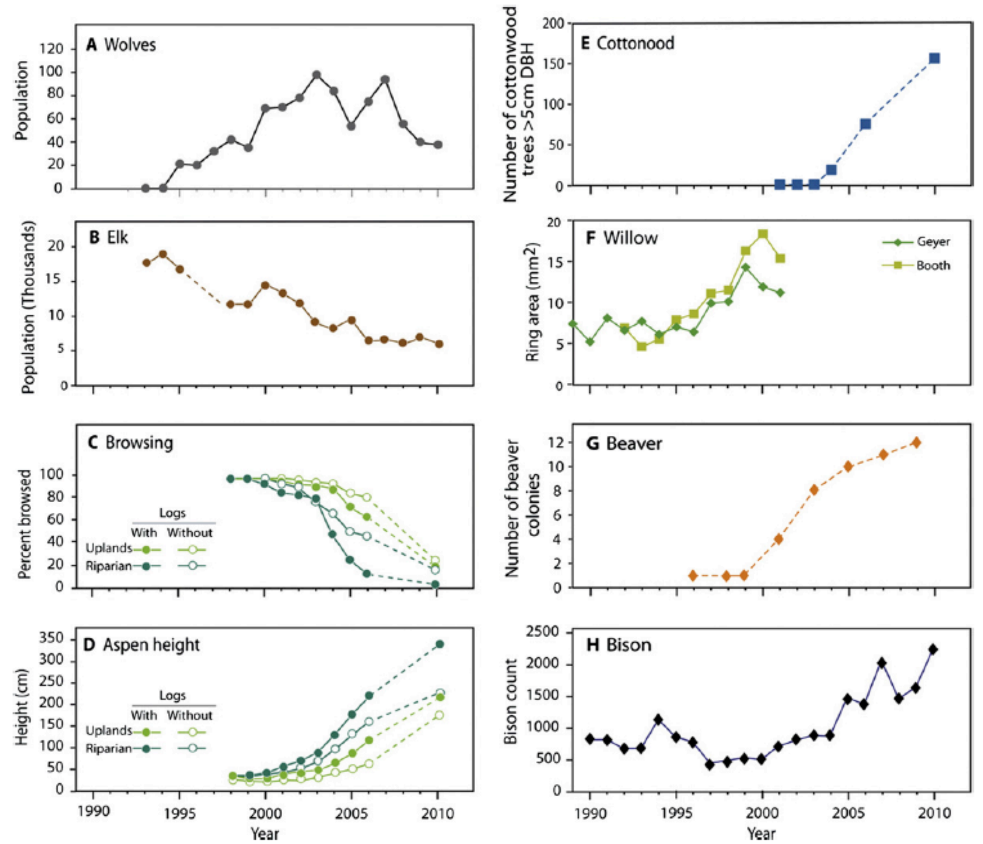


Figure 1: Trends in (A) wolf populations, (B) elk populations, (C) percentage of aspen leaders browsed, (D) mean aspen heights, (E) cottonwood recruitment, (F) willow ring area, (G) number of beaver colonies, and (H) summer bison counts in the Yellowstone National Park. Modified from Ripple and Beschta 2012

Certain small scale habitat characteristics that decrease visibility or act as escape impediments are considered to cause avoidance and increasing vigilance behavior in ungulates (Halofsky & Ripple 2008; Ripple & Beschta 2004). The same researchers indicated in their studies increasing vigilance behavior and reduced browsing rates in the presence of coarse woody debris (CWD), which suggest a riskiness of this habitat characteristic for elk (Halofsky & Ripple 2008; Ripple & Beschta 2006). CWD is contemplated as escape impediment for ungulates, since they may hinder escape routes (Halofsky & Ripple 2008). Nevertheless, the evidence for increasing perceived predation risk combined with small scale habitat features persists to be strongly debated (Kauffman et al. 2010; Winnie 2012).

Figure 2: A) Aspen recruitment (3–4m tall) and (B) a lack of recent aspen recruitment (aspen <1m tall) caused by elk. Modified from Ripple and Beschta 2012

In small-scale European systems with dense forests, fine scale habitat characteristics as well as gap dynamics seem to be more influential for seedling occurrence (Kuijper et al. 2013). So far, the study of behavioral mediated trophic cascade effects is rather scarce in Europe. Possible reasons for that lack of research are the absence of large predators in most areas and the poverty in undisturbed habitats.

An exception is the Białowieża Primeval Forest in Poland, where the coexistence of large predators such as the wolf (*Canis lupus*) with several ungulate species, including their most abundant prey species, the red deer (*C. elaphus*) facilitates research on trophic cascade effects. The Białowieża Primeval Forest was formerly protected by the monarchy as a hunting reserve and became declared as a National Park in 1921. Because of that, anthropogenic influence used to be low and since the establishment of the strict protected area, human intervention became minimized in that area. In this forest, there are no areas where predators are absent, as in large scales of North American systems (Schmidt et al. 2009). Ungulates can reduce predation risk by avoiding areas with high predator frequency and by reacting to small scale habitat features (Kuijper et al. 2013).

Red deer is considered to have a significant impact on tree regeneration and tree stand dynamics (Kuijper et al. 2010; Kuijper et al. 2010). Recent studies in the Białowieża forest indicate perceived predation risk by an increase of red deer vigilance behavior in wolf territories with low visibility (Kuijper et al. 2014). In addition, CWD presence caused decreasing browsing rates on seedlings in wolf core areas (Kuijper et al. 2013).

In the present study, I tested the effect of CWD combined with a wolf core area and a gradient for wolf activity on seedling numbers and tree recruitment. My hypothesis was that the presence of wolf combined with CWD would overweigh the negative effect of ungulate browsing on seedlings, and thereby facilitates higher seedling numbers and tree recruitment (Figure 3). In addition, I tested the effect of CWD features that might lead to decreasing red deer browsing rates close to CWD, and that way enable the occurrence of higher seedling numbers. My expectation was that certain CWD features are likely to strength the perceived predation risk and that my study would contribute to understand the behavioral mechanism behind this effect.

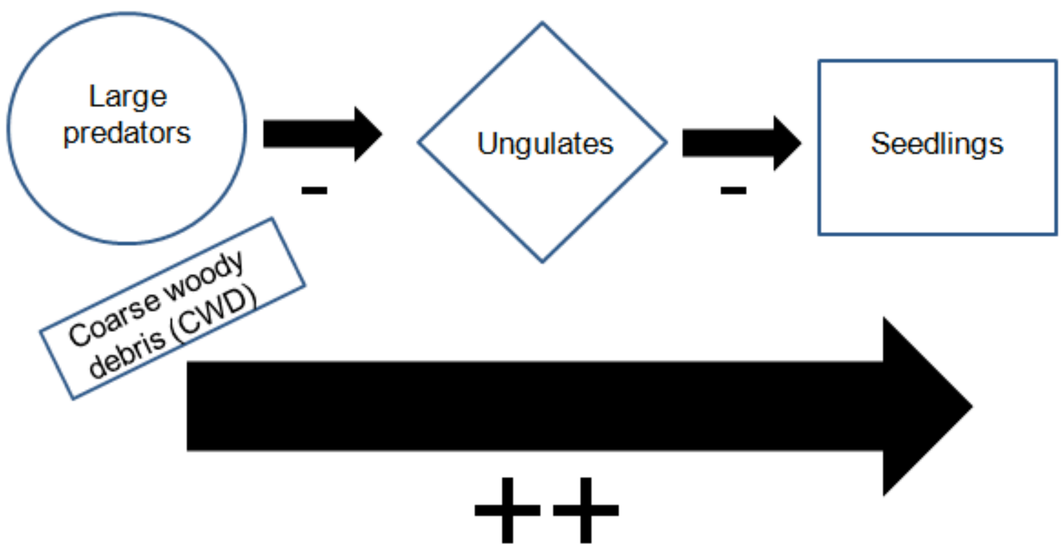


Figure 3: Conceptual model of effects of simultaneous wolf presence and coarse woody debris occurrence on ungulate behavior and seedling occurrence. Ungulates are expected to perceive higher predation risk (-) in the presence of wolf and close to CWDs, and, consequently, seedling numbers and or tree recruitment are expected to enhance (++)

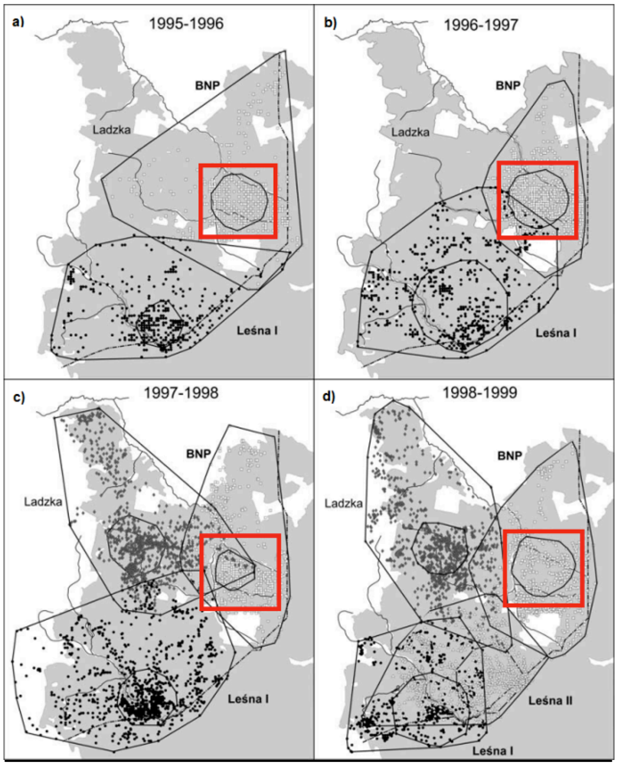
Methods

2.1. Study area

The study site is located in the polish part of the Białowieża Primeval Forest that ranges from eastern Poland to western Belarus (52° 45 'N, 24°00' E). The polish Białowieża forest has a size of 103 km^2, including 79 km^2 of strictly protected area. It consists of a mosaic of different forest types dominated by deciduous forests about 54% (*Quercus robur, Tilia cordata, Carpinus betulus*) and mixed deciduous forest about 23% (*Picea abies, Quercus robur, Tilia cordata, Carpinus betulus*). Mean annual temperature of the area is 6.8 °C and mean annual precipitation is 641 mm.

The Białowieża lowland forests are considered to be the best preserved European forest systems with very low human influence. The remoteness and protection status of the forest since decades is facilitating habitat to many species that are rare or endangered on a European scale.

In the polish part of the forest, there are four wolf territories that occupy the whole area (Figure 4). Jedrezejewski et al. (2007) established the concept of wolf core areas, which is defined as part of the territory, where packs are abundant >50%/ year and dens are located (Jedrzejewski et al. 2007). Another concept includes the idea of a gradient of perceived wolf risk. Centroids were a result of several data, indicating the center of wolf activity, including a telemetry study showing locations of den sites (Schmidt et al. 2008) and a road survey by the Mammal Research Institute for wolf signs (scats, tracks, urination, territorial scratching) in the strict reserve (Figure 5). Following, data were weighted and centroids of wolf activity were calculated (Churski, M., *unpublished*).



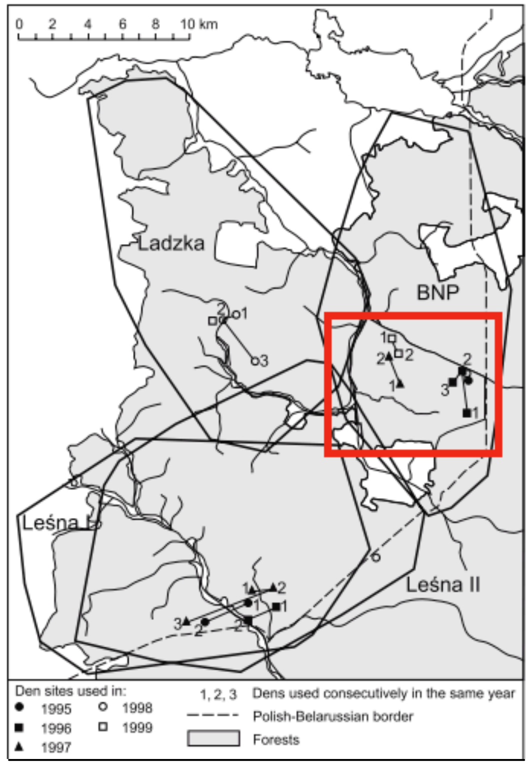


Figure 5: Maps of annual territories of 2 to 4 wolf packs inhabiting the Polish part of Białowieża Primeval Forest from a) 1995 till d) 1999. The strict reserve wolf pack is marked in red, their territory remains constant. d) Data were used as a model for the core area borders I used. Modified from Jedrzejewski et al 2000

Figure 4: Locations of den sites in the territories of wolf packs in the Białowieża Primeval Forest, Poland in 1996- 1999. The pack of the strict reserve is highlighted in red. Modified from Schmidt et al 2008

The main prey species of Białowieżan wolves is red deer (*Cervus elaphus*), which account up to 63% of the diet. Red deer represents the most abundant ungulate species (~12 individuals/ km^2) and is considered to cause high impact on forest structure by browsing (Jedrzejewski et al. 2002). Other ungulate species occur in lower densities such as wild boar (*Sus scrofa)* with approximate 10 individuals/km^2, roe deer (*Capreolus capreolus)* with 2 individuals/km^2, European bison (*Bison bonasus*) with 0.8 individuals/km^2 and moose (*Alces alces*) with 0.4 individuals/km^2). (Schmidt et al. 2008).

2.2.1. Seedling sampling on CWD and control plots

Data collection took place between May and mid June 2014. The sampled forest types were deciduous and wet deciduous forests because food resources of these forests are determinant in the ungulate diet (Jedrzejewska et al. 1994; Kamler et al. 2008). All transects were set up in the strict reserve to exclude anthropogenic effects. I used random transects with a length of 200m and a width of 40m. Transects had a buffer of 10m to walkways and other forest types. Kuijper et al (2013) established starting points of transects inside and outside the wolf core area that were used. In addition, I created new random transects inside and outside the wolf core area and with different distances to centroids of wolf activity. Walking directions of transects changed clockwise. In order to define the border of wolf core area, a GIS layer was used with similar borders of the core area by Jedrzejewski et al 2007. Centroids were also inserted to the GIS map and exact distances to transect starting points were calculated (Figure 6).

Along the transects, I established a plot around each CWD that had a minimum of >10m length and >1m height. Plot centers were set centric, at each site of the CWD in order to receive an equal radius. Control plots were set 20m away from the CWD center.

A total of 48 plots were sampled (12 CWD plots inside wolf core area, 12 CWD plots outside wolf core area and 24 control plots, respectively) (Appendix III).

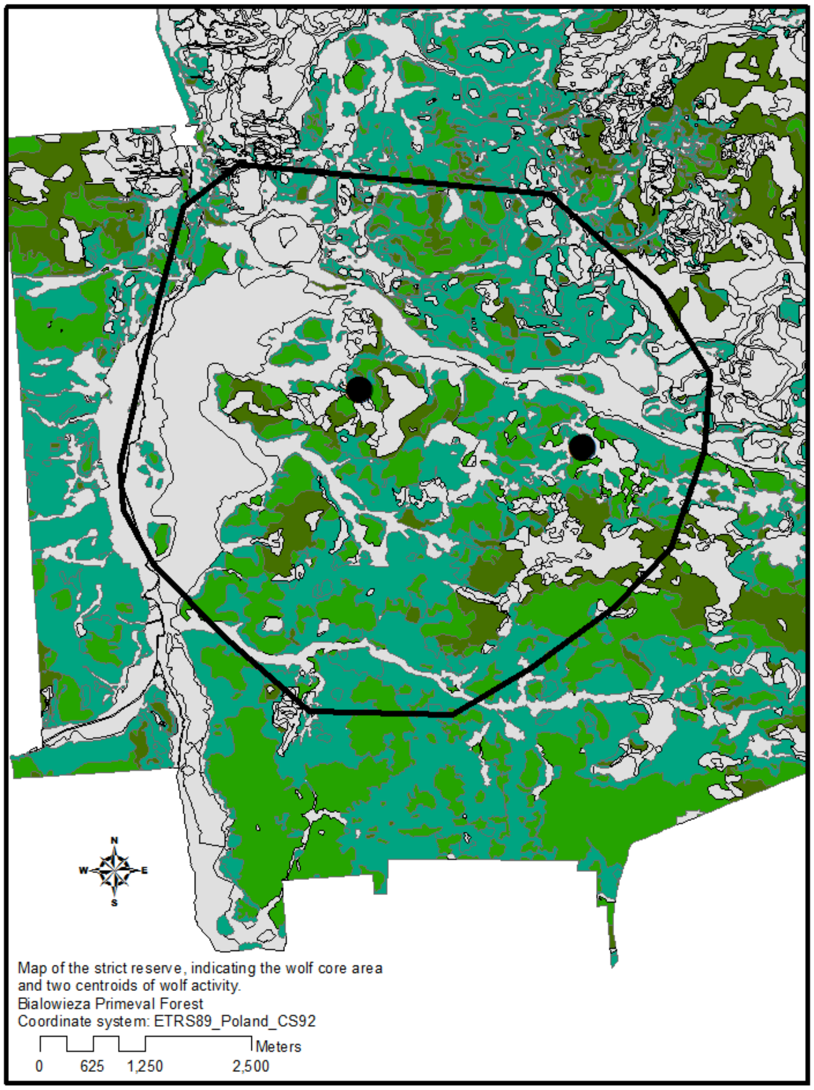


Figure 6: Map of the strict reserve, indicating the wolf core area and the centroids of wolf activity in the Białowieża Primeval Forest. Decidous forest areas are indicated in green and blue: Data obtained: Jedrzejewski et al 2007 and Mammal Research Institute Białowieża

I used field map equipment (www.ifer.cz) to store and map data about seedling species, seedling numbers and seedling heights in each plot. Heights were categorized in classes 1-7 (in 30cm intervals). Class 1 represented the smallest and 7 the tallest size class. Seedling heights were recorded up to 2m, because at this height they are considered to be out of reach for browsing ungulates and may be part of the mature forest after tree recruitment (Figure 7) (Painter et al. 2014a; Kuijper et al. 2013).

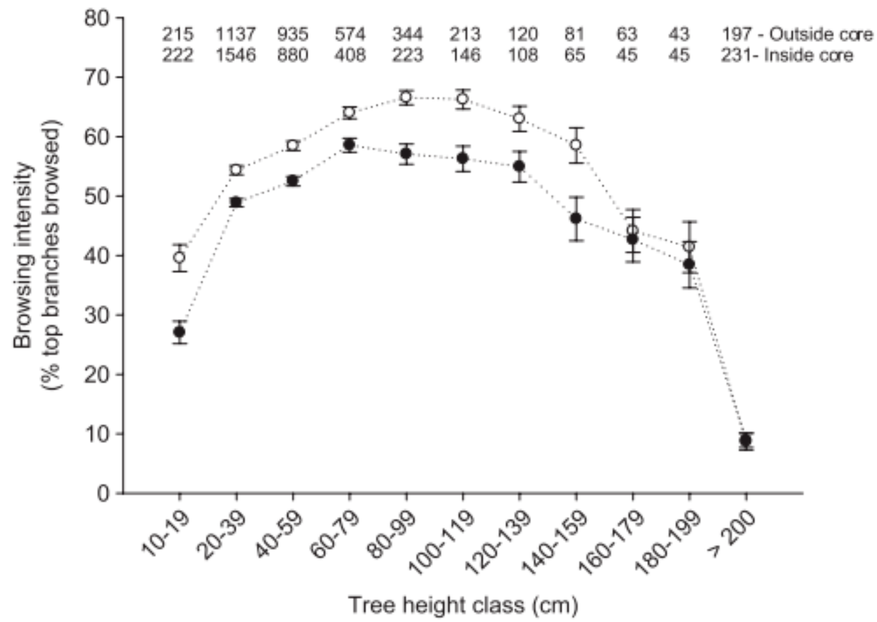


Figure 7: Browsing intensity of tree sapling per height class outside ( ) and inside (•) the wolf core area measured as the proportion of browsed top 10 branches at different classes of tree sapling height. Averages (SE) are based on 17 transects inside and outside the wolf core area. Sample sizes are indicated at the top of the graph. Modified from Kuijper et al 2013.

