Habitat suitability for wolves in the Netherlands

A modelling approach

L. Biersteker, A. Planillo, D.R. Lammertsma, T. van der Sluis, F. Knauer, S Kramer-Schadt, E.A. van der Grift, M. Van Eupen, & H.A.H. Jansman

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With several wolf packs now established in the Netherlands, the return of this species to our country is a fact. The question now is what the potential range of the wolf in the Netherlands might look like in the long term, and how large the wolf population might become. This report answers these questions based on a data-driven modelling analysis of habitat suitability for wolves in the Netherlands.

Keywords: Habitat suitability, wolf, *Canis lupus*, LARCH, number of packs

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Summary

With several wolf packs now established in the Netherlands, the return of this species to our country is a fact. At the time of writing, there are seven packs living in the Veluwe, one in Drenthe and one in Drenthe and Friesland. When a large predator like the wolf returns to a human- and livestock-dense country like the Netherlands, it is useful to assess where the species might settle so that policymakers and society at large can prepare accordingly. A habitat suitability analysis is a key part of this process. The present habitat suitability analysis was commissioned by the Ministry of Agriculture, Fisheries, Food Security and Nature (Ministry of LVVN) in 2023. It was originally published in Dutch (Biersteker et al, 2024), and now translated in English. The aim of this project is to assess habitat suitability for wolves in the Netherlands using a data-driven modelling analysis. In consultation with Ministry of LVVN, this led to the following research questions, which are answered in this report:

- What is the wolf's potential range in the Netherlands?
- Given this range, how large could the wolf population become?
  - What is the relationship between this range and tree cover in the Netherlands?
  - What is the relationship between this range and the distribution of four prey species?
  - What is the relationship between this range and the distribution of damage incidents?
  - What is the relationship between this range and the centres of the current territories?
- Is it possible to predict which parts of the potential range are most likely to see habitat establishment first?

To reliably estimate the Netherlands' habitat suitability and ecological carrying capacity for wolves, information is needed on the animal's preferred habitat types and the conditions found there. While no transmitter research has been carried out in the Netherlands, wolves have been tracked in Germany, providing information on their habitat use and dispersal capacity. This data was used to create a statistically valid carrying capacity model. In the present study, this German model was applied to the Dutch situation, resulting in a map showing the wolf's range in 10x10 km grid sections. This resolution is quite low for a country the size of the Netherlands. To increase the granularity of the German model, two analyses based on the LARCH knowledge system were added. First, LARCH was run using a suitability map with a 10x10 km resolution to demonstrate its similarity to the German model. The resolution was then increased by carrying out a LARCH-SCAN analysis with a resolution of 100x100 m.

The results show that the wolf's potential range in the Netherlands is concentrated in the north and east of the country, including the Utrechtse Heuvelrug and eastern North Brabant. With its low threshold for habitat suitability, the German model yields a distribution covering almost all of the northeastern Netherlands, Flevoland, the Utrechtse Heuvelrug and large parts of North Brabant. Under a scenario with a higher threshold, a much smaller range remains, primarily covering the Veluwe, southeastern Flevoland, Drents-Friese Wold and parts of North Brabant. The LARCH model yields an almost identical range for both scenarios, while the LARCH-SCAN model predicts a larger distribution and potential range than the 10x10 km analyses. For instance, LARCH-SCAN identifies a number of dune areas in the western Netherlands as suitable habitats, but with a carrying capacity of less than one pack. Even when using a higher threshold, LARCH-SCAN yields a larger range than the other models, which can be attributed to its higher level of detail. For carrying capacity, the LARCH-SCAN analysis provides a lower limit of 23 packs and an upper limit of 56.

The results show a clear difference in suitability between the eastern and western parts of the country, which is likely related to the level of human influence. The level of human influence in the west is such that, given the parameters used in the model, the establishment of a pack is unlikely. However, there are several things to note in this context. Some areas, for instance, are just below the threshold for pack establishment, so it is not inconceivable that pack establishment could still occur there. Moreover, the area requirement of a pack used in this study (200 km^2) is not a hard lower limit, as wolf territories show considerable variation in terms of size, ranging between 80 and 400 km^2. It should also be emphasised that this modelling study only estimates the suitability of areas for permanent wolf establishment. However, dispersing wolves can turn up

anywhere and stay for shorter or longer periods. This may include environments that are unsuitable as permanent habitats, such as urban areas.
The current occurrence of wolves in the Netherlands (based on damage incidents involving livestock) and the location of the current territories (based on monitoring) provide an indication of the degree of uncertainty underlying the modelled range. The results of the model appear to be consistent with both damage incidents and territory locations.

A visual validation of the modelled range against forest cover and the occurrence of ungulate species gives an indication of the areas likely to be colonised first, as forest cover and wild ungulate abundance are important factors in the habitat preferences of wolves. The model only identifies areas it deems suitable as wolf habitats, without ranking them in terms of suitability. Based on the additional data, the Veluwe, with its high degree of forest cover and the presence of four wild ungulate species, appears to be a highly suitable environment. This can also be seen in practice, as the Veluwe is already home to seven packs. Wooded areas with two ungulate species in Drenthe, Friesland and eastern North Brabant are also highly suitable for colonisation, which appears to be confirmed by the current establishment of wolves in Drents-Friese Wold and eastern North Brabant.

The present analysis was conducted based on data obtained from wolves in Germany. In order to improve the quality of the models and reduce uncertainty, further research is needed on the habitat use of wolves in the Netherlands, preferably using multiple methods such as telemetry, DNA and trace research. The data this would yield could serve as a basis for a new model for the Dutch situation, with a higher predictive value.

1 Introduction

1.1 Background

With several wolf packs now established in the Netherlands, the return of this species to our country is a fact.[1] At the time of writing, there are seven packs living in the Veluwe, one in Drenthe and one in Drenthe and Friesland. In 2012, in preparation for the expected return of the wolf, a fact-finding study was conducted by Wageningen Environmental Research (WENR) on behalf of the Ministry of Economic Affairs, the Association of Provincial Authorities (IPO) and BIJ12. This was six years before the establishment of the first pack (Groot Bruinderink et al., 2012).

Due to the growing population of wolves in the Netherlands – and Europe – and the more frequent occurrence of roaming wolves in the Netherlands, interactions between humans, livestock and wolves are now increasingly common. The Interprovincial Wolf Plan (IPO, 2019) and Addendum (IPO, 2023) set out a number of policy principles for the management of wolves. For the revision of this plan, two additional factual reports were commissioned by the above-mentioned authorities, which together form the legal and ecological basis for the updated document. The legal framework for the protection and management of wolves is described in Boerema et al. (2021)[2], while the report by Jansman et al. (2021) discusses issues surrounding the ecology of wolves, such as their lifestyle, diet, distribution, occurrence and origin, but also ecological carrying capacity. In addition, Jansman et al. (2021) address questions regarding problem behaviour, human-wolf coexistence, policy, damage, monitoring and management.

When a large predator like the wolf returns to a human- and livestock-dense country like the Netherlands, it is desirable to assess where the species might settle so that policymakers and society at large can prepare accordingly. A habitat suitability analysis is a key part of this process. Two such analyses have previously been conducted for the wolf in the Netherlands (Lelieveld, 2012; Potiek et al., 2012), both of which made assumptions based on the literature and expert knowledge. However, a modelling study using a data-driven approach can provide a more reliable prediction of potential distribution. After more than 20 years of experience with wolves in Germany, researchers there have gained insight into the animal's habitat use. This makes it possible to carry out a new analysis of potentially suitable habitats in the Netherlands using modelling tools.

The present habitat suitability analysis was commissioned by the Ministry of Agriculture, Fisheries, Food Security and Nature (Ministry of LVVN) in 2023. It was originally published in Dutch (Biersteker et al, 2024)[3], and now translated in English. The aim of this project is to assess habitat suitability for wolves in the Netherlands using a data-driven modelling analysis.

1.2 Research questions

In consultation with Ministry of LVVN, this led to the following research questions, which are answered in this report:

- What is the wolf's potential range in the Netherlands?
- Given this range, how large could the wolf population become?
  - What is the relationship between this range and tree cover in the Netherlands?
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  - What is the relationship between this range and the centres of the current territories?
- Is it possible to predict which parts of the potential range are most likely to see habitat establishment first?

[1] https://www.bij12.nl/onderwerp/wolf/.
[2] Boerema L., L. Freriks. A.A. and D.B. van den Brink. 2021. The legal protection of wolves in the Netherlands and in a number of other European countries: A legal study to support the formulation of Dutch wolf policy in the light of the implementation of nature legislation, Boerema and Van den Brink B.V., Houwerzijl/Element Advocaten, Best.
[3] https://doi.org/10.18174/654770 Habitatgeschiktheid voor de wolf in Nederland – een modelanalyse. Biersteker et al, 2024.

Section 2 presents the methodology, describing the wolf’s specific requirements and the models used. The results, boundary conditions and assumptions are set out in Section 3. Section 4 discusses the results in relation to other studies and the validation process, before concluding with several recommendations.

2 Method

2.1 Introduction

To reliably estimate the Netherlands' habitat suitability and ecological carrying capacity for wolves, information is needed on the animal's preferred habitat types and the conditions found there. The habitat size required for a pack to settle somewhere permanently (carrying capacity) must also be considered. Finally, the distances wolves can travel to reach new areas need to be taken into account. This information can be obtained from expert estimates or from field data (based on transmitters or derived from sightings of tracks and droppings).

While no transmitter research has been carried out in the Netherlands, there is tracking data from two German wolves that passed through the Netherlands (Jansman et al., 2021). This data gives an impression of the animal's migratory behaviour, but does not provide insight into how it uses its environment. German researchers, however, have carried out several field studies, collaring wolves to collect information on their habitat use and dispersal capacity. This data was then used to create a statistically valid model for carrying capacity (Planillo et al., 2023; Kramer-Schadt et al., 2020).

In the present study, this German model was applied to the Dutch situation, resulting in a map showing the wolf's range in 10x10 km grid sections. This resolution is quite low for a country the size of the Netherlands.

To increase the granularity of the German model, two analyses based on the LARCH knowledge system were added. First, LARCH was run using a suitability map with a 10x10 km resolution to demonstrate its similarity to the German model. The resolution was then increased by carrying out a LARCH-SCAN analysis with a resolution of 100x100 m.

Conceptually, the German model is very similar to the LARCH(-SCAN) knowledge system (Pouwels et al., 2008; Rüter et al., 2014; Pazurova, 2018; Van der Sluis 2021). This model has previously been used in wolf studies as well, for example in the Umbria region of Italy (Klaver, 2003; Van der Sluis & Pedroli, 2004), the Abruzzo region of Italy – in the heart of the Apennines (Van der Sluis et al., 2003) – and two areas in Lugansk Oblast, Ukraine (Van der Sluis et al., 2011). The LARCH model is described in Section 2.3.2.

In summary, the present study aims to determine the habitat suitability for wolves in the Netherlands through three modelling analyses:

1. An analysis using the model developed in Germany;
2. An analysis using the LARCH model;
3. An analysis using the LARCH-SCAN model.

2.2 Species description – ecology of the wolf

The wolf is a generalist species (Boitani, 2000). Although it has a clear preference for wooded areas, it also uses agricultural land and wetlands (Jędrzejewski et al., 2004; Fechter & Storch, 2014). The wolf's territory is typically made up of approximately 50% forest, ensuring sufficient nesting sites and prey (Jędrzejewski et al., 2004; Jansman et al., 2021). While the animal generally avoids human-made structures such as motorways and urban areas (Jędrzejewski et al., 2004; Fechter & Storch, 2014), secondary roads, lakes and rivers do not affect habitat use.
The wolf's diet is highly varied, as it feeds on whatever is most readily available in its habitat to meet its nutritional needs (Boitani, 2000). Nevertheless, it prefers habitats with several different species of wild ungulates, allowing for flexible use of the range depending on the season (Jansman et al., 2021).

