Potential for Grey wolf *Canis lupus* in the Netherlands

Effects of habitat fragmentation and climate change on the carrying capacity and population dynamics

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Abstract

Recolonization of the Netherlands by wolves is likely to occur within 5 to 10 years, and for management reasons the habitat suitability should be understood. Therefore, I predicted the carrying capacity and population dynamics of the wolf in the Netherlands, and studied the effects of habitat fragmentation and climate change. The effects of climate change on soil processes, vegetation structure and prey abundance for wolves were simulated with the models SMART2 and SUMO2. I assessed the effects of habitat fragmentation by comparing a scenario with and without wildlife overpasses. Population dynamics were simulated applying the model METAPHOR. Due to climate change, primary productivity increased, resulting in higher prey availability. Wolf carrying capacity and population dynamics are hence positively affected by climate change, although the effect was smaller than for habitat fragmentation. The average number of adults after a 110 year model run more than doubled in the presence of overpasses compared to the scenario without. Population persistence is negatively affected by habitat fragmentation. This study indicates the importance of overpasses for carnivores, which therefore should be an integrated part of nature management.

Keywords: Canis lupus, wolf, habitat fragmentation, population dynamics, persistence, overpasses, climate change.

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Contents

1   Introduction

Within an ecosystem, populations of producers, carnivores and decomposers are generally limited by resources, whereas herbivores are in general predator-limited (Hairston et al., 1960). Many studies have shown that carnivores can have strong direct effects on the structure and dynamics of herbivore prey communities (Sih et al., 1985; Schmitz et al., 2000) through reducing prey abundance or biomass (Hairston et al., 1960). However, predator populations may be limited by prey availability (a.o. Jaksic et al., 1997). Both climate change and habitat fragmentation might alter predator-prey relationships by affecting both prey and predator abundances.

Due to climate change, many species, both prey and predator species, have shifted their distributions towards higher latitudes and elevations (Thomas, 2010; Chen et al., 2011). This may lead to changed interactions if species differ in their ability to track changing climates, which is found in several ecosystems (Voigt et al., 2003; Dunson and Travis, 1991; Gilman et al., 2010; Walther et al., 2002). Higher trophic levels are more sensitive to climate change than lower levels (e.g. Voigt et al., 2003; Vasseur and McCann, 2005), because of their relatively greater metabolic needs and smaller population sizes (Gilman et al., 2010). However, it is predicted that rainfall and temperature will increase in the future (Van den Hurk et al., 2006), which both are expected to increase net primary production (Lieth, 1995; Schuur, 2003; Del Grosso, 2008). This increased primary productivity is expected to positively affect herbivore prey abundance (Walther, 2010) which may subsequently affect predator abundance. In this way, climate change might lead to changed predator-prey interactions.

Habitat loss generally affects predators more than their prey, and hence prey species may benefit from decreased predation risk (Ryall and Fahrig, 2006; Baggio et al., 2011; Moorcroft et al., 2006). Mammalian carnivores, such as the wolf *(Canis lupus)* and the lynx *(Lynx lynx)*, are particularly vulnerable to habitat loss and fragmentation as a result of traits such as large body sizes, large area requirements, low densities and slow population growth rates (Hunter et al., 2003; Crooks, 2002). Mammalian carnivores need spatially heterogeneous landscapes for dispersal, territorial defence, resource acquisition and reproduction (McKenzie, 2006; Crooks et al., 2011). Fragmentation results in decreased connectivity of these different habitat types and may hence disturb movement and decrease population viability (Crooks et al., 2011; Taylor et al., 1993). In addition, habitat fragmentation might provide spatial refuges for prey, i.e. places with lower predation risk, which may lead to reduced predator efficiency in fragmented habitats (Sih et al., 1985; McNair, 1986). For the lynx, habitat fragmentation is the most detrimental factor for population survival due to barriers like highways and resulting road kills (Schmidt, 2011; Zimmermann et al., 2007).

Although both habitat fragmentation and climate change are intensively studied (e.g. Thomas, 2010; Chen et al., 2011; Fahrig, 2003), less is known about their interactive effects on predator-prey interactions due to both negative and positive effects on either prey or predator, which might depend on specific traits of both trophic levels. In this thesis, the effects of habitat fragmentation and climate change on predator-prey relationships will be studied. The wolf will be used as a case study. Herbivore prey abundance is predicted to increase as a result of increased primary productivity due to climate change (Jaksic et al., 1997; Timmerman et al., 1999). This increased prey availability may positively affect wolf carrying capacity. However, recent habitat fragmentation might limit the expansion of wolf habitat due to roads and urban areas.

Originally, until the 18th century, wolves *(Canis lupus* L., 1758, ord. *Carnivora*, fam. *Canidae)* were present in all European countries except for Great Britain and Ireland. As a result of hunting, the wolf has nearly been exterminated in central and western Europe during the 19th century (Boitani, 2000; Glenz, 2001), with mainly small isolated populations remaining in Portugal, Spain, Italy, Greece and Finland (Boitani, 2000). During the last 30 years, the wolf has recovered in France, Germany, Switzerland, Sweden and Norway (Boitani, 2000). The nearest wolf packs in Germany and France are at a distance of 400 km from the border of the Netherlands (www.wolveninnederland.nl). Having in mind the high mobility of the wolf, with dispersal distances of hundreds of kilometres, and even observations of dispersal distances of up to 1500 km (Mech and Boitani, 2003), wolf experts (a.o. Leo Linnartz, Stichting ARK) stated that the wolf is expected to colonize the Netherlands within 10 years. The presence of wildlife overpasses in the Netherlands decreases the degree of habitat fragmentation, and thus may facilitate colonization and positively affect population persistence. As survival of local wolf populations may depend on the health of neighbouring populations, evaluation and management of the fragmented populations in Europe is needed (Boitani, 2000). For that reason, factors limiting the recolonization and establishment of the wolf in the Netherlands should be understood.

The carrying capacity of the Netherlands for the wolf might be determined by climate change and habitat fragmentation. Wolves are expected to be highly negatively affected by habitat fragmentation, mainly due to large area requirements (Hunter et al., 2003; Mladenoff et al., 1999; Whittington et al., 2004). Several studies have shown that wolves avoid areas with a high probability of encountering people (e.g. Whittington et al., 2004; Theuerkauf et al., 2003) and habitats within the range of 250 meters from roads (Kaartinen et al., 2005). This might exclude wolves from the habitats where prey populations are highest (Whittington et al., 2005) and lead to disturbance of den sites (Theuerkauf et al., 2003).

In this study, I will address the question what the carrying capacity of the Netherlands is for the wolf, and simulate their population dynamics. Attention will be to the following sub questions:
– What is the effect of vegetation change due to climate change on prey abundance, and how does this affect wolf carrying capacity and population dynamics?
– What is the effect of wildlife overpasses on wolf carrying capacity and population dynamics?
– Is there an interaction between the effect of climate change and habitat fragmentation on wolf carrying capacity and population dynamics?

First, the effects of climate change on the vegetation are modelled. These changes in vegetation are translated to changes in abundances of the (herbivore) prey species of the wolf. Subsequently, the effects of changed prey abundance on wolf carrying capacity and population dynamics are assessed. The effects of habitat fragmentation are studied by comparing a scenario with overpasses with a scenario without overpasses.

2 Materials and methods

2.1 Study area

The Netherlands is a highly cultivated landscape, with a high road density of 372 km roads per km^2 land area (2005, World Bank). The total forest cover in the Netherlands is about 10.8% (FAO).

2.2 Ecological profile wolf

Wolves live in packs, usually consisting of a breeding pair and their offspring from one or more generations. These packs cooperate in hunting and defending their territories. Reproduction is limited to the alpha male and female, which are the dominant pack members. In general, wolves reproduce once a year. They give birth in dens, usually to three to ten pups. Sexual maturity is reached after three years (Mech and Boitani, 2003). Juveniles around the age of one or two years generally leave the pack in order to form a new pack. With a dispersal distance of around 200 km, these animals may facilitate recolonization (Mech and Boitani, 2003).

Wolves are able to survive in a wide range of habitats. The quality of habitat is mainly determined by human disturbance and prey densities (Boitani, 2000; Mladenoff, 1995). Areas occupied by wolves have higher degrees of forest cover, higher prey availability, lower human population densities and lower densities of roads and human settlements (Jedrzejewski et al., 2004; Oakleaf et al., 2006). As wolves are territorial (Boitani, 2000), large areas are required to support viable populations (Woodroffe and Ginsberg, 1998). In the cultivated landscape of Europe, the minimum area requirement is about 120 km^2 per pack, with larger area requirements in areas with low prey abundance (www.wolveninnederland.nl). The diet of the wolf is very diverse, consisting of the most available food in its habitat (Boitani, 2000). In Germany, for example, 52% of its diet consists of roe deer (Capreolus capreolus), 25% of red deer (Cervus elaphus) and 17% of wild boar (Sus scrofa) (http://www.wolfsregion-lausitz.de/nahrungszusammensetzung). In the Netherlands, roe deer, red deer, fallow deer, wild boar, hares and rabbits are expected to become the main prey species for the wolf (Leo Linnartz, Stichting ARK, personal communication). Roe deer are abundant throughout the whole country, with in total 70.000 individuals, and may therefore be important during dispersal to new habitats (Leo Linnartz, Stichting ARK, personal communication).

2.3 Models

The models SMART2, SUMO2 and METAPHOR are used in this study. First, soil processes and vegetation succession are modelled for two climate scenarios by using the model chain SMART2-SUMO2. In addition, in SUMO2, these changes in vegetation are translated to changes in abundance of the (herbivore) prey species of the wolf. Subsequently, the effects of changed prey abundance and changed vegetation on population dynamics of the wolf are modelled for two scenarios of habitat fragmentation: one without overpasses and one with overpasses. For the simulation of population dynamics of the wolf an individual-based metapopulation model, METAPHOR, is used. See Figure 1 for an overview.
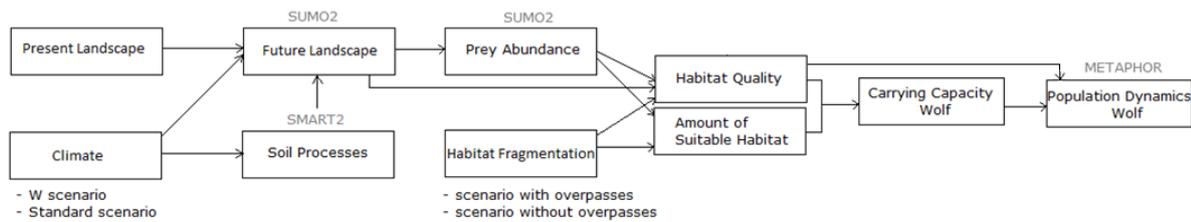
Figure 1

Overview of factors studied in this project, with in grey the models used. Two climate scenarios and two scenarios of habitat fragmentation are used, resulting in four combinations.

The two climate scenarios are referred to as the 'W scenario' and the 'standard scenario'. In the W scenario, the predicted global increase of temperature until 2100 is four degrees Celsius, no change of air-circulation is assumed, and precipitation in both summer and winter increases with 3% per degree temperature-increase (Van den Hurk et al., 2006; Figure 2). In the 'standard scenario', the temperature, precipitation and air-circulation are assumed to remain constant.
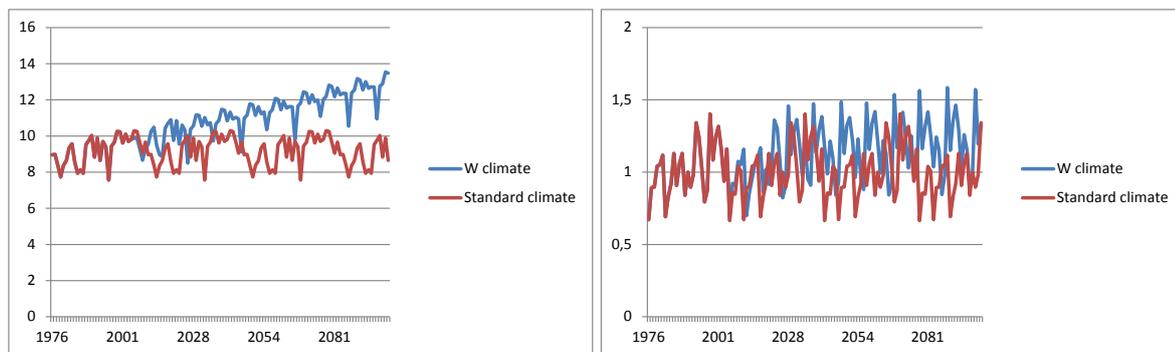
Figure 2

Trend in temperature (left) and precipitation (right) over the years for the W and standard climate scenario. Modified after Van den Hurk et al. (2006).

The effect of habitat fragmentation is assessed by comparing a scenario with overpasses with a scenario without overpasses for both climate scenarios, resulting in a total of four scenarios. When overpasses are present, wolves are assumed to freely cross roads that would normally act as barrier, which may result in larger habitat areas. Only overpasses large enough for the wolf are taken into account. Both finished and planned overpasses are considered (Figure 3).

2.3.1   SMART-SUMO

SMART2 (Kros, 2002; Mol-Dijkstra et al., 2009) and SUMO2 (Wamelink et al., 2009a,b) are used for the simulation of respectively soil processes and vegetation succession. In both models, the time step is one year. The standard and w-climate scenario are used as input for SMART2 to assess the effects of climate change on soil processes. The processes simulated in SMART2 include the gross element input from the atmosphere, geochemical interactions in the soil, foliar uptake and exudation, root decay, litterfall, mineralization, nutrient uptake, nitrification and denitrification.