2.2.2. Sampling of CWD features and canopy openness

In addition to the seedling counts, I used the field map equipment to record CWD features that might influence ungulates behavior in the presence of CWD and result in higher seedling numbers and enhance tree recruitment. The considered features include length, height, volume, CWD species, CWD age class, presence of branches and uprooted tree.

I expected that canopy cover could have an influence on seedling numbers. In order to integrate this confounding factor to the data analysis, a fisheye objective was used to take a picture of the canopy in the plot center.

2.3. Statistical analysis

2.3.1 Seedling numbers

For the analysis of seedling numbers, all size classes were considered together, being interested on the number of plants <2m in plots depending on CWD proximity and wolf occurrence. More in detail, I considered the total number of seedlings occurring in each of the 48 plots (24 CWDs, 24 no-CWDs). The cumulative dataset was clearly zero-truncated, having always at least one seedling per plot.

I used the vglm function from the VGAM package in R to fit the data in a zero-truncated model with Poisson distribution of errors. The model fit indicated a strong significant interaction between wolf area and CWD presence as well as centroids and CWD presence in affecting seedling numbers. However, after checking for overdispersion, I needed to switch to a zero truncated negative binomial model that models zero- truncated count data and allows an overdispersion. Canopy openness was included in the model to take into account of light effect on seedling numbers. I included a quadratic term to allow for non-linear relationships.

After modeling, I used the boot package for bootstrapping to get confidence intervals for the parameters and the exponentiated parameters of CWD presence and wolf area. In this case, confidence intervals were not created for the predicted value themselves, but for the mean predicted value. In order to apply it to a negative binomial model, incident risk ratios were used based on the existing coefficients. I used the boot function to execute 2000 replicates to achieve stable results.

2.3.2 Tree recruitment

I used the Kaplan Meier survival estimate (survival package in R) to calculate tree recruitment rates. The main assumption for any survival analysis is the distribution of the positive value T that indicates the moment when a specific event takes place. The Kaplan Meier estimate is a right continuous step function that uses events as time intervals. In my estimate, T is representing the size class of a seedling at the time of its disappearance/ death.

I used this estimation to compare differences in browsing pressure / mortality for all seedling species on CWD vs control, and wolf core area vs non core area. In addition, I checked for significant interaction of CWD presence and wolf area. For the centroids of wolf activity, I created categories of transect starting points with "small" and "tall" distances to the centroids. Categories were set at < 2km and >2km and <4km and >4km. By the creation of these categories, at least 1/3 of the data remained in each category.

I assumed tree recruitment (seedling survival), where T=7. The Kaplan Meier index is defined as a nonparametric maximum likelihood estimate (Griess et al. 2012):

$$\hat{S}(t) = \prod_{t_i<t} \frac{n_i - d_i}{n_i}. \qquad \text{(Eq 1)}$$

where S(t) is the estimated survival probability for the t events, n_i represents the number of individuals at the start of time t_i and d_i is the number of dead individuals at ti (Eq 1).

2.3.3 CWD features

For the analysis of the effects of certain CWD features on seedling numbers, I used the glmmADMB package in R. I utilized a zero inflated negative binomial mixed model to model the effect on number of seedlings in proximity of CWD spots. Zero-inflated negative binomial models are used for count data with excessive zeros (more than those predicted by a Poisson distribution) combined with overdispersion.

In the full models, I used seedling number as a response variable and I tested for interactions with wolf core area, distance to centroids of wolf activity and canopy openness, which I included as a quadratic term. In addition, I used several variables of CWD features: CWD height, length and uprooted tree and seedling species. Plot ID was set as random effect. I did backward stepwise selection to remove non significant variables.

2.3.4 Canopy openness

For the estimation canopy openness, I imported the fisheye photographs in the Gap Light Analyser. This imaging software can be used to extract canopy structure and gap light. I improved the color contrast into a separate RGB plane and corrected the picture according to distorted light conditions (Figure 8, Figure 9). Finally, canopy openness was estimated.

Figure 9: Fisheye photograph of canopy for the estimation of Canopy openness

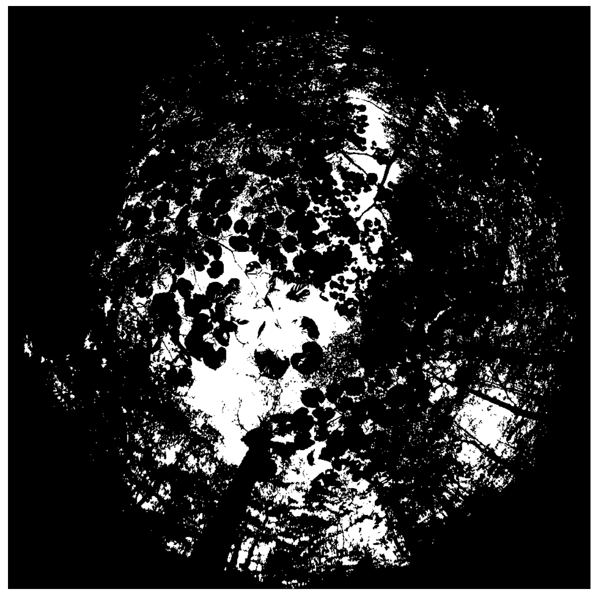


Figure 8: Edited fisheye picture for the estimation of canopy openness using Gap Light Analyser software

Results

3.1. Seedling numbers

I modeled the data using a zero truncated negative binomial model. I used seedling number as response variable and wolf core area, seedling height and canopy openness as independent variables. The interaction of seedling numbers and wolf core area was removed, as well as the non significant variable of seedling height. The same selection process resulted the best fitting model for centroid data of wolf activity.

Seedling numbers were not different depending on wolf occurrence (inside and outside wolf core area) or CWD presence (Table 1). I observed a slight trend of increasing seedling numbers in the wolf core area, not significant though (Figure 10). In my dataset, canopy openness ranged between 11.3% and 28.3% with a mean of 18.41%. Canopy openness had a slightly significant quadratic effect, indicating an optimum at a canopy openness of 20% for seedling occurrence (Figure 10). Wide confidence intervals for predicted values of the effect of CWD and wolf core area on seedling numbers are clearly wide suggesting a fairly weak effect (Appendix I).

Table 1: Exponentiated parameter estimates with percentile and bias adjusted confidence intervals. Confidence intervals overlapping 1 indicate the lack of significance of the effect of CWD and wolf presence on seedling numbers

	Estimate	PLL	PUL
CWD	1.013	0.616	1.590
Wolf	1.2141	0.818	2.111
Canopy openness	1.337	0.834	2.119
Canopy openness^2	0.993	0.980	1.004

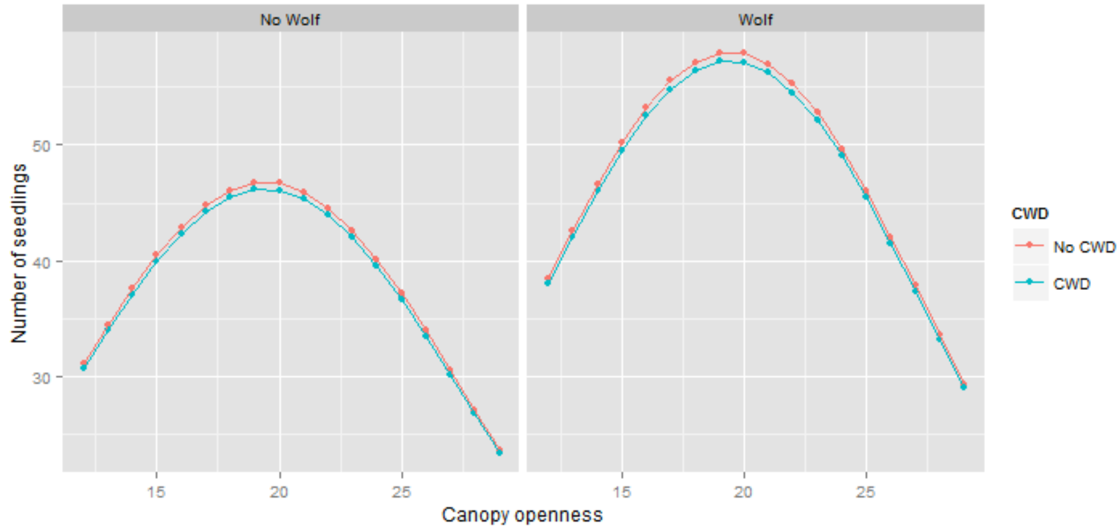


Figure 10: Plots of CWD presence per wolf area. CWD does not have an effect on number of plants,. Canopy openness has an optimum at 20% in affecting seedling numbers.

Distance to the center of wolf activity did not affect seedling numbers (Table 2), although I observed a slightly increasing trend on seedling numbers with decreasing distance to the centroids (Figure 11). However, the effect of wolf activity on seedling numbers was not significant (Table 2).

Table 2: Exponentiated parameter estimates with percentile and bias adjusted confidence intervals. Confidence intervals overlapping 1 indicate the lack of significance for CWD and distance to wolf centroids

	Estimate	PLL	PUL
CWD	1.002	0.565	1.596
Distance to Wolf	0.897	0.727	1.027
Canopy openness	1.282	0.760	2.131
Canopy openness^2	0.994	0.980	1.010

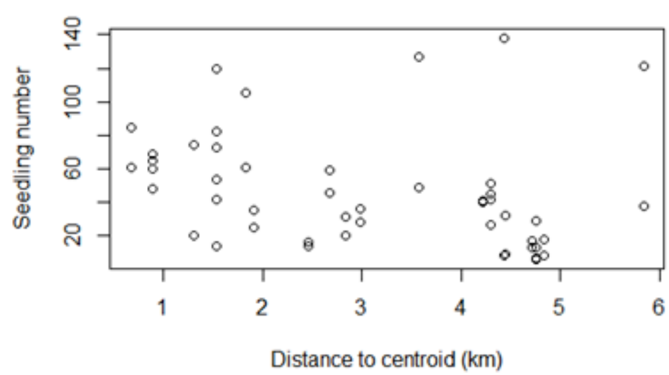


Figure 11: Scatterplot of seedling number depending on distance to centroid of wolf activity. There is a slightly increasing trend on seedling numbers with decreasing distance to the centroid

3.2. Tree recruitment

Tree recruitment (i.e. seedlings reaching size class 7) was facilitated for all seedlings only inside CWD plots (Kaplan Meier Survival Analysis, p <0.0001). In the CWD free control plots, seedling browsing and/or other mortality events resulted in discontinuance of seedlings to higher height classes (Figure 12).

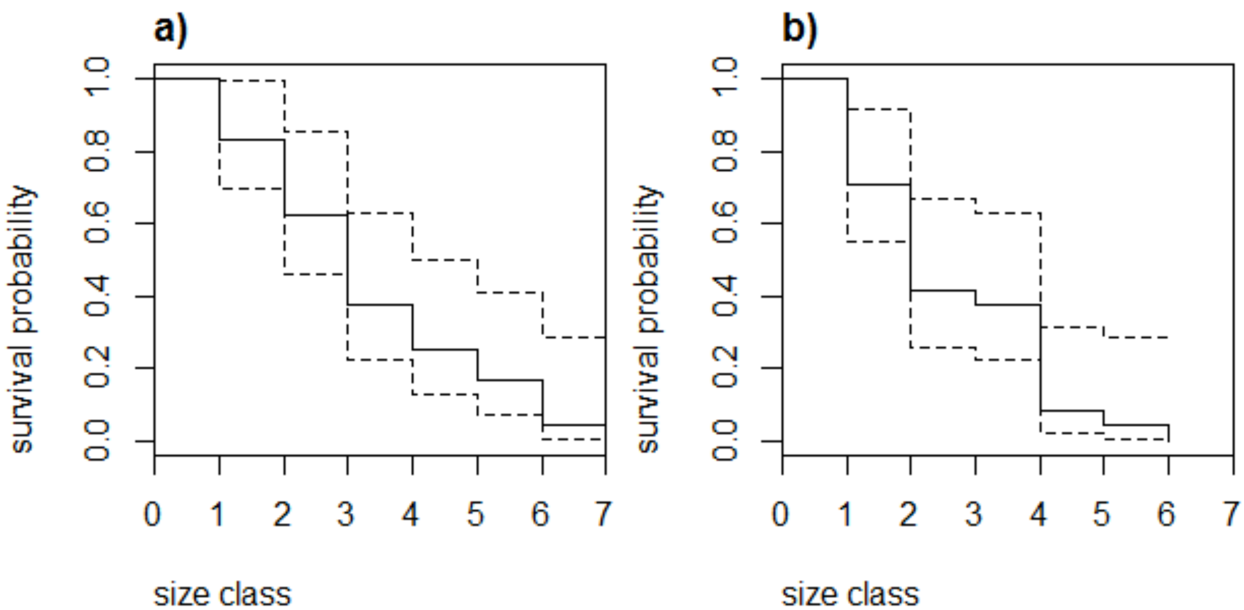


Figure 12: Kaplan Meier Survival Analysis for seedling size class and CWD presence. Size classes are categorized in 30cm intervals. a) represents plots close to CWD. Seedlings reach size class 7 (2m) and b) CWD free (control) plots: Seedlings reach size class 6. Thus only seedlings close to CWD contribute to tree recruitment. Generalized Wilcoxon test p <0.0001

Tree recruitment was independent of wolf presence; the difference between wolf core area compared to outside the wolf core area was not significant (p= 0.124). The interaction of wolf area and CWD was also not significant (p= 0.23). The Kaplan Meier survival analysis considering plots depending on distance to centroids of wolf activity indicated CWD presence as determinant for the occurrence of tree recruitment (Figure 13, Figure 14). Gradient of wolf activity were tested separately for the two different distances. Results of both categories ~2km distance to centroid and ~4km distance to centroid showed no significance (p=0.146 and p= 0.224 respectively) (Appendix II).

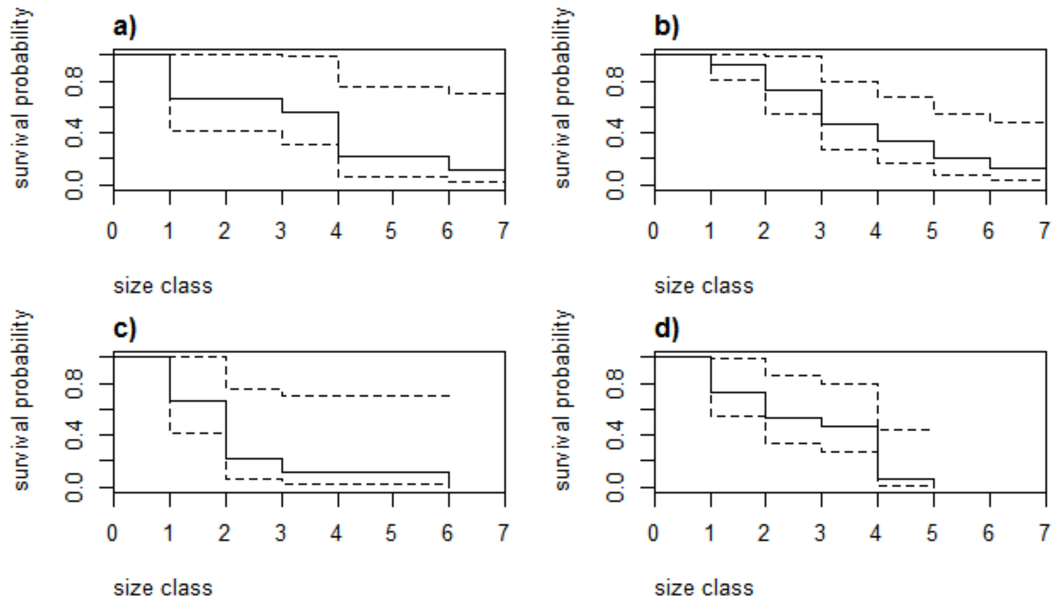


Figure 13: Kaplan Meier Survival Analysis for Seedling size class, distance to centroid (in km) and CWD presence. a) and b) represent CWD plots with a distance to centroids of < 2km (a) and > 2km (b). c) and d) are CWD free (control) plots with a distance to centroid of <2km (c) and >2km (d) .Seedlings reach size class 7 (2m) and contribute to tree recruitment only inside CWD plots.
Generalized Wilcoxon test p =0.146

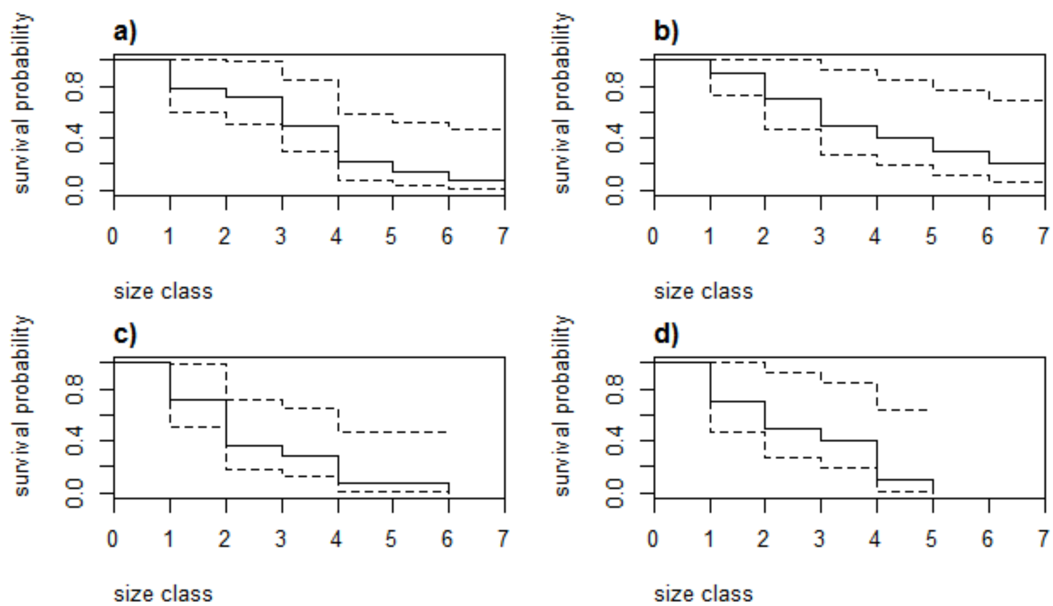


Figure 14: Kaplan Meier Survival Analysis for Seedling size class, distance to centroid (in km) and CWD presence. a) and b) represent CWD plots in distances to centroids of < 4km (a) and > 4km (b). c) and d) are control plots in a distance to kernel of <4km (c) and >4km (d). Seedlings reach size class 7 and contribute to tree recruitment in CWD plots only. Generalized Wilcoxon test p =0.244

3.3. CWD features

I used a zero inflated negative binomial mixed model to model seedling counts within CWD plots. I checked the variables for collinearity. CWD volume and height were clearly collinear (r>0.75). Collinear variables got excluded and I used the variables that were more meaningful for testing my hypothesis. That way, I reduced the non-significant features presence of branches, uprooted tree, CWD length, CWD species, CWD age class and CWD volume. As in the other models, wolf area and distance to centroids were not significant and got excluded.