The size of wolf territories varies depending on the availability of prey, population density, time of year, geographical location and land cover (Jędrzejewski et al., 2007; Mysłajek et al., 2018). Wolves are highly territorial, and will claim and defend an area from conspecifics. Their local presence is usually limited to a pair of parents with their young, sometimes accompanied by a few young from the previous year. While the size of these packs can fluctuate over time depending on the number of young born each year and their survival rate, it always remains within certain bounds. Young adults will usually leave the pack at one or two years of age, and occasionally a pack may accept a roaming lone wolf. Packs can range from two to nine animals, with the average pack consisting of five animals (Fechter & Storch, 2014). Without human intervention, it can be predicted with a high degree of certainty that this will be the number of wolves living in a habitat or territory in the short, medium and long term.

In Europe, a pack’s home range is usually around 200 km^2, but this can vary from 80 to 400 km^2 (Reinhardt & Kluth, 2016; Jansman et al., 2021; Planillo et al., 2024). In the present study, the typical home range of 200 km^2 was used to parameterise the models and determine the number of wolves that could potentially settle in the Netherlands.

The daily distances wolves travel vary depending on the food supply. According to Kusak et al. (2005), the linear distance travelled by wolves in Europe (Italy, Croatia and Poland) ranges from 2.5 to 9 km/day. Reinhardt & Kluth (2016), on the other hand, found that adult wolves travelled a daily distance of approximately 9 to 13 km, with a maximum of 68 km, whereas Jędrzejewski et al. (2001) reported average daily distances of 20-27 km, with a maximum of 64 km. This would mean that a wolf could theoretically travel up to 30 km in one direction to forage and return to its starting point the same day. Based on the average home range from their telemetry study, Mysłajek et al. (2018) plotted circles around known wolf dens (assuming these dens were in the centre of the home range). The home range of 378 km^2 they used resulted in circles with an 11 km radius around the centres of established wolf territories. This radius also corresponds to the wolf’s average daily travel distance. In North America, wolves are known to travel up to 80 km/day when food supply is low, and will typically travel 1.6 to 9 km/day when food supply is high (Kusak et al., 2005). Combined with the average and maximum distances reported by Jędrzejewski et al. (2001), this implies that wolves travel an average of about 10 km out and 10 km back to forage. This value was used to parameterise the models.

Detailed dispersal studies are scarce for the Central European wolf population. Most reported dispersal distances are under 100 km (Kojola et al., 2006; 2009; Linnell et al., 2005; Blanco & Cortes, 2007). Kojola et al. (2006; 2009) found a median dispersal distance of 98.5 km (range 35-445 km) in Finland. In Linnell et al. (2005), 65% of dispersal is under 100 km, 20% between 100 and 200 km and 17% above 200 km. Long-distance dispersal is regularly observed as well, with linear distances ranging from 400 to more than 1,000 km (Wabakken et al., 2007; Ciucci et al., 2009; Mancinelli & Ciucci, 2018; Ražen et al., 2016; Reinhardt & Kluth, 2016; Andersen et al., 2015). Of the 298 published dispersal distances in the US, only 10 are above 500 km (Linnell et al., 2005). Jiminez et al. (2017) reported no significant difference in the linear dispersal distances of males and females, which were 98.1 km and 87.7 km respectively, and that only 10 of the 297 collared wolves travelled more than 300 km. For the parameterisation of the models, we assumed a dispersal distance of 100 km.

2.3 Modelling analysis

2.3.1 German model

The German model (Planillo et al., 2024) was developed based on an analysis of observations of collared wolves combined with land cover maps and indicator maps related to human impacts (population density, distance to infrastructure and distance to roads). A human footprint (HFP) map was used as well.[4] The researchers used these map layers together with observational data to train two different types of models: a generalised linear mixed model and a maximum entropy model. The combination of these models resulted in what is known as an ensemble or composite model, which is created by taking a weighted average of a number of different models, each with its own strengths and weaknesses. This will result in a more robust prediction than would be possible with any single model.

In the present study, the ensemble model was run using input maps from the Netherlands (Table 1) at a resolution of 100x100 m. The model's output is a map with the same resolution, showing a habitat suitability score for each cell. This is the habitat suitability index (HSI), which ranges between 0 and 1, with 0 representing 'completely unsuitable' and 1 representing 'habitat of optimal quality'. For a detailed description of the HSI model, see Planillo et al. (2024).

Table 1 *Source and year per source map.*

Name	Year	Description	Source
CORINE Land Cover	2018	Land cover, modified based on classes that are relevant to the wolf	https://land.copernicus.eu/pan-european/corine-land-cover/clc2018
Population density	2010	Human population densities	https://www.eea.europa.eu/data-and-maps/data/population-density-disaggregated-with-CORINE-landcover-2000-2
Human footprint	2018	Degree of human impact on an area	https://www.nature.com/articles/s41597-022-01284-8
Distance from settlements	2016	Distance from built-up areas	https://ghsl.jrc.ec.europa.eu/esm_R2019.php
Distance from roads	2016	Distance from motorways, only larger roads included	https://hub.worldpop.org/geodata/summary?id=17447

The resolution of the suitability map was then reduced to 10x10 km and resampled using a threshold, with all cells below the threshold receiving a suitability score of 0. This ensured that only cells of sufficient quality were retained for range modelling, as highly fragmented habitats and habitats of insufficient quality were filtered out. In order to create a potential range map? with an upper and lower limit, this was done twice (see Section 2.3.4).

The German model's final population estimates were calculated by retaining only those areas with at least two adjacent 10x10 km (100 km^2) cells, including diagonally adjacent cells. This is equivalent to an area of 200 km^2, which is the average size of a wolf's territory, with a 10 km range for the animal's daily activity (see Section 2.2).

Applying the German model (Planillo et al., 2023) to the Dutch situation involved the following steps:
1. Creating a map showing the estimated habitat suitability (resolution of 100x100 m).
2. Reducing the resolution of this suitability map to 10x10 km.
3. Filtering this map to exclude highly unsuitable or fragmented patches or cells from the carrying capacity calculations.
4. Determining the ranges? by retaining only areas ('patches') with two or more adjacent 10x10 km cells, corresponding to the area requirement of one pack.
5. Calculating the total carrying capacity by dividing the total potential range in the Netherlands by the area required by one pack.

[4] An HFP map scores the extent to which an area has been adapted by humans on a scale of 0 to 50, where 0 represents 'not adapted' and 50 represents 'highly adapted'. The HFP map used here was created using maps of eight different variables: built environment, population density, nighttime lighting, agricultural land, pastures, roads, railways and navigable waterways.

2.3.2 LARCH model

In the present study, the HSI map from the German model was used as the basis for two LARCH analyses. For the first analysis, the LARCH input was a version of the HSI map aggregated to a resolution of 10x10 km. Similar to Planillo et al. (2024), the outcome of the HSI model was first translated to a 10x10 km resolution, after which a suitability threshold was applied to retain the suitable habitats. LARCH determines metapopulations: networks of spatially distinct populations that interact at different levels, such as exchange of specimens, colonisation and extinction of populations.

In determining metapopulations LARCH also includes the resistance of infrastructure such as motorways, waterways and urban centres. This is based on a resistance map with the same resolution as the habitat suitability map. For a species that has no chance to cross a motorway or waterway (it is an absolute mortal barrier), the patches on either side of such an element are not part of the same metapopulation since no exchange can take place between these populations. Due to the use of a 10x10 km suitability map, however, the current analysis does not consider absolute barriers, as this would require 10x10 km resistance maps unsuited to the scale of these mostly linear elements.

The wolf's range was set at 10 km (see 3), the range of daily activity rather than the dispersal distance, which is many times greater. Given the distances regularly covered by dispersing wolves (see Section 2.2) and the omission of resistance from the present analysis, it can be assumed that all wolf populations in the Netherlands belong to the same network.
The following description of the LARCH knowledge system is largely based on the description given by Van der Sluis et al. (2020):

For the spatial analysis of habitats, the landscape ecological model LARCH (Landscape-Ecological Analysis and Rules for the Configuration of Habitat) was used. This model is based on principles from metapopulation theory and provides information on the structure and viability of populations in relation to the configuration and carrying capacity of breeding, foraging and resting areas. Metapopulation theory views landscapes as networks of spatially distinct populations interacting at different levels (Hanski & Gilpin, 1997; Opdam et al., 2002; Foppen, 2001). Interactions between habitat patches include exchange of individuals and colonisations or extinctions. Exchange of terrestrial species often takes place through corridors, or incrementally via 'stepping stones' (Van der Sluis et al., 2004). The metapopulation approach is particularly useful in fragmented landscapes.

LARCH is a knowledge system that integrates spatial information with ecological species characteristics. It is used for scenario analysis and policy evaluation. The system was developed by Alterra (predecessor of WENR) and has been fully described and has been applied in analyses worldwide (Chardon et al., 2000; Franz et al., 2013; Groot Bruinderink et al., 2003; Van der Sluis & Chardon, 2001; Van der Sluis et al., 2007; Verboom et al., 2001; Pouwels et al., 2002).
The principles underpinning the LARCH model are simple: a species of conservation concern or an indicator species (sometimes called an umbrella species) that is representative of several other species is selected, and the suitability of an area to support a population of the species is assessed. The size of an area and its vegetation structure determine the potential number of individuals of a particular species it can support. The distance to adjacent areas (network distance) determines whether these areas are part of a species' network with which exchange still takes place. All areas in a network contribute to the population, and the size of the network population is determined based on the species' characteristics.

As input, LARCH requires a habitat map (e.g. a vegetation or land cover map) and ecological species parameters (e.g. home range, dispersal distance and carrying capacity for all habitats). LARCH does not require distribution or abundance data, as the assessment is based on the potential of a species' ecological network given optimal habitat quality.

2.3.3 LARCH-SCAN

The second analysis used the SCAN module of LARCH, which clusters metapopulations based on species range, taking into account the degree of habitat connectivity. The degree of habitat connectivity is based on Hanski (1989), who calculates the connective strength between patches using an exponential function of the distance a species can move (dispersal) and habitat size.

The LARCH-SCAN module was run with the HSI map at its original resolution of 100x100 m, providing a more accurate estimate of the range and number of packs.

At the time of writing, it is not yet possible to properly estimate landscape resistance with the LARCH-SCAN model due to insufficient Dutch field data for wolf movements. Infrastructure resistance was therefore not included in the metapopulation modelling.

In this analysis, the wolf's range was set at 10 km, equal to the 10x10 km LARCH analysis (see Sections 2.2 and 2.3.2).

2.3.4 Uncertainty/upper and lower limits of the range

To cater for the uncertainty in their predictions, Planillo et al. (2024) use a 'lenient' (0.17) and a 'strict' (0.28) threshold level to resample or convert the HSI map before determining the range and calculating the number of packs, resulting in two different HSI maps. This means that the range and number of packs are calculated twice, once for each filtered HSI map, yielding an upper and lower range limit.

The thresholds are determined based on the HSI scores with the highest number of observations. The lower limit is defined as the lowest value within the 95% confidence interval, while the upper limit is calculated as the mean HSI score for the observations, minus one standard deviation. This ensures that cells of insufficient quality are not included in the calculation of the total number of packs.

In order to provide transparency regarding the uncertainty of the LARCH and LARCH-SCAN analyses, we decided to use the above approach as well.

2.3.5 Numbers

The unit used to express the size of (meta)populations or networks is the reproductive unit (RU). This is the number of units in a population that are able to reproduce. The reproductive unit for wolves is a pack, typically consisting of two to nine animals (Fechter & Storch, 2014).

In calculating the number of RUs per population, we assumed a home range of 200 km^2, which is consistent with what Planillo et al. (2024) infer from the observational data. The number of packs that, according to the models, could settle in the Netherlands was calculated by taking the sum of all populations that could contain at least one pack based on their area.

For each modelling analysis, the range's carrying capacity in terms of number of packs was calculated as follows:

1. The different sub-areas within the range were divided by the area required by a pack.
2. All areas large enough to support at least one pack were added together.

In order to obtain a lower limit for the carrying capacity, the above procedure was used to calculate the range according to the strict threshold, and in order to obtain an upper limit the lenient threshold was used. The carrying capacity range is the difference between this upper and lower limit.

2.4 Visual interpretation of model results

The model used by Planillo et al. (2024) is based in part on the CORINE Land Cover map that was developed as part of the EU Copernicus programme. This map includes a variety of land cover types with large differences in tree cover and prey availability, two key factors in the wolf's habitat preferences that are not included in the model (Krammer-Schadt et al., 2020, Planillo et al., 2024). These factors can be used to give an indication of which parts of the range (as calculated by the LARCH-SCAN model) are most likely to see pack establishment, or where this will happen first. To facilitate this process, maps were created of the average tree cover in the Netherlands and the distribution of four ungulate species, namely Roe deer, Fallow deer, Red deer and Wild boar were made.