In SUMO2, succession is simulated based on information on soil processes, provided by SMART2. Biomass and nitrogen dynamics are simulated for five functional plant types: herbs and grasses, dwarf shrubs, shrubs, and two site specific tree species. In addition, SUMO2 simulates vegetation type. Six vegetation types are distinguished: grassland, heathland, reed land, shrub vegetation, salt marsh and forest. The model accounts for different types of management. In this study, management is assumed to remain constant. Grazers are modelled to decrease the vegetation biomass through eating, and to put nitrogen back into the soil via manure. With high food availability, the amount of grazers will increase gradually until a maximum. In case of food shortage, the number of grazers is adjusted to the amount of food available. By changing the vegetation, climate change will affect herbivore abundance, which will subsequently affect carrying capacity and population dynamics of wolves.

Initial prey numbers
For the calculation of the initial prey numbers, data on prey presence were kindly provided by the Dutch Mammal Society. As no data on prey abundance was available, the current abundance of the different species was estimated by using data on density in different habitats (Groot Bruinderink et al., 2000, 2001). For red deer, roe deer and wild boar, density data were available per habitat type. For fallow deer, an average density was available, which is used as constant density for all habitat types. For hare and rabbit, the density was estimated based on literature (Smith et al., 2005; Serrano Pèrez et al., 2008; Tompson and King, 1994). The distinguished vegetation types are the following: coniferous forest, deciduous forest, grassland and heathland, as defined in the VIRIS database (provided by Alterra). For the other vegetation types in which the species were present, an average density is chosen (Appendix 1, Table 1). If more than one vegetation type was present, the density was calculated according to their relative cover.

Species parameters
For every species, the relative biomass of roots, stems and leafs eaten per individual is used as input for SUMO2. In addition, amount of faeces, and concentrations of N, ureum, phosphorus, potassium, magnesium and calcium in faeces are used to assess the amount of nutrients going back into the soil (Appendix 1, Table 2). Data on these parameters for all species except for hare were obtained from Wamelink et al. (2009b), in which these values are estimated. For hares, the concentrations of the different nutrients and the fraction faeces are assumed to be the same as for rabbits. The amount of biomass grazed by European hares is adapted from Kronfeld and Shkolnik (1996).

2.3.2 METAPHOR

METAPHOR (Verboom et al.; 2001, Vos et al.; 2001, Schippers et al., 2009) is an individual-based model, simulating the dynamics of a metapopulation. It is often used to predict the effects of habitat fragmentation on the presence and stability of populations. Patches of suitable habitat, with corresponding habitat quality, are used as input for this model. For the wolf, habitat quality is mainly affected by prey availability, habitat area, forest cover and human disturbance (Boitani, 2000; Massolo and Meriggi, 1998; Jedrzejewski et al., 2004). The latter three are assumed to remain constant over the years, whereas prey availability changes due to climate change. Every ten years, the outcome of the simulations of prey biomass from SMART2-SUMO2 is used to predict the quality of every habitat patch. METAPHOR is initialized with 30 adult individuals, and is run from 1990 to 2100.

Identification of suitable habitats
First, habitats suitable for the wolf had to be identified. Wolves are able to live in diverse types of habitat, from desert to tundra, and from open field to dense forest (Geffen et al., 2004). The main criterion for habitat in order to be suitable for wolves is sufficient prey availability (Boitani, 2000; Jedrzejewski et al., 2004; Massolo and Meriggi, 1998). In the Netherlands, prey occurs everywhere. For that reason, it is not taken into account

for the identification of suitable habitats, but prey density is used for the calculation of the habitat quality and the carrying capacity for METAPHOR.

Because of avoidance of areas within 250 meters from roads (Kaartinen et al., 2005), roads are used as border of habitats. As traffic intensity influences this avoidance behaviour of wolves (Whittington et al., 2005), two areas in the Netherlands are distinguished: the more urbanized provinces Utrecht, Noord-Holland and Zuid-Holland, in which roads are more intensively used, versus the rest of the Netherlands. In the more urbanized provinces, both main roads and highways are taken into account, whereas for the rest of the Netherlands only highways are assumed to form a barrier (see Figure 3).

As wolves avoid areas within 250 meters from buildings (Kaartinen et al., 2005), these areas were excluded as suitable habitat. For every area surrounded by roads, the total area is subtracted by the area within 250 meters from roads and buildings, giving the area that can be used by wolves (Box 1: Equation 1). The minimum required area for a wolf pack in cultivated Europe is 120 km^2 (www.wolveninnederland.nl). For that reason, a habitat is only considered suitable when the usable area meets this minimum area requirement.

Carrying capacity
The carrying capacity for wolves is assumed to be either limited by prey abundance or by area. For that reason, both the carrying capacity based on prey availability and the carrying capacity based on area requirements are calculated.

Carrying capacity based on prey availability
The total consumable biomass of prey (in kg) is calculated based on the densities of the different prey species. A method provided by Leo Linnartz (Stichting ARK) is used for this, in which the prey abundance is assumed to remain constant, with the amount of predation being equal to the mortality of prey without predation. Wolves are known to mainly predate on weak individuals (Leo Linnartz, personal communication). For that reason, it is assumed that wolf predation will have no large effects on prey numbers. Parameters shown in Table 3 (Appendix 1) are used. For every species, the yearly number of individuals available for predation is calculated as the population size multiplied by the population growth factor. Subsequently, the total consumable biomass is calculated as the consumable biomass per individual (kg) times the number of individuals available for predation (Box 1: Equation 2).

For every suitable habitat, the total consumable biomass is calculated. The carrying capacity based on prey availability is calculated as the total consumable biomass of prey (kg/yr) divided by the yearly consumption per wolf (kg/yr) (Box 1: Equation 3). As prey availability may change due to climate change, the carrying capacity based on prey availability may also change.
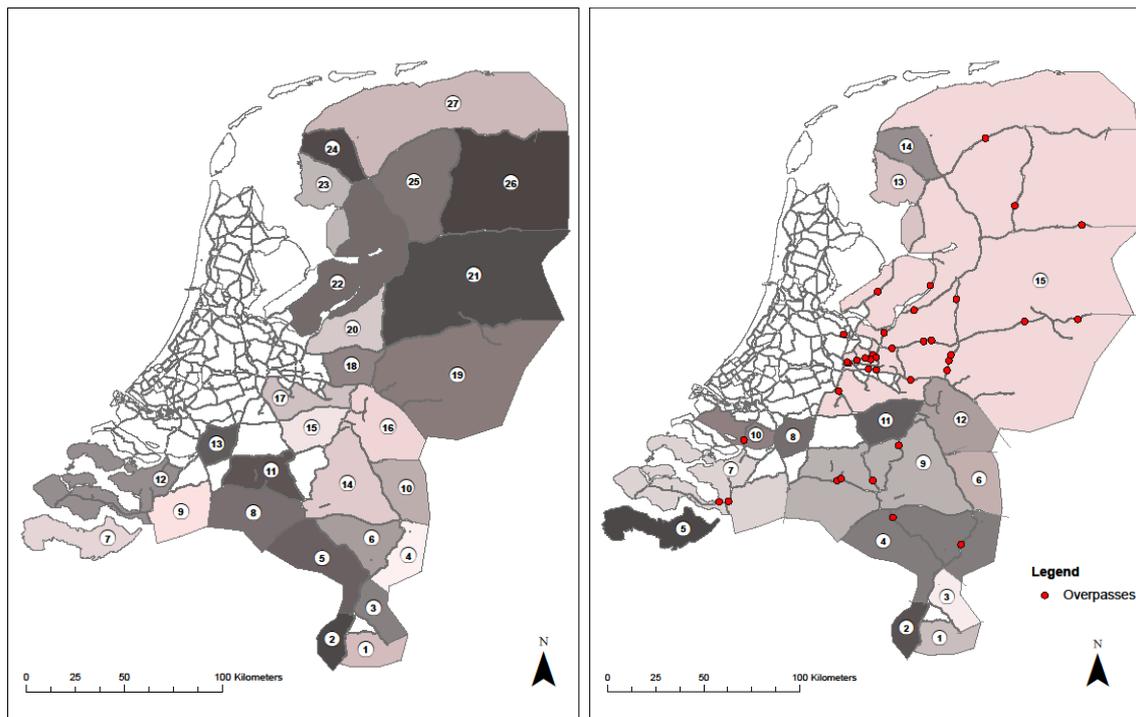
Figure 3

*Suitable habitats in the Netherlands for the scenario without (left) and with overpasses (right). Overpasses large enough
for the wolf are displayed as red dots. Every suitable habitat is displayed in a different colour and numbered.*

Carrying capacity based on area requirements

The maximal number of packs based on area requirements is calculated as the total usable area divided by the
minimal area restriction of 120 km^2 (www.wolveninnederland.nl) (Box 1: Equation 4). As pack size is dependent
on prey density, consumable prey biomass per m^2 is calculated for every habitat (Box 1: Equation 5).
Predicted pack sizes are shown in Table 4 (Appendix 1) for different ranges of consumable prey biomass.
Subsequently, the maximum number of wolves based on area is calculated as the number of packs multiplied
by the pack size (Box 1: Equation 6).

For every habitat, the carrying capacities based on prey availability and area are compared, and the lowest
value is used in METAPHOR (Box 1: Equation 7). For example, when $CC_{prey} > CC_{area}$, the area seems to be more
restricting than the prey abundance. In this case, CC_{area} will be used in the model.

Habitat Quality

As processes in METAPHOR are influenced by habitat quality, every habitat is assigned a value between
0 and 1 representing respectively poor and very suitable habitats. For wolves, the main factor affecting habitat
quality is prey availability (Theuerkauf et al., 2003; Boitani, 2000; Jedrzejewski et al., 2004). Forest cover also
has a positive effect on the quality (Jedrzejewski et al., 2004; Massolo and Meriggi, 1998). In addition, the
area of a habitat is assumed to affect quality positively. Human disturbance negatively affects habitat quality
for wolves (Jedrzejewski et al., 2004; Oakleaf et al., 2006). In this study, the relative area of buildings is used
as an indicator of human disturbance. Prey availability, forest cover, area and the relative area covered with
buildings are divided into ranges, to which quality factors are assigned (Table 5, Appendix 1). The overall
quality of a habitat is calculated as the average of the four different quality factors (Box 1: Equation 8).

Population dynamics
METAPHOR is initialized with 50 adult individuals, with 50% chance of being either male or female. For the scenario without overpasses, the individuals are introduced in habitat 19, 21 and 16 (Figure 3, left map), with respectively 35, 10 and 5 adult individuals. For the scenario with overpasses, habitat 15 (Figure 3, right map) is used as initial habitat.
For the wolf, three different life stages are distinguished: pup (0-1 years), juvenile (1-3 years) and adult (>3 years). For every individual, four processes are simulated: aging, dispersal, survival and reproduction. The occurrence and parameters of the last three processes are assumed to be dependent on the current life stage of the individual. In addition, dispersal, survival and litter size are assumed to be dependent on habitat quality.

Dispersal
In the model METAPHOR, wolves of one and two years old disperse, with a basic dispersal rate of 80%, which varies according to quality and pack size. In a study in Canada (Hayes and Harestad, 1999), dispersal rates were higher in larger packs and in lower quality habitats. In the model, wolves are assumed to disperse a minimum distance of 100 km, after which they choose a habitat of sufficient quality. The chance of settling increases with distance and depends on quality of the patch (Figure 4; Box 1: Equation 9).
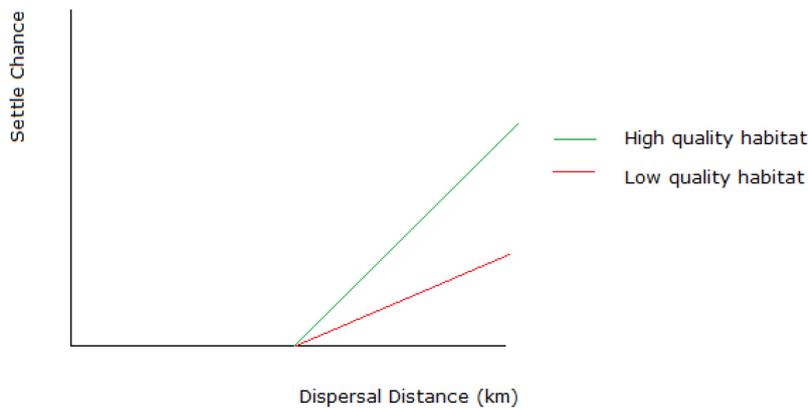
Figure 4
Relation between dispersed distance and settle chance, for high and low quality habitat.

For every individual, a number between 0 en 1 is drawn from a random distribution. If the settle chance exceeds this number, the wolf is assumed to settle if the carrying capacity is not reached. If the chance of settlement is not sufficient or the maximum number of packs in the patch has already been reached, the wolf continues its dispersal. When a wolf arrives in a patch where one or more of individuals of the opposite sex are present, but less than the maximum number of reproductive units in that habitat, the wolf is assumed to settle and form a new pack with an individual of the opposite sex (Box 1: Equation 10). If the wolf has not settled after 500 km, it is assumed to die. In this way, an increased mortality during dispersal, due to crossing roads and not finding suitable habitat, is taken into account.

Although wolves avoid roads in their habitat, dispersal is not affected by roads (Kohn et al., from Wydeven et al. (Eds.), 2009). The direction of dispersal is assumed to be random. Therefore, the chance of dispersal to a neighbouring habitat is assumed to be relative to the length of the interface between the habitats (Box 1: Equation 11). It is assumed that for every wolf going out of the Netherlands, a wolf from Germany or Belgium comes back, meaning that net no wolves will be leaving the Netherlands.

Survival

Wolf yearly survival is dependent on age, with pups having lower survival rates. Basic survival rates from Boitani (2000) are used, which are shown in Table 6 (Appendix 1). Survival rate is affected by quality (Boitani, 2000), with lower survival in poor habitats. For the interpolation of survival rates in habitats of intermediate quality, a linear relationship is assumed.

Reproduction

After three years, sexual maturity is reached (Mech and Boitani, 2003). For that reason, only for individuals older than three years, reproduction takes place. In every pack, only one female (the alpha-female) reproduces. The number of reproducing females in a habitat therefore equals the number of packs in that habitat.