CWD height was the only significant feature from my model that had an effect on seedling numbers (Table 3). This result demonstrates the underlying mechanism of the perceived fear in red deer: increasing height of CWD leads to increasing fear and avoidance of this habitat characteristic.

Table 3: Model output of the zero inflated, negative binomial mixed model

	Estimate	**Std. Error**	**z value**	**Pr(>z)**
Canopy_open	1.2187	0.5240	2.33	0.202 *
Canopy_open^2	-0.0304	0.0133	-2.30	0.022 *
Size class	-1.1058	0.0891	-12.41	<2e-16***
CWD height	0.0421	0.0213	1.98	0.048 *

Accordingly, higher CWD height is associated with higher seedling numbers, as model predictions suggested (Figure 15 a). Based on the model predictions, I again appreciated a quadratic effect of canopy cover, with an optimum at around 20% (Figure 15 b). In addition, my model predict an almost negative exponential distribution for the numbers of seedlings depending on size class, indicating very low seedling numbers in size class 5-7 (Figure 15 c). This result demonstrates the small amount of seedlings that actually grow up to 2m and will be part of the tree recruitment.

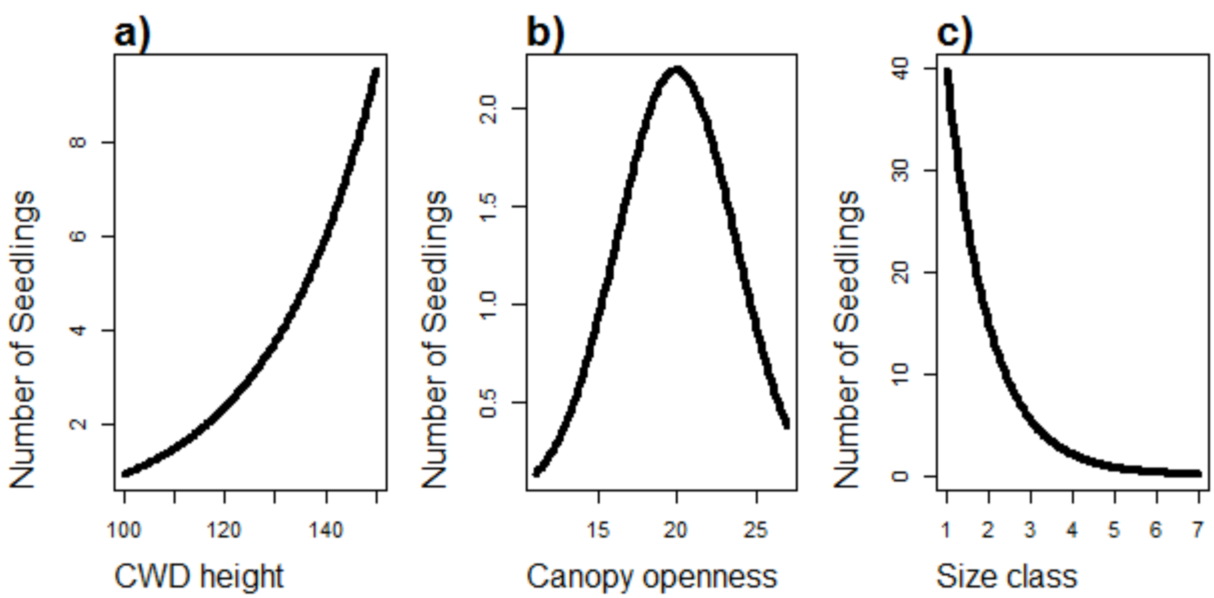


Figure 15: Predictions from the zero inflated negative binomial mixed model with different seedling numbers on the Y axis. a) Number of seedlings depending on CWD height. Increasing CWD height is associated with increasing seedling numbers. b) demonstrates an optimum of canopy openness for the number of seedlings. c) shows the decreasing number of seedlings with increasing height class.

Discussion

My study showed that CWD and wolf presence do not have an effect on seedling densities. CWD is functioning as important small scale habitat characteristics that protect seedlings from overbrowsing and facilitated tree recruitment. This process of seedlings growing up to 2m and thereby out of browsing reach was independent from wolf presence. CWD height act as a crucial feature for the occurrence of seedling numbers: the higher the CWD, the higher the number of seedlings. This behavioral mediated effect leaded to an increase of perceived fear in red deer close to high CWD, because of the reduced visibility and increasing function as an escape impediment.

For data analysis, I did not separate the species, since some seedling species such as *Carpinus betulus* were overrepresented. According to studies on forest structures in the area, increasing ungulate numbers caused a shift in tree recruitment rates towards preferred browsing species which will lead to a dominance of deciduous species such as *Carpinus* and *Tilia* (Kuijper et al. 2010). Thus, reduced herbivore numbers (either anthropogenic or natural induced) facilitate increasing tree recruitment and higher forest dynamics (Kuijper et al. 2010). In the strict reserve, some species including *Carpinus betulus, Alnus glutinosa, Tilia cordata, Betula spp., Acer platanoides* and *Pinus silvestres* increased regeneration rates, compared to standing numbers of the mature forest (Miscicki 2012). Declining species include *Picea abies* and *Quercus robur*, whereas the latter usually follows an spatial and temporal discontinuous regeneration scheme (Bernadzki et al. 1998; Bobiec et al. 2011). Contrariwise to the lack of tree recruitment, *Quercus robur* increases in basal area (Bernadzki et al. 1998). However, depending on the season, forage species of red deer include all tree species that occur in deciduous forest areas, varying from *Carpinus betulus, Quercus robur, Picea excels, Betula spp, Populus tremula, Acer platanoides, Corylus avellana* to *Tilia cordata* (Gebczynska 1980; Kuijper et al. 2010).

Use of wolf core area vs centroids

The results of my study indicated no significant effect of wolf core area. This independence of wolf area shows that perceived predation risk in red deer is not operating on large scales as in the Yellowstone National park, where elk is avoiding areas with high risk of wolf (Mao et al. 2005; Creel et al. 2005). Comparing the sizes of the Białowieża Primeval Forest (600km² in Poland) to the Yellowstone National Park (~9000km²), it is obvious that ungulates possibilities are little to avoid predators completely in the small scale Białowieża Primeval Forest. In addition, the Białowieża Forest has a dense structure that is limiting the view and impede detection of predators over large distances (Kuijper et al. 2014). This might result in an inability for ungulates to react to an unexpected predator presence. The Yellowstone system has a high heterogeneity in habitat types including forests, river valleys and meadows, which allows ungulates to shift their habitats away from risky areas to less risky habitats such as in higher elevations (Ripple & Beschta 2003). Risky habitats for elk and the resulting reduced browsing rates facilitated recovery of overbrowsed tree species (Painter et al. 2014a; Brown 1999). However, there is much debate on this topic and other studies from Yellowstone indicate no impacts of ungulate browsing in Aspen growing on risky sites (Kauffman et al. 2010).

A crucial factor in the Białowieża Primeval Forest is that there are no predator free areas, since wolf territories are considered to overlap each other (Schmidt et al. 2009). Recent studies indicated immediate ungulate reactions to evidence of wolf presence such as scent markings (Kuijper et al. 2014). In the areas of high wolf activity, such as den sites, the amount of scat and wolf smell is concentrated and ungulates are likely to perceive an increase in wolf risk. That way, I consider the concept of a gradient related to wolf activity based on centroids as more suitable compared to the use of a strict border to define a wolf core area in the Białowieża Primeval Forest.

Effects on numbers of seedlings

Results of my study indicated no significant effect of wolf and CWD presence on numbers of seedlings. I observed a slight trend of increasing seedling number with decreasing distance to the centroids of wolf activity. To achieve evidence for the non significance of this trend, a power analysis should be done to calculate the minimum sample size. If results indicate that the sample size of 48 plots was too small, data collection should be expanded to achieve stable results.

Anyway, earlier studies in the area suggested that habitat selection by ungulates was not that much driven by predator presence as formerly expected, but depend more on anthropogenic influences (Theuerkauf & Rouys 2008). Laundré et al assessed that animals have the ability to identify and alter their behaviour according to different amounts of predation risks (Laundré et al. 2010). In the Białowieża Primeval Forest, behavioural adaptations of roe deer (*Capreolus capreolus*) were observed according to temporal factors as hunting season (Sönnichsen et al. 2013). Red deer numbers in the strict reserve of Białowieża Primeval Forest densities are high (~12 individuals per km²) and they are browsing throughout the whole area. The results of no significant effects in seedling numbers suggested that the perceived predation risk was not strong enough for ungulates to avoid areas of high wolf activity as in large scale Yellowstone ecosystems.

Effects on tree recruitment

Tree recruitment was defined as seedlings growing up to 2m (size class 7). In this study, tree recruitment was facilitated in the presence of CWD only (Kaplan Meier estimate). Simultaneously, tree recruitment was independent of wolf presence. This trend is contrary to earlier findings in the study area, where browsing rates could be related to the presence of CWD and wolf core area (Kuijper et al. 2013). A reason for this dissimilarity could be due to the differences in scale. The focus of this former study was on a finer scale, directed towards individual seedlings that were growing in the presence or absence of CWD.

In the Yellowstone area, several tree species got suppressed by overbrowsing of ungulates. After wolf reintroduction, aspen, willows and cottonwood increased in height and stem growth in risky elk habitats (Ripple & Beschta 2006; Beyer et al. 2007).

For my study, the Kaplan Meier estimate was not representative as a survival analysis, since seedlings might be maintained small by browsing. In addition, in the presence of CWD, growth rates of plants are considered to be slower because of lower nutrient and mineral concentrations, compared to most organic soils (Harmon et al. 1986). Anyway, seedling densities may be delusive in terms of tree recruitment rates, since disturbance frequencies are higher compared to the forest floor of undisturbed, dense forest systems. Actual seedling settlement and tree recruitment rates in the presence of CWD are not only a matter of browsing pressure, but also determined by moisture, species interactions, decay state of the CWD and amount of snow. Protection of seedlings and small trees exist at the sites of CWD by the creation of shaded microsites (Harmon et al. 1986). In Białowieża, vicinity to CWD is considered to increase seedling survival of *Quercus robur*, whereas herbivory limits tree recruitment of the species in the absence of CWD (Ginkel van et al. 2013; Smit et al. 2012)

The effect of CWD on tree recruitment may indicate a general fear of red deer in presence of these small scale habitat features. This perceived fear is considered to occur throughout the whole area, since there are no predator free areas (Schmidt et al. 2009). Increasing vigilance rates of ungulates in the area of CWD give evidence for the perceived fear (Halofsky & Ripple 2008; Kuijper et al. 2014).

Influence of CWD height

My results show that CWD height is the only significant feature that affects seedling numbers. Higher CWD height resulted in increasing seedling densities.

A former study in the Białowieża Primeval Forest indicated reduced browsing intensity with increasing amount of CWD (Kuijper et al. 2013). Combining these facts with higher rates in vigilance behavior close to CWD (Halofsky & Ripple 2008; Altendorf et al. 2001), I presume an increasing effect of the perceived fear when amount or height of CWD include less chance to escape and horizontal view of browsing ungulates.

Conclusions

The results of my study indicate no difference in seedling densities in the presence of wolf or CWD. The slightly increasing trend of seedling numbers with decreasing distance to wolf activity center should be confirmed by establishing a power analysis. According to my results, CWD was crucial for tree recruitment and the contribution of seedlings growing up to the adult forest stand. With increasing height, CWD presence is associated with higher seedling numbers.

Based on this, I conclude that CWD is creating hotspots of fear throughout the whole area, independent of wolf. This general fear in red deer associated with CWD should be used in forest management of natural stands to ensure tree recruitment and to create heterogeneous habitat structures. The presence of large predators is crucial in this case, although effects of CWD should be verified in semi natural European ecosystems including absence of natural predators.

Future studies should prove the hypothesis of generalized fear in Białowieżan red deer in the presence of CWD. Evidence for the perceived fear could be obtained by the use of an exclosure experiment, in order to compare seedling numbers and recruitment rates in fenced sites without browsing to areas with natural browsing.

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Appendix I: Additional graph on seedling density

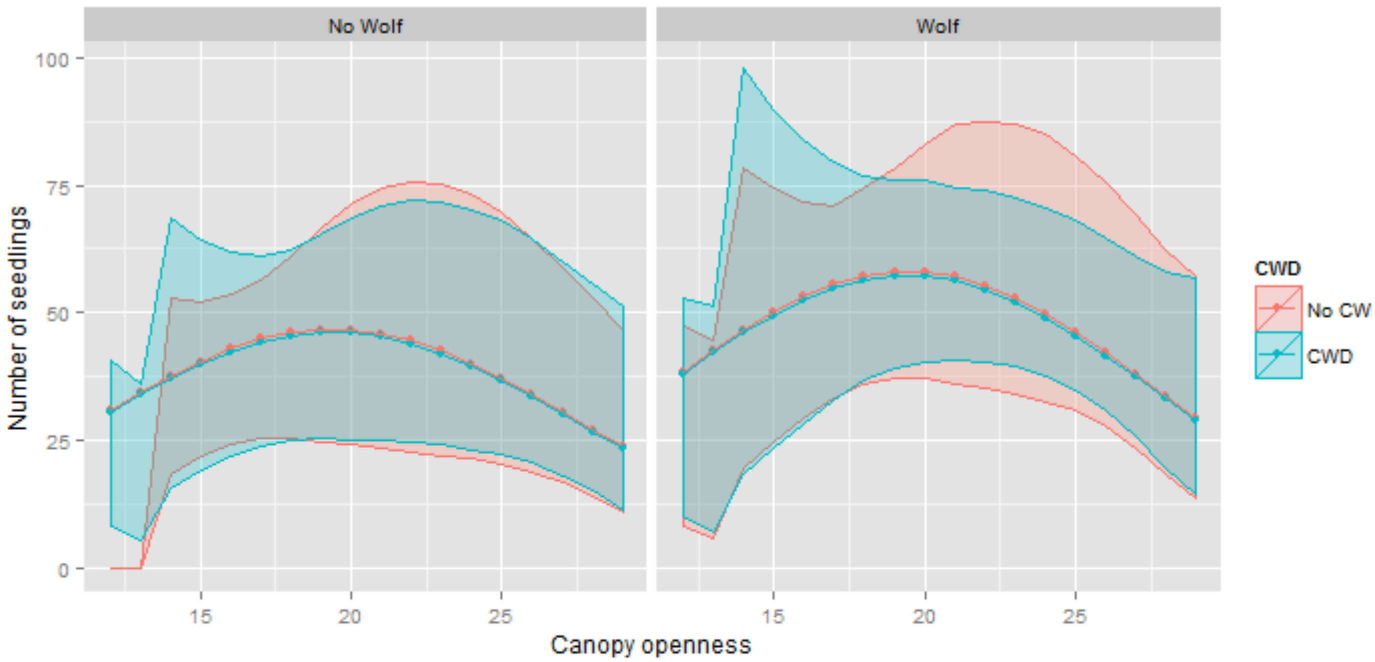

Figure A 1: Plots of CWD presence per wolf area. CWD does not have an effect on number of seedlings; confidence intervals for predicted values are overlapping. Canopy openness has an optimum at 20%.

Appendix II: Kaplan Meier Analysis for two different distances to centre of wolf activity

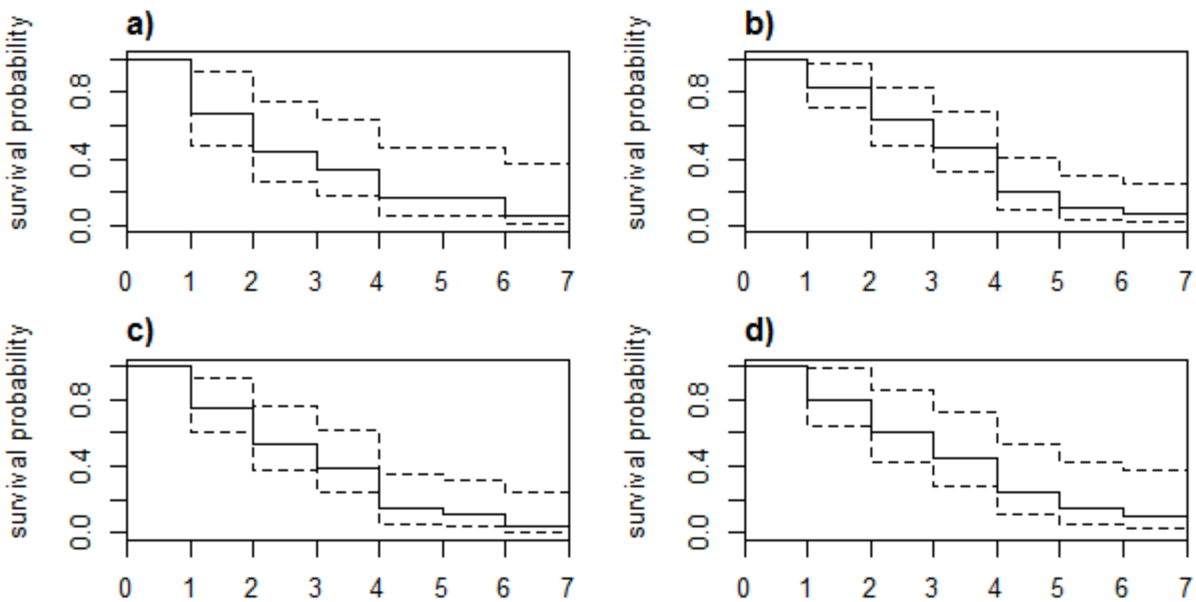

Figure A 2: Kaplan Meier Survival Analysis for Seedling size class and different distances to centroid (in km). a) and b) represent distances to centroid of < 2km (a) and >2km (b). Generalized Wilcoxon test p =0.252. c) and d) represent distances to centroid of <4 (c) and .>4km (d). Generalized Wilcoxon test p =0.511. Seedlings can reach size class 7 (2m) in all distances. Tree recruitment is thus independent from distance of wolf activity centre

Appendix III Overview of all plots

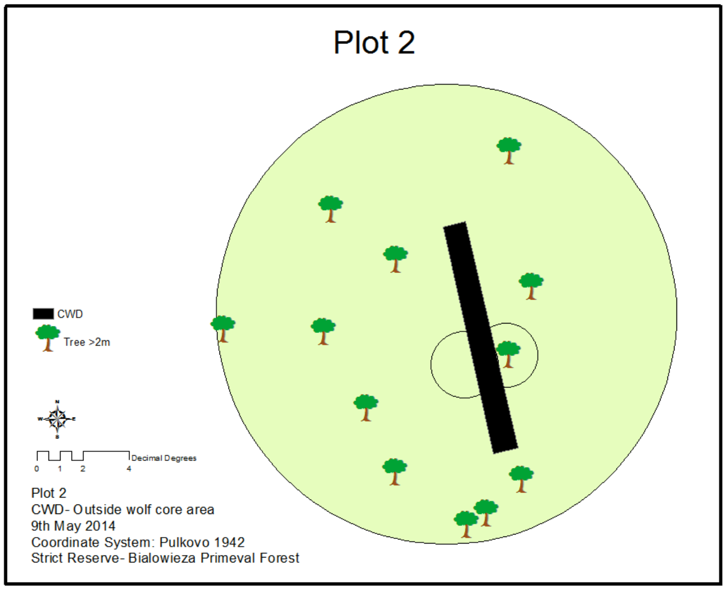

Figure A 3: Overview map of plot 2 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 4: Overview photo of plot 2