Two additional maps were created to provide insight into how the LARCH-SCAN range compares with what is observed in practice: one showing the centres of established territories and another providing an overview of incidents involving livestock damage. In both maps, the points are plotted on the modelled range.

Below we describe how each additional map was created and which sources were used.

2.4.1 Forest cover in the Netherlands

This map shows the percentage of tree cover for 1x1 km sections within the LARCH-SCAN range; the data for mean tree cover is from the EU Copernicus Land Monitoring Service (https://sdi.eea.europa.eu/catalogue/copernicus/api/records/c7bf34ea-755c-4dbd-85b6-4efc5fd302a2?language=all).

2.4.2 Range of wild ungulates in the Netherlands

To map the occurrence of ungulate species, all observations within the last year for Roe deer, and within the last five years for Fallow deer, Red deer and Wild boar, were retrieved from the National Flora and Fauna Database. These figures were converted to the level of hourly section presence (5x5 km^2), by scoring all hour sections with at least five observations as 'present'.

In addition, these hourly sections were used to create a map of the number of species occurring in different parts of the LARCH-SCAN range.

2.4.3 Damage to livestock

In the Netherlands, a large proportion of land-based livestock farms are insufficiently protected, for example by wolf-resistant fencing (link: BIJ12 December 2023 progress report: <2% sufficiently protected). As a result, wolves are not only preying on wild ungulates, as they normally do, but also causing damage to livestock. As a visual comparison between the distribution of such damage incidents and the modelled range can provide an indication of the plausibility of the model results, BIJ12 damage data from roughly the past eight years (2015-2023) was mapped onto the wolf's range according to the LARCH-SCAN model.

2.4.4 Centres of current territories/monitoring in the Netherlands

In the Netherlands, monitoring is coordinated by BIJ12 on behalf of the provinces. DNA samples are collected from bitten livestock, deer and boar, as well as from found faeces. These samples are used to determine if a wolf is present, and whether it has settled or is still roaming. This is how the centres of the territories currently established in the Netherlands were identified and mapped onto the modelled range.

3 Results

3.1 Modelling analysis

3.1.1 Habitat suitability

The habitat suitability modelling results in a map with values between 0 and 1, where 1 represents an optimal habitat for wolves, the highest attainable score. Areas with natural vegetation and low anthropogenic pressure are marked as highly suitable (Figure 1). In particular, these are the Veluwe, the Oostvaardersplassen, Drents-Friese Wold, the Biesbosch National Park, the dune areas in the west of the Netherlands and the wooded areas in the south of North Brabant and on the border between Limburg and Germany. Non-natural areas with low anthropogenic pressure are also reasonably suitable, despite their lower suitability scores compared to areas with natural vegetation. Examples of such non-natural areas include the Alblasserwaard, Flevoland and rural areas in the north and east of the country.

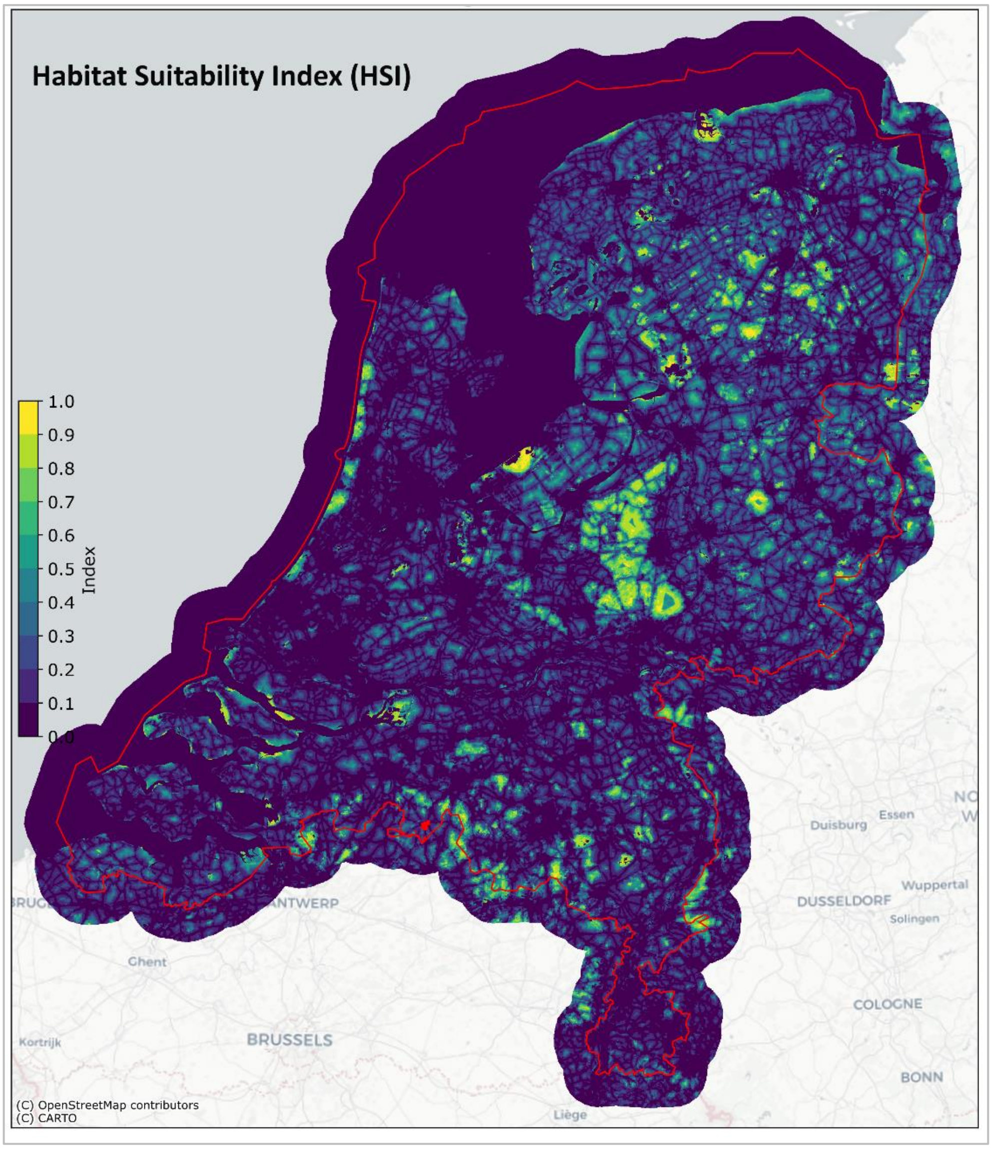

Figure 1 *The habitat suitability map for wolves in the Netherlands, based on the German model (Planillo et al., 2024).*

3.1.2 Range according to three methods

Below are the wolf population estimates and range maps for each of the three models. These maps should be interpreted as follows.

1. **Orange** is the range when the **strict threshold** (0.28) is used to calculate the HSI. This is the highest quality ‘core area’, where wolf establishment is most likely and will likely happen first. The actual distribution of wolves in the Netherlands is expected to include at least this area, which therefore represents the **lower limit** of wolf distribution in the Netherlands.
2. **Blue** is the range when the **lenient threshold** (0.17) is used to calculate the HSI. This can be seen as a broad estimate of wolf distribution. Although wolf establishment may occur in this area, it is less likely than in the orange area. It is not likely that the actual distribution of wolves will include this area in its entirety, as is the case with the orange area. The blue area therefore represents the **upper limit** of wolf distribution in the Netherlands, and is unlikely to see establishment in the short term.
3. **Grey** areas are potentially suitable for wolves (based on the lenient threshold), but **not large enough** to support at least one pack (200 km^2).

3.1.2.1 German model

Applying the German model (Planillo et al., 2024) to the Dutch situation results in the map shown in Figure 2. The modelled range has two centres of gravity: one in the northeastern Netherlands and another in the south of North Brabant. Using the low threshold, the wolf's range covers the entire northeast of the country. This region has many agricultural areas scattered with natural elements, which are sufficiently suitable for the wolf, especially considering the low anthropogenic pressure in this part of the Netherlands. Besides the larger core areas, there are a number of smaller cores in the west, around the Biesbosch, the Utrechtse Heuvelrug and various agricultural areas in North and South Holland. When the high threshold is used, the remaining core areas are the Veluwe, a cluster in Drenthe, Friesland and Overijssel, and the forest and moorland areas in the south of North Brabant. These areas have the highest suitability scores and are thus most likely to be settled by wolves.

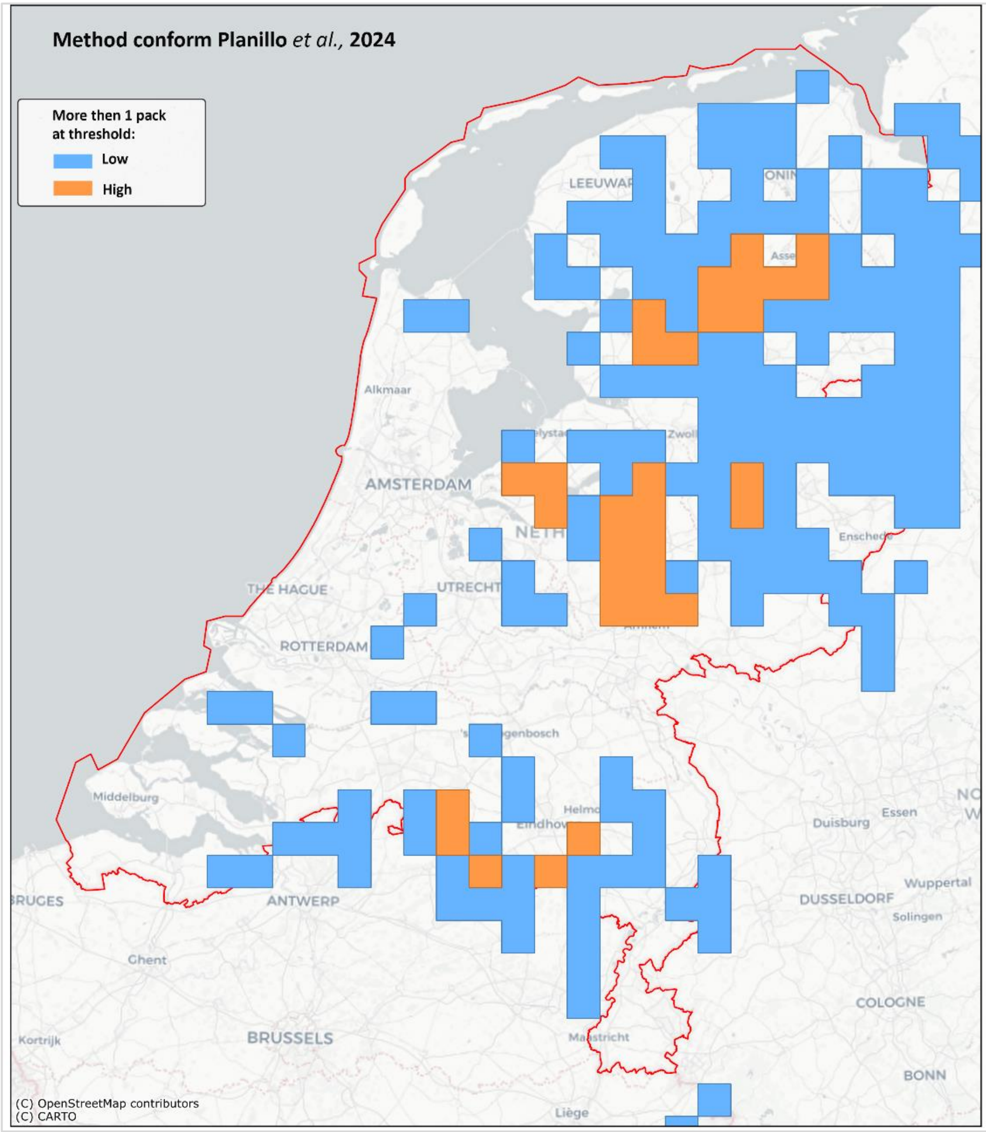

Figure 2 *Potential range of wolves in the Netherlands according to the German method (Planillo et al., 2024). The blue areas can support one pack or more at the low threshold. The orange areas can support at least one pack at the high threshold.*

3.1.2.2 LARCH model

Figure 3 shows the result of the LARCH model using the same parameter settings. Despite small, one-cell differences here and there, the outcome is almost identical to that of the German method.