The number of pups is dependent on habitat quality, and assumed to be density independent. In a high quality habitat, the number of pups per litter were taken as 6 (± 1), and in a low quality habitat, the number of pups were 2 (± 1). For intermediate qualities, the number of pups is interpolated by assuming a linear relationship.

The total number of adult wolves in the Netherlands is calculated for every year in each run. The average number of adults over the runs is plotted against the time in order to see the trend in average number of wolves.

In addition, as indicator for population persistence, the average maximum year over the 150 runs is calculated. Every run ends in year 2100. However, if the population becomes extinct, the run stops earlier. A low number therefore indicates a low population persistence.

Box 1: Equations

Eq. 1: $Area_j = Area_{T,j} - Area_{Build,j}$

Eq. 2: $ConsB_{ij} = ConsB_{ind,i} * N_{i,j} * r$

Eq. 3: $CC_{preyav,\,j} = \frac{\sum_{i=1}^{n} ConsB_{ij}}{Cons_{Wolf}}$

Eq. 4: $N_{packs,j} = \frac{Area_j}{MAR}$

Eq. 5: $DensPrey_j = \frac{\sum_{i=1}^{n} ConsB_{ij}}{Area_j}$

Eq. 6: $CC_{area,j} = PS_j * N_{packs,j}$

Eq. 7: If $(CC_{preyav,\,j} < CC_{area,\,j})$: $CC_j = CC_{prey\_av,\,j}$

If $(CC_{area,\,j} < CC_{prey\_av,\,j})$: $CC_j = CC_{area,\,j}$

Eq. 8: $Q_{habitat,\,j} = \frac{Q_{human,j} + Q_{prey,j} + Q_{forest,j} + Q_{area,j}}{4}$

Eq. 9: If $(Dist_w < Dist_{min})$: $P_{settle,\,wj} = 0$

If $(Dist_w > Dist_{min})$: $P_{settle,\,wj} = (Dist_w - Dist_{min}) * D * Q_{habitat,\,j}$

Eq. 10: If $(N_{pop.\,sex,\,j} >= 1$ & $N_{opp.\,sex,\,j} < N_{packs,\,j})$: $P_{settle,\,j} = 1$

Eq. 11: $P_{a,b} = \frac{IF_{a,b}}{\sum_{k=1}^{m} IF_{a,k}}$

Indices: i: prey species; j: suitable habitat patch; k: habitat adjacent to habitat a; w: individual wolf; m: total number of habitats adjacent to habitat a.

Variables:

$Area_j$: Usable area in habitat j (m²) ; $Area_{T,j}$: Total area in habitat j (m²); $Area_{Build,j}$: Area within 250m around aggregated buildings in habitat j (m²); $ConsB_{i,j}$: Total consumable biomass of species i in habitat j (kg yr⁻¹); $ConsB_{ind,i}$: Consumable biomass per individual of species i (kg); $N_{i,j}$: Population size of species i in habitat j (-); r: Population growth factor (yr⁻¹); $CC_{prey\_av,\,j}$: Carrying capacity based on prey availability for habitat j (-); $Cons_{Wolf}$: Yearly consumption per wolf (kg yr⁻¹); $N_{packs,\,j}$: Maximal number of packs in habitat j (-); $CC_{area,\,j}$: Carrying capacity in habitat j based on area requirements (-); PS_j: pack size in habitat j (-); CC_j: Carrying Capacity in habitat j (-); Q_j: Overall quality of habitat j, value between 0 and 1 (-); $Q_{human,j}$: Quality factor based on human disturbance in habitat j (-); $Q_{prey,\,j}$: Quality factor based on prey availability in habitat j (-); $Q_{forest,\,j}$: Quality factor based on forest cover in habitat j (-); $Q_{area,\,j}$: Quality factor based on total usable area in habitat j (-); $Dist_w$: travelled distance by wolf w (m); $Dist_{min}$: minimal travelled distance after which the chance of settlement increases (m); $N_{pop.\,sex,\,j}$: Number of individuals of the opposite sex in patch j (-); $P_{settle,\,w,j}$: Chance of settlement of wolf w in habitat j (-); D: Rate of increase of settle chance with dispersed distance (m⁻¹); $P_{a,b}$: Chance of dispersing from habitat a to habitat b (-); $IF_{a,b}$: Interface of habitat a with habitat b (m); $IF_{a,k}$: Interface of habitat a with habitat k (m).

3 Results

3.1 Effect of habitat fragmentation on carrying capacity

I studied the effect of habitat fragmentation on carrying capacity and population dynamics by comparing a scenario with overpasses with a scenario without overpasses. In the scenario with overpasses, several habitats became connected, including areas not large enough to be suitable without overpasses (Figure 3). As a result, availability of prey significantly increased for both climate scenarios with 7% (Figures 5 and 6; Appendix 2: Tables 1 and 2; $P<0.0005$; For the W climate: Repeated measures ANOVA, $n=22$, $F=40193.988$, $P<0.0005$; For the standard climate: Repeated measures ANOVA, $n=22$, $F=20144.061$, $P<0.0005$). This led to a significant increase in total carrying capacity of the Netherlands (Figures 7 and 8; Figures 9 and 10; Appendix 2: Tables 3 and 4; for the W climate: Repeated measures ANOVA, $n=22$, $F=5377.804$, $P<0.0005$; for the standard climate: Repeated measures ANOVA, $n=22$, $F=2905.288$, $P<0.0005$). Over the years, the average carrying capacity for the W scenario increased from 355 to 443 (sd = resp. 3.36 and 7.07), and for the standard scenario an increase from 338 to 429 is found (sd = resp. 6.59 and 11.35).

3.2 Effect of climate change on carrying capacity

Climate change, as simulated in the W scenario, resulted for all functional plant types in all years in a significantly larger biomass compared to the standard climate scenario (Appendix 2: Figure 1 and Table 5; for the difference in total vegetation biomass: repeated measures ANOVA, $n=11$, $F=14.720$, $P=0.003$). The total biomass of grasses and herbs, and shrubs significantly decreased over time in the standard scenario, whereas no significant change is found for the W scenario (Appendix 2: Table 6; For grasses and herbs in the standard scenario: $n=11$, $\beta=-0.806$, $t=-4.079$, $P=0.003$; For shrubs in the standard scenario: $n=11$, $\beta=-0.868$, $t=-5.253$, $P=0.001$; For grasses and herbs in the W scenario: $n=11$, $\beta=-0.488$, $t=-1.678$, $P=0.128$; for shrubs in the W scenario: $n=11$, $\beta=0.539$, $t=1.920$, $P=0.087$).

Biomass of prey was predicted to be affected by vegetation biomass, and thus by climate. Indeed, climate was found to significantly affect consumable prey biomass (Figures 5 and 6; Appendix 2: Tables 7 and 8; For the scenario without overpasses: Repeated measures ANOVA, $n=22$, $F=18.119$, $P=0.002$; For the scenario with overpasses: Repeated measures ANOVA, $n=22$, $F=18.312$, $P=0.002$). However, the average absolute difference between the climate scenarios was only 3% for both scenarios of habitat fragmentation. My results show in the standard climate scenario a significant decrease in prey biomass of 7% over 110 years, whereas in the W scenario the prey biomass remained relatively constant (Figure 5; Appendix 2: Table 9, for standard scenario with overpasses: Linear regression, $n=11$, $\beta=-0.713$, $t=-3.050$, $P=0.014$; for standard scenario without overpasses: Linear regression, $n=11$, $\beta=-0.723$, $t=-3.136$, $P=0.012$; for W scenario with overpasses: Linear regression, $n=11$, $\beta=-0.317$, $t=1.003$, $P=0.342$; for W scenario without overpasses: Linear regression, $n=11$, $\beta=-0.337$, $t=1.074$, $P=0.311$). A remarkable trend in total vegetation biomass was observed, with an increase followed by a decrease every 30 years. In both climate scenarios, for plots in which succession occurred, this occurred in the first 10 years. For prey biomass, a trend similar to the trend in vegetation biomass is observed.

The difference in prey biomass resulted in a significantly smaller carrying capacity for the standard scenario compared to the W scenario (Figures 9 and 10; Appendix 2: Tables 10 and 11; for the scenario with overpasses: Repeated measures ANOVA, n=22, F=17.317, P=0.002; for the scenario without overpasses: Repeated measures ANOVA, n=22, F=15.350, P=0.03). For the W-climate, the scenario with overpasses resulted in an average carrying capacity over the years of 443 (± 7.07) wolves, whereas the carrying capacity in the standard scenario was slightly smaller with an average of 429 (± 11.35) wolves. For the scenario without overpasses, the results were similar (average ± sd = 355 ± 3.36 vs. 338 ± 6.59).

3.3 Effect of habitat fragmentation on population dynamics

The higher carrying capacities for the scenarios with overpasses significantly affected wolf population dynamics in METAPHOR. For every year, the average number of adults over the runs was calculated. In the scenario with overpasses, the number of adults averaged resp. 39 and 37 (sd = resp. 28.0 and 30.7) for the W and standard climate, which was statistically significantly higher than in the scenario without overpasses, in which it averaged resp. 17.2 ±21.3 and 17.2 ± 20.1 (Figure 11; Appendix 2: Tables 12 and 13; for the W scenario: Repeated measures ANOVA, n=222, F=748.511, P<0.0005; for the standard scenario: Repeated measures ANOVA, n=222, F=606.782, P<0.0005).

The maximum year of the run gives an indication of the population persistence. If the maximum year was smaller than 110, the population became extinct before the end of the simulation. In absence of overpasses, the population persistence was statistically significantly lower than with overpasses (Figure 12; Appendix 2: Tables 14 and 15; for the W scenario: Repeated measures ANOVA, n=300, F=191.682, P<0.0005; for the standard scenario: Repeated measures ANOVA, n=300, F=143.575, P<0.0005).

3.4 Effect of climate change on population dynamics

The significant effect of climate on carrying capacity was reflected in the population dynamics as simulated in METAPHOR. In presence of overpasses, the average number of wolves per year was significantly larger for the W scenario with 36.83 (± 3.55) adults, compared to 33.82 (± 5.48) for the standard climate (Figure 11, Appendix 2: Table 16; Repeated Measures ANOVA, n=222, F=38.386, P<0.0005). Although climate seemed to have no effect in the first decades, from year 80 onwards the difference in total number of adults between the climate scenarios increased, with in year 110 for the standard climate scenario on average 23.2 adults and for the W scenario 38.9 adults (Figure 11). This increasing difference over time can be explained by the increasing difference in carrying capacity over time between the climate scenarios.
Similarly, for the scenario without overpasses, a significant effect of climate on average number of wolves per year was found (Appendix 2: Table 17; Repeated Measures ANOVA, n=222, F=18.198, P<0.0005). However, in Figure 11, no effect of climate can be observed in absence of overpasses. For that reason, this significance seems to be caused by the low variation in the data instead of by a large effect of climate. Population persistence as measured by the maximum year of the run was not significantly affected by climate (Figure 12; Appendix 2: Tables 18 and 19; for the scenario with overpasses: Repeated measures ANOVA, n=222, F=1.903; P=0.170; for the scenario without overpasses: Repeated measures ANOVA, n=222, F=0.371, P=0.543).

3.5 Effect of initial number of wolves on wolf population dynamics

Increasing the initial number of wolves from 50 to 150 did not largely affect the outcome of METAPHOR (Figures 11 and 12). Again, a strong decline in average number of adults was found in the scenario without overpasses. For the scenarios with overpasses, the number of wolves increased in the first five years (after the initialization period), after which it declined. Over the years, the number of adults in presence of overpasses was higher for the W scenario. For the W scenario, after 90 years an equilibrium of around 50 adults seemed to be reached, whereas the number of adults in the standard scenario declined. The equilibrium in the runs starting with 150 adult wolves seemed to be similar to the equilibrium when starting with 50 wolves. This suggests robustness of the model. However, it may also indicate that METAPHOR is relatively insensitive to the initial number of adults.

3.6 Interaction effect of climate and habitat fragmentation

The effect of habitat fragmentation differed between the climate scenarios, indicating an interaction effect. The relative effect of overpasses on carrying capacity was calculated for both climate scenarios as the carrying capacity with overpasses divided by the carrying capacity without overpasses. A positive effect of climate change on primary production and prey biomass was predicted to mitigate the negative effects of habitat fragmentation. The effect of overpasses on the carrying capacity was indeed significantly smaller for the W scenario compared to the standard scenario (Figure 13; Appendix 2: Table 20; Repeated measures ANOVA, n=22, F=87.602, P<0.0005). For the W scenario, the carrying capacity increased with a factor 1.25 (± 0.010) after including overpasses. For the standard scenario, the relative effect was a factor 1.27 (± 0.013). The positive effect of overpasses was caused by either increased prey biomass or increased area due to habitats becoming suitable which were unsuitable without overpasses. As a result of a higher prey biomass for the W climate, the prey availability was more limited in the standard scenario. This stronger limitation of prey biomass may have caused the stronger relative effect of overpasses in the standard climate scenario. The relative effect of overpasses followed a fluctuating trend, similar to the trend in available prey biomass. In years with lower available prey biomass, the effect of wildlife overpasses was smaller. Wildlife overpasses increase the available area, and hence the number of packs. Lower prey density results in smaller pack sizes, and hence results in a smaller effect of overpasses on carrying capacity.