Figure A 6: Fisheye photo of plot 2. Taken in 1m height at the plot center

Figure A 5: Edited fisheye photo of plot 2 using Gap light Analyser

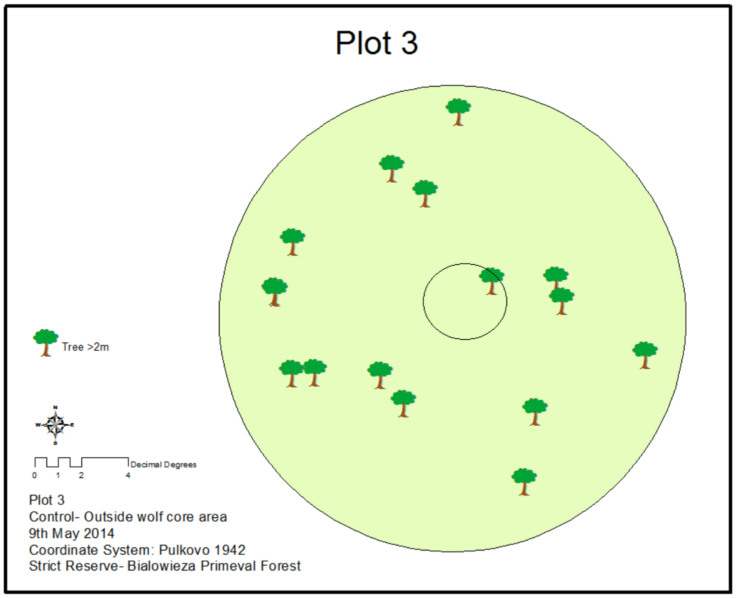

Figure A 7: Overview map of plot 3 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 8: Overview photo of plot 3

Figure A 10: Fisheye photo of plot 3. Taken in 1m height at the plot center

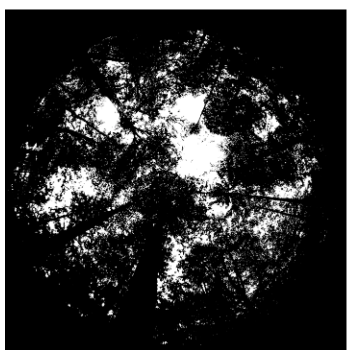

Figure A 9: Edited fisheye photo of plot 3 using Gap light Analyser

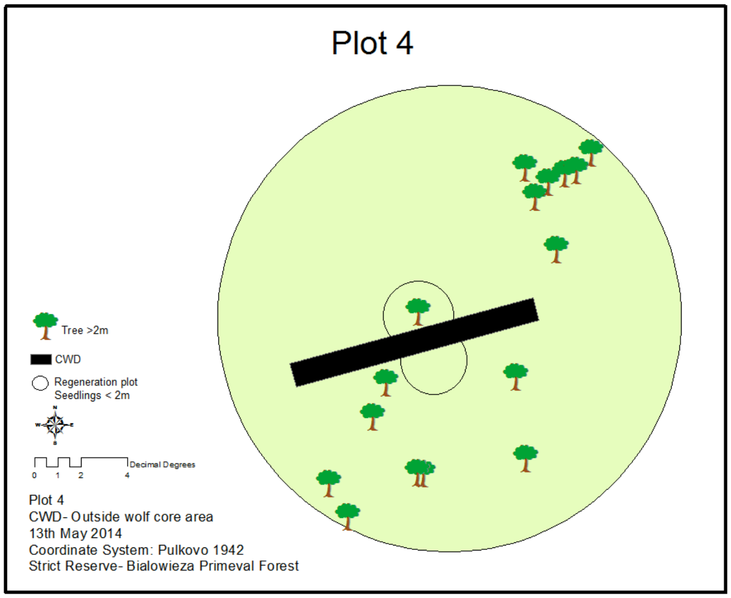

Figure A 11: Overview map of plot 4 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 12: Overview photo of plot 4

Figure A 14: Fisheye photo of plot 4. Taken in 1m height at the plot center

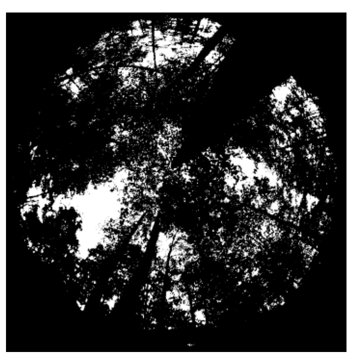

Figure A 13: Edited fisheye photo of plot 4 using Gap light Analyser

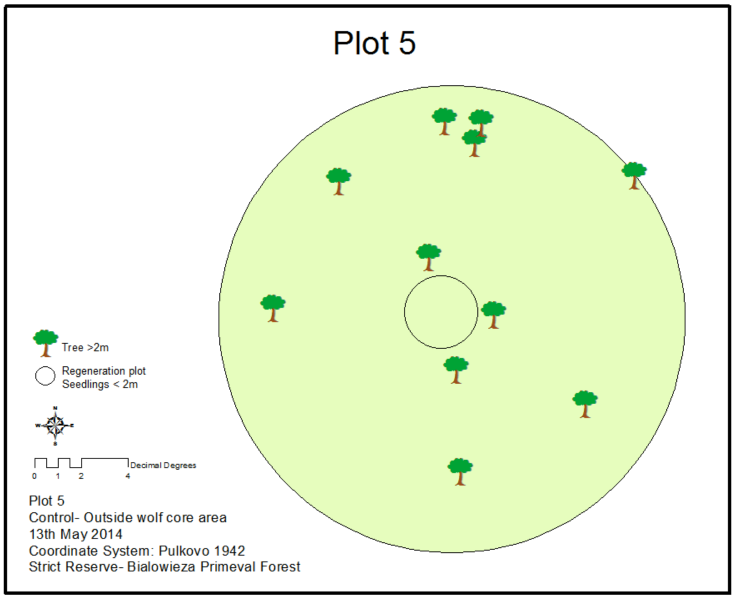

Figure A 15: Overview map of plot 5 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 16: Overview photo of plot 5

Figure A 18: Fisheye photo of plot 5. Taken in 1m height at the plot center

Figure A 17: Edited fisheye photo of plot 5 using Gap light Analyser

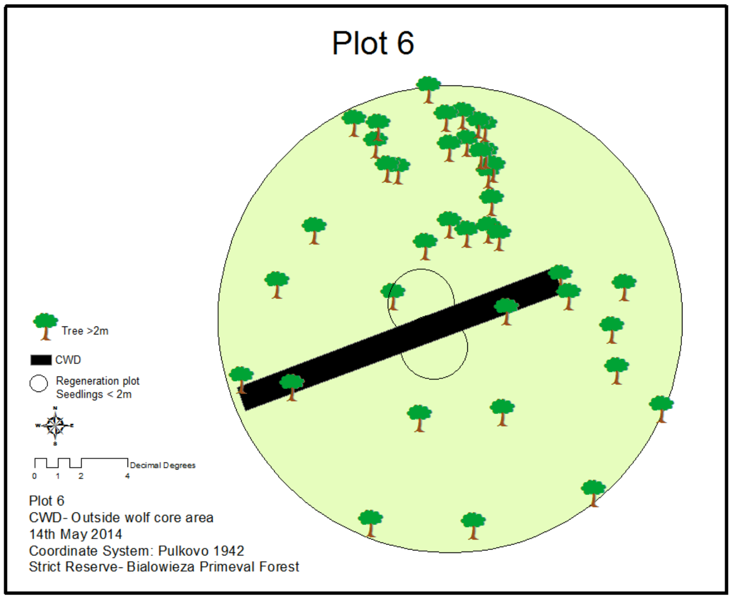

Figure A 19: Overview map of plot 6 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 20: Overview photo of plot 6

Figure A 22: Fisheye photo of plot 6. Taken in 1m height at the plot center

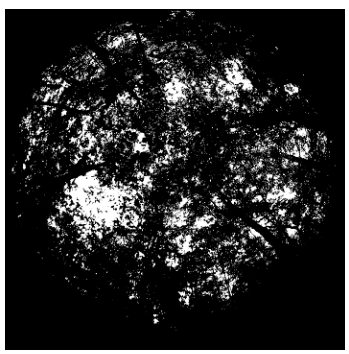

Figure A 21: Edited fisheye photo of plot 6 using Gap light Analyser

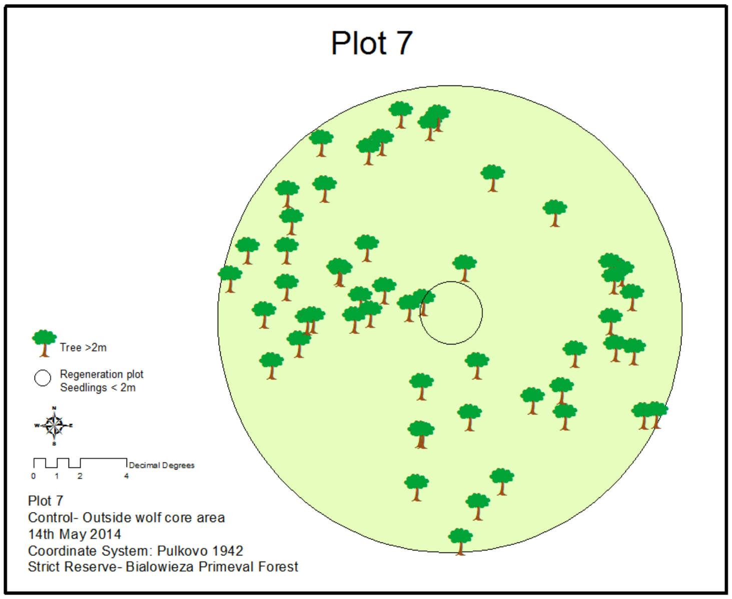

Figure A 23: Overview map of plot 7 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 24: Overview photo of plot 7

Figure A 26: Fisheye photo of plot 7. Taken in 1m height at the plot center

Figure A 25: Edited fisheye photo of plot 7 using Gap light Analyser

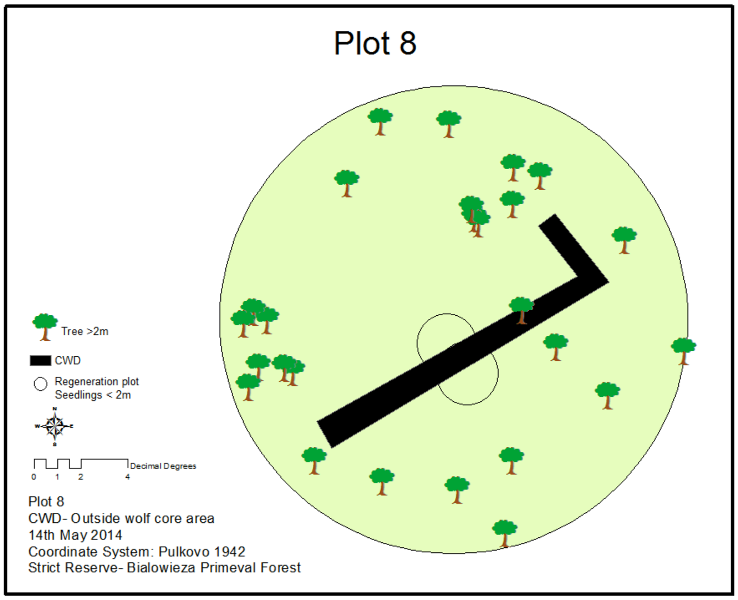

Figure A 27: Overview map of plot 8 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 28: Overview photo of plot 8

Figure A 30: Fisheye photo of plot 8. Taken in 1m height at the plot center

Figure A 29: Edited fisheye photo of plot 8 using Gap light Analyser

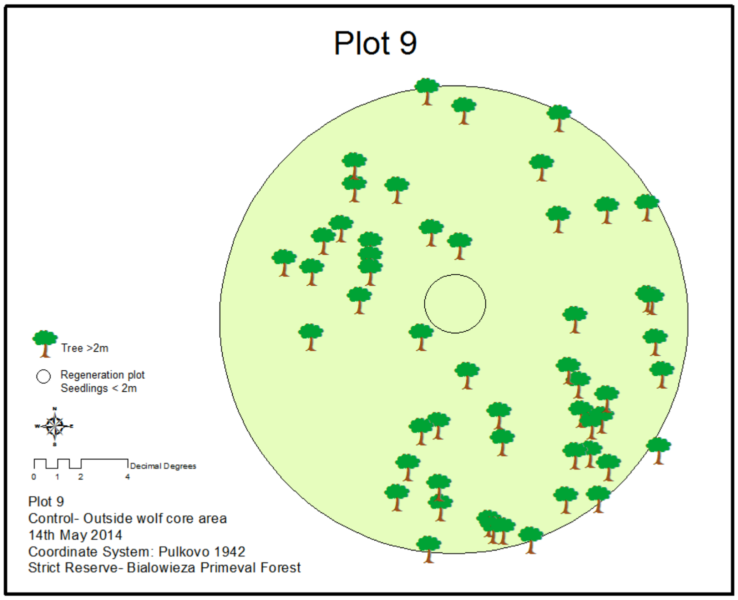

Figure A 31: Overview map of plot 9 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 32: Overview photo of plot 9

Figure A 34: Fisheye photo of plot 9. Taken in 1m height at the plot center

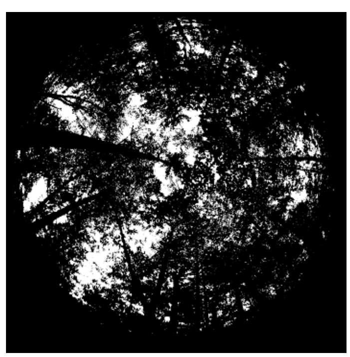

Figure A 33: Edited fisheye photo of plot 9 using Gap light Analyser

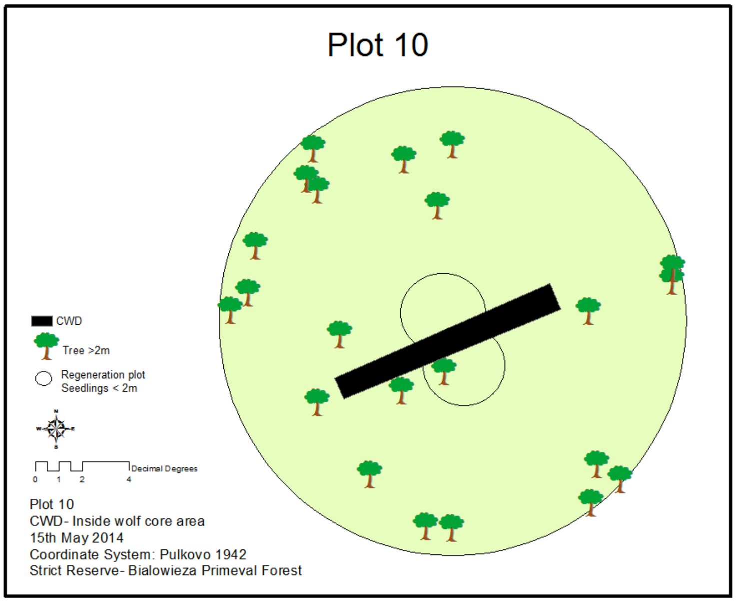

Figure A 35: Overview map of plot 10 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 36: Overview photo of plot 10

Figure A 38: Fisheye photo of plot 10. Taken in 1m height at the plot center

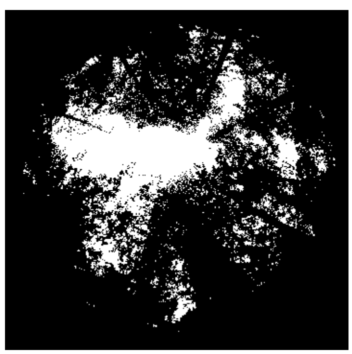

Figure A 37: Edited fisheye photo of plot 10 using Gap light Analyser

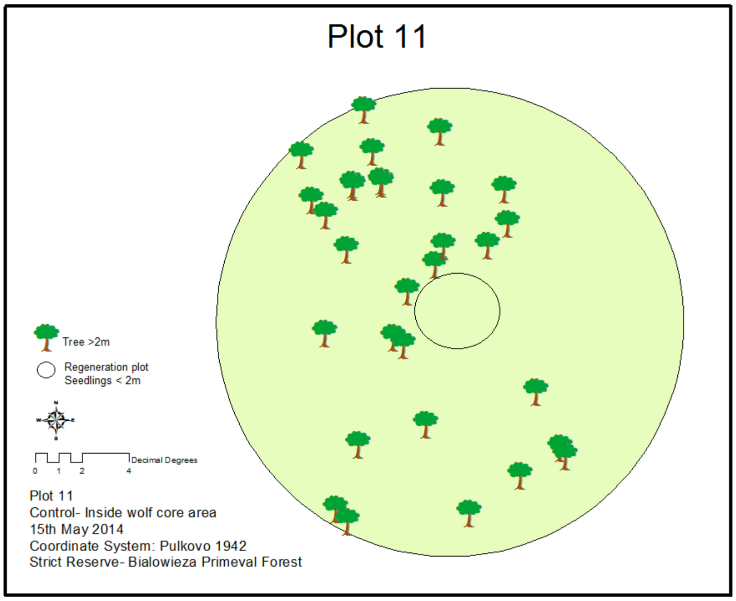

Figure A 39: Overview map of plot 11 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 40: Overview photo of plot 11

Figure A 42: Fisheye photo of plot 11. Taken in 1m height at the plot center

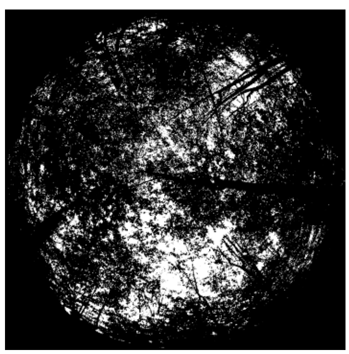

Figure A 41: Edited fisheye photo of plot 11 using Gap light Analyser

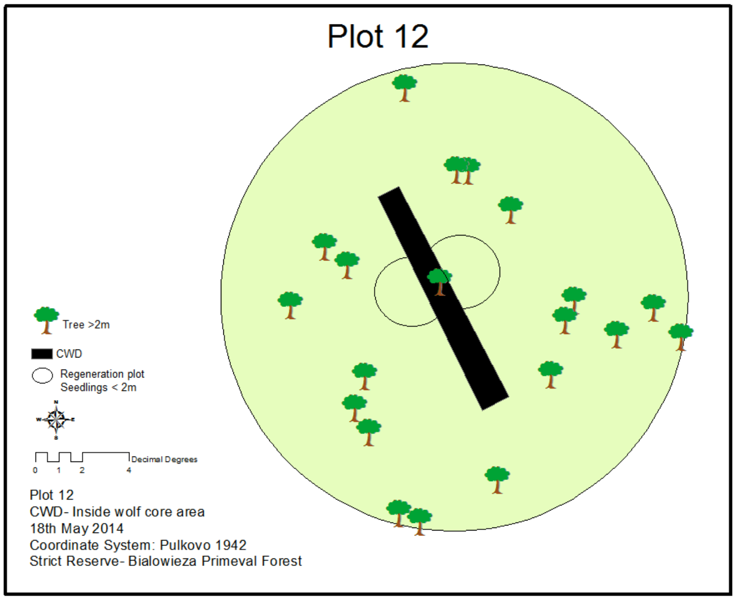

Figure A 43: Overview map of plot 12 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 44: Overview photo of plot 12