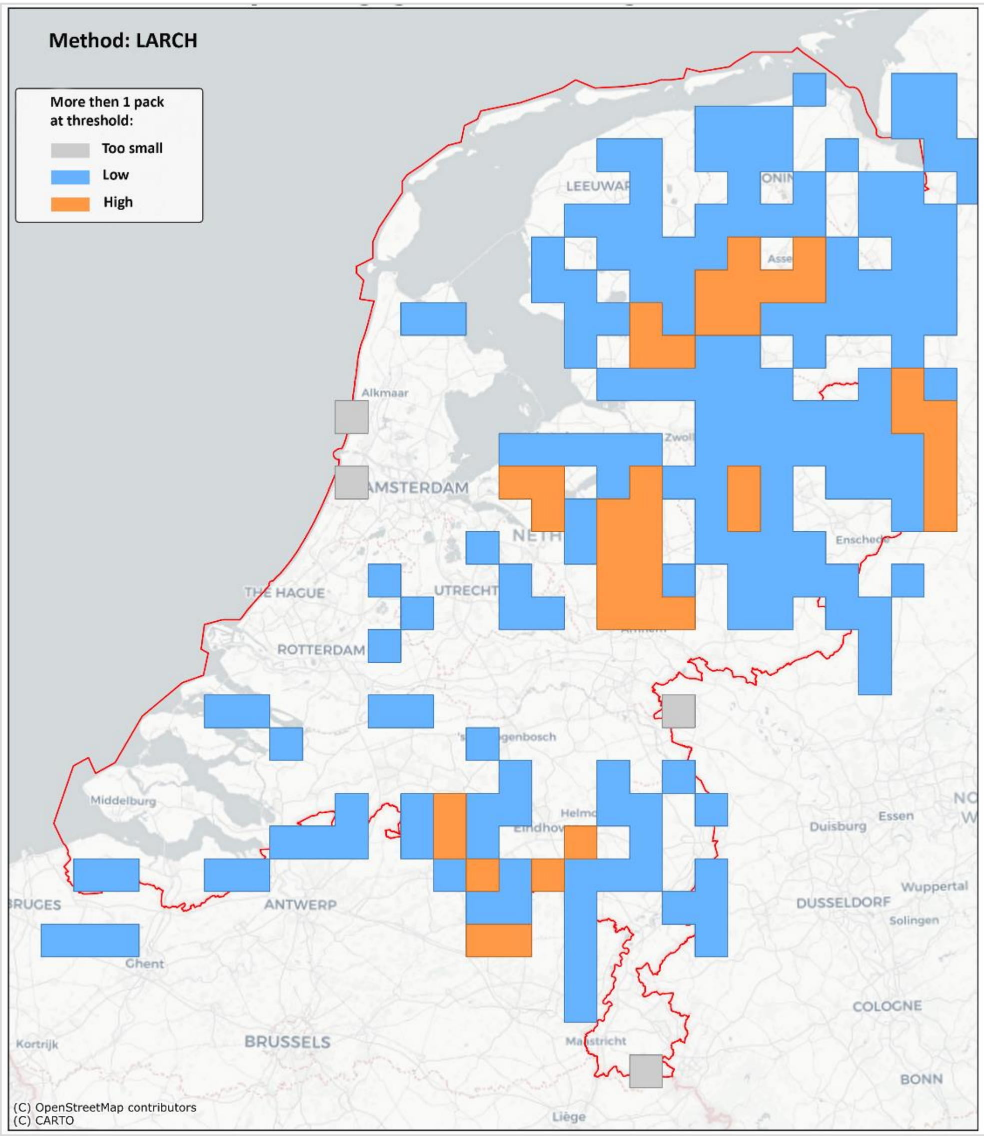

Figure 3 *Potential range of wolves in the Netherlands according to the LARCH model, at a resolution of 10x10 km. The grey areas are too small to support one pack. The blue areas are large enough for one pack at the low threshold, and the orange areas can support one pack at the high threshold. The grey areas were calculated using the low threshold.*

3.1.2.3 LARCH-SCAN model

The distribution picture resulting from the LARCH-SCAN model is broadly the same: a high probability of occurrence in the northeastern Netherlands and the south of North Brabant, with centres of gravity in the Veluwe, Drents-Friese Wold and forest and heathland areas in North Brabant (Figure 4).

Nevertheless, a number of differences stand out. Certain areas with carrying capacity for at least one pack in the 10 km LARCH model (at the low threshold) are not large enough to support a pack according to the LARCH-SCAN model. This applies to the Biesbosch, the Alblasserwaard, Robbenoordbos and its surroundings, the agricultural area in Zeelandic Flanders and the wooded areas on the border between Limburg and Germany (De Maasduinen National Park/ Klever Reichswald and De Meinweg National Park).

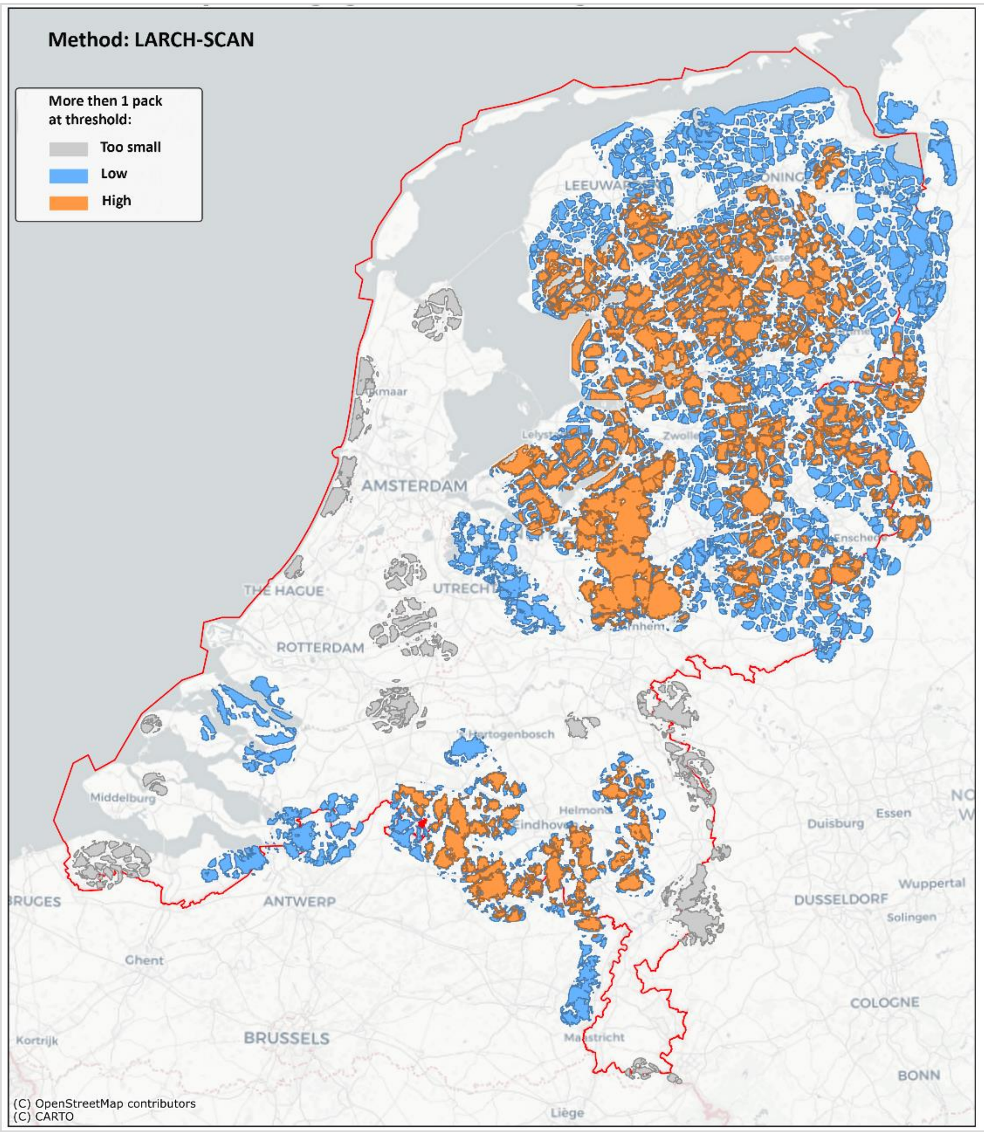

Figure 4 *Potential range of wolves in the Netherlands according to LARCH-SCAN. The blue areas are large enough for one pack at the low threshold, and the orange areas can support one pack at the high threshold. The grey areas, which are only identified by the model at the low threshold, are too small to support one pack.*

3.1.3 Numbers

The lower and upper limits for the number of packs that could occur in the Netherlands according to each of the three models are given in Table 2.

Table 2 *Total number of packs in the Netherlands according to the different methods.*

Method	Lower limit	Upper limit
German model	15.5	99.5
LARCH model	19.5	104
LARCH-SCAN model	22.86	55.65

3.2 Visual interpretation of the models

3.2.1 Tree cover

The average tree cover in the Netherlands is shown in Figure 5. In general, tree cover is relatively high in the east and south of the country compared to the west and far north. In the west, high tree cover is mostly limited to the dune areas.

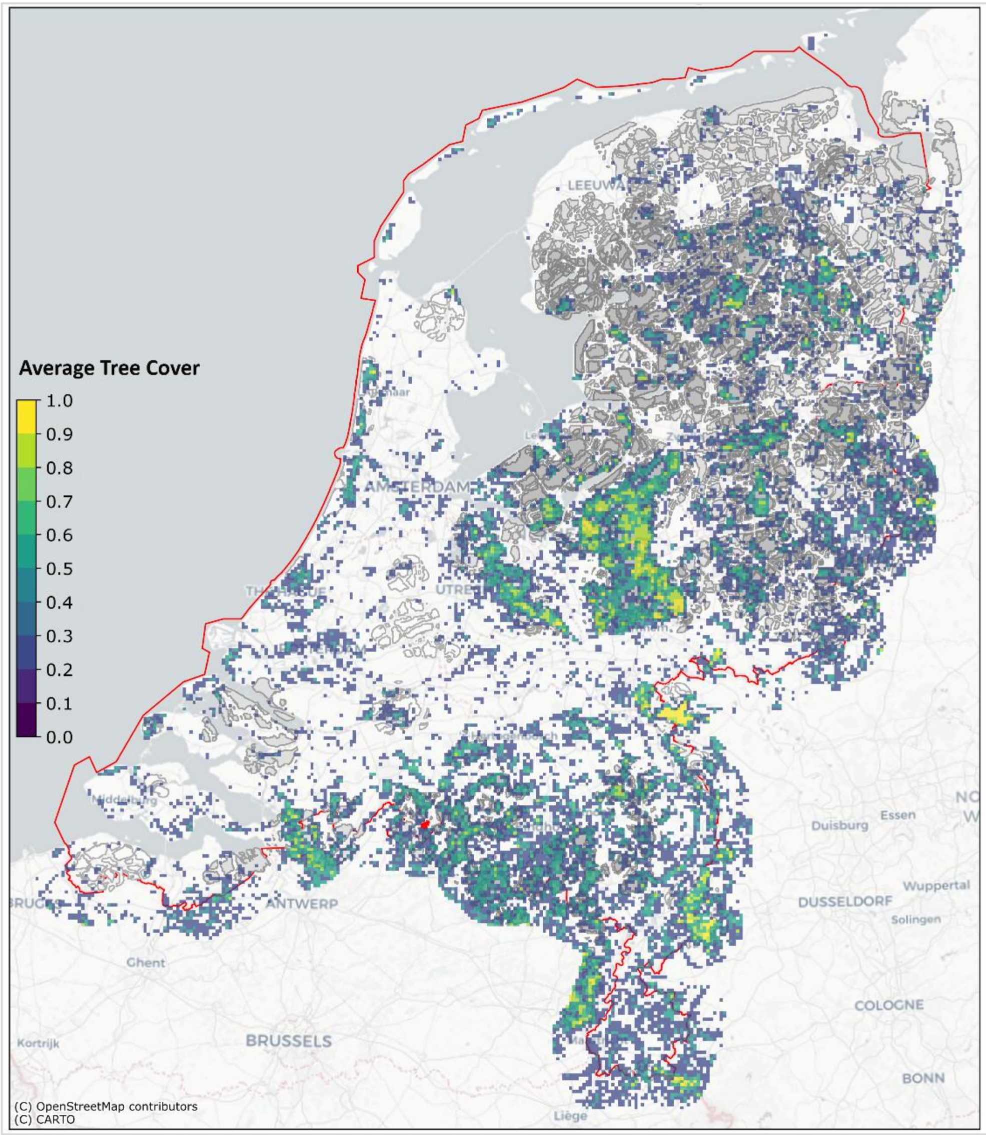

Figure 5 *The percentage of tree cover at the level of 1x1 km sections mapped onto the distribution area according to LARCH-SCAN (grey). Sections with less than 10% cover have been left blank.*

3.2.2 Ungulate species available

The availability of Roe deer, Fallow deer, Red deer and Wild boar is shown in Figure 6. In the Veluwe, each of these ungulates is available as prey. Roe deer is also available in Limburg, as is Wild boar in certain regions. In Drents-Friese Wold and the dune areas along the coast, Roe and Fallow deer are available.