Due to this interaction effect, the difference in carrying capacity between the climate scenarios increases over time (Figure 9). As a result, the effect of climate on population dynamics differed between the scenario with and the scenario without overpasses. Climate change resulted in an increase in the average number of adults in the scenario with overpasses, whereas no effect could be observed in the scenario without overpasses (although significance was found, see Chapter 3.4).
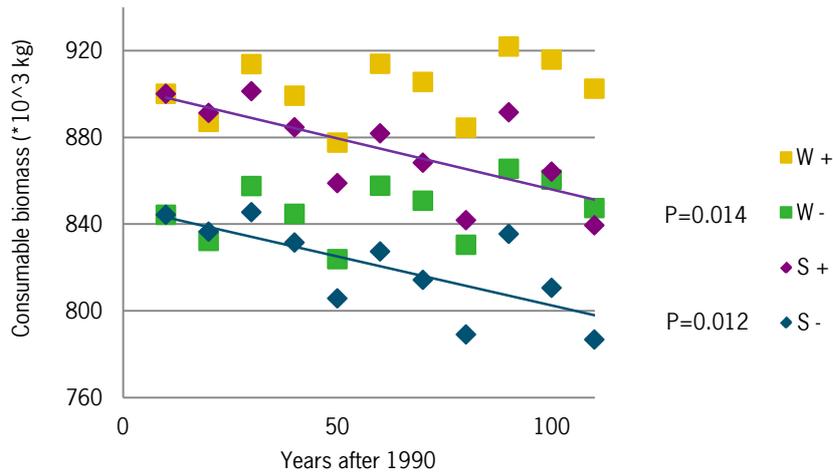
Figure 5

Effect of climate scenario and presence of wildlife overpasses on total consumable biomass prey. Lines indicate a significant trend (See Appendix 2: Table 9).
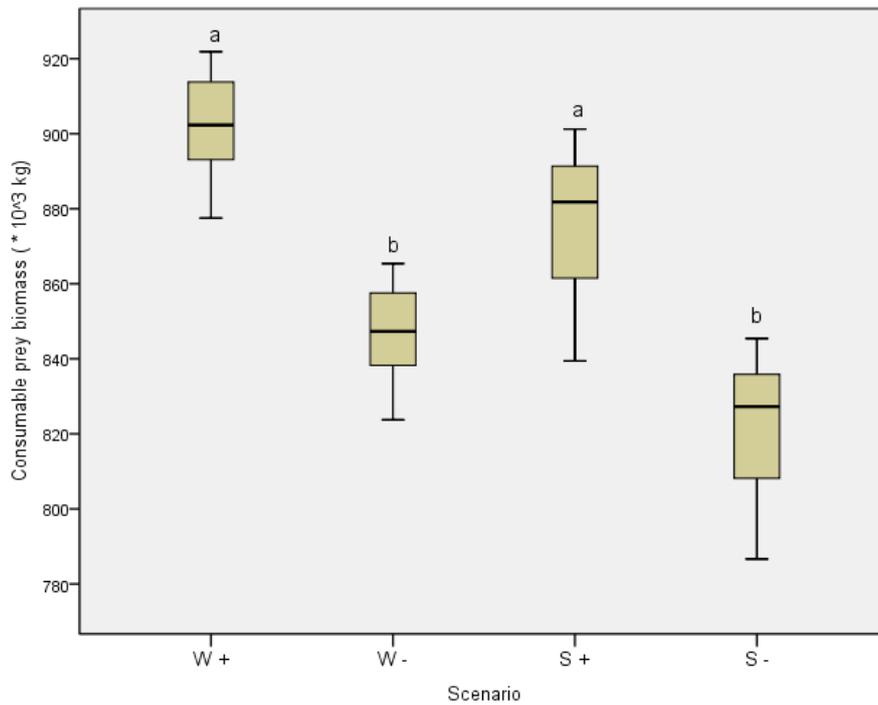
Figure 6

Boxplot showing the effects of overpasses and climate on total consumable biomass of prey (in thousands of kgs), summed over all suitable habitats. Boxes represent the range between the upper and lower quartile, with the median represented as a horizontal line in the box. Error bars represent the variation per scenario.
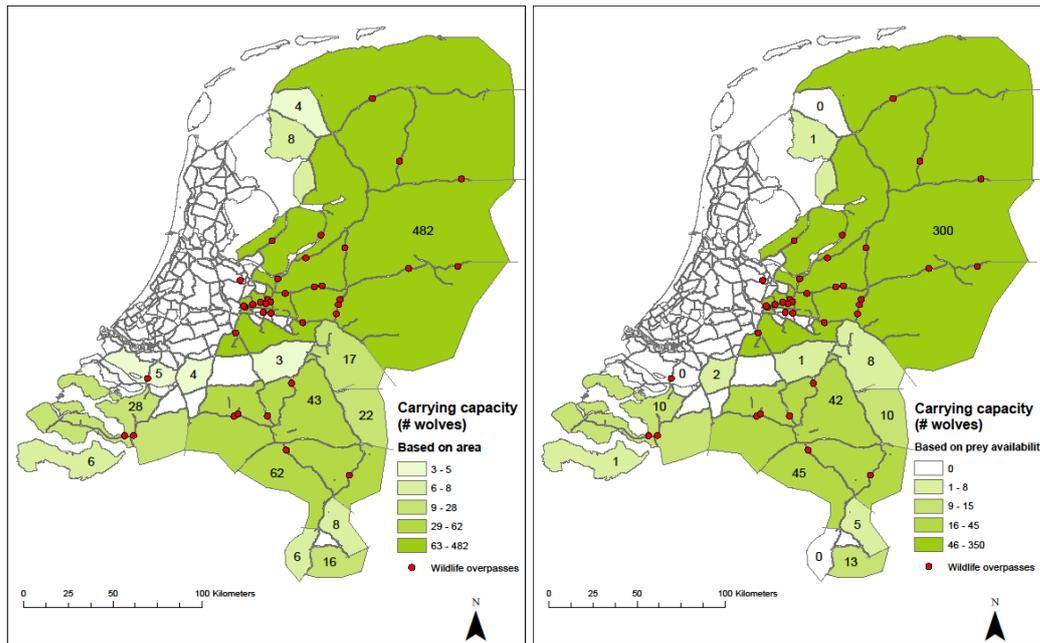
Figure 7

Carrying capacity of wolves in the Netherlands with wildlife overpasses, based on area (left) and prey availability (right). Numbers represent the carrying capacity in the year 2010 for the standard climate scenario in the corresponding habitat, colours represent ranges. Overpasses are displayed as red dots. Either area of prey availability is limiting, so the lowest carrying capacity is used in METAPHOR. Prey availability turns out to be limiting for all habitats.
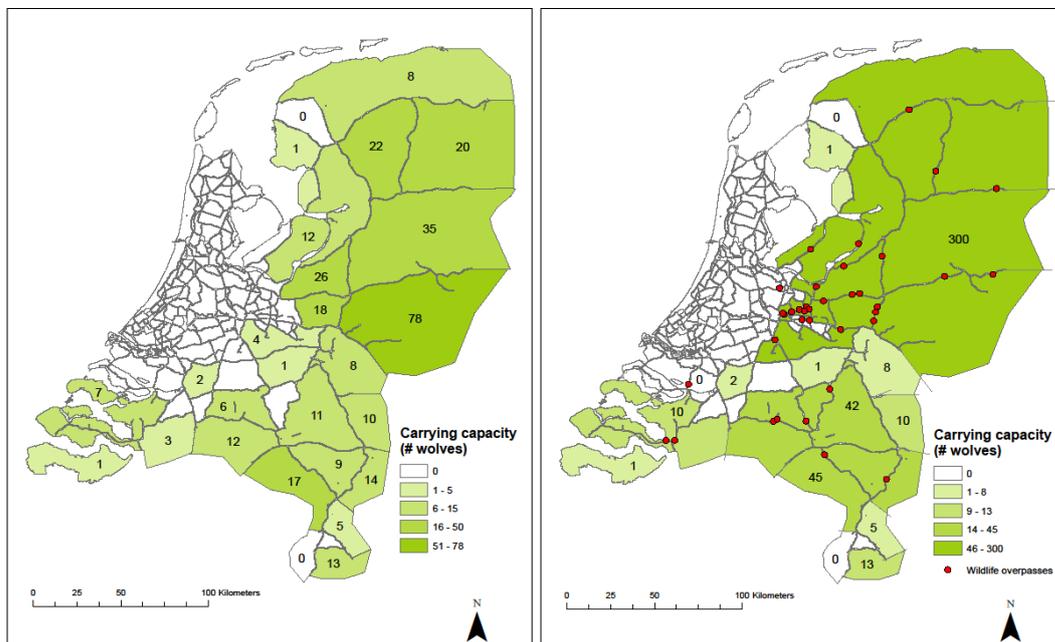
Figure 8

Carrying capacity of wolves in the Netherlands without (left) and with (right) wildlife overpasses. Numbers represent the carrying capacity in the year 2010 in the corresponding habitat, colours represent ranges. In the right picture, overpasses are displayed as red dots. Either area of prey availability is limiting, so the lowest carrying capacity is displayed. Prey availability turns out to be limiting for all habitats.
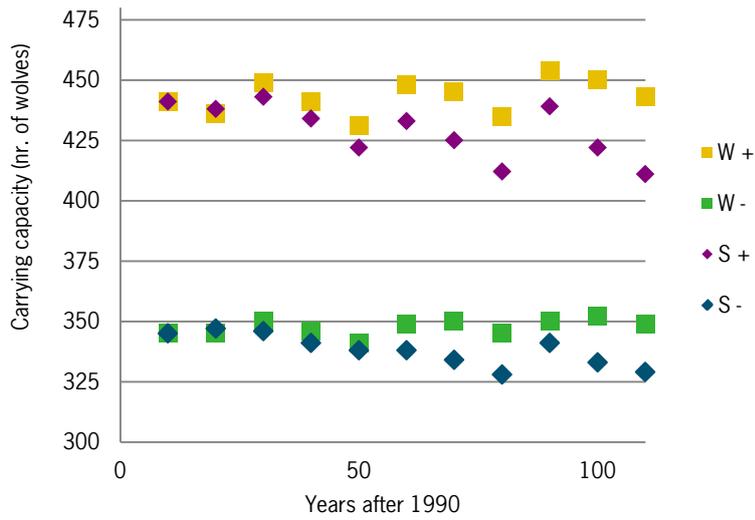
Figure 9
Effect of climate scenario and presence of overpasses on total carrying capacity for the Netherlands.
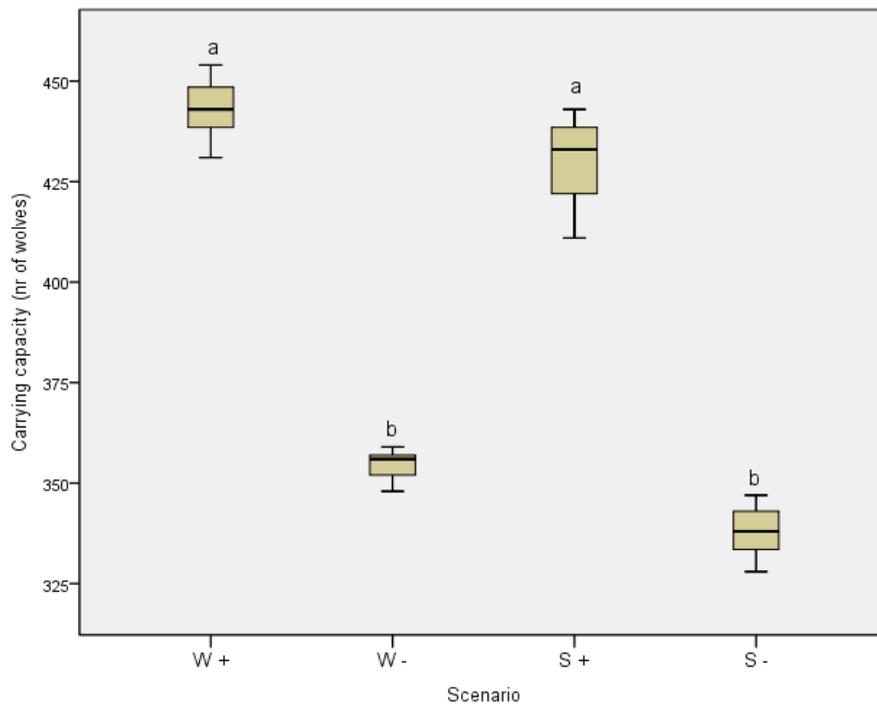
Figure 10
Boxplot showing the effects of wildlife overpasses and climate scenario on the carrying capacity of the Netherlands.
Boxes represent the range between the upper and lower quartile, with the median represented as a horizontal line in the box.
Error bars represent the variation per scenario.
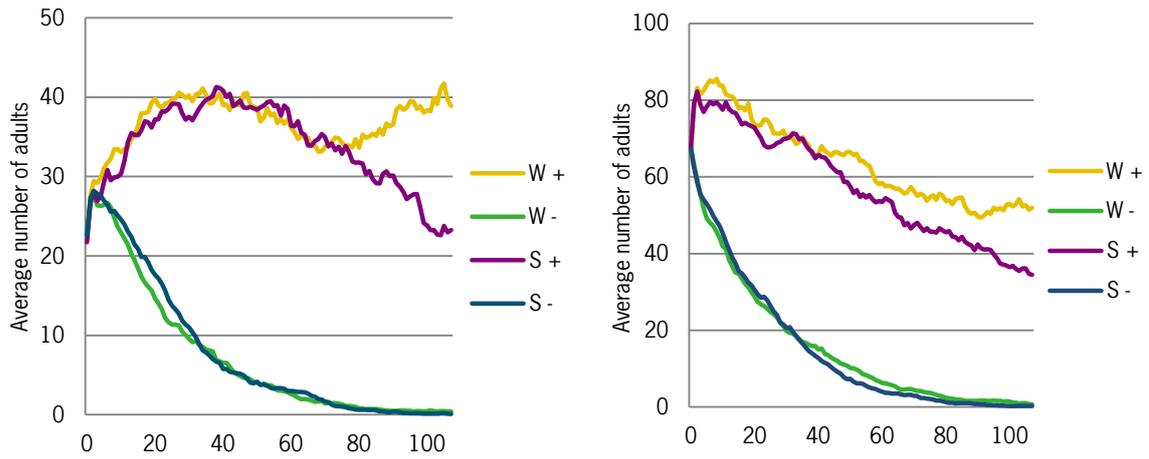
Figure 11