Figure A 45: Fisheye photo of plot 12. Taken in 1m height at the plot center

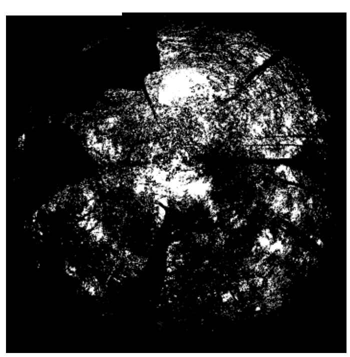

Figure A 46: Edited fisheye photo of plot 12 using Gap light Analyser

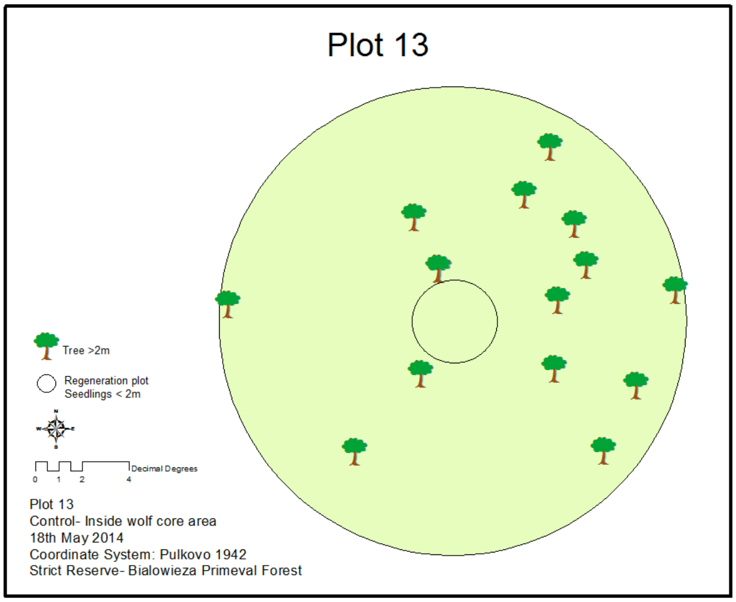

Figure A 47: Overview map of plot 13 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 48: Overview photo of plot 13

Figure A 50: Fisheye photo of plot 13. Taken in 1m height at the plot center

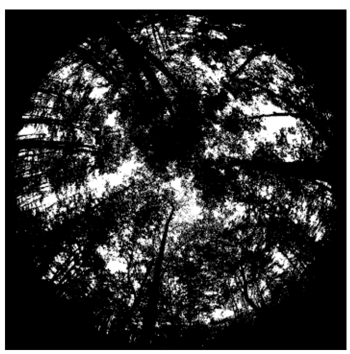

Figure A 49: Edited fisheye photo of plot 13 using Gap light Analyser

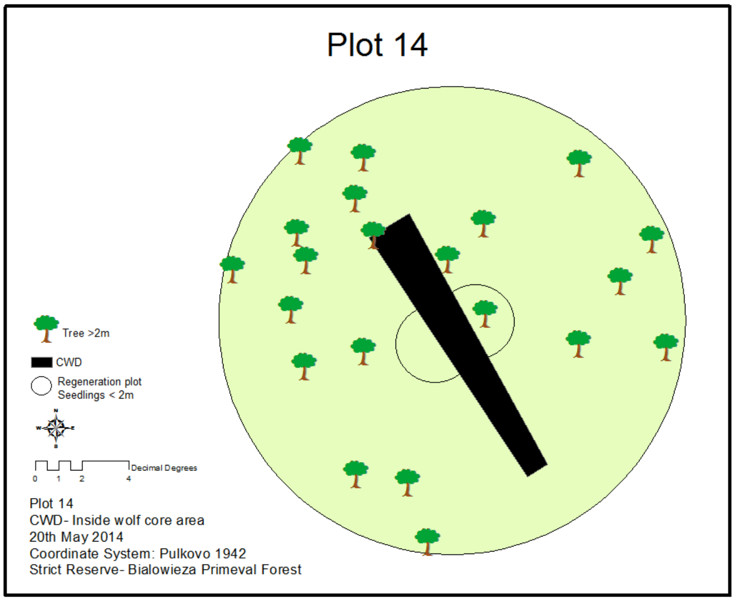

Figure A 51: Overview map of plot 14 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

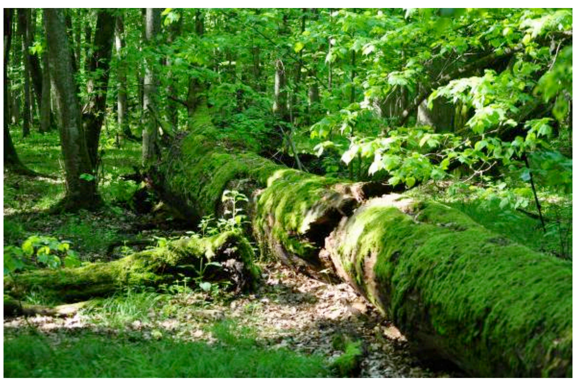

Figure A 52: Overview photo of plot 14

Figure A 53: Fisheye photo of plot 14. Taken in 1m height at the plot center

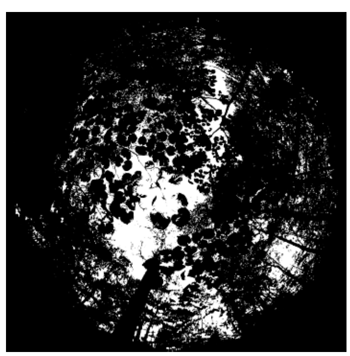

Figure A 54: Edited fisheye photo of plot 14 using Gap light Analyser

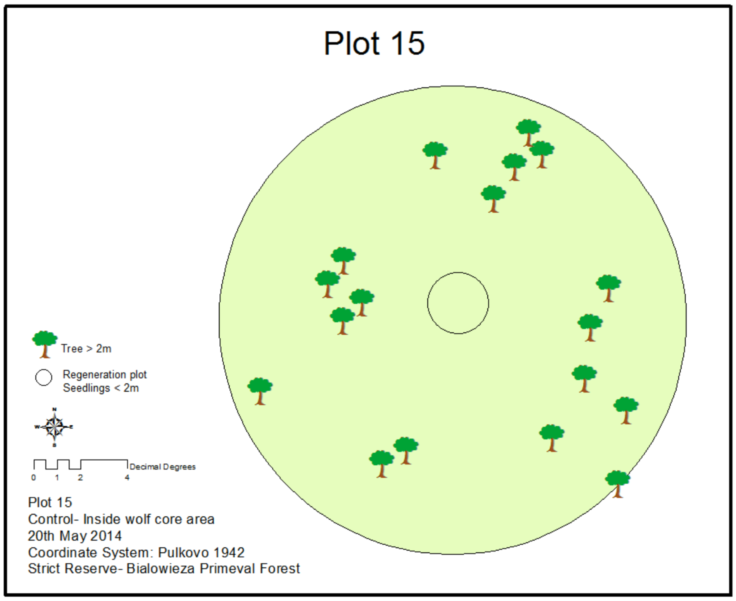

Figure A 55: Overview map of plot 15 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 56: Overview photo of plot 15

Figure A 58: Fisheye photo of plot 15. Taken in 1m height at the plot center

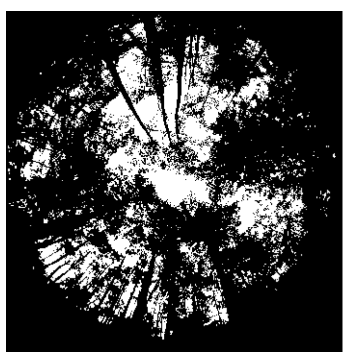

Figure A 57: Edited fisheye photo of plot 14 using Gap light Analyser

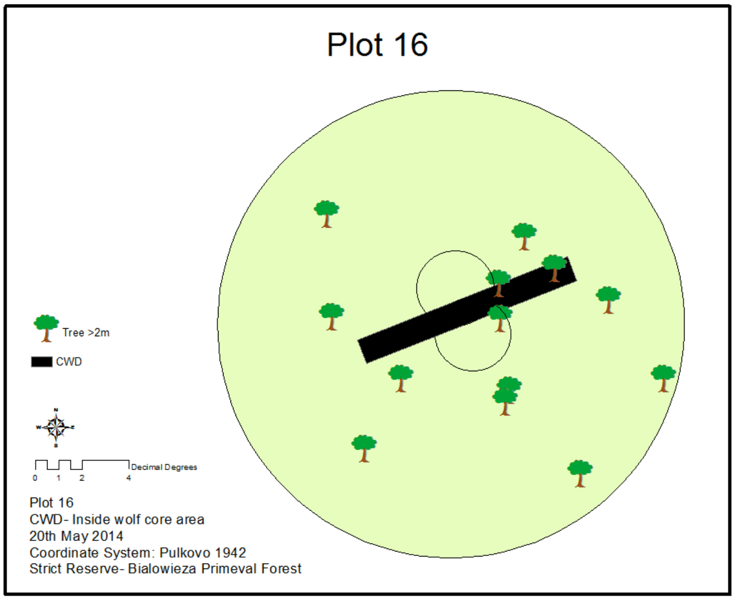

Figure A 59: Overview map of plot 16 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 60: Overview photo of plot 16

Figure A 62: Fisheye photo of plot 16. Taken in 1m height at the plot center

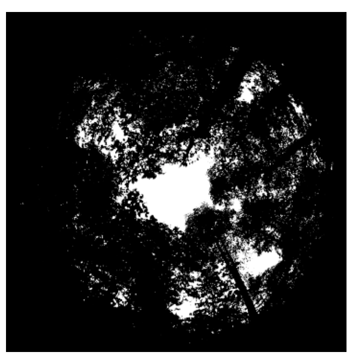

Figure A 61: Edited fisheye photo of plot 16 using Gap light Analyser

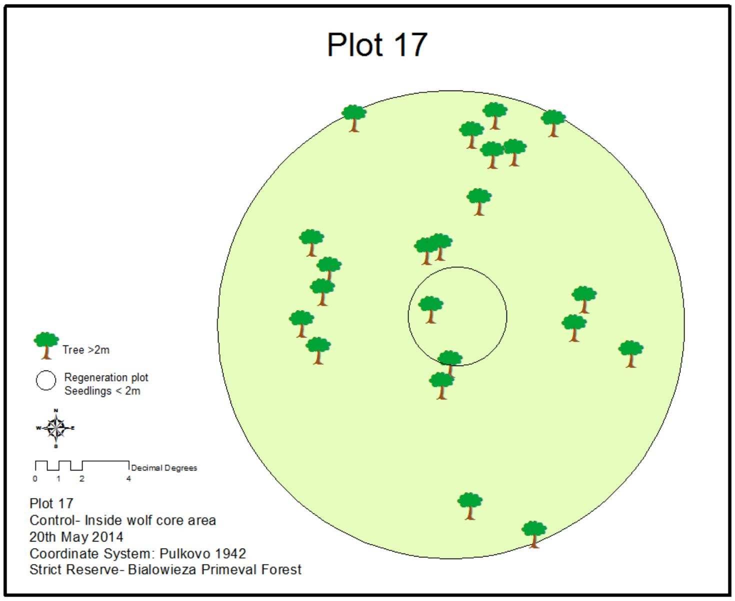

Figure A 63: Overview map of plot 17 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 64: Overview photo of plot 17

Figure A 66: Fisheye photo of plot 17. Taken in 1m height at the plot center

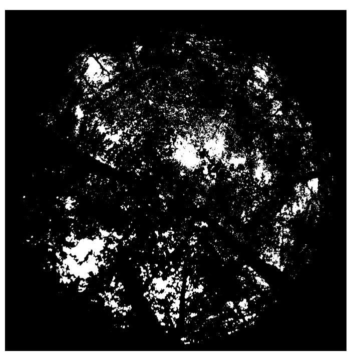

Figure A 65: Edited fisheye photo of plot 17 using Gap light Analyser

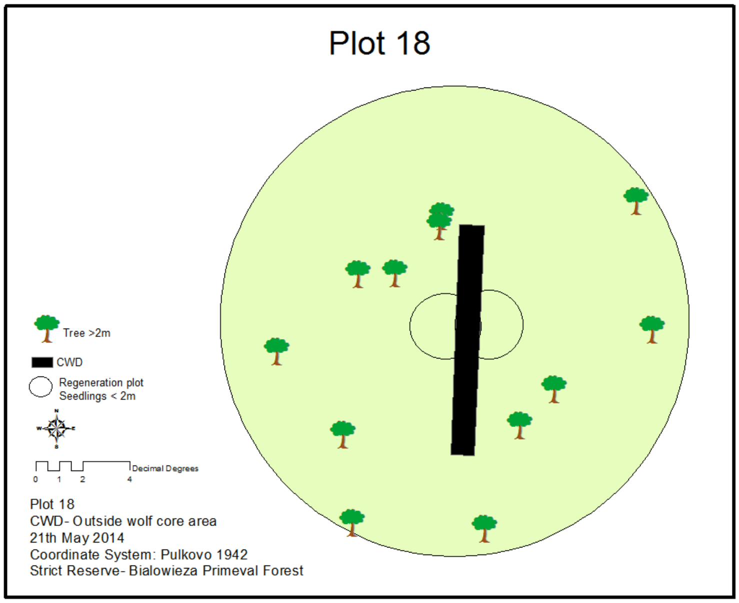

Figure A 67: Overview map of plot 18 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 68: Overview photo of plot 18

Figure A 70: Fisheye photo of plot 18. Taken in 1m height at the plot center

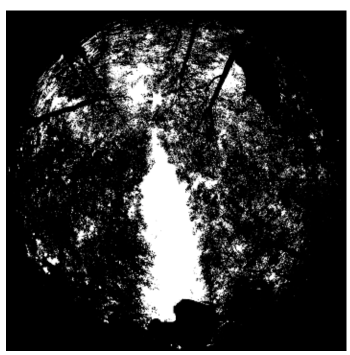

Figure A 69: Edited fisheye photo of plot 18 using Gap light Analyser

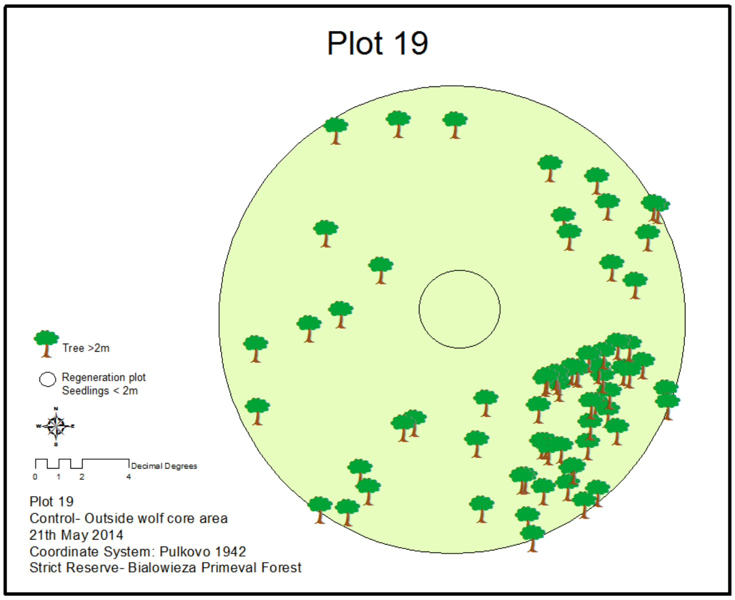

Figure A 71: Overview map of plot 19 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 72: Overview photo of plot 19

Figure A 74: Fisheye photo of plot 19. Taken in 1m height at the plot center

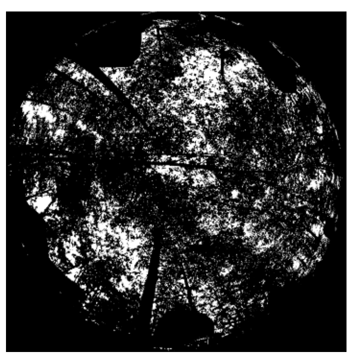

Figure A 73: Edited fisheye photo of plot 19 using Gap light Analyser

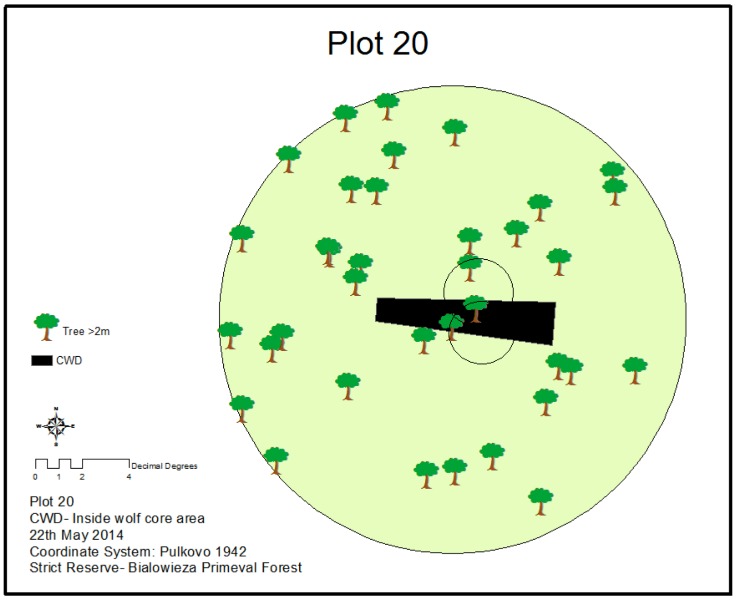

Figure A 75: Overview map of plot 20 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 76: Overview photo of plot 20

Figure A 78: Fisheye photo of plot 20. Taken in 1m height at the plot center

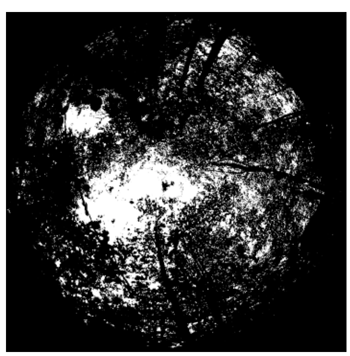

Figure A 77: Edited fisheye photo of plot 20 using Gap light Analyser

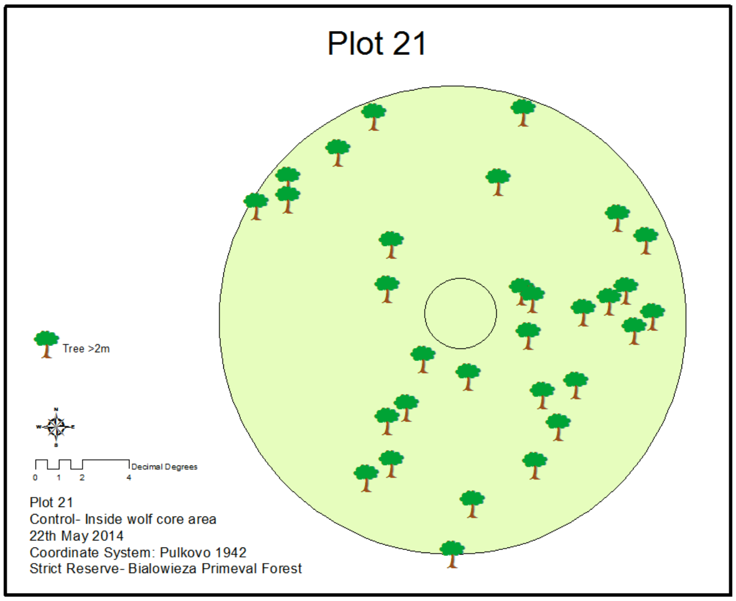

Figure A 79: Overview map of plot 21 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 80: Overview photo of plot 21