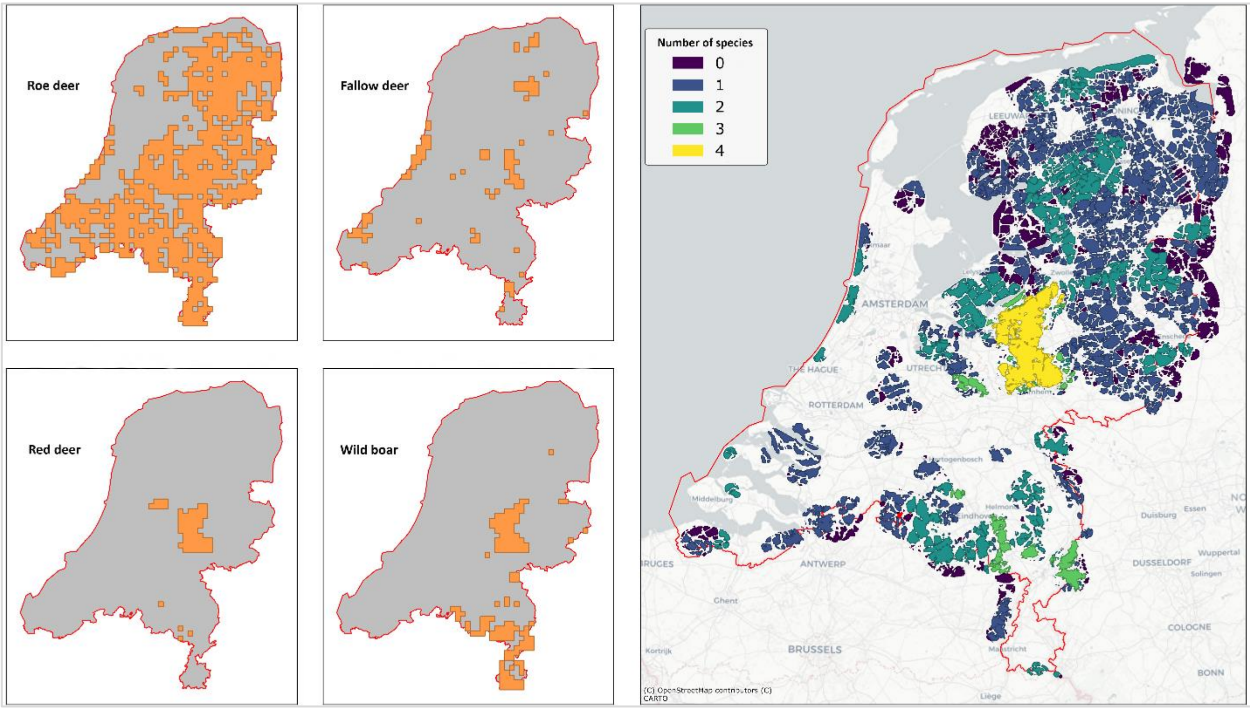

Figure 6 *Availability of four ungulate species in the Netherlands and the number of ungulate species occurring in different parts of the range.*

3.2.3 Map versus practice: territories & damage

To validate the model output, Figure 7 shows the centres of gravity of the current territories as well as locations where damage to livestock has been reported (confirmed cases), mapped onto the modelled potential range.

For the territories, there appears to be a complete overlap, with all the packs located in the core area. One territory, belonging to a solitary animal, is located in the wide range (the blue areas on the maps).

There is also a high degree of overlap between damage incidents and the potential range. The areas around Drents-Friese Wold, Strabrechtse Heide and the Veluwe show the highest concentration of damage incidents. These are also the focal areas of the modelled range.

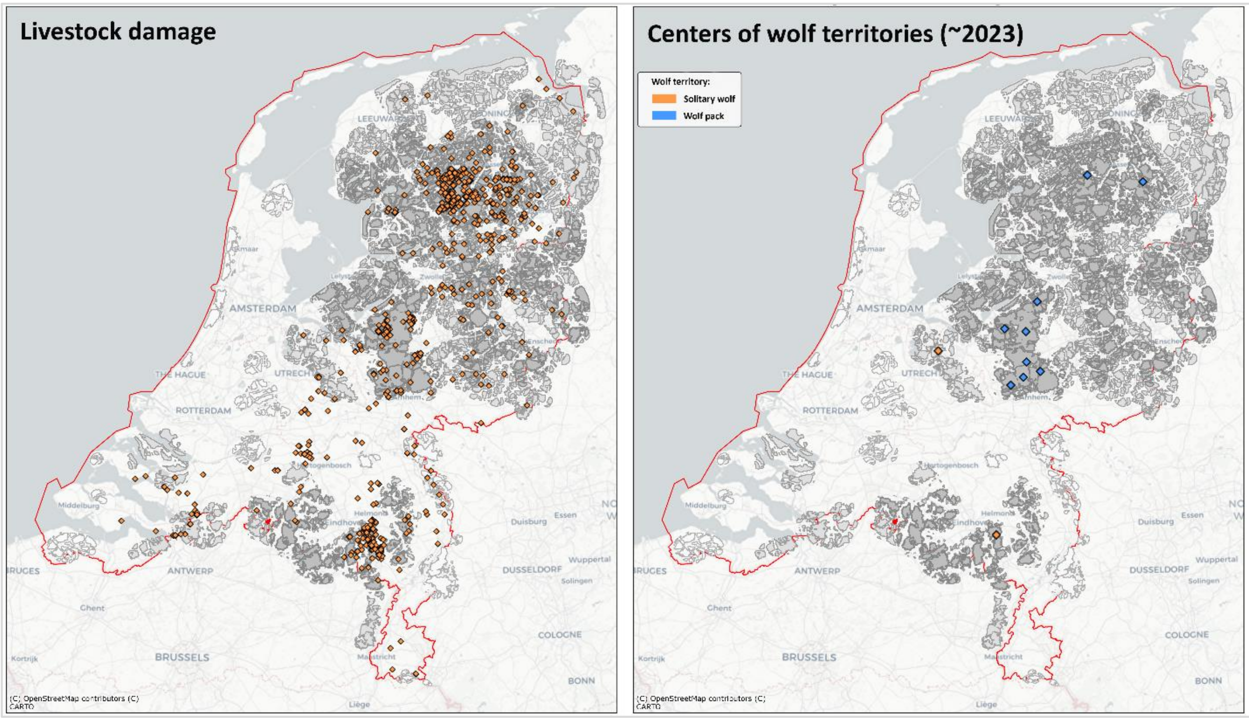

Figure 7 *The map on the left shows reported and confirmed incidents of livestock damage (date boundaries). Each orange dot represents one reported incident. The map on the right shows the global centres of established wolf territories in 2023. The blue dots show the territories of packs, the orange dots those of solitary animals. The light and dark grey areas are the LARCH-SCAN ranges at the low and high thresholds respectively (see also Figure 4).*

4 Discussion

4.1 Range

This report mapped the potential range of wolves in the Netherlands based on modelling analyses. These analyses were based on the habitat use of wolves in Germany. As the wolf populations in the Netherlands and Germany are closely related, it is reasonable to assume similar preferences. Nevertheless, a certain degree of caution is warranted when interpreting the results. Large parts of the Netherlands, such as the Veluwe and the Achterhoek, resemble Germany in terms of habitat, but the same cannot be said of the open agricultural areas in other parts of the country. Uncertainties regarding the model results are discussed below.

4.1.1 Range according to this study

The results show that the wolf's potential range in the Netherlands is concentrated in the north and east of the country, including the Utrechtse Heuvelrug and eastern North Brabant. With its lower threshold (HSI 0.17), the German model yields a distribution covering almost all of the northeastern Netherlands, Flevoland, the Utrechtse Heuvelrug and large parts of North Brabant (Figure 2). Under a scenario with a higher threshold (HSI 0.28), a much smaller range remains, mainly covering the Veluwe, southeastern Flevoland, Drents-Friese Wold and parts of North Brabant. The LARCH model yields an almost identical range for both scenarios (Figure 3). The LARCH-SCAN model (Figure 4, Annex 1) predicts a wider distribution and potential range than the 10x10 km analyses. For instance, LARCH-SCAN identifies a number of dune areas in the western Netherlands as suitable habitats, but with a carrying capacity of less than one pack. When using the strict threshold, LARCH-SCAN yields a larger range than the other models, which can be attributed to its higher level of detail. While the German model identifies suitable habitats using 10x10 km cells, the LARCH-SCAN grid is more granular (100x100 m). Lowering the resolution to 10x10 km means that cells will be identified as unsuitable when they do not contain sufficient suitable habitat, for example when the land cover is predominantly agricultural with high anthropogenic pressure. However, this also excludes parts of cells that may be suitable from further analysis. Due to its finer resolution, the LARCH-SCAN model does include these areas.

The results show a clear difference in suitability between the eastern and western parts of the country, which is likely related to the level of human influence. The level of human influence in the west is such that, given the parameters used, the establishment of a pack is unlikely. However, there are several things to note in this context. Some areas, for instance, are just below the low threshold for pack establishment. The Alblasserwaard, De Maasduinen National Park and Reichswald Kleve, and De Meinweg National Park have scores of 98, 97 and 81% respectively. Given their size, it is not inconceivable that pack establishment could still occur in these areas. Whether or not these areas are actually suitable for establishment is likely to depend primarily on the degree of forest cover and the availability of prey animals. This means that establishment in Maasduinen appears more likely than in the Alblasserwaard. Moreover, the area requirement of a pack used in this study (200 km^2) is not a hard lower limit, as wolf territories show considerable variation in terms of size, ranging between 80 and 400 km^2 (Reinhardt & Kluth, 2016; Jansman et al., 2021, Planillo et al., 2024). As a result, pack establishment in areas assessed as too small cannot be ruled out. Particularly in the dune areas of North and South Holland, it is conceivable that a pack could make do with a smaller area, given the availability of prey animals (Fallow and Roe deer) and high degree of forest cover. In addition, there are areas that are not large enough for a pack at the high threshold, but that almost meet the area requirement. Examples include the Utrechtse Heuvelrug and the agricultural land surrounding Lauwersmeer, which meet 68 and 87% of the area requirement respectively. In addition to packs, a solitary wolf may also settle in an area. This has already happened in a number of places around the country (Figure 7).

4.1.2 Previous habitat suitability studies

Several attempts have been made to identify potential wolf habitats in Europe based on modelling analyses (Jędrzejewski et al., 2008; Fechter & Storch, 2014; Louvrier et al., 2018; Marucco & McIntire, 2010; Nowak et al., 2017; Gwynn & Symeonakis, 2022). Such habitat suitability studies have also been carried out for the Netherlands (Potiek, 2012; Lelieveld, 2012). The assumptions used in these studies vary widely, and it is not always clear whether the factors used are representative of wolf preferences, or whether the underlying data have introduced artefacts into the model output. These artefacts can occur when the data used comes from different habitats and relates to different habitat types, different degrees of anthropogenic influence and different wolf population densities. However, they can also occur when the data only covers a relatively small subarea (Planillo et al., 2024).