Trend of the average number of adults over the years, per scenario with an initial number of adults of 50 (left) and 150 (right). Year 0 is the first year after the initialization period of three years. Averages are taken from 150 model runs with METAPHOR.
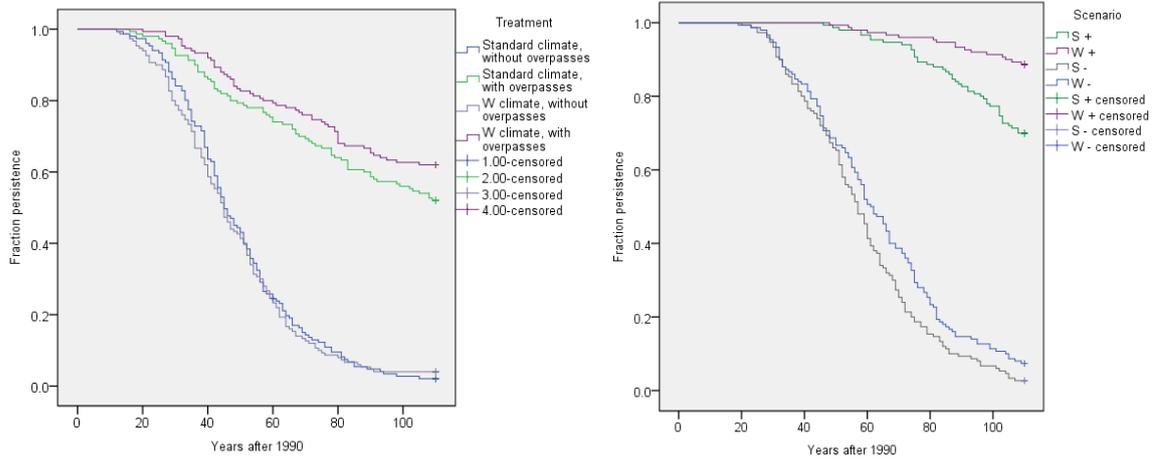
Figure 12

Survival analysis for the different scenarios, with population extinction as event for 150 runs. The vertical axis shows the fraction of runs in which the population persisted. Every year the population in a run becomes extinct, the fraction persistence decreases. The initial number of wolves was 50 (left) or 150 (right).
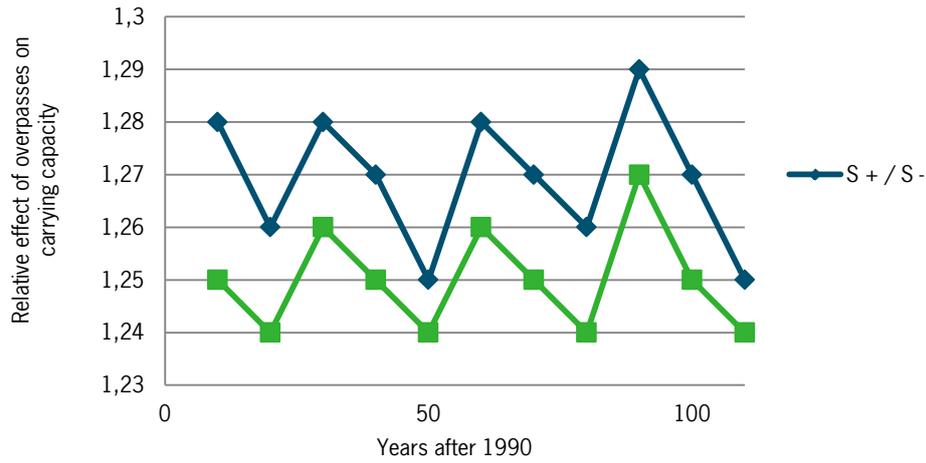
Figure 13

Relative effect of overpasses on total carrying capacity over the years, for both climate scenarios. The relative effect of overpasses is calculated as the carrying capacity in the scenario with overpasses, divided by the carrying capacity in the scenario without overpasses. This gives the fraction of increase in carrying capacity due to presence of overpasses.

4   Discussion

Many mammalian carnivores are threatened by habitat fragmentation. In this study, the results show that this is also the case for the wolf. Future climate change will positively affect the wolf through increased prey availability, but the negative effect of current habitat fragmentation is much larger. Presence of wildlife overpasses decreases these effects of habitat fragmentation, and increases wolf carrying capacity and population persistence in the Netherlands. Upon inclusion of overpasses, several habitats become connected, including areas that were not large enough without overpasses. These larger areas resulted in larger prey availability and potential for more packs, and therefore higher carrying capacity for several habitats.
As a result of including overpasses, the total carrying capacity for the Netherlands for the year 2010 increased from 343 to 438 wolves (for the standard climate scenario). It should be noted that this is the maximal number of wolves, and this number of wolves will not be reached in the Netherlands as it is now. The model runs with METAPHOR area expected to give a better indication of the potential number of wolves in the Netherlands. In the scenario with climate change and in presence of overpasses, the number of adults seems to stabilize at around 50 individuals by 2100. Although Geert Groot-Bruinderink considers this number to be large (personal communication), Staatsbosbeheer (Dutch Nature management organization) predicts room for 100 wolves in the Oostvaardersplassen (Staatsbosbeheer, 2008), which is a nature reserve in the Netherlands of only 56 km^2. No consensus exists on the maximal number of wolves for the Netherlands. However, this study is based on well justified assumptions, and therefore is expected to be reliable.

Presence of overpasses increased the percentage of runs in which the population persisted until the year 2100 from almost zero to resp. 52 and 62 (for resp. standard and W scenario), and the average number of adults over the first 110 years more than doubled. This indicates the importance of overpasses for wolf persistence. Similar negative effects of fragmentation on population persistence of large carnivores are found (grizzly bears: Proctor et al., 2012; black bears: Hostetler et al., 2009; lynx: Schmidt et al., 2011; bobcats and coyotes: Riley et al., 2003). Loss of connectivity might additionally result in loss of genetic variation (Kojola et al., 2009; Proctor et al., 2012; Schmidt et al., 2011), further decreasing population persistence. Moreover, several studies found increased mortality of carnivores in fragmented landscapes (Hostetler et al., 2009; Riley et al., 2003), which is not taken into account in this study, and may further increase the difference between the situation with and without overpasses.

Climate change is predicted to increase primary productivity (Holmgren et al., 2001), and hence positively affect herbivore abundance (Jaksic et al., 1997; Walther, 2010). In this study, I found a small increase in primary productivity and prey biomass due to the predicted climate change, which is simulated in the W scenario. In contrast, in the standard scenario, the prey biomass declined with 7% over 110 years due to a decreased biomass of grasses and herbs, and shrubs. Although the absolute effect is small, climate change may have had a positive effect on primary productivity, and hence may have prevented prey biomass from declining in the W scenario.

The larger prey biomass in the W scenario resulted in a higher carrying capacity than in the standard scenario. For the scenario with overpasses, this positively affected population dynamics, resulting in a larger number of adult wolves for the scenario simulating future climate change. Similarly, Jaksic et al. (1997) found that the top predators hawks, owls and foxes respond to increased prey abundance upon climate change with a delayed increase in density, suggesting a bottom up regulation for these species. However, the effects of climate change on interactions between vegetation and herbivores are more complex than simulated in my study (see a.o. Van der Putten et al., 2010). On the long term, climate change can result in an altered C/N ratio

(Tylianakis et al., 2008), to which herbivores respond with increased consumption of up to 40% (Coley, 1998). This may counteract the positive effect of climate change on primary production, and hence decrease the effect of climate change on prey biomass and wolf carrying capacity.

In this study, in the Netherlands prey availability turned out to be more limiting for carrying capacity than the size of suitable habitat. However, as generalists, wolves will be able to change to additional prey species when prey abundance is low. For that reason, actual prey abundance may be higher than in this study, and hence the effects of climate change on wolf carrying capacity may have to be reconsidered.

An important assumption in this study is the definition of roads as habitat boundary. Although wolves are known to avoid roads, it is unclear if roads act as habitat boundary (Kohn et al., 2000; Keenlance, 2002). Unfortunately, no data on traffic intensity, which determines avoidance behaviour (Whittington et al., 2005), for the whole of the Netherlands was available. The assumption that in the more urbanized provinces both main roads and highways form a barrier, and in the other provinces only highways, highly affected the outcome of this study. The actual carrying capacity might be higher if main roads would not form a barrier. Therefore, this assumption might have to be reconsidered. In addition, the avoidance of cities is debated. Although several studies report this avoidance behaviour, in Southern and Eastern Europe, wolves also live in cities (for example the Romanian city Brasov) (www.wolveninnederland.nl).

Although this study predicts that wolves will be able to persist in the Netherlands, the probability of colonization is unclear. An important addition to this thesis would be to study this chance of recolonization. Corridors suitable for wolves should be identified in order to get an indication on the chance that wolves will spread from existing packs to the Netherlands.
Moreover, as only the Netherlands are taken into account, habitats along the border may be underestimated in size. For a metapopulation of wolves, the Netherlands is expected to be too small. Exchange with individuals from Germany, Belgium and France is expected to occur, and even the entire Europe may form a etapopulation. For that reason, the study area should be extended with at least Germany, Belgium and France, and probably the entire Europe. Although this will not affect the carrying capacity of the Netherlands, it may affect population dynamics. If habitat in neighbouring countries is of higher quality, dispersal in METAPHOR will be more directed towards these countries, resulting in less wolves in the Netherlands. In addition, although hunting on wolves is not allowed in Europe, illegal hunting may occur. Therefore, this may have to be considered as additional mortality factor in METAPHOR.

According to SMART2-SUMO2, in places where succession occurs, this happened already in the first 10 years, which may not be realistic. In addition, the effect of management appeared to be large. Every 30 years, the dwarf shrub biomass is decreased by sod cutting, resulting in a remarkable trend in biomass of dwarf shrubs, prey availability and wolf carrying capacity. In SMART2-SUMO2, this sod cutting occurs for all dwarf shrubs in the Netherlands in one time, resulting in a strong decline in dwarf shrub biomass and hence in prey availability and carrying capacity. Although this decreased plant biomass may affect prey, the observed response in prey biomass and carrying capacity may not be realistic. In future research, it should be considered to spread management over the years, instead of applying the management type for the whole of the Netherlands in one time.

In this study, random dispersal is assumed. However, through scent marking and howling, wolves are expected to find each other more often than ad random (Mech and Boitani, 2003). For that reason, adapting the simulation of dispersal in METAPHOR accordingly is expected to improve the model outcome. The number of adults and population persistence are expected to be positively affected.

Moreover, the initial prey abundance in SUMO2 could be improved. This initial abundance of prey is estimated based on density data, instead of actual measured data or hunting statistics. Although the prey density remained relatively constant after an initialization period, the model could be improved by using more accurate data. In addition, the importance of hare and rabbit in the wolf's diet is debatable. Although these species are known to be prey species, the fraction in the wolf diet is small. For that reason, these species might have to be excluded. In contrast, sheep and goats might have to be included, although in Germany their fraction in the diet is small as well (http://www.wolfsregion-lausitz.de/nahrungszusammensetzung).

Moreover, wolf predation is assumed to be compensatory, and therefore does not affect prey abundance. It is not clear if this assumption is realistic. In Poland, wolves have been reported to remove only 6.3 to 9.0% of the total available biomass of ungulates (Glowacinski and Profus, 1997), suggesting that the effect of wolf predation on ungulates is rather small. In contrast, for example in Yellowstone, elk density has declined upon wolf introduction (Ripple and Beschta, 2011). Through addition of a feedback between METAPHOR and SMART2-SUMO2, the effect of predation on prey abundance can be simulated, which may improve the results. Moreover, behavioural changes of prey species should be studied, as these may affect the vegetation.

Behavioural changes of prey species
Prey species may change their behaviour due to presence of predators (Van der Merwe and Brown, 2008; Willems and Hill, 2009), by reducing foraging time, changing habitat choice, reducing their movement, and/or becoming more vigilant (Bednekoff, 2007; Stephens et al., 2007). This may result in release of herbivorous pressure, and therefore in changes in the vegetation (Strong and Frank, 2010). Similarly, new habitats experience increased grazing or browsing pressure (Ripple and Beschta, 2004). For example, in Yellowstone National Park, after introduction of the wolf, its prey species elk *(Cervus elaphus)* and bison *(Bison bison)* showed increased levels of vigilance (Laundré et al., 2001), and elk changed its movement patterns to staying more in forested patches of lower quality, because of lower predation risk (Mao et al., 2005; Fortin et al., 2005; Hernandez and Laundré, 2005). This, in combination with a decline in elk density of about 60% since wolf introduction, has resulted in a large decrease of browsing intensity, and an increase of recruitment of aspen, willows and cottonwoods. Moreover, probably related to the increased availability of woody plants and herbaceous forage, beaver and bison numbers increased (Ripple and Beschta, 2011). In Canada, similar effects have been found (Hebblewhite et al., 2005). Compared to low-wolf areas, areas with high wolf density contained lower elk densities and lower browsing intensities, which had positive effects on the vegetation and on beaver and songbird densities. These studies show that the presence of wolves or other predators may increase biodiversity. Similar results have been found for bobcats. In Georgia (USA), the reintroduction of bobcats led to declining deer populations and increased oak regeneration (Diefenbach et al., 2009). If these interactions would have been considered in this study, the outcome may have been different. Due to increased vigilance, the prey availability may decrease, hence negatively affecting wolf carrying capacity. In addition, vegetation may change as a result of increased vigilance, which may affect habitat quality for both the wolf and its prey species. In areas with high predation pressure, increased vigilance is expected to result in more dense forests, hence increasing habitat quality for the wolf. In contrast, in areas with low predation pressure and therefore high prey abundance, the habitat quality for the wolf is expected to decrease. In this way, wolves may avoid these areas, despite the high prey abundance. This might result in a further decrease in carrying capacity.