Figure A 82: Fisheye photo of plot 21. Taken in 1m height at the plot center

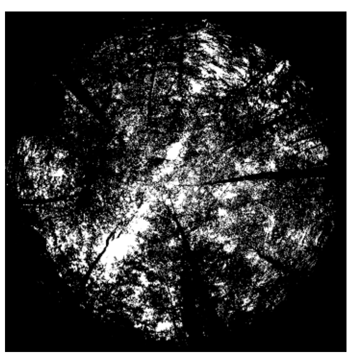

Figure A 81: Edited fisheye photo of plot 21 using Gap light Analyser

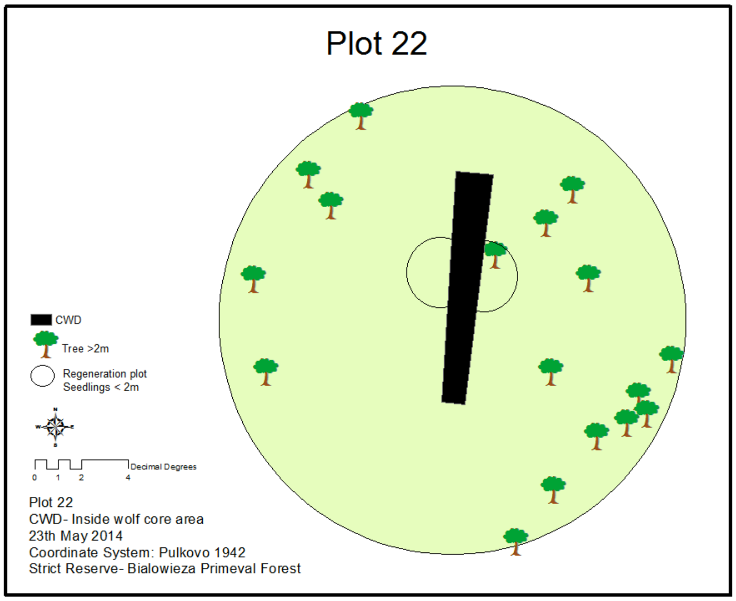

Figure A 83: Overview map of plot 22 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 84: Overview photo of plot 22

Figure A 86: Fisheye photo of plot 22. Taken in 1m height at the plot center

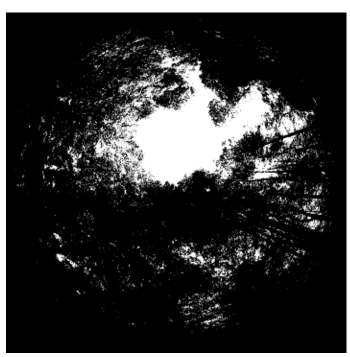

Figure A 85: Edited fisheye photo of plot 22 using Gap light Analyser

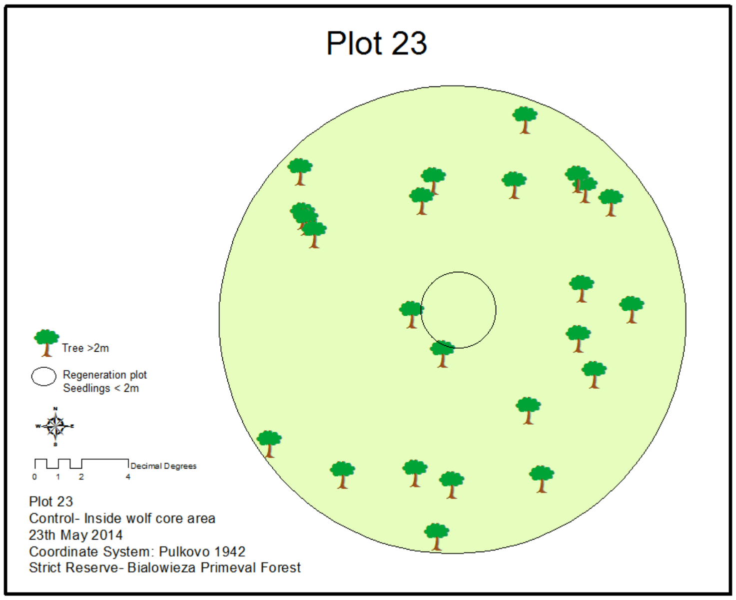

Figure A 87: Overview map of plot 23 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 88: Overview photo of plot 23

Figure A 90: Fisheye photo of plot 23. Taken in 1m height at the plot center

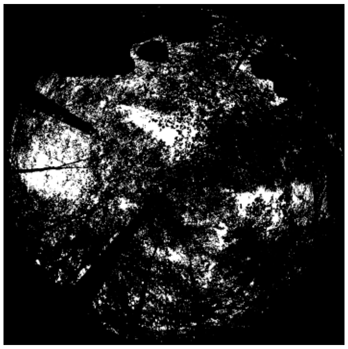

Figure A 89: Figure A4 Edited fisheye photo of plot 23 using Gap light Analyser

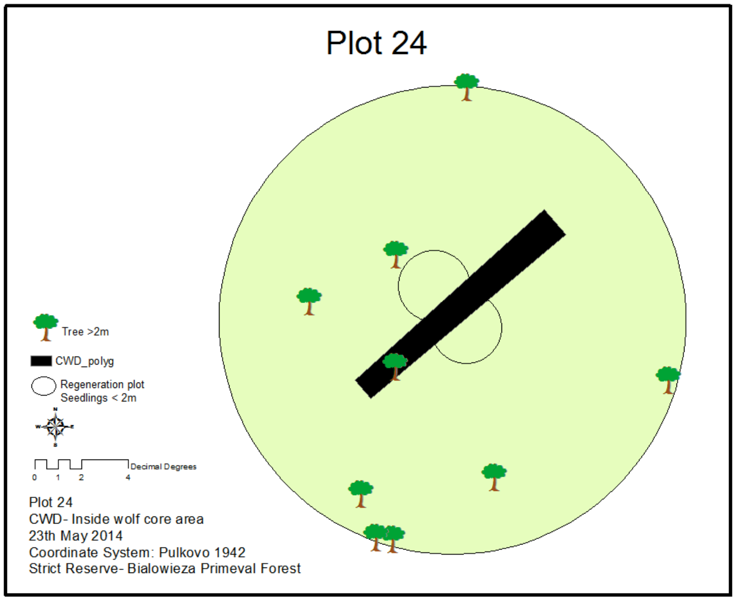

Figure A 91: Overview map of plot 24 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

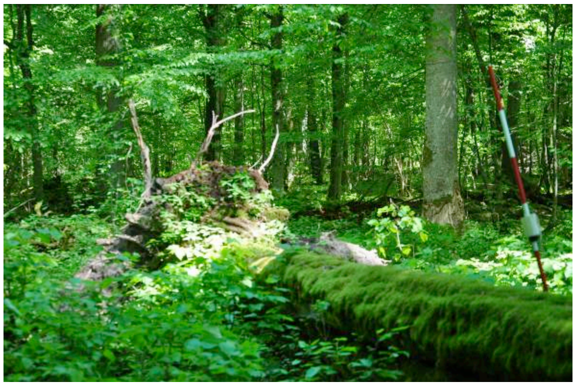

Figure A 92: Overview photo of plot 24

Figure A 94: Fisheye photo of plot 24. Taken in 1m height at the plot center

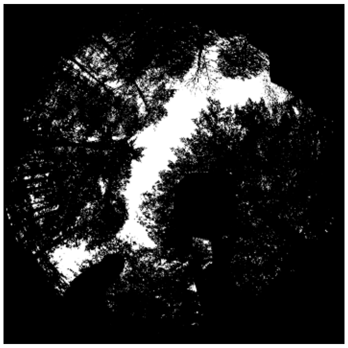

Figure A 93: Edited fisheye photo of plot 24 using Gap light Analyser

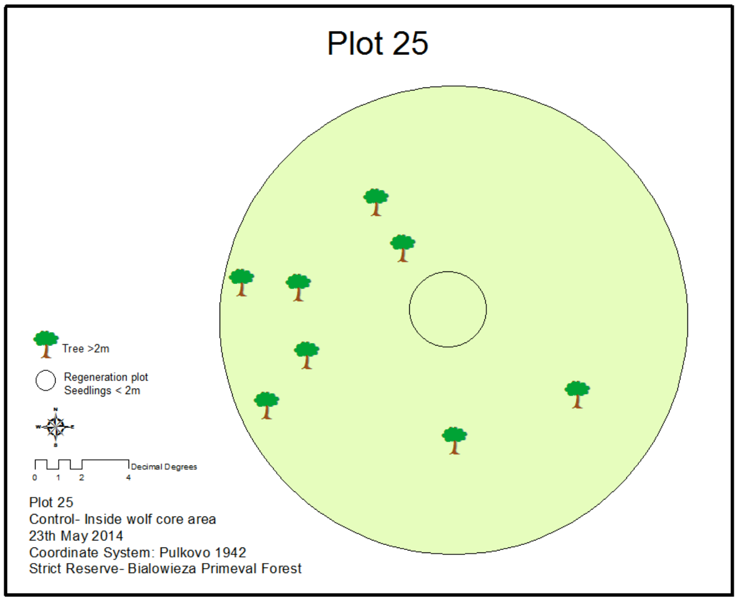

Figure A 95: Overview map of plot 25 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 96: Overview photo of plot 25

Figure A 98: Fisheye photo of plot 25. Taken in 1m height at the plot center

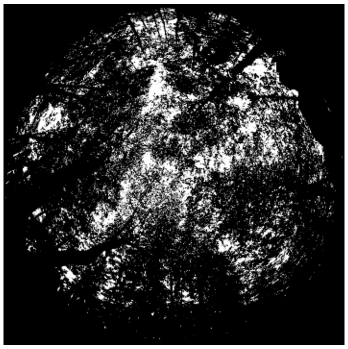

Figure A 97: Edited fisheye photo of plot 25 using Gap light Analyser

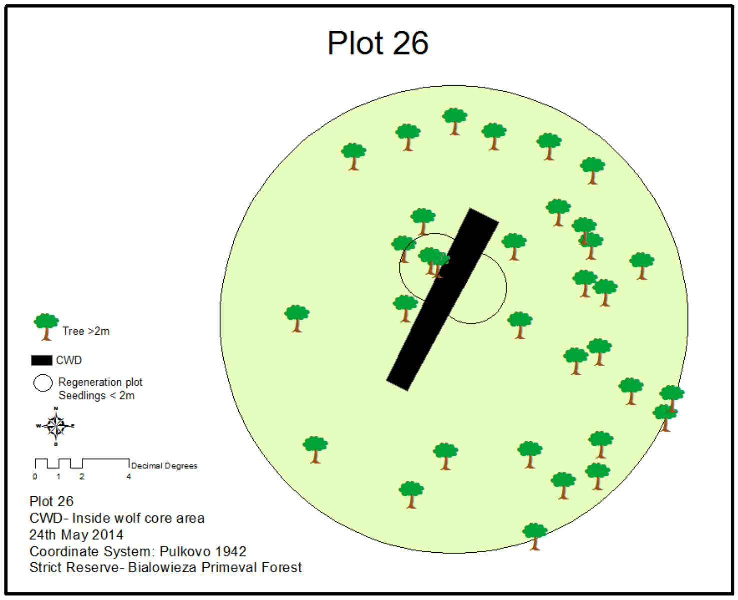

Figure A 99: Overview map of plot 26 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 100: Overview photo of plot 26

Figure A 102: Fisheye photo of plot 26. Taken in 1m height at the plot center

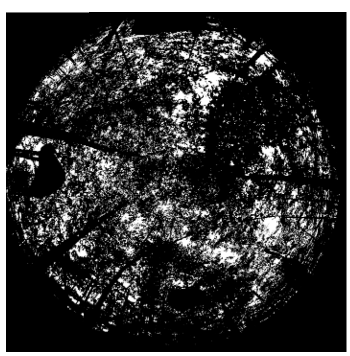

Figure A 101: Edited fisheye photo of plot 26 using Gap light Analyser

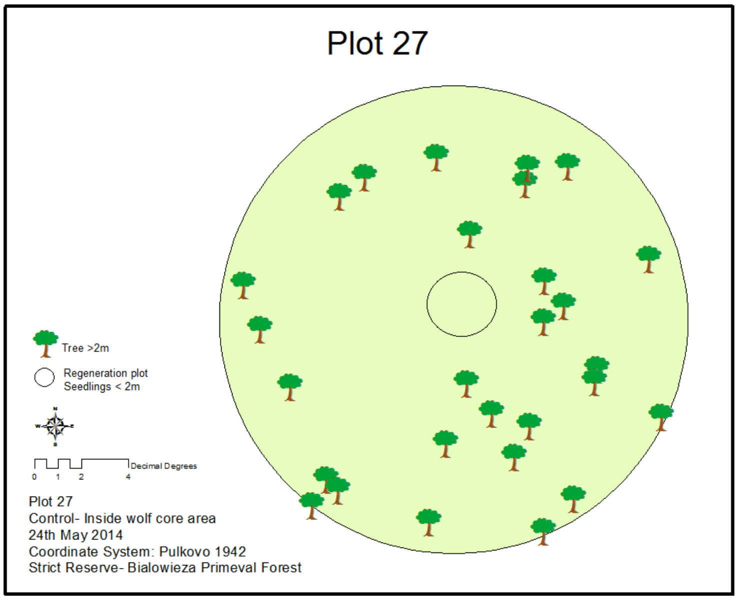

Figure A 103: Overview map of plot 27 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 104: Overview photo of plot 27

Figure A 106: Fisheye photo of plot 27. Taken in 1m height at the plot center

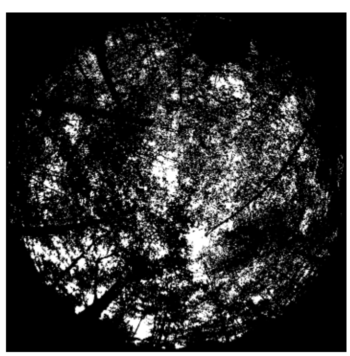

Figure A 105: Edited fisheye photo of plot 27 using Gap light Analyser

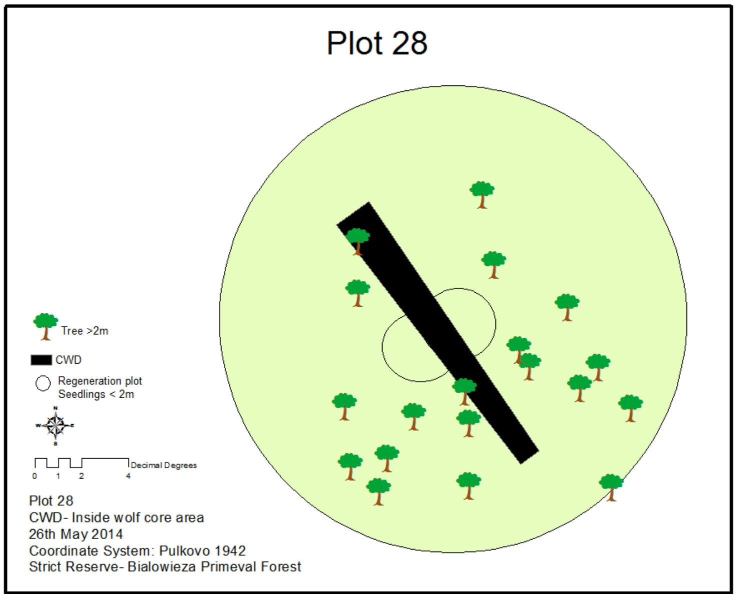

Figure A 107: Overview map of plot 28 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 108: Overview photo of plot 28

Figure A 110: Fisheye photo of plot 28. Taken in 1m height at the plot center

Figure A 109: Edited fisheye photo of plot 28 using Gap light Analyser

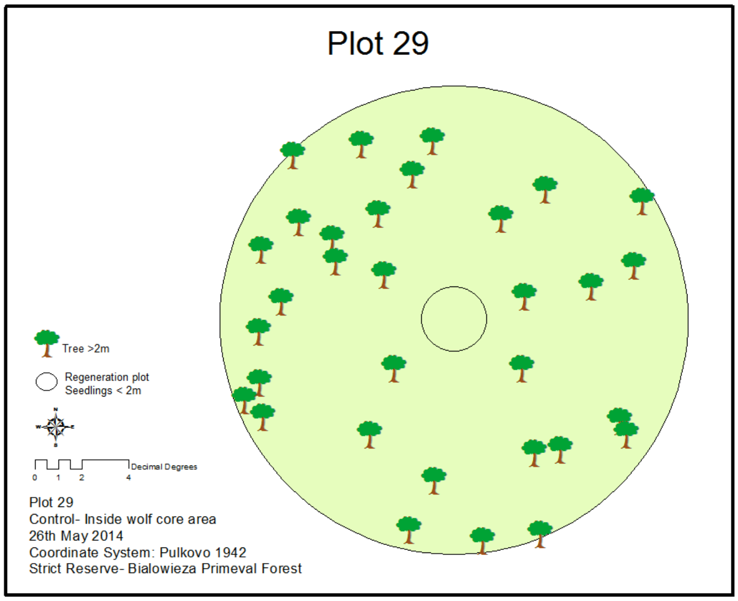

Figure A 111: Overview map of plot 29 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 112: Overview photo of plot 29

Figure A 114: Fisheye photo of plot 29. Taken in 1m height at the plot center

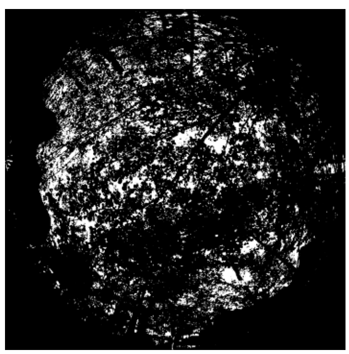

Figure A 113: Edited fisheye photo of plot 29 using Gap light Analyser

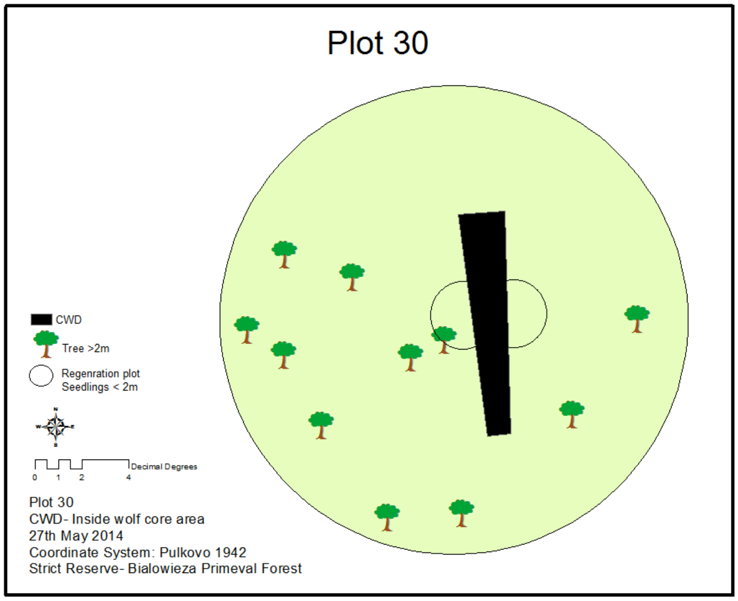

Figure A 115: Overview map of plot 30 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