The range in the present study is consistent with the area modelled by Lelieveld (2012), with both models yielding a centre of gravity in the northeast of the country. There are also suitable areas in eastern North Brabant, the Utrechtse Heuvelrug and De Maasduinen National Park. Potiek et al. (2012) arrived at a distribution covering almost the entire country, with the exception of North and South Holland and certain parts of Utrecht. This was likely an overestimate, which can be attributed to the fact that they divided the country into sections using motorways. The centre of gravity, however, is similar to that of Lelieveld (2012) and the present study, located in the northeast.

All three habitat suitability studies for the Netherlands (Lelieveld, Potiek and the present study) identify almost the entire northeast of the country as suitable for wolf establishment, making it highly likely that the centre of gravity of the Dutch population will be in this area. The present and previous studies also show that models based on expert estimates are sufficient to give a rough indication of the wolf's range. Indeed, the present model, with its higher granularity and input quality, shows roughly the same picture. As the level of detail increases, the differences become more pronounced and more nuances emerge in the modelled range. The similarity between the results of the previous studies and the present one is remarkable given the differences in terms of methodology and input. Analyses based on anthropogenic pressure, prey availability and a combination of these factors all yielded similar distributions.

However, models that assume general habitat requirements may underestimate an area's suitability for wolves. A modelling study by Gwynn & Symeonakis (2022) argues that agricultural land (fields and grassland) is unsuitable, while Planillo et al. (2023) find increasing colonisation of open areas in northern and western Germany. It is unclear to what extent open areas with little cover (thickets and forest) in the Netherlands provide sufficient prey, or whether they are suitable for burrowing. Roe deer occur almost everywhere in the Netherlands (Figure 6), which means that even agricultural areas could be partly suitable provided there is sufficient cover nearby. However, pastures and farmland are not suitable, as wild ungulates are not present (or are present at too low a density) and livestock are not usually available as prey (provided that sufficient protective measures are in place).

4.1.3 Range development/expansion

Predicting potential range expansion is complex, as the response of individuals to anomalous habitat may differ from habitat use in modelling studies (Louvrier et al., 2018; Planillo et al., 2024). As a 'plastic species', the wolf is also an opportunist that adapts to new conditions. Hence, modelling studies based on early establishment data yield different predictions than those based on data from areas that have been colonised for longer. In areas that have been colonised for some time, suboptimal habitat also becomes part of wolf territories once all optimal habitat is occupied.

When using only telemetry data, there is a risk that a few individuals with specific habitat preferences will have an outsized influence on the model results. In Germany, Planillo et al. (2024) recently found wolf territories in areas with higher levels of human disturbance in an area colonised 20 years ago. The first areas that were established, however, had high forest cover and low levels of human disturbance. Using only the German data from recently colonised areas as model input would lead to an underestimation of habitat suitability compared to the actual observed distribution (Planillo et al., 2024).

It should be emphasised that this modelling study estimates the suitability of areas for permanent wolf establishment. However, dispersing wolves can turn up anywhere and stay for shorter or longer periods. This may include environments that are unsuitable as permanent habitats, such as urban areas.

4.1.4 Numbers

For carrying capacity, the LARCH-SCAN analysis provides a lower limit of 23 packs and an upper limit of 56. It therefore seems unlikely that fewer than 23 packs or more than 56 packs will occur in the Netherlands.

Potiek et al. (2012) calculated the maximum number of packs that could occur in the Netherlands to be between 68 and 89. Using the population dynamics analysis they carried out based on this carrying capacity (METAPHOR analysis), they estimated that 10 packs (50 animals) could occur in the Netherlands. Lelieveld (2012) estimated that the Netherlands could support between 16 and 44 packs, depending on the modelling scenario.

The estimate of the present study is similar to the results of the previous studies, although there is a greater difference with the study by Potiek et al. (2012), which found a fairly wide spread in carrying capacity, from 10 to 89 packs. The spread in the present study (33) is about the same as that in Lelieveld (2012) (28), while the numbers are slightly higher: the lower limit is seven packs higher and the upper limit is 12 packs higher.

4.1.5 Trends in wolf numbers

In practice, the wolf population in a given region is largely determined by the animal’s highly territorial nature, so numbers tend to be fairly constant (see Section 2.2; Van Den Berge & Gouwy, 2021).

This is an essential difference with non-territorial species, such as Wild boar, whose numbers can fluctuate greatly (Briedermann, 2009).

Due to the wolf’s territorial nature, population changes manifest in localised spatial patterns of local presence and absence, as with other medium and large predators. Wolves’ territories can be seen as pieces in a jigsaw puzzle, not necessarily adjacent to one another and often with intervening gaps. The variation in the size of wolf territories can sometimes be considerable, and local conditions such as food availability are a factor in this: more abundant food allows for smaller territories and vice versa.

The density of a wolf population is ultimately determined primarily by the number of territories, viewed across a wider region, plus lone wolves roaming within that same area. As the density of wolves increases, negative density-dependent factors come into play. These can include smaller litter sizes, lower survival rates among young wolves, an increase in aggressive interactions between wolves and the spread of disease. Smith et al. (2020a) report that population regulation in wolves is determined by density-dependent mortality as a result of aggression between packs.
For the time being, there is plenty of space for wolves in the Netherlands, as their numbers still appear to be low. While the wolf population in the Netherlands is growing, density-dependent factors will curb the rate of growth as numbers increase. Eventually, the population will stabilise and fluctuate around the ecological carrying capacity of the ecosystem, a situation that now appears to have been achieved in the Lusatia region in eastern Germany. In the US, the population in Yellowstone National Park also stabilised after growing rapidly in the years following reintroduction, partly as a result of disease (Smith et al., 2020b). Annual wolf population growth in the states of Idaho, Wyoming and Montana has been around 25% for the past three decades (Wielgus & Peebles, 2014). In Germany, the wolf population grew from one pack to 67 packs between 2000 and 2015, at an average annual growth rate of 36% (Reinhardt et al., 2019). It then levelled off slightly, to around 25% per year (Reinhardt et al., 2021). In 2022 and 2023, the number of packs in Germany was around 184[5], while the range continued to increase.

Most wolves colonising the Netherlands come from the Central European population, especially from Germany. As this population continues to grow, it is likely that more wolves will migrate to the Netherlands

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[5] https://www.dbb-wolf.de/wolf-occurrence/confirmed-territories/map-of-territories.

from Germany. In addition, due to wolves' high capacity for dispersal and growth in other subpopulations in Europe, such as the Alpine wolf population, individuals may also come to the Netherlands from other regions. Whether these newcomers can find a place to settle will depend on the amount of suitable territory that is still available. The amount of available habitat may also change in the coming years due to spatial developments (e.g. forest expansion, nature development and housing development).

4.2 Visual validation of model results

Figures 5, 6 and 7 show a visual validation of the modelled range against forest cover, the occurrence of ungulate species, the centres of current wolf territories and validated incidents of livestock damage. Figures 5 and 6 give an indication of the areas likely to be colonised first, as the degree of forest cover and the availability of wild ungulates are important factors in the habitat preferences of wolves (Jędrzejewski et al., 2004; Fechter & Storch, 2014, Jansman et al., 2021). The current occurrence of wolves in the Netherlands (based on damage incidents involving livestock) and the location of the current territories (based on monitoring) provide an indication of the degree of uncertainty underlying the modelled range.

4.2.1 Forest cover and ungulate availability

In general, areas identified as suitable habitats by the models have relatively high levels of forest cover (Figure 5). This is particularly the case for the core area (calculated using the strict threshold, shown in orange on the maps). The core area according to the LARCH-SCAN model mainly comprises natural areas with high levels of forest cover. However, when looking at the range calculated by the LARCH-SCAN model at the lenient threshold (shown in blue on the distribution map), the picture becomes less clear. At this threshold, more agricultural land is included in the range. Forest cover in these areas is generally much lower than in predominantly natural areas. It is therefore more likely that wolves will settle in an area such as the Veluwe or the Utrechtse Heuvelrug than in agricultural areas identified as suitable by the model based on land use and anthropogenic pressure.

The calculations in the present study did not include data on prey abundance, as food availability was not shown to be a key factor in the habitat suitability analysis of the German study. It was assumed that ungulate densities were sufficient throughout Germany. Home range size is partly dependent on the availability of prey (Jędrzejewski et al., 2007; Mysłajek et al., 2018). European wolves prey mainly on ungulates, such as Red deer, Roe deer and Wild boar (Fechter & Storch, 2014; Merrigi et al., 2011; Zlatanova et al., 2014; Khorozyan & Heurich, 2022; Jansman et al., 2021). Roe deer are especially popular. It is generally assumed that ungulate densities are high in Europe (Massei et al., 2015; Reinhardt et al., 2020). The Netherlands also has high densities of wild ungulates in some regions, but a zero population policy applies to Red deer, Fallow deer and Wild boar in large parts of the country (Figure 6).

When wild ungulates are in limited supply, other animals become prey, including unprotected livestock, beavers and lagomorphs. Wolves will switch prey species depending on their sex and age, as well as the benefits (supply) and costs (own safety/vulnerability of prey) (Sovie et al., 2023). A habitat with multiple species of wild ungulates provides more food security for wolves in situations where prey numbers fluctuate (Glenz et al., 2001). For the Dutch situation, this implies that areas with multiple species of wild ungulates provide optimal habitat, as this allows wolves to switch between prey species depending on the season. Small-scale cultivated landscapes and intensively used open agricultural areas appear to be less suitable due to the monotonous prey supply (Roe deer and small mammals), assuming that livestock are well protected and not available. Roe deer, the wolf's favourite prey, is found almost everywhere in the Netherlands. Other wild ungulates (Red deer, Fallow deer, Wild boar) that could serve as alternative prey have a more limited distribution (Figure 6). Semi free-living ungulates (Heck cattle, Highland cattle, Konik horses, Galloway cattle, European bison, etc.) could also serve as prey, especially the calves and weaker individuals. It therefore seems plausible that the early establishment phase will mainly see colonisation in forest areas with multiple species of wild ungulates (and higher densities), as has already happened in the Veluwe in recent years. Establishment in the open cultivated landscapes of the Flevopolders, Zeeland or Friesland seems less likely, but cannot be ruled out based on the models. It is not known whether and for how long the less suitable areas would remain populated; wolves may only be transient in these areas, but they may also prove suitable for permanent establishment.

4.2.2 Sequence of establishment

The model only identifies areas it deems suitable as wolf habitats, without ranking them in terms of suitability. Forest cover and prey availability should give an indication of which parts of the modelled range are likely to be established by packs first. Based on the additional data, the Veluwe, with its high degree of forest cover and the presence of four wild ungulate species, appears to be a highly suitable environment. This can also be seen in practice, as the Veluwe is already home to seven packs. Wooded areas with two ungulate species in Drenthe, Friesland and eastern North Brabant are also highly suitable for colonisation, which appears to be confirmed by the current establishment of wolves in Drents-Friese Wold and eastern North Brabant.

4.2.3 Overlap with current territories

The visual comparison between the modelled range and the territory centres shows a high degree of overlap (Figure 7). All of the territories are located within the range. Moreover, all pack territories, unlike those of solitary animals, are also within the core area. This shows that the modelled range is consistent with what is observed in practice.

4.2.4 Overlap with incidents of livestock damage

To validate the model results, the distribution of damage incidents was mapped onto the LARCH-SCAN range (Figure 7). The significant overlap between the two areas confirms the plausibility of the modelled range.

The high concentration of incidents around Drents-Friese Wold and in North Brabant, and the low number of incidents around the Veluwe – the area where most wolves are currently found – are noteworthy. The differences between these areas are likely due to the Veluwe's abundance of wild ungulates. There are at least four different prey species in this region, all of which occur in fairly high densities. As a result, wolves do not have to venture outside the nature reserve to find food, limiting their contact with unprotected livestock. In Drenthe, Friesland and North Brabant, the supply of wild ungulates is lower, which means that wolves have to move around more in search of prey. In addition, the natural areas in these regions are more fragmented than in the Veluwe, with a lot of agricultural land cutting through nature reserves. As wolves move between these fragmented natural areas, they are more likely to encounter unprotected livestock.