5 Conclusions

This study shows that wolf carrying capacity is highly affected by habitat fragmentation. Presence of overpasses increases carrying capacity from 355 (±3.36) to 443 (±7.07) for the W scenario, and from 338 (±6.59) to 429 (±11.35) for the standard climate scenario. This resulted in a larger number of adults in METAPHOR than without the overpasses. In addition, the population persistence, as measured by the fraction of populations surviving until 2100, was significantly higher for the scenarios with overpasses.

Climate change is found to positively affect the wolf, although the effects were smaller than the effects of mitigating habitat fragmentation by overpasses. In the standard climate scenario, prey availability significantly decreased over the years, whereas the prey availability in the W scenario remained relatively constant. This resulted in a higher carrying capacity in the scenario with climate change, compared to the standard scenario. In METAPHOR, the average number of adults was significantly higher for the W scenario. The difference between the climate scenarios increased over the years, caused by the increasing difference in prey availability due to climate change.

It can be concluded that management of wolves in Europe should be focussed on limiting the effects of habitat fragmentation, for example by construction of overpasses.

6   Acknowledgements

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7   Literature

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Appendix 1. Model input parameters

Table 1
Density of prey species of the wolf (#/100ha).

	Coniferous Forest	Deciduous forest	Grassland	Heathland	Other vegetation
Fallow Deer	4	4	4	4	4
Hare	35	35	35	35	35
Rabbit	100	100	100	100	100
Red Deer	4.5	2	5	5	4
Roe Deer	4	2	8	6	5
Wild Boar	0.54	2.4	6	0.6	1

Table 2
Parameter values used as input for SUMO2 for simulating the effect of herbivores on vegetation (Wamelink et al. (2009b), supplemented with data for rabbit).

Species	Biomass grazed (ton/yr)	Fraction faeces	[N] faeces	[N] Ureum	[P] faeces	[K] faeces	[Mg] faeces	[Ca] faeces
Hare	0.014	0.65	0.007	0	0.007	0.007	0.007	0.007
Roe deer	0.24	0.65	0.007	0.003	0.007	0.007	0.007	0.007
Red deer	0.67	0.65	0.007	0.003	0.007	0.007	0.007	0.007
Fallow deer	0.513	0.65	0.007	0.003	0.007	0.007	0.007	0.007
Wild boar	0.522	0.65	0.0075	0.003	0.02	0.02	0.02	0.02
Rabbit	0.0032	0.65	0.007	0	0.007	0.007	0.007	0.007

Table 3
Parameters of prey species. Values are provided by Leo Linnartz (Stichting Ark).

Species	Weight ♂ (kg)	Weight ♀ (kg)	Average weight (kg)	% Consumable	Consumable biomass per individual (kg)	% Mortality
Hare	3.6	3.4	3.5	75%	2.63	20%
Roe deer	27	22	25	75%	18	20%
Red deer	220	150	185	75%	139	20%
Fallow deer	130	60	95	75%	71	20%
Wild boar	130	60	95	75%	71	20%
Rabbit	130	60	95	75%	71	20%

Table 4
Predicted pack size based on available prey density.

Consumable biomass prey per m² (kg/m²)	Pack size
>= 0.9	10
0.7 - 0.9	8
0.5 - 0.7	7
0.3 - 0.5	6
0.2 - 0.3	5
0.1 - 0.2	4
<0.1	3

Table 5
Factors affecting habitat quality. Used ranges and their corresponding quality factors.

Prey density (kg/m²)	Quality factor	Suitable Area (in km²)	Quality factor
<0.1	0.5	<200	0.4
0.1 - 0.2	0.6	200 - 350	0.5
0.2 - 0.3	0.7	350 - 500	0.65
0.3 - 0.4	0.8	500 - 700	0.75
0.4 - 0.6	0.9	700 - 1000	0.9
>0.6	1	>1000	1

Relative forest cover (% of total area)	Quality factor	Relative area buildings (% of total area)	Quality factor
<0.015	0.1	0 - 30	1
0.015 - 0.04	0.2	30 - 50	0.7
0.04 - 0.07	0.4	50 - 70	0.5
0.07 - 0.1	0.65	70 - 100	0.3
0.1 - 0.15	0.8		
>0.15	1		

Table 6
Survival rates of wolves in Europe for different life stages (with use of Boitani, 2000).

Life Stage	Basic survival rate (± std. dev.)		Survival rate in low quality (± std. dev.)	
Pup (0-1 yr old)	0.45	(± 0.05)	0.2	(± 0.05)
Juvenile (1-2 yr old)	0.6	(± 0.1)	0.45	(± 0.1)
Adult (3yr or older)	0.8	(± 0.1)	0.6	(± 0.1)

Appendix 2. Results

2.1 Effects of overpasses on carrying capacity

a) Effects of overpasses on total consumable prey biomass

Table 1

Repeated measures ANOVA, followed by a post hoc test (Bonferroni), on the effect of overpasses on total consumable prey biomass (kg) in the Netherlands for the W climate scenario. Hypothesis of sphericity is rejected. Greenhouse-Geisser correction is therefore used (shown in bold font). The test of Within-subjects effects shows a significant effect of overpasses on prey biomass for the Greenhouse-Geisser method.

a) Repeated measures ANOVA

Descriptive statistics

	Mean	Std. Deviation	N
W +	901926.1836	14204.73530	11
W -	846750.5000	13420.29184	11

Mauchly's Test of Sphericity[b]

Measure: Prey_Biomass

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Overpasses	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a. May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b. Design: Intercept.

Within Subjects Design: Overpasses.

Tests of Within-Subjects Effects

Measure: PreyBiomass

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Fragmentation	Sphericity Assumed	1.674E10	1	1.674E10	40193.988	.000	1.000
	Greenhouse-Geisser	**1.674E10**	**1.000**	**1.674E10**	**40193.988**	**.000**	**1.000**
	Huynh-Feldt	1.674E10	1.000	1.674E10	40193.988	.000	1.000
	Lower-bound	1.674E10	1.000	1.674E10	40193.988	.000	1.000
Error (Fragmentation)	Sphericity Assumed	4165786.785	10	416578.678			
	Greenhouse-Geisser	4165786.785	10.000	416578.678			
	Huynh-Feldt	4165786.785	10.000	416578.678			
	Lower-bound	4165786.785	10.000	416578.678			

b) Post hoc test: Bonferroni

Measure: Prey_Biomass

(I) Ecoducten	(J) Ecoducten	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
W +	W -	55175.684[*]	275.212	.000	54562.473	55788.894

Based on estimated marginal means.

* The mean difference is significant at the .05 level.

a. Adjustment for multiple comparisons: Bonferroni.

Table 2

Repeated measures ANOVA, followed by a post hoc test (Bonferroni), on the effect of overpasses on total consumable prey biomass (kg) in the Netherlands for the standard climate scenario.

a) Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
S +	874806.7555	21858.86691	11
S -	820578.9182	20783.60676	11

Mauchly's Test of Sphericity[b]

Measure: Prey_Biomass

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Overpasses	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a. May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b. Design: Intercept.

Within Subjects Design: Overpasses.

Tests of Within-Subjects Effects

Measure: Prey_Biomass

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Ecoducten	Sphericity Assumed	1.617E10	1	1.617E10	20144.061	.000	1.000
	Greenhouse-Geisser	**1.617E10**	**1.000**	**1.617E10**	**20144.061**	**.000**	**1.000**
	Huynh-Feldt	1.617E10	1.000	1.617E10	20144.061	.000	1.000
	Lower-bound	1.617E10	1.000	1.617E10	20144.061	.000	1.000
Error (Ecoducten)	Sphericity Assumed	8028977.351	10	802897.735			
	Greenhouse-Geisser	8028977.351	10.000	802897.735			
	Huynh-Feldt	8028977.351	10.000	802897.735			
	Lower-bound	8028977.351	10.000	802897.735			

b) Post hoc test: Bonferroni

Measure: Prey_Biomass

(I) Overpasses	(J) Overpasses	Mean Difference(I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
S +	S -	54227.837[*]	382.075	.000	53376.521	55079.154

Based on estimated marginal means.

* The mean difference is significant at the .05 level.

a. Adjustment for multiple comparisons: Bonferroni.

b) Effects of overpasses on total carrying capacity.

Table 3

Repeated measures ANOVA (a), followed by a post hoc test (Bonferroni) (b), on the effect of overpasses on total carrying capacity for the W climate scenario.

a) Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
W +	443.0000	7.07107	11
W -	347.4545	3.26691	11

Mauchly's Test of Sphericity[b]

Measure: Carcap

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Overpasses	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a. May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.
b. Design: Intercept.

Within Subjects Design: Overpasses.

Tests of Within-Subjects Effects

Measure: Carcap

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Overpasses	Sphericity Assumed	50209.136	1	50209.136	5377.804	.000	.998
	Greenhouse-Geisser	**50209.136**	**1.000**	**50209.136**	**5377.804**	**.000**	**.998**
	Huynh-Feldt	50209.136	1.000	50209.136	5377.804	.000	.998
	Lower-bound	50209.136	1.000	50209.136	5377.804	.000	.998
Error (Overpasses)	Sphericity Assumed	93.364	10	9.336			
	Greenhouse-Geisser	93.364	10.000	9.336			
	Huynh-Feldt	93.364	10.000	9.336			
	Lower-bound	93.364	10.000	9.336			

b) Post hoc test: Bonferroni

Measure: Carcap

(I) Overpasses	(J) Overpasses	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
W +	W -	95.545[*]	1.303	.000	92.642	98.448

Based on estimated marginal means.

*   The mean difference is significant at the .05 level.

a.   Adjustment for multiple comparisons: Bonferroni.

Table 4

Repeated measures ANOVA (a), followed by a post hoc test (Bonferroni) (b), on the effect of overpasses on total carrying capacity for the standard climate scenario.

a) Repeated measures ANOVA

Descriptive statistics

	Mean	Std. Deviation	N
S +	429.0909	11.35301	11
S -	338.1818	6.58511	11

Mauchly's Test of Sphericity[b]

Measure: Carcap

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Overpasses	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a.   May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b.   Design: Intercept.

Within Subjects Design: Overpasses.

Tests of Within-Subjects Effects

Measure: Carcap

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Overpasses	Sphericity Assumed	45454.545	1	45454.545	2905.288	.000	.997
	Greenhouse-Geisser	**45454.545**	**1.000**	**45454.545**	**2905.288**	**.000**	**.997**
	Huynh-Feldt	45454.545	1.000	45454.545	2905.288	.000	.997
	Lower-bound	45454.545	1.000	45454.545	2905.288	.000	.997
Error (Overpasses)	Sphericity Assumed	156.455	10	15.645			
	Greenhouse-Geisser	156.455	10.000	15.645			
	Huynh-Feldt	156.455	10.000	15.645			
	Lower-bound	156.455	10.000	15.645			

b) Post hoc test: Bonferroni

Measure: Carcap

(I) Overpasses	(J) Overpasses	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
1	2	90.909[*]	1.687	.000	87.151	94.667
2	1	-90.909[*]	1.687	.000	-94.667	-87.151

Based on estimated marginal means.

*   The mean difference is significant at the .05 level.

a.   Adjustment for multiple comparisons: Bonferroni.

2.2   Effects of climate on carrying capacity

a) Effects of climate on vegetation biomass
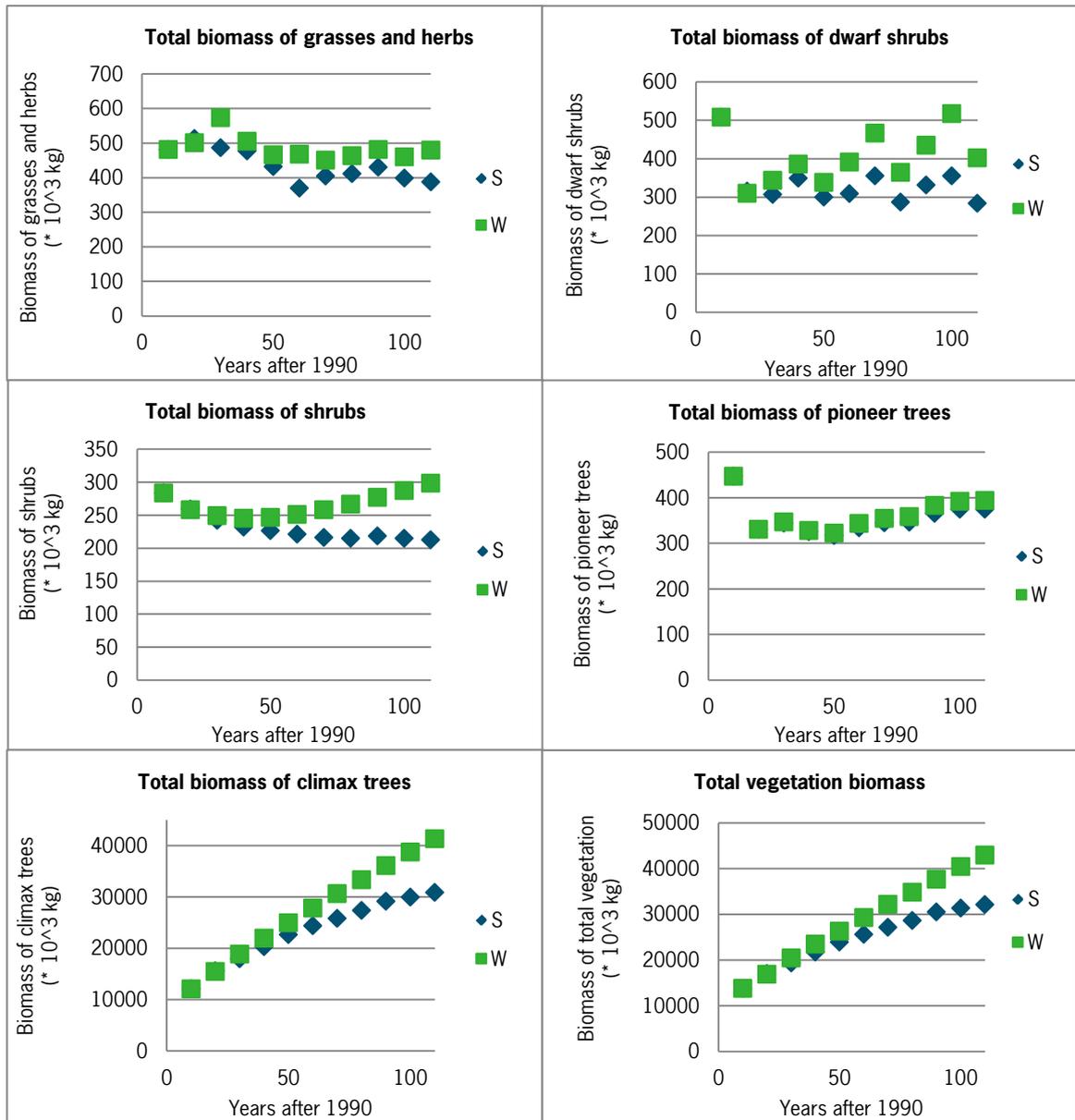
Figure 1

Effects of the climate scenarios on the total biomass in the Netherlands per functional plant type, over the years.