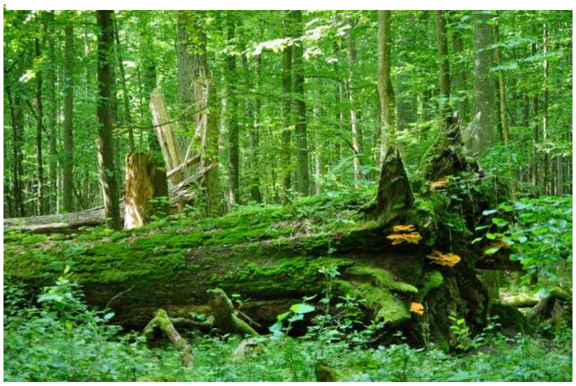

Figure A 116: Overview photo of plot 30

Figure A 118: Fisheye photo of plot 30. Taken in 1m height at the plot center

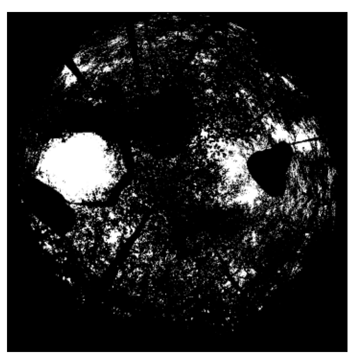

Figure A 117: Edited fisheye photo of plot 30 using Gap light Analyser

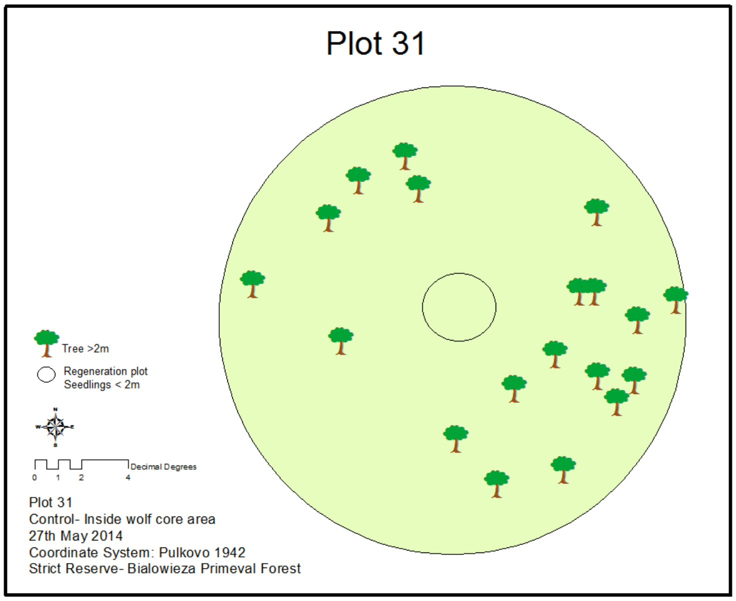

Figure A 119: Overview map of plot 31 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 120: Overview photo of plot 31

Figure A 122: Fisheye photo of plot 31. Taken in 1m height at the plot center

Figure A 121: Edited fisheye photo of plot 31 using Gap light Analyser

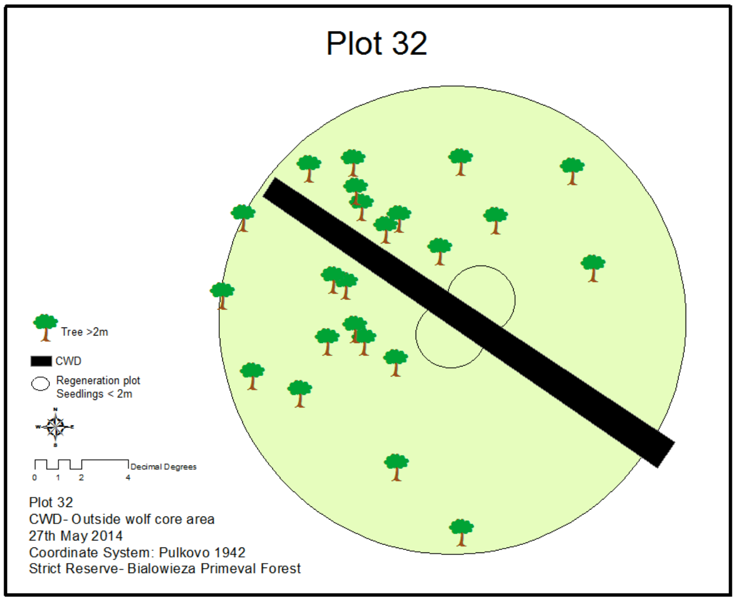

Figure A 123: Overview map of plot 32 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 124: Overview photo of plot 32

Figure A 125: Fisheye photo of plot 32. Taken in 1m height at the plot center

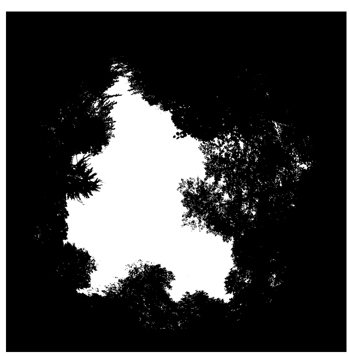

Figure A 126: Edited fisheye photo of plot 32 using Gap light Analyser

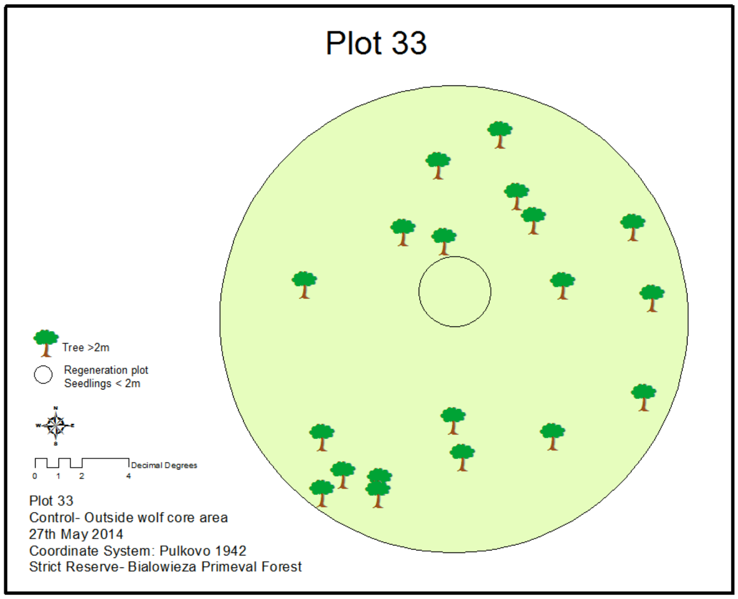

Figure A 127: Overview map of plot 33 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 128: Overview photo of plot 33

Figure A 129: Fisheye photo of plot 33. Taken in 1m height at the plot center

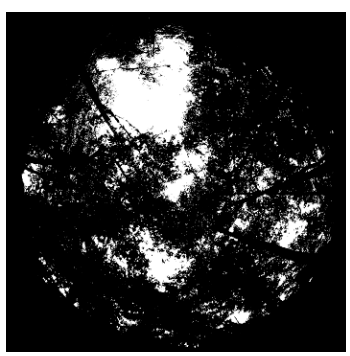

Figure A 130: Edited fisheye photo of plot 33 using Gap light Analyser

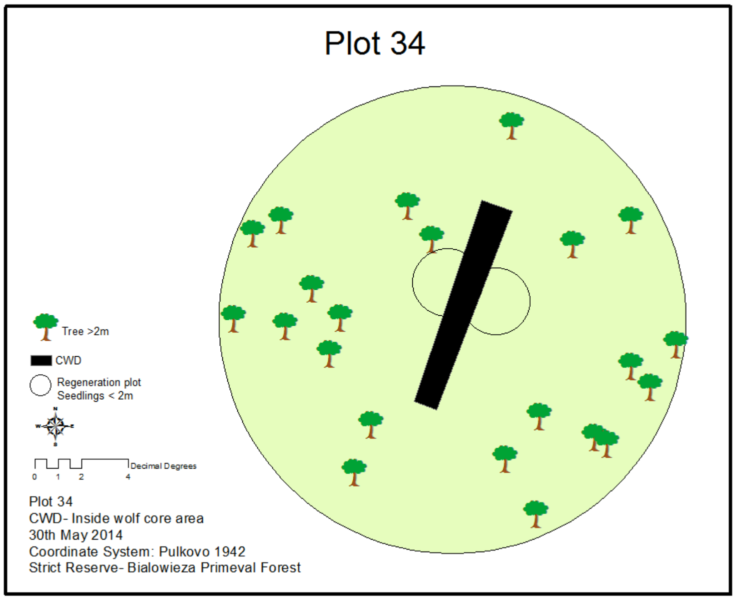

Figure A 131: Overview map of plot 33 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 132: Overview photo of plot 34

Figure A 134: Fisheye photo of plot 34. Taken in 1m height at the plot center

Figure A 133: Edited fisheye photo of plot 34 using Gap light Analyser

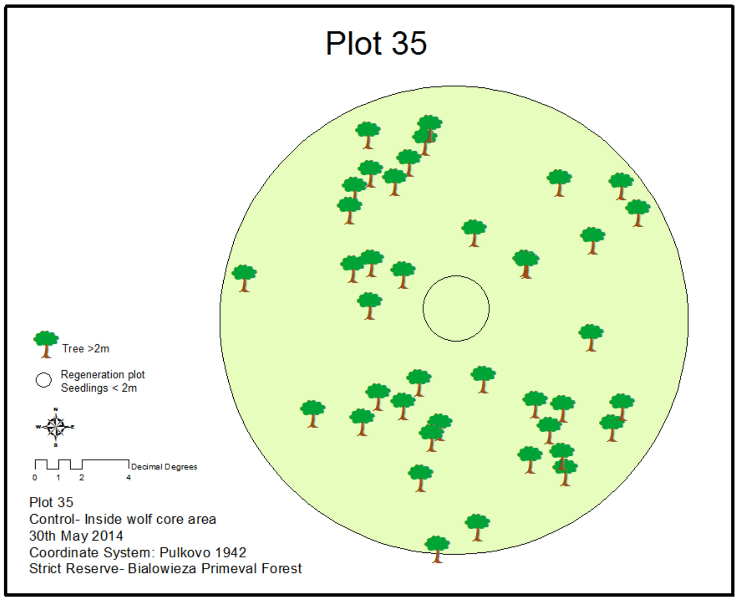

Figure A 135: Overview map of plot 35 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 136: Overview photo of plot 35

Figure A 137: Fisheye photo of plot 35. Taken in 1m height at the plot center

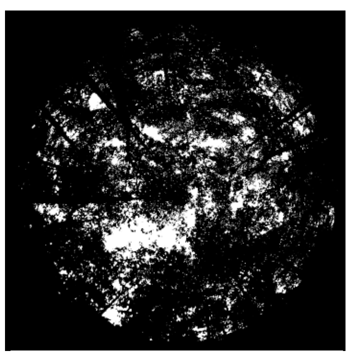

Figure A 138: Edited fisheye photo of plot 35 using Gap light Analyser

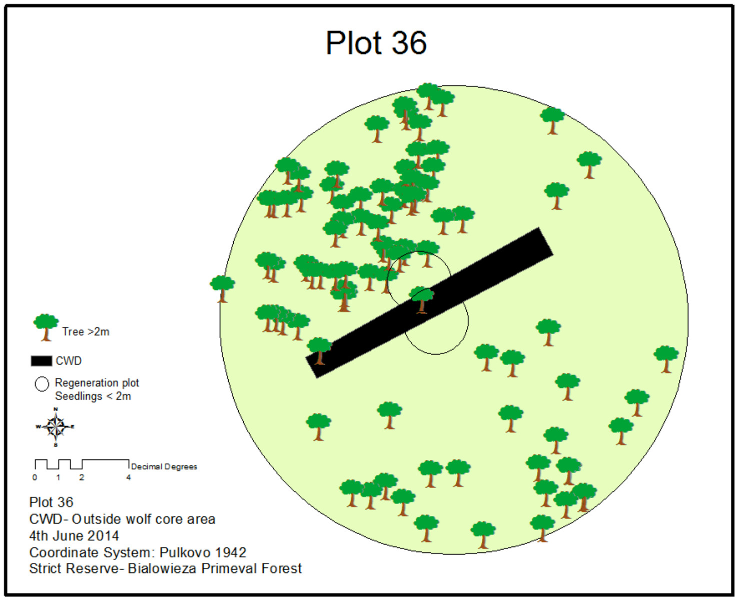

Figure A 139: Overview map of plot 36 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

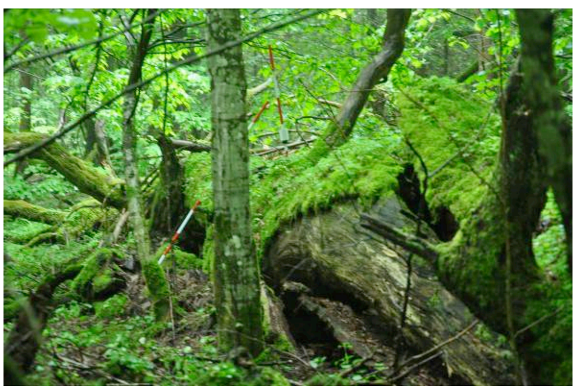

Figure A 140: Overview photo of plot 36

Figure A 141: Fisheye photo of plot 36. Taken in 1m height at the plot center

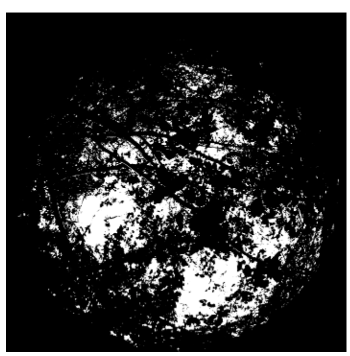

Figure A 142: Edited fisheye photo of plot 36 using Gap light Analyser

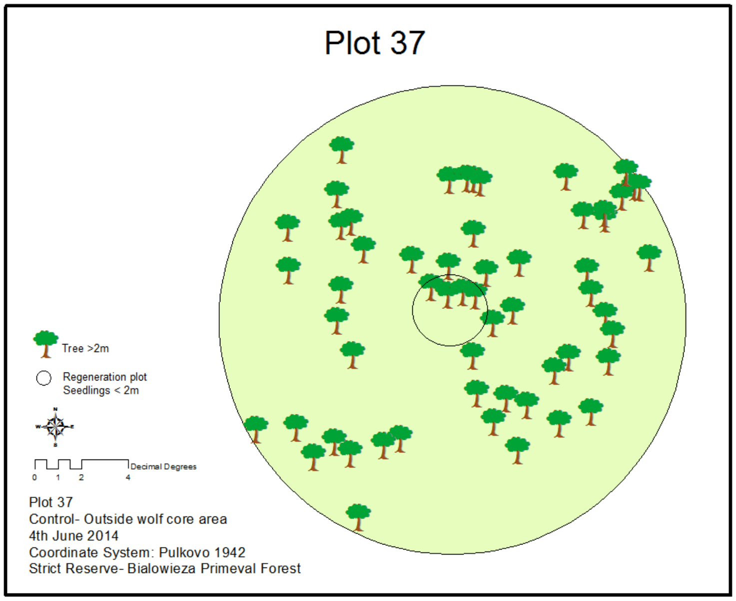

Figure A 143: Overview map of plot 37 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 144: Overview photo of plot 37

Figure A 146: Fisheye photo of plot 37. Taken in 1m height at the plot center

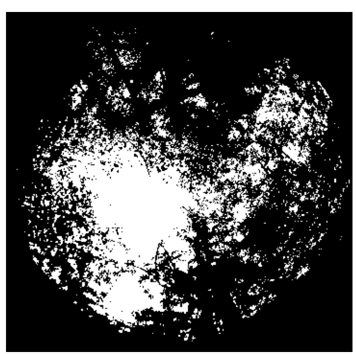

Figure A 145: Edited fisheye photo of plot 36 using Gap light Analyser

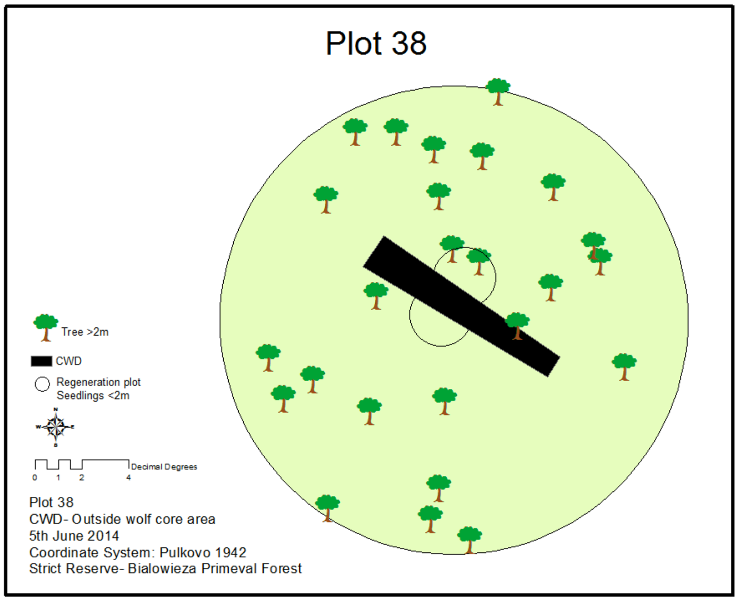

Figure A 147: Overview map of plot 38 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 148: Overview photo of plot 38

Figure A 150: Fisheye photo of plot 38. Taken in 1m height at the plot center

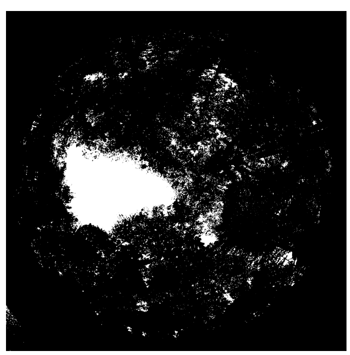

Figure A 149: Edited fisheye photo of plot 38 using Gap light Analyser

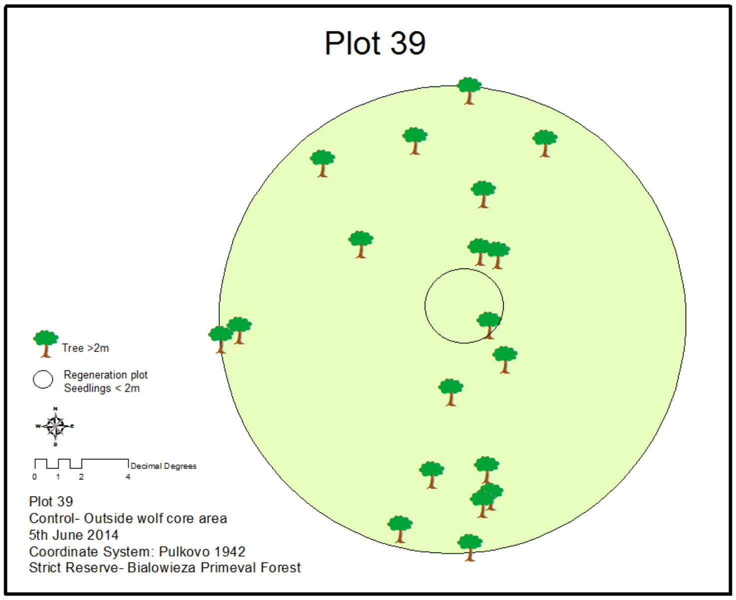

Figure A 151: Overview map of plot 39 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 152: Overview photo of plot 39