The map also shows damage incidents outside the range. These can probably be attributed to dispersing wolves, which can travel long distances and come into contact with unprotected livestock along the way.

4.3 Recommendations

In terms of modelling wolf distribution and pack numbers, the present study provides sufficient background for policymakers. The modelled distribution, combined with future research and existing knowledge, can be used to anticipate potential problems. However, the present analysis was based on data obtained from wolves in Germany. In order to improve the quality of the models and reduce uncertainty, further research is needed in particular on habitat use and movements of wolf in the Netherlands, preferably using multiple methods such as telemetry, DNA and trace research. The data this would yield could serve as a basis for a new model for the Dutch situation, with a higher predictive value. To gain a better understanding of human-wildlife coexistence, research is also needed on the possibility of wolves adapting to a landscape with high anthropogenic pressure, as is the case in the Netherlands.

In order to manage the wolf's return to the Netherlands in the best possible way, future research should pay more attention to human-wildlife coexistence., e.g. effective strategies to prevent damage to livestock, increase public support and limit conflicts with recreational activities.

References

Andersen et al. 2015. Long-distance dispersal of a wolf, Canis lupus, in northwestern Europe. Mamm. Res. 60: 163-168.

Biersteker, L., Planillo, A., Lammertsma, D. R., van der Sluis, T., Knauer, F., Kramer-Schadt, S., van der Grift, E. A., van Eupen, M., & Jansman, H. A. H. (2024). *Habitatgeschiktheid voor de wolf in Nederland: een modelanalyse*. (Rapport / Wageningen Environmental Research; No. 3350). Wageningen Environmental Research. https://doi.org/10.18174/654770.

Blanco, J.C. & Y. Cortes 2007. Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain. Journal of Zoology 273: 114-124.

Blanco, J.C., Y. Cortes & E. Virgos 2005. Wolf response to two kinds of barriers in an agricultural habitat in Spain. Can. J. Zool. 83: 312–323.

Boerema L., L. Freriks. A.A. & D.B. van den Brink 2021. De juridische bescherming van de wolf in Nederland en in een aantal andere Europese landen; een juridisch onderzoek ter ondersteuning van het opstellen van Nederlands wolvenbeleid in het licht van de uitvoering van de natuurwetgeving, Boerema en Van den Brink B.V., Houwerzijl/Element Advocaten, Best.

Briedermann, L. 2009. Schwarzwild. Kosmos Verlag, Stuttgart.

Chardon, J., R. Foppen & N. Geilen 2000. LARCH-RIVER: a method to assess the functioning of rivers as ecological networks. European Water Management, 3: 35-43.

Ciucci, P., W. Reggioni, L. Maiorano & L. Boitani 2009. Long-distance dispersal of a rescued wolf from the Northern Apennines to the Western Alps. Journal of Wildlife Management 73(8): 1300-1306.

Fechter D. & I. Storch 2014. How Many Wolves (Canis lupus) Fit into Germany? The Role of Assumptions in Predictive Rule-Based Habitat Models for Habitat Generalists. PLoS ONE 9(7): e101798. https://doi.org/10.1371/journal.pone.0101798.

Foppen, R.F.B. 2001. Bridging gaps in fragmented marshland: applying landscape ecology for bird conservation. (PhD). Wageningen University, [S.l.].

Franz, K.W., J. Romanowski, K. Johst & V. Grimm 2013. Ranking landscape development scenarios affecting natterjack toad (Bufo calamita) population dynamics in Central Poland. PLoS One, 8(5), e64852. doi:10.1371/journal.pone.0064852.

Groot Bruinderink, G., H.A H. Jansman, M.H. Jacobs & M. Harmsen 2012. De komst van de wolf (Canis lupus) in Nederland: een 'factfinding study'. Rapport 2339. Alterra, Wageningen.

Groot Bruinderink, G., T. Van Der Sluis, D. Lammertsma, P. Opdam & R. Pouwels 2003. Designing a Coherent Ecological Network for Large Mammals in Northwestern Europe. Conservation Biology, 17(2): 549-557. doi:10.1046/j.1523-1739.2003.01137.x.

Gwynn V. & E. Symeonakis 2022. Rulebased habitat suitability modelling for the reintroduction of the grey wolf (Canis lupus) in Scotland. PLoS ONE 17(10): e0265293. https://doi.org/10.1371/journal.pone.0265293.

Hanski, I. & M.E. Gilpin (ed.) 1997. Metapopulation biology: ecology, genetics, and evolution. London, UK: Academic Press.

IPO, 2019. Interprovinciaal wolvenplan. IPO, Den Haag.

IPO, 2023. Addendum Interprovinciaal wolvenplan. IPO, Den Haag.

Jansman, H.A.H., J. Mergeay, E.A. van der Grift, G.A. de Groot, D.R. Lammertsma, K. van den Berge, F.G.W.A. Ottburg, J. Gouwy, R. Schuiling, T. van der Veken & C. Nowak 2021. De wolf terug in Nederland: Een factfinding study. Wageningen Environmental Research, Rapport 3107.

Jędrzejewski, W., B. Jędrzejewska, B. Zawadzka, T. Borowik, S. Nowak & R.W. Mysłajek 2008. Habitat suitability model for Polish wolves based on long-term national census. Animal Conservation, 11(5), 377–390. https://doi.org/10.1111/j.1469-1795.2008.00193.x.

Jędrzejewski, W., K. Schmidt, J. Teuerkauf, B. Jedrzejewska & H. Okarma 2001. Daily movements and territory use by radio collard wolves (Canis lupus) in Bialowieza primeval forest in Poland. Canadian J. Zool. 79(11): 1993-2004.

Jędrzejewski, W., K. Schmidt, J. Teuerkauf, B. Jedrzejewska & R. Kowalczyk 2007. Territory size of wolves Canis lupus: linking local (Bialowieza Primeval Forest, Poland) and Holarctic-scale patterns. Ecography 30: 66-76.

Jędrzejewski, W., M. Niedziałkowska, S. Nowak & B. Jędrzejewska, B. 2004. Habitat variables associated with wolf (Canis lupus) distribution and abundance in northern Poland. Diversity and Distributions, 10: 225-233. https://doi.org/10.1111/j.1366-9516.2004.00073.x.

Jimenez, M. D., E.E. Bangs, D.K. Boyd, D.W. Smith, S.A. Becker, D.E. Ausband, ... & K. Laudon 2017. Wolf dispersal in the rocky mountains, Western United States: 1993–2008. The Journal of Wildlife Management, 81(4): 581-592.

Khorozyan, I. & M. Heurich 2022. Large-scale sheep losses to wolves (Canis lupus) in Germany are related to the expansion of the wolf population but not to increasing wolf numbers. Frontiers in Ecology and Evolution, 10, 778917.

Kojola, I., J. Aspi, A. Hakala, S. Heikkinen, C. Ilmoni & S. Ronkainen 2006. Dispersal in an expanding wolf population in Finland. Journal of Mammalogy, 87(2): 281–286.

Kojola, I., S. Kaartinen, A. Hakala, S. Heikkinen, & H.M. Voipio 2009. Dispersal behavior and the connectivity between wolf populations in Northern Europe. Journal of Wildlife Management 73(3): 309-313.

Kramer-Schadt, S., M. Wenzler, P. Gras & F. Knauer 2020. Habitatmodellierung und Abschätzung der potenziellen Anzahl von Wolfsterritorien in Deutschland. Deutschland/Bundesamt für Naturschutz.

Kusak, J., A.M. Skrbinšek & D. Huber 2005. Home ranges, movements, and activity of wolves (Canis lupus) in the Dalmatian part of Dinarids, Croatia. Eur. J. Wildl. Res. 51(4): 254–262. doi:10.1007/s10344-005-0111-2.

Lelieveld, G. 2012 (VU; studentenverslag): Room for wolf comeback in the Netherlands.

Linnell, J.D.C., H. Broseth, E.J. Solberg & S.M. Brainerd 2005. The origins of the southern Scandinavian wolf Canis lupus population: potential for natural immigration in relation to dispersal distances, geography and Baltic ice. Wildlife Biology 11(4): 383-391.

Louvrier, J., C. Duchamp, V. Lauret, E. Marboutin, S. Cubaynes, R. Choquet, C. Miquel & O. Gimenez 2018. Mapping and explaining wolf recolonization in France using dynamic occupancy models and opportunistic data. Ecography, 41(4), 647–660.

Mancinelli, S. & P. Ciucci 2018. Beyond home: Preliminary data on wolf extraterritorial forays and dispersal in Central Italy. Mammalian Biology 93: 51–55.

Mancinelli, S., L. Boitani & P. Ciucci 2018. Determinants of home range size and space use patterns in a protected wolf (Canis lupus) population in the central Apennines, Italy. Can. J. Zool. 96: 828–838.

Marucco, F. & E.J.B. McIntire 2010. Predicting spatio-temporal recolonization of large carnivore populations and livestock depredation risk: Wolves in the Italian Alps. Journal of Applied Ecology, 47(4), 789–798. https://doi.org/10.1111/j.1365-2664.2010.01831.x.

Meriggi, A., A. Brangi, L. Schenone, D. Signorelli & P. Milanesi 2011. Changes of wolf (Canis lupus) diet in Italy in relation to the increase of wild ungulate abundance, Ethology Ecology & Evolution, 23:3, 195-210, DOI: 10.1080/03949370.2011.577814.

Merrill, S.B. 2000. Details of Extensive Movements by Minnesota Wolves (Canis Lupus). The American Midland Naturalist 144 (2): 428-433.

Mysłajek, R.W., M. Tracz, M. Tracz, P. Tomczak, M. Szewczyk, N. Niedzwiecka & S. Nowak 2018. Spatial organization in wolves Canis lupus recolonizing north-west Poland: Large territories at low population density. Mammalian Biology 92: 37–44.

Opdam, P., R. Foppen, & C. Vos 2002. Bridging the gap between ecology and spatial planning in landscape ecology. Landscape Ecology, 16(8), 767-779.

Pazúrová, Z., R. Pouwels, J. Ružičková, J. Bolliger, J. Krokusová, J. Oťaheľ, et al. 2018. Effects of Landscape Changes on Species Viability: A Case Study from Northern Slovakia. Sustainability 2018 10(10).

Planillo A., M. Wenzler-Meya, I. Reinhardt, G. Kluth, F.U. Michler, N. Stier, J. Louvrier, K. Steyer, B. Gillich, S. Rieger, F. Knauer, T. Kuemmerle & S. Kramer-Schadt 2024. Understanding habitat selection of range-expanding populations of large carnivores: 20 years of grey wolves (Canis lupus) recolonizing Germany. Diversity and Distributions, 30: 71–86. doi:10.1111/ddi.13789.

Potiek, G., W.W. Wamelink, R. Jochem & F. van Langevelde, 2012. Potential for Grey wolf Canis lupus in the Netherlands, Effects of habitat fragmentation and climate change on the carrying capacity. Wageningen, Alterra, Alterra Report 2349.

Pouwels, R., R. Jochem, M.J.S.M. Reijnen, S.R. Hensen & J.G.M. Van der Greft 2002. LARCH voor ruimtelijk ecologische beoordelingen van landschappen.

Ražen, N., A. Brugnoli, C. Castagna et al. 2016. Long-distance dispersal connects Dinaric-Balkan and Alpine grey wolf (Canis lupus) populations. Eur J Wildl Res 62(1): 137-142. https://doi.org/10.1007/s10344-015-0971-.

Reinhardt I., G. Kluth, C. Nowak C., et al. 2019. Military training areas facilitate the recolonization of wolves in Germany. Conservation Letters.;12:e12635. https://doi.org/10.1111/conl.12635.

Reinhardt I., P. Kaczensky, J. Frank., F. Knauer & G. Kluth 2020. How to deal with bold wolves. 10.19217/skr577.

Reinhardt, I. & G. Kluth 2011. Pilotstudie zur Abwanderung und zur Ausbreitung von Wölfen in Deutschland [Pilot study on the dispersal and expansion of wolves in Germany]. Unpublished Final Report, F+E Vorhaben (FKZ 806 86 080). LUPUS. https://www.bfn.de/0304_wolf-woelfe-telemetrie-pdm.html.