Table 5

Repeated measures ANOVA on the difference in vegetation biomass between the climate scenarios, per functional plant type. The mean difference represents the biomass in the W scenario minus the biomass in the standard scenario.

Functional plant type	Mean difference (W - S)	Standard Error	F	Significance
Grasses and herbs	48675.945	10706.630	20.669	0.001
Dwarf shrubs	69333.725	15830.903	19.181	0.001
Shrubs	34623.698	8951.987	14.959	0.003
Pioneer trees	8844.762	2195.289	16.233	0.002
Climax trees	4112210.034	1082227.127	14.438	0.003
Total vegetation	4273688.580	1113913.837	14.720	0.003

Table 6

Regression analysis on the change in primary productivity of different functional plant type over time, per climate scenario.

Functional plant type	Climate		Unstandardized coefficients		Standardized coefficients	t	P-value
			B	Std. Error	Beta		
Grasses and Herbs	S	Constant	503892.862	18915.919		26.639	.000
		Year	-1137.500	278.900	-.806	-4.079	.003
	W	Constant	514192.648	20118.637		25.558	.000
		Year	-497.897	296.633	-.488	-1.678	.128
Dwarf Shrubs	S	Constant	388958.506	37859.941		10.274	.000
		Year	-873.087	558.214	-.462	-1.564	.152
	W	Constant	370120.735	44940.115		8.236	.000
		Year	596.438	662.606	.287	.900	.391
Shrubs	S	Constant	266279.999	7576.703		35.145	.000
		Year	-586.792	111.712	-.868	-5.253	.001
	W	Constant	247848.447	10506.253		23.591	.000
		Year	297.462	154.906	.539	1.920	.087
Pioneer trees	S	Constant	357995.811	24574.010		14.568	.000
		Year	-47.557	362.324	-.044	-.131	.898
	W	Constant	353885.062	25180.067		14.054	.000
		Year	168.369	371.260	.149	.454	.661
Climax trees	S	Constant	12252434.257	719174.623		17.037	.000
		Year	183871.653	10603.651	.985	17.340	.000
	W	Constant	9977000.964	291856.091		34.185	.000
		Year	290332.375	4303.183	.999	67.469	.000

b) Effects of climate on consumable prey biomass

Table 7
Repeated measures ANOVA, followed by a post hoc test (Bonferroni), on the effect of climate on total consumable prey biomass (kg) in the Netherlands for the scenario without overpasses.

a) Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
W -	846750.5000	13420.29184	11
S -	820578.9182	20783.60676	11

Test of Sphericity

Measure: Prey Biomass

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Climate	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a. May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b. Design: Intercept.

Tests of Within-Subjects Effects

Measure: Biomass

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Climate	Sphericity Assumed	3.767E9	1	3.767E9	18.119	.002	.644
	Greenhouse-Geisser	**3.767E9**	**1.000**	**3.767E9**	**18.119**	**.002**	**.644**
	Huynh-Feldt	3.767E9	1.000	3.767E9	18.119	.002	.644
	Lower-bound	3.767E9	1.000	3.767E9	18.119	.002	.644
Error(Climate)	Sphericity Assumed	2.079E9	10	2.079E8			
	Greenhouse-Geisser	2.079E9	10.000	2.079E8			
	Huynh-Feldt	2.079E9	10.000	2.079E8			
	Lower-bound	2.079E9	10.000	2.079E8			

b) Post hoc test: Bonferroni

(I) Climate	(J) Climate	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
W -	S -	26171.582[*]	6148.408	.002	12472.075	39871.088

Based on estimated marginal means.

* The mean difference is significant at the .05 level.

a. Adjustment for multiple comparisons: Bonferroni.

Table 8

Repeated measures ANOVA, followed by a post hoc test (Bonferroni), on the effect of climate on total consumable prey biomass (kg) in the Netherlands for the scenario with overpasses.

a) Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
W +	901926.1836	14204.73530	11
S +	874806.7555	21858.86691	11

Mauchly's Test of Sphericity[b]
Measure: Prey_Biomass

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Climate	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a. May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b. Design: Intercept.

Within Subjects Design: Climate.

Tests of Within-Subjects Effects

Measure: Prey_Biomass

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Climate	Sphericity Assumed	4.045E9	1	4.045E9	18.312	.002	.647
	Greenhouse-Geisser	**4.045E9**	**1.000**	**4.045E9**	**18.312**	**.002**	**.647**
	Huynh-Feldt	4.045E9	1.000	4.045E9	18.312	.002	.647
	Lower-bound	4.045E9	1.000	4.045E9	18.312	.002	.647
Error(Climate)	Sphericity Assumed	2.209E9	10	2.209E8			
	Greenhouse-Geisser	2.209E9	10.000	2.209E8			
	Huynh-Feldt	2.209E9	10.000	2.209E8			
	Lower-bound	2.209E9	10.000	2.209E8			

b) Post hoc test: Bonferroni

Pairwise Comparisons

Measure: Prey_Biomass

(I) Climate	(J) Climate	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
W +	S +	27119.428[*]	6337.464	.002	12998.678	41240.179

Based on estimated marginal means.

*   The mean difference is significant at the .05 level.

a.   Adjustment for multiple comparisons: Bonferroni.

Table 9

Outcome of linear regression on the effect of time on total consumable prey biomass (kg) for the different scenarios. Results were similar for the scenario with and the scenario without overpasses. For the W climate scenario, no significant change over the years is found. For the standard climate scenario, the total consumable biomass decreases significantly over time.

Scenario		Unstandardized Coefficients		Standardized Coefficients	t	P-value
		B	Std. Error	Beta		
W +	Constant	893780.274	9183.296	.317		.000
	Year	135.765	135.400		1.003	.342
W -	Constant	838569.802	8612.971	.337	97.361	.000
	Year	136.345	126.991		1.074	.311
S +	Constant	902996.908	10449.266	-.713	86.417	.000
	Year	-469.836	154.066		-3.050	.014
S -	Constant	847747.694	9793.361	-.723	86.564	.000
	Year	-452.813	144.395		-3.136	.012

Dependent Variable: Consumable Biomass.

c) Effects of climate on total carrying capacity

Table 10
Repeated measures ANOVA (a), followed by a post hoc test (Bonferroni) (b), on the effect of climate on total carrying capacity for the scenario with overpasses.

a) Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
W +	443.0000	7.07107	11
S +	429.0909	11.35301	11

Mauchly's Test of Sphericity[b]

Measure: Carcap

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Climate	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a. May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b. Design: Intercept.
Within Subjects Design: climate.

Tests of Within-Subjects Effects

Measure: Carcap

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Climate	Sphericity Assumed	1064.045	1	1064.045	17.317	.002	.634
	Greenhouse-Geisser	**1064.045**	**1.000**	**1064.045**	**17.317**	**.002**	**.634**
	Huynh-Feldt	1064.045	1.000	1064.045	17.317	.002	.634
	Lower-bound	1064.045	1.000	1064.045	17.317	.002	.634
Error(climate)	Sphericity Assumed	614.455	10	61.445			
	Greenhouse-Geisser	614.455	10.000	61.445			
	Huynh-Feldt	614.455	10.000	61.445			
	Lower-bound	614.455	10.000	61.445			

b) Post hoc test: Bonferroni

Measure: Carcap

(I) climate	(J) climate	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
W +	S +	13.909[*]	3.342	.002	6.462	21.357

Based on estimated marginal means.

* The mean difference is significant at the .05 level.

a. Adjustment for multiple comparisons: Bonferroni.

Table 11

Repeated measures ANOVA (a), followed by a post hoc test (Bonferroni) (b), on the effect of climate on total carrying capacity for the scenario without overpasses.

a) Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
W -	347.4545	3.26691	11
S -	338.1818	6.58511	11

Mauchly's Test of Sphericity[b]

Measure: Carcap

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Climate	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a. May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b. Design: Intercept.

Within Subjects Design: climate.

Tests of Within-Subjects Effects

Measure: Carcap

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Climate	Sphericity Assumed	472.909	1	472.909	15.350	.003	.606
	Greenhouse-Geisser	**472.909**	**1.000**	**472.909**	**15.350**	**.003**	**.606**
	Huynh-Feldt	472.909	1.000	472.909	15.350	.003	.606
	Lower-bound	472.909	1.000	472.909	15.350	.003	.606
Error(climate)	Sphericity Assumed	308.091	10	30.809			
	Greenhouse-Geisser	308.091	10.000	30.809			
	Huynh-Feldt	308.091	10.000	30.809			
	Lower-bound	308.091	10.000	30.809			

b) Post hoc test: Bonferroni

Measure: Carcap

(I) climate	(J) climate	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
W -	S-	9.273[*]	2.367	.003	3.999	14.546

Based on estimated marginal means.

*   The mean difference is significant at the .05 level.

a. Adjustment for multiple comparisons: Bonferroni.

2.3 Effect of overpasses on population dynamics

a) Effect of overpasses on average number of adults

Table 12
Repeated measures ANOVA (a) followed by a post hoc test (Bonferroni) (b) on the effect of overpasses on the average number of adults per year for the W climate scenario.

a) Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
W -	8.1569	9.77679	111
W +	36.8268	3.54913	111

Mauchly's Test of Sphericity[b]

Measure: Adults

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Fragmentation	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix

a. May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b. Design: Intercept.

Within Subjects Design: Fragmentation.

Tests of Within-Subjects Effects

Measure: Adults

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Fragmentation	Sphericity Assumed	45618.796	1	45618.796	748.511	.000	.872
	Greenhouse-Geisser	**45618.796**	**1.000**	**45618.796**	**748.511**	**.000**	**.872**
	Huynh-Feldt	45618.796	1.000	45618.796	748.511	.000	.872
	Lower-bound	45618.796	1.000	45618.796	748.511	.000	.872
Error (Fragmentation)	Sphericity Assumed	6704.069	110	60.946			
	Greenhouse-Geisser	6704.069	110.000	60.946			
	Huynh-Feldt	6704.069	110.000	60.946			
	Lower-bound	6704.069	110.000	60.946			

b) Post hoc test: Bonferroni

Measure: Adults

(I) Fragmentation	(J) Fragmentation	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
W -	W +	-28.670[*]	1.048	.000	-30.747	-26.593

Based on estimated marginal means.

* The mean difference is significant at the .05 level.

a. Adjustment for multiple comparisons: Bonferroni.

Table 13

Repeated measures ANOVA (a) followed by a post hoc test (Bonferroni) (b) on the effect of overpasses on the average number of adults per year for the standard climate scenario.

a) Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
S -	8.5846	10.24225	111
S +	33.8202	5.47816	111

Mauchly's Test of Sphericity[b]

Measure: Adults

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Fragmentation	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a. May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b. Design: Intercept.

Within Subjects Design: Fragmentation.

Tests of Within-Subjects Effects

Measure: Adults

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Fragmentation	Sphericity Assumed	35344.246	1	35344.246	606.782	.000	.847
	Greenhouse-Geisser	**35344.246**	**1.000**	**35344.246**	**606.782**	**.000**	**.847**
	Huynh-Feldt	35344.246	1.000	35344.246	606.782	.000	.847
	Lower-bound	35344.246	1.000	35344.246	606.782	.000	.847
Error (Fragmentation)	Sphericity Assumed	6407.351	110	58.249			
	Greenhouse-Geisser	6407.351	110.000	58.249			
	Huynh-Feldt	6407.351	110.000	58.249			
	Lower-bound	6407.351	110.000	58.249			

b) Post hoc test: Bonferroni

Measure: Adults

(I) Fragmentation	(J) Fragmentation	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
S -	S +	-25.236[*]	1.024	.000	-27.266	-23.205

Based on estimated marginal means.

*   The mean difference is significant at the .05 level.

a. Adjustment for multiple comparisons: Bonferroni.

b) *Effect of overpasses on population persistence*

Table 14

Repeated measures ANOVA (a) followed by a post hoc test (Bonferroni) (b) on the effect of overpasses on population persistence for the W climate scenario. Population persistence is measured as the end-year of the simulated. If no extinction occurs, the end-year is year 110.

a) Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
W -	48.1800	21.27578	150
W +	90.8133	27.99602	150

Mauchly's Test of Sphericity[b]

Measure: Max_Year

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Fragmentation	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a. May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b. Design: Intercept.

Within Subjects Design: Fragmentation.