Figure A 153: Fisheye photo of plot 39. Taken in 1m height at the plot center

Figure A 154: Edited fisheye photo of plot 39 using Gap light Analyser

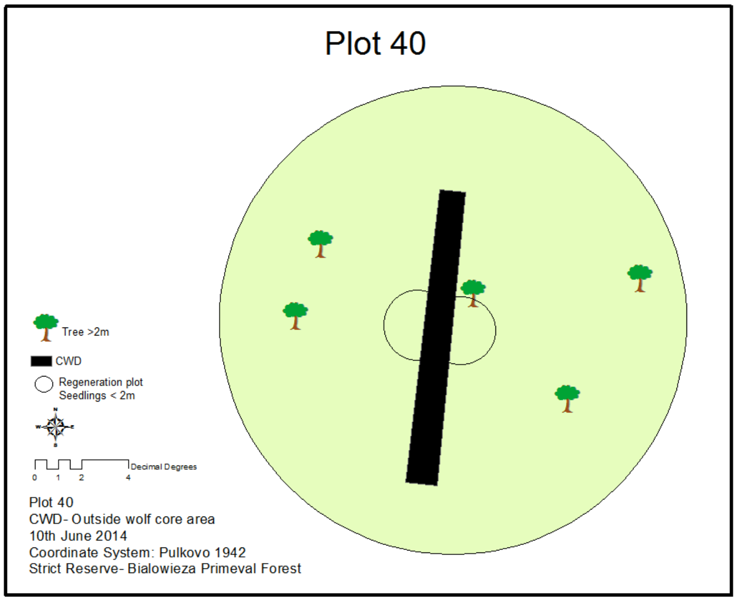

Figure A 155: Overview map of plot 40 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 156: Overview photo of plot 40

Figure A 158: Fisheye photo of plot 40. Taken in 1m height at the plot center

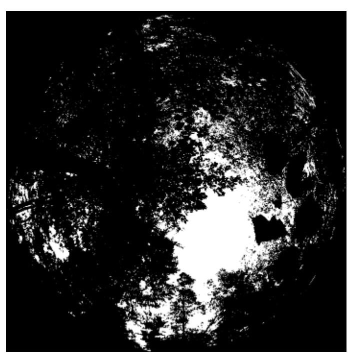

Figure A 157: Edited fisheye photo of plot 40 using Gap light Analyser

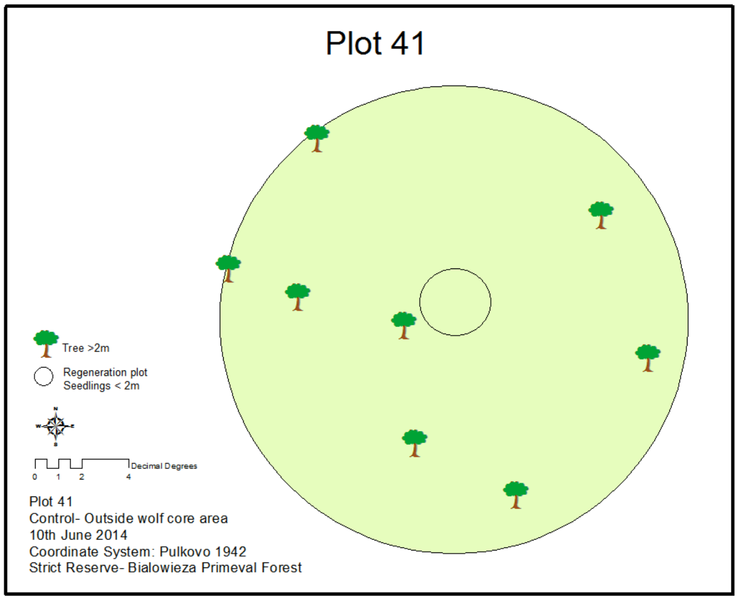

Figure A 159: Overview map of plot 41 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 160: Overview photo of plot 41

Figure A 162: Fisheye photo of plot 41. Taken in 1m height at the plot center

Figure A 161: Edited fisheye photo of plot 41 using Gap light Analyser

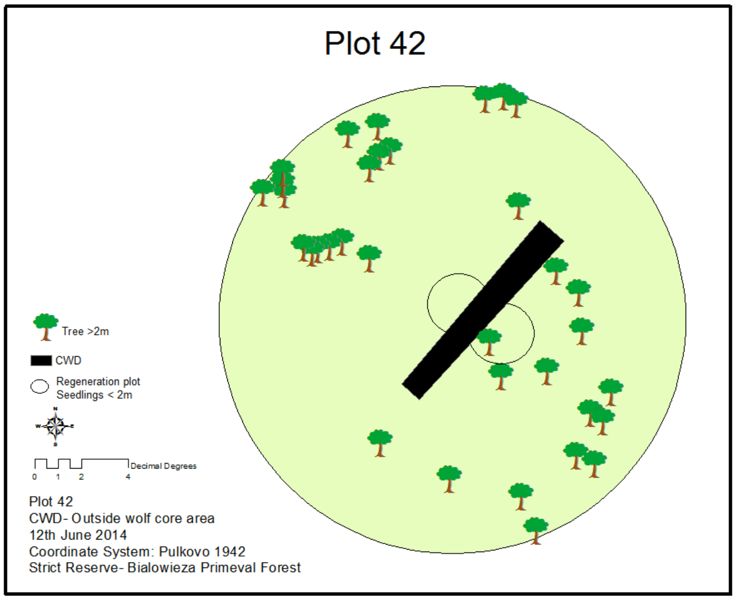

Figure A 163: Overview map of plot 42 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 164: Overview photo of plot 42

Figure A 165: Fisheye photo of plot 42. Taken in 1m height at the plot center

Figure A 166: Edited fisheye photo of plot 42 using Gap light Analyser

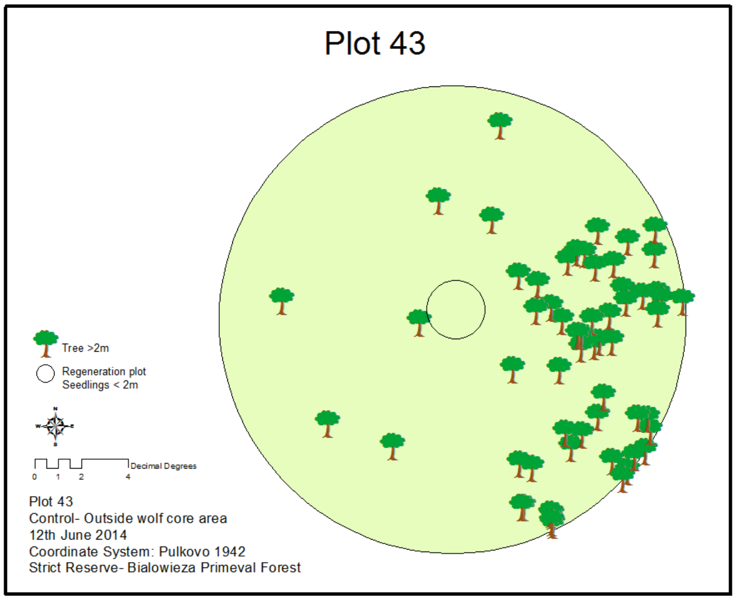

Figure A 167: Overview map of plot 43 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 168: Overview photo of plot 43

Figure A 169: Fisheye photo of plot 43. Taken in 1m height at the plot center

Figure A 170: Edited fisheye photo of plot 42 using Gap light Analyser

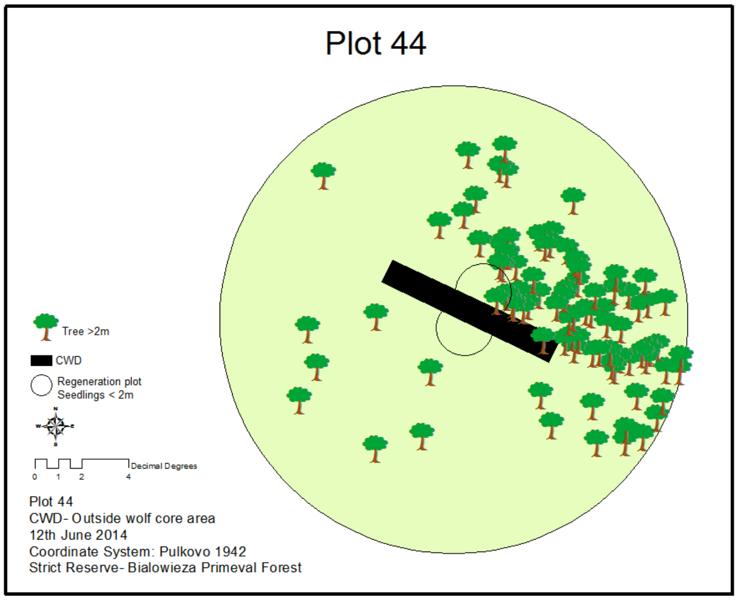

Figure A 171: Overview map of plot 44 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 172: Overview photo of plot 44

Figure A 173: Fisheye photo of plot 44. Taken in 1m height at the plot center

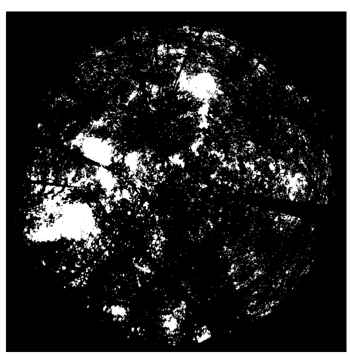

Figure A 174: Edited fisheye photo of plot 44 using Gap light Analyser

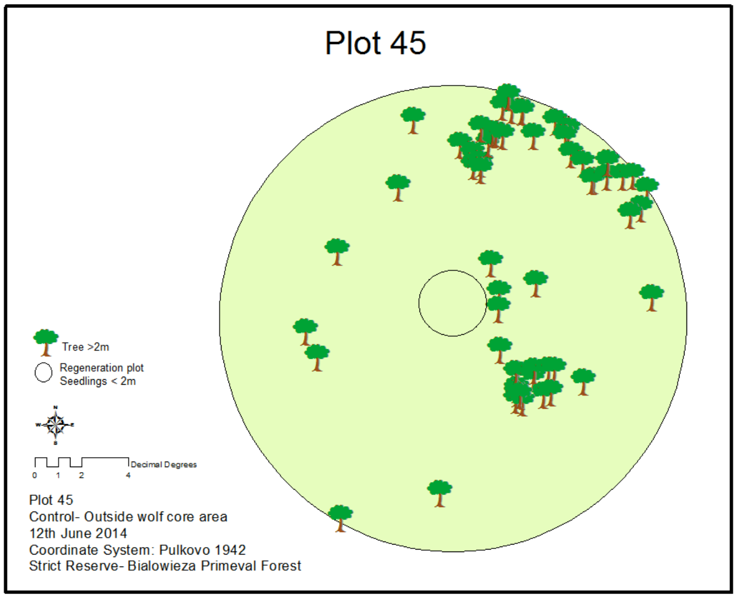

Figure A 175: Overview map of plot 45 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 176: Overview photo of plot 45

Figure A 177: Fisheye photo of plot 45. Taken in 1m height at the plot center

Figure A 178: Edited fisheye photo of plot 45 using Gap light Analyser

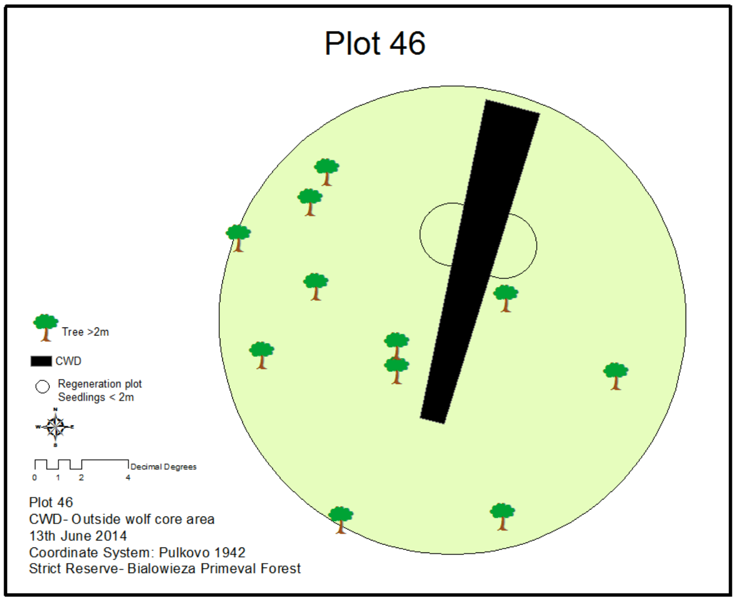

Figure A 179: Overview map of plot 46 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 180: Overview photo of plot 46

Figure A 181: Fisheye photo of plot 46. Taken in 1m height at the plot center

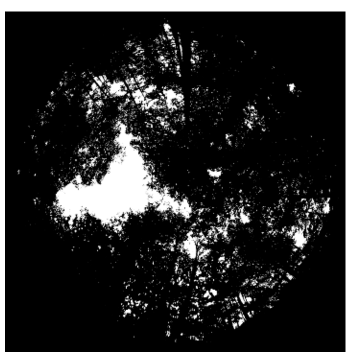

Figure A 182: Edited fisheye photo of plot 46 using Gap light Analyser

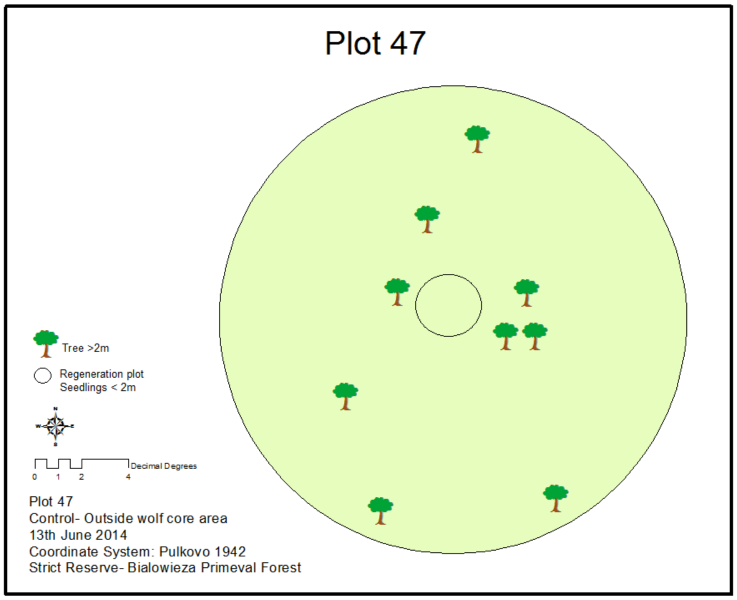

Figure A 183: Overview map of plot 47 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 184: Overview photo of plot 47

Figure A 186: Fisheye photo of plot 47. Taken in 1m height at the plot center

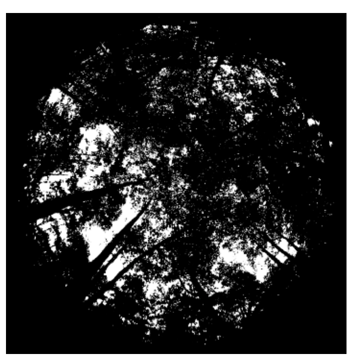

Figure A 185: Edited fisheye photo of plot 47 using Gap light Analyser

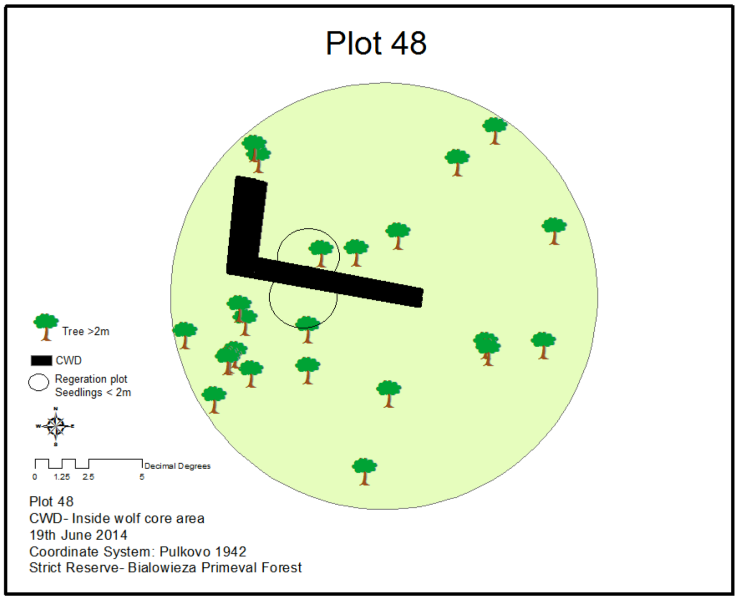

Figure A 187: Overview map of plot 48 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 188: Overview photo of plot 48

Figure A 190: Fisheye photo of plot 48. Taken in 1m height at the plot center

Figure A 189: Edited fisheye photo of plot 48 using Gap light Analyser

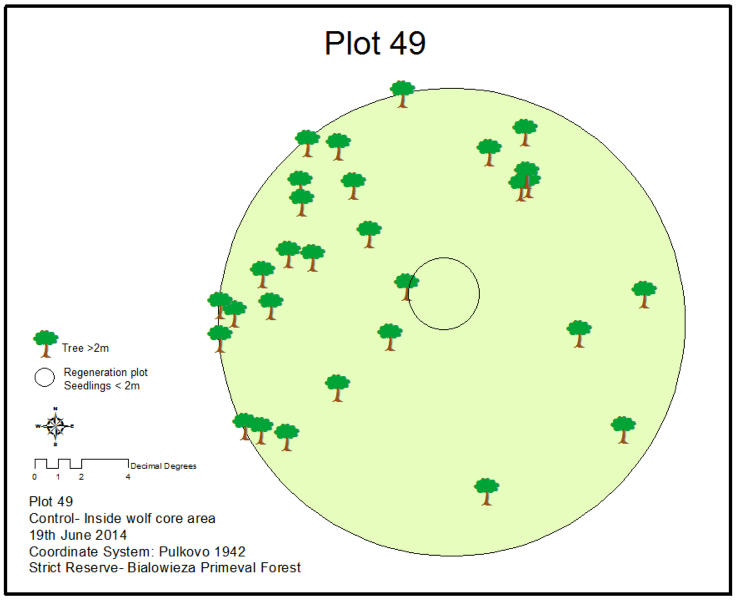

Figure A 191: Overview map of plot 49 including circular regeneration plot of seedlings <2m in the center, CWD and trees >2m

Figure A 192: Overview photo of plot 49

Figure A 193: Fisheye photo of plot 49. Taken in 1m height at the plot center

Figure A 194: Edited fisheye photo of plot 49 using Gap light Analyser