Reinhardt, I. & G. Kluth 2016. Abwanderungs- und Raumnutzungsverhalteen von Wólfen (Canis lupus) in Deutschland. Natur und Landschaft 91(6): 262-271.

Rüter, S., C.C. Vos, M. van Eupen & H. Rühmkorf 2014. Transboundary ecological networks as an adaptation strategy to climate change: The example of the Dutch – German border. Basic and Applied Ecology 15(8): 639-650.

Smith, D.W., D.R. Stahler & D.R. MacNulty 2020a. Yellowstone Wolves Science and Discovery in the World's First National Park. University of Chicago Press.

Smith, D.W., D.R. Stahler, R. McIntyre, E.E. Stahler & K.A. Cassidy 2020b: Wolves and Humans in Yellowstone. In: Smith, D.W., D.R. Stahler en D.R. MacNulty (editors). 2020. Yellowstone Wolves Science and Discovery in the World's First National Park. University of Chicago Press.

Sovie, A.R., M.C. Romanski, E.K. Orning, D.G. Marneweck, R. Nichols, S. Moore & J.L. Belant 2023. Temporal variation in translocated Isle Royale wolf diet. Ecology and Evolution, 13(3), e9873.

Stier, N., V. Meissner-Hylanova & M. Roth 2016. Wolfstelemetrie in Mecklenburg-Vorpommern. Zwischenbericht 2016, TU Dresden.

Van der Sluis, T. & B. Pedroli 2004. Ecological network analysis for Umbria (Italy) – RERU, rete ecologica della regione Umbria. Alterra report 1013.

Van der Sluis, T. & J.P. Chardon 2001. How to define European ecological networks. In Advances in Ecological Sciences (10): 119-128.

Van der Sluis, T., B. Pedroli, I. Woltjer, E. van Elburg, E. & G. Maas, G. 2020. Uitwerking PAGW Natuuropgave Hotspots Grote Rivieren: eindrapport. Wageningen Environmental Research, Rapport 3031.

Van der Sluis, T., G. Maas, E. van Elburg, I. Woltjer & B. Pedroli 2021. Robuuste en klimaatbestendige riviernetwerken. Hotspots voor natuurontwikkeling langs de grote rivieren. Landschap 38(1): 58-67.

Van der Sluis, T., H. Baveco. G. Corridore, H. Kuipers, F. Knauer, B. Pedroli, R. Jochems & J. Dirksen 2003. Networks for LIFE: An Ecological Network. Analysis for the Brown bear (Ursus arctos) - and indicator species in Regione Abruzzo. Wageningen, Alterra, Green World Research. Alterra-rapport 697.

Van der Sluis, T., J. Buijs, E. Koopmanschap, J. Gosselink, V. Kliuiev & M. Eupen 2011. Development of an ECONET for Lugansk Oblast: rural development and sustainable development in Ukraine. Rapport no 2153 Alterra.

Van der Sluis, T., J. Romanowski, I.M. Bouwma & J. Matuszkiewicz 2007. Comparison of scenarios for the Vistula river, Poland. In Landscape Ecological Applications in Man-Influenced Areas. Linking Man and Nature Systems (pp. 417-433.). Dordrecht: Springer.

Van der Sluis, T., M. Bloemmen & I.M. Bouwma 2004. European corridors: strategies for corridor development for target species. Tilburg/Wageningen, The Netherlands.

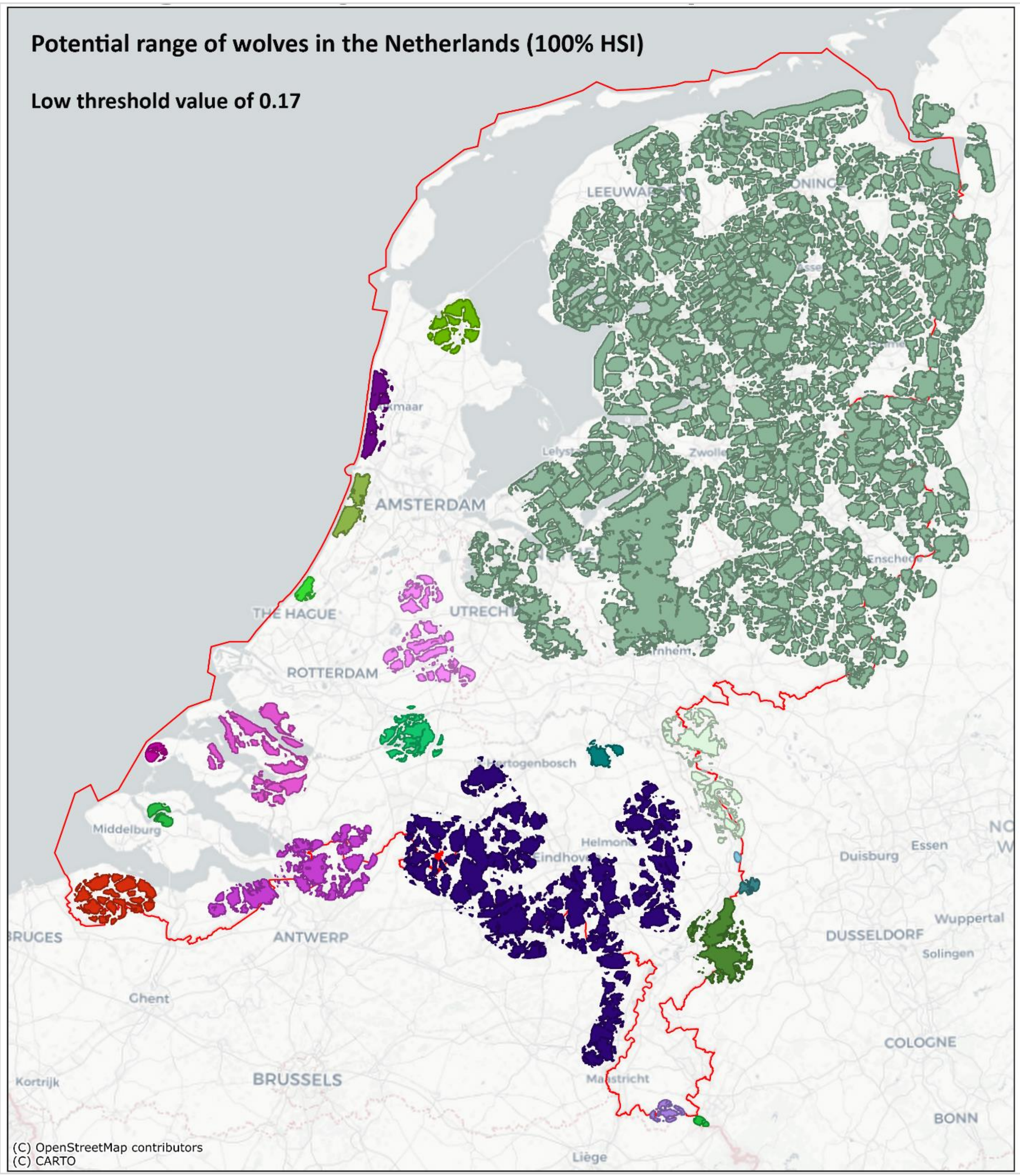
Verboom, J., R. Foppen, P. Chardon, P., Opdam & P. Luttikhuizen 2001. Introducing the key patch approach for habitat networks with persistent populations: an example for marshland birds. Biological Conservation, 100(1): 89-101.

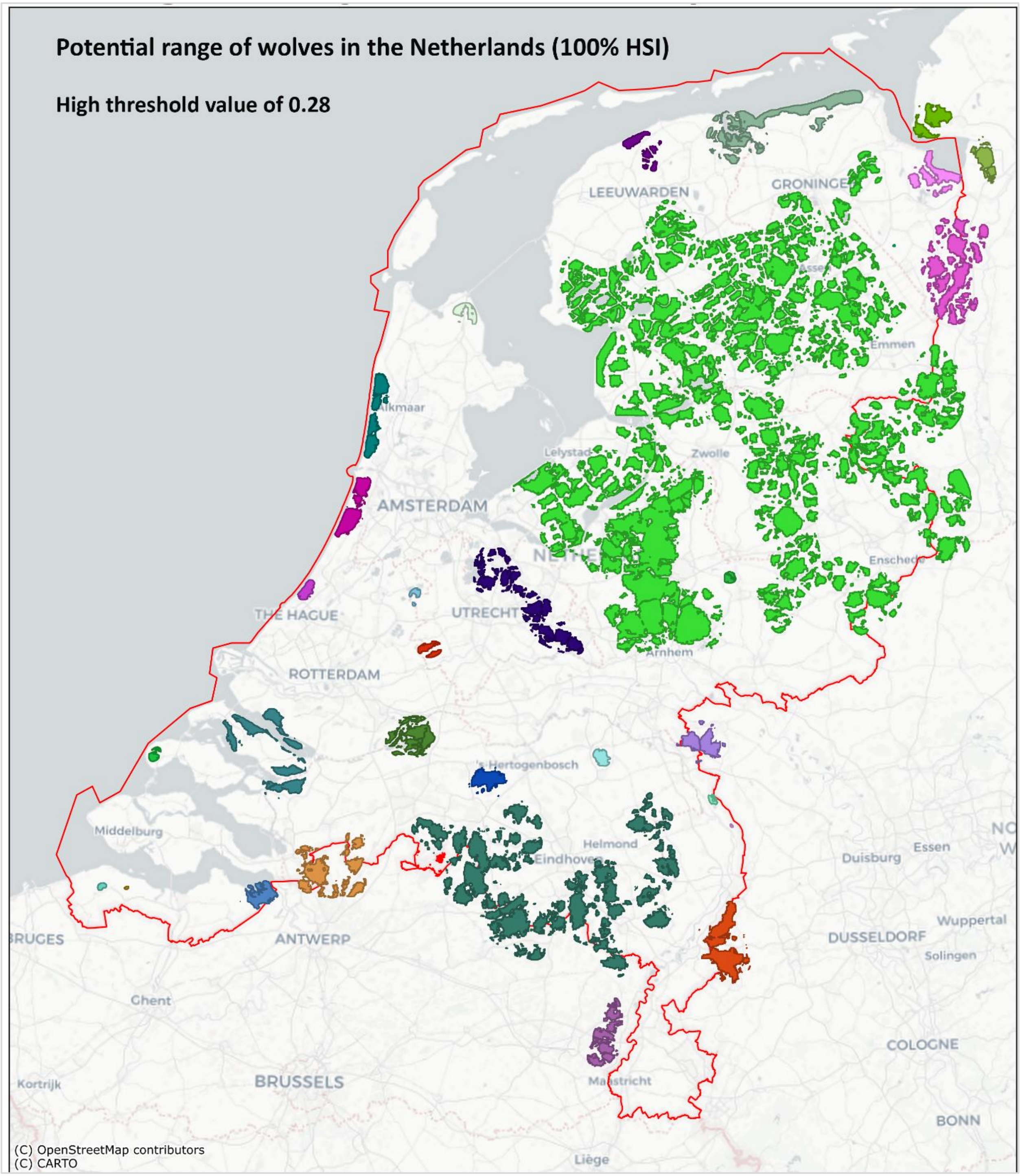
Wabakken, P., H. Sand, I. Kojola, B. Zimmermann, J.M. Arnemo, H.C. Pedersen & O. Liberg 2007. Multistage, Long-Range Natal Dispersal by a Global Positioning System–Collared Scandinavian Wolf.

Wielgus, R.B. & K.A. Peebles 2014. Effects of wolf mortality on livestock depredations. PloS one, 9(12), e113505.

Zlatanova, D., A. Ahmed, A. Valasseva & P. Genov 2014. Adaptive diet strategy of the wolf (Canis lupus L.) in Europe: a review. Acta Zoologica Bulgarica 66(4): 439-452.

Annex 1 Model outputs




Potential range of wolves in the Netherlands (100% HSI)
High threshold value of 0.28
LEEUWARDEN
GRONINGEN
Emmen
Alkmaar
Lelystad
Zwolle
AMSTERDAM
THE HAGUE
UTRECHT
Enschede
ROTTERDAM
Arnhem
's-Hertogenbosch
Middelburg
Helmond
Eindhoven
Essen
Duisburg
Wuppertal
BRUGES
ANTWERP
DUSSELDORF
Solingen
Ghent
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