Tests of Within-Subjects Effects

Measure: Max_Year

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Fragmentation	Sphericity Assumed	136320.083	1	136320.083	191.682	.000	.563
	Greenhouse-Geisser	**136320.083**	**1.000**	**136320.083**	**191.682**	**.000**	**.563**
	Huynh-Feldt	136320.083	1.000	136320.083	191.682	.000	.563
	Lower-bound	136320.083	1.000	136320.083	191.682	.000	.563
Error (Fragmentation)	Sphericity Assumed	105965.417	149	711.177			
	Greenhouse-Geisser	105965.417	149.000	711.177			
	Huynh-Feldt	105965.417	149.000	711.177			
	Lower-bound	105965.417	149.000	711.177			

b) Post hoc test: Bonferroni

Measure: Max_Year

(I) Fragmentation	(J) Fragmentation	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
W -	W +	-42.633[*]	3.079	.000	-48.718	-36.549

Based on estimated marginal means.

*   The mean difference is significant at the .05 level.

a. Adjustment for multiple comparisons: Bonferroni.

Table 15

Repeated measures ANOVA (a) followed by a post hoc test (Bonferroni) (b) on the effect of overpasses on population persistence for the standard climate scenario. Population persistence is measured as the end-year of the simulated. If no extinction occurs, the end-year is year 110.

a)   Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
S -	49.6267	20.05581	150
S +	85.9533	30.70783	150

Mauchly's Test of Sphericity[b]

Measure: Max_Year

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Fragmentation	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a.   May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b.   Design: Intercept.

Within Subjects Design: Fragmentation.

Tests of Within-Subjects Effects

Measure: Max_Year

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Fragmentation	Sphericity Assumed	98972.003	1	98972.003	143.575	.000	.491
	Greenhouse-Geisser	**98972.003**	**1.000**	**98972.003**	**143.575**	**.000**	**.491**
	Huynh-Feldt	98972.003	1.000	98972.003	143.575	.000	.491
	Lower-bound	98972.003	1.000	98972.003	143.575	.000	.491
Error (Fragmentation)	Sphericity Assumed	102711.497	149	689.339			
	Greenhouse-Geisser	102711.497	149.000	689.339			
	Huynh-Feldt	102711.497	149.000	689.339			
	Lower-bound	102711.497	149.000	689.339			

b) Post hoc test: Bonferroni

Measure: Max_Year

(I) Fragmentation	(J) Fragmentation	Mean Difference(I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
S -	S +	-36.327[*]	3.032	.000	-42.317	-30.336

Based on estimated marginal means.

*   The mean difference is significant at the .05 level.

a.   Adjustment for multiple comparisons: Bonferroni.

2.4   Effect of climate on population dynamics

a) Effects of climate on average number of adults per year

Table 16

Repeated measures ANOVA (a) followed by a post hoc test (Bonferroni) (b) on the effect of climate on the average number of adults per year for the scenario with overpasses.

a)   Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
S +	33.8202	5.47816	111
W +	36.8268	3.54913	111

Mauchly's Test of Sphericity[b]

Measure: Adults

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Climate	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a.   May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b.   Design: Intercept.

Within Subjects Design: climate.

Tests of Within-Subjects Effects

Measure: Adults

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Climate	Sphericity Assumed	501.702	1	501.702	38.386	.000	.259
	Greenhouse-Geisser	**501.702**	**1.000**	**501.702**	**38.386**	**.000**	**.259**
	Huynh-Feldt	501.702	1.000	501.702	38.386	.000	.259
	Lower-bound	501.702	1.000	501.702	38.386	.000	.259
Error (climate)	Sphericity Assumed	1437.709	110	13.070			
	Greenhouse-Geisser	1437.709	110.000	13.070			
	Huynh-Feldt	1437.709	110.000	13.070			
	Lower-bound	1437.709	110.000	13.070			

b) Post hoc test: Bonferroni

Measure: Adults

(I) climate	(J) climate	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
S +	W +	-3.007[*]	.485	.000	-3.968	-2.045

Based on estimated marginal means.

* The mean difference is significant at the .05 level.

a. Adjustment for multiple comparisons: Bonferroni.

Table 17
Repeated measures ANOVA (a) followed by a post hoc test (Bonferroni) (b) on the effect of climate on the average number of adults per year for the scenario without overpasses.

a) Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
S -	8.5846	10.24225	111
W -	8.1569	9.77679	111

Mauchly's Test of Sphericity[b]

Measure: Adults

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Climate	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix

a. May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b. Design: Intercept.

Within Subjects Design: climate.

Tests of Within-Subjects Effects

Measure: Adults

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
climate	Sphericity Assumed	10.152	1	10.152	18.198	.000	.142
	Greenhouse-Geisser	**10.152**	**1.000**	**10.152**	**18.198**	**.000**	**.142**
	Huynh-Feldt	10.152	1.000	10.152	18.198	.000	.142
	Lower-bound	10.152	1.000	10.152	18.198	.000	.142
Error(climate)	Sphericity Assumed	61.364	110	.558			
	Greenhouse-Geisser	61.364	110.000	.558			
	Huynh-Feldt	61.364	110.000	.558			
	Lower-bound	61.364	110.000	.558			

a) Post hoc test: Bonferroni

Measure: Adults

(I) climate	(J) climate	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
S -	W -	.428[*]	.100	.000	.229	.626

Based on estimated marginal means.

* The mean difference is significant at the .05 level.

a. Adjustment for multiple comparisons: Bonferroni.

b) Effect of climate on population persistence

Table 18
Repeated measures ANOVA (a) followed by a post hoc test (Bonferroni) (b) on the effect of climate on population persistence for the scenario with overpasses. Population persistence is measured as the end-year of the simulated. If no extinction occurs, the end-year is year 110.

b) Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
S +	85.9533	30.70783	150
W +	90.8133	27.99602	150

Mauchly's Test of Sphericity[b]
Measure: Max_Year

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Climate	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a. May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b. Design: Intercept
 Within Subjects Design: Climate

Tests of Within-Subjects Effects
Measure: Max_Year

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Climate	Sphericity Assumed	1771.470	1	1771.470	1.903	.170	.013
	Greenhouse-Geisser	**1771.470**	**1.000**	**1771.470**	**1.903**	**.170**	**.013**
	Huynh-Feldt	1771.470	1.000	1771.470	1.903	.170	.013
	Lower-bound	1771.470	1.000	1771.470	1.903	.170	.013
Error(Climate)	Sphericity Assumed	138684.030	149	930.765			
	Greenhouse-Geisser	138684.030	149.000	930.765			
	Huynh-Feldt	138684.030	149.000	930.765			
	Lower-bound	138684.030	149.000	930.765			

c) Post hoc test: Bonferroni

Measure: Max_Year

(I) Climate	(J) Climate	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
S +	W +	-4.860	3.523	.170	-11.821	2.101

Based on estimated marginal means.

a. Adjustment for multiple comparisons: Bonferroni.

Table 19

Repeated measures ANOVA (a) followed by a post hoc test (Bonferroni) (b) on the effect of climate on population persistence for the scenario without overpasses. Population persistence is measured as the end-year of the simulated. If no extinction occurs, the end-year is year 110.

d) Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
S -	49.6267	20.05581	150
W -	48.1800	21.27578	150

Mauchly's Test of Sphericity[b]

Measure: Max_Year

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Climate	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a. May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b. Design: Intercept.

Within Subjects Design: Climate.

Tests of Within-Subjects Effects

Measure: Max_Year

Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Climate	Sphericity Assumed	156.963	1	156.963	.371	.543	.002
	Greenhouse-Geisser	**156.963**	**1.000**	**156.963**	**.371**	**.543**	**.002**
	Huynh-Feldt	156.963	1.000	156.963	.371	.543	.002
	Lower-bound	156.963	1.000	156.963	.371	.543	.002
Error(Climate)	Sphericity Assumed	63013.537	149	422.910			
	Greenhouse-Geisser	63013.537	149.000	422.910			
	Huynh-Feldt	63013.537	149.000	422.910			
	Lower-bound	63013.537	149.000	422.910			

e) Post hoc test: Bonferroni

Measure: Max_Year

(I) Climate	(J) Climate	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
S -	W -	1.447	2.375	.543	-3.246	6.139

Based on estimated marginal means.

Adjustment for multiple comparisons: Bonferroni.

2.5 Difference in relative effect of overpasses on carrying capacity between the climate scenarios

Table 20

Repeated measures ANOVA on the difference in relative effect of wildlife overpasses on carrying capacity between both climate scenarios. The relative effect of overpasses is calculated as the carrying capacity in the scenario with overpasses, divided by the carrying capacity in the scenario without overpasses.

f) Repeated measures ANOVA

Descriptive Statistics

	Mean	Std. Deviation	N
W	1.2494	.00992	11
S	1.2687	.01322	11

Test of sphericity
Measure: Effect_Overpasses

Within Subjects Effect	Mauchly's W	Approx. Chi-Square	df	Sig.	Epsilon[a]		
					Greenhouse-Geisser	Huynh-Feldt	Lower-bound
Climate	1.000	.000	0	.	1.000	1.000	1.000

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a. May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the Tests of Within-Subjects Effects table.

b. Design: Intercept.

Tests of Within-Subjects Effects
Measure: Effect_Overpasses

| Source		Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Climate	Sphericity Assumed	.002	1	.002	87.602	.000	.898
	Greenhouse-Geisser	**.002**	**1.000**	**.002**	**87.602**	**.000**	**.898**
	Huynh-Feldt	.002	1.000	.002	87.602	.000	.898
	Lower-bound	.002	1.000	.002	87.602	.000	.898
Error (climate)	Sphericity Assumed	.000	10	2.330E-5			
	Greenhouse-Geisser	.000	10.000	2.330E-5			
	Huynh-Feldt	.000	10.000	2.330E-5			
	Lower-bound	.000	10.000	2.330E-5			

g) Post hoc test: Bonferroni

Measure: Effect_Overpasses

(I) climate	(J) climate	Mean Difference (I-J)	Std. Error	Sig.[a]	95% Confidence Interval for Difference[a]	
					Lower Bound	Upper Bound
W	S	-.019[*]	.002	.000	-.024	-.015

Based on estimated marginal means.

* The mean difference is significant at the .05 level.

a. Adjustment for multiple comparisons: Bonferroni.
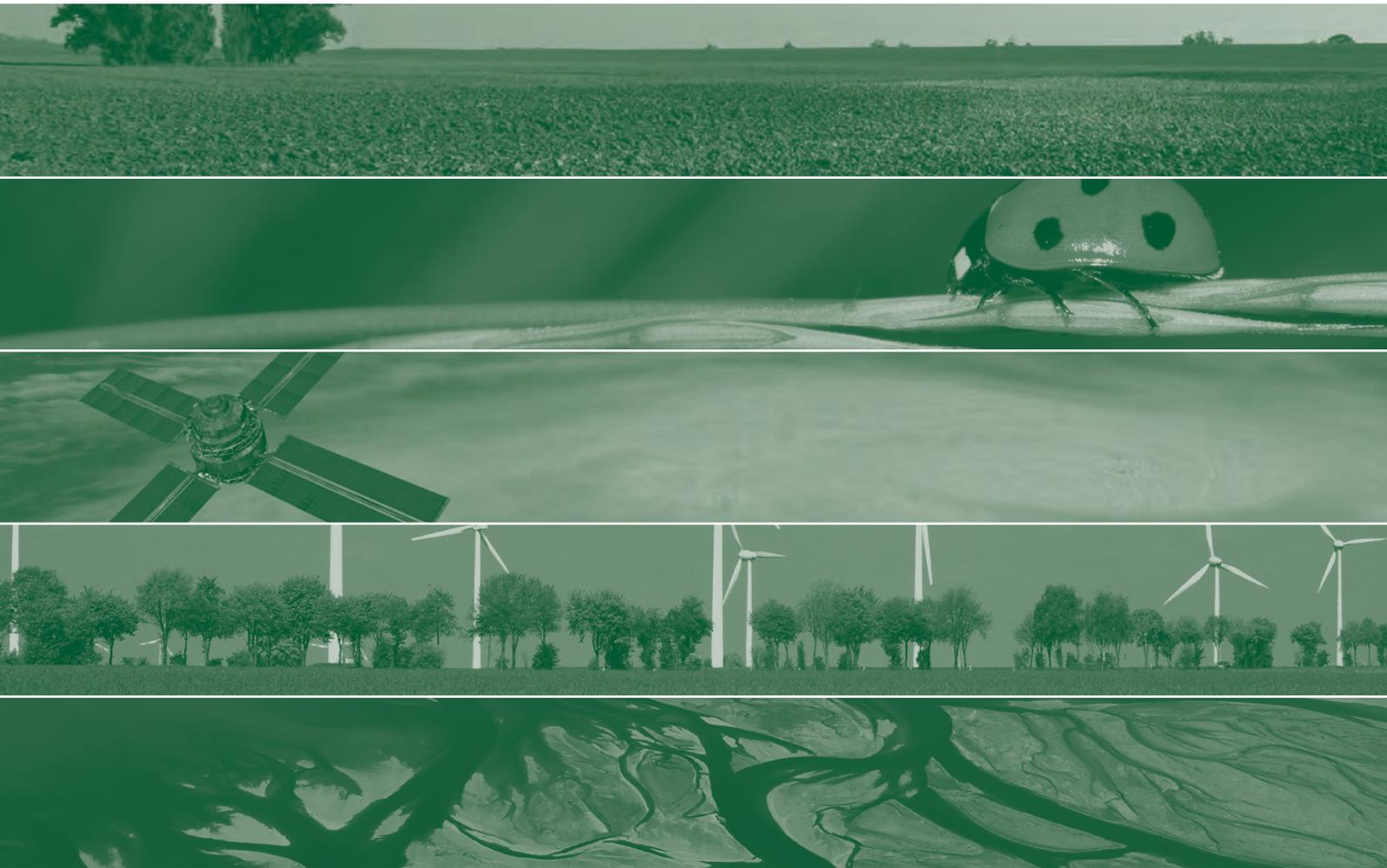
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