

Exploring potential areas for rewilding aurochs in Europe

A suitability analysis



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Summary

The last aurochs (*Bos primigenius*) became extinct in a Polish forest in 1627 CE. This megafauna species is the wild ancestor of domesticized cattle and is considered to have had a significant influence on shaping the European cultural and ecological landscape. *Bos primigenius* provided a multitude of ecosystem services to its environment and its extinction may have contributed to global warming and the coextinction of other species, illuminating its potential as a species to rewild areas in Europe. Even though the aurochs has been extinct for centuries, its DNA is still alive. “The Tauros Programme” aims to breed back the aurochs in a new species called Tauros that resembles the old domestic ancestor of cattle as closely as possible. Building on “The Tauros Programme” this research aims to explore areas that would be suitable to rewild this keystone species with, once the breeding process has been finalized. The following research question will be answered: “What are suitable areas in Europe for the rewilding of aurochs?”

This research is divided into two phases: identifying where aurochs used to thrive in the past and subsequently exploring where they can be rewilded under current conditions for different scenarios. This was done for the following scenario: protected areas scenario, low population density scenario and RCP4.5 2050 scenario. A Species Distribution Model (SDM) was used to determine under which bioclimatic conditions, elevations and in which anthromes aurochs were able to thrive in the past. Outcome of this analysis was used as input for the reclassification and rescaling of different criteria layers in the weighted suitability analysis. From the suitability analysis it can be concluded that Northwestern- and Central Europe contain the biggest share of suitable areas to rewild aurochs with, also in the face of climate change. Rewilding of sparsely populated areas would be most suitable in Northern United Kingdom and parts of Scandinavia and the Baltic. This research could inform policymakers in deciding where to rewild aurochs in Europe. This way, the cultural and ecological value of this megafauna species could be restored on the European continent, potentially contributing to the mitigation of climate change.

Key words: aurochs, rewilding, Species Distribution Model (SDM), weighted suitability analysis

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1. Introduction

The wild ancestor of domestic cattle, *Bos primigenius*, commonly known as aurochs, has significantly influenced the European cultural and ecological landscape (Wright, 2013). Described by Julius Caesar as: “These are a little below the elephant in size” (Stokstad, 2015). After the extinction of the woolly mammoth, the aurochs lived on to be the heaviest mammal in Europe (Stokstad, 2015). This imposing herbivore featured heavily in Paleolithic cave art (Soubrier et al., 2016). Also, it is believed that the Celtic horned god of the underworld Cernunnos was inspired by *Bos primigenius* (Hubbell, 2022). Historically, the habitat of aurochs was distributed over almost all of Europe, and parts of Asia and North Africa (van Vuure, 2005).

Aurochs provided a multitude of ecosystem services to its environment. Whilst roaming the European landscapes they altered its physical structure by consuming the shoots of young trees and shrubs, consequently creating and sustaining open vegetation (Hofman-Kamińska et al., 2019; van Vuure, 2005). Next to grazing, this keystone species shaped European ecosystems through several pathways by the (re)distribution of nutrients through animal waste, dispersing seeds and pathogens and physical impacts (Malhi et al., 2016; Smith et al., 2016). Furthermore, it is hypothesized by Cromsigt et al. (2018) that structural changes induced by grazing of megafauna species, like aurochs, can cause changes in carbon sequestration and the global methane budget, and large-scale vegetation shifts. As a result, contributing to mitigating global warming (Cromsigt et al., 2018).

Regrettably, the last individual of this astounding megafauna species became extinct in a Polish forest in 1627CE, with most extinctions taking place in the period from 1300BCE until 1500CE (van Vuure, 2005; Wright, 2013). The extinctions were most likely triggered by hunting and the introduction of domesticized cattle into the habitat of aurochs (van Vuure, 2005). This keystone species often had many other species depending on them. Galetti et al. (2018) state that the extinction of aurochs may have resulted in the concurrent loss of other species, also known as co-extinction. Mainly species that are strongly dependent on megafauna, like mutualistic or parasitic species, were affected (Galetti et al., 2018). Co-extinction of predators and scavengers could have taken place in a more indirect way, through trophic cascade effects within an ecosystem (Galetti et al., 2018).

The reintroduction or rewilding of aurochs could prove to be beneficial in restoring European ecosystems, maintaining biodiversity and mitigating global warming. Rewilding is defined as the transformation of a non-wild area back to its original wild state (Corlett, 2016). According to Monbiot (2013), it is a shift away from the western worldview of human dominion over nature that has shaped our relationship with the natural world in the past centuries. In the context of this research, rewilding concerns the reintroduction of megafauna species that could contribute to restoring the population of this species and the ecosystem in which it was found.

Even though this species has been extinct for centuries, its DNA is still present in contemporary European cattle species (*Tauros / Rewilding Europe*, n.d.). “The Tauros Programme” aims to breed back the aurochs in a new species called Tauros that resembles *Bos primigenius* as closely as possible (Pereira & Navarro, 2015). The breeding process is currently materializing in six European countries: Croatia, Czech Republic, the Netherlands, Portugal, Romania and Spain (*Tauros / Rewilding Europe*, n.d.). This research aims to build on “The Tauros Programme” by exploring potential rewilding areas in Europe in which this bred back aurochs species could be reintroduced, once the breeding process has been completed. In this research, the term aurochs will be used to refer to both the extinct species and the bred back species, known as Tauros.

Research of this kind has not been done before. Leonardi et al. (2020) have researched whether the niche and habitat suitability of four European ungulates, including aurochs, changed between 40 and 8 kya. They demonstrated that aurochs changed their niche after the Last Glacial Maximum (LGM), before the effect of domestication and significant human influence (Leonardi et al., 2020). The research by

Leonardi et al. (2020) establishes that during this period suitable habitat for aurochs expanded to Northern Europe, ultimately encompassing most of Europe. Yet, no analysis has been done that aims to explore the habitat suitability of aurochs under current conditions. Furthermore, human influence was not taken into account in the study by Leonardi et al. (2020), which this research will include in its analysis.

1.1 Research aim and research questions

The primary goal of this research is to identify rewilding opportunities for aurochs across Europe. First, it is aimed to establish where aurochs were able to thrive in the past. After determining the preferred conditions, a weighted suitability analysis will be done to shed light on the areas that have a suitable habitat for aurochs under current conditions. This analysis will be done for the following scenarios: a protected areas scenario, low population density scenario and RCP4.5 2050 scenario. The resulting suitability maps will be used to answer the **main research question**: “What are suitable areas in Europe for the rewilding of aurochs?”

In order to answer the main research question, answers need to be formulated for the following **sub questions**:

- “What kind of habitats did aurochs occupy formerly?”
- “Under which environmental conditions were aurochs able to thrive in the past?”
- “Where in Europe can land be repurposed into wilderness?”
- “Will the identified suitable rewilding areas still be suitable in the face of climate change?”

2. Methods

2.1 Study area

This research aimed to identify suitable areas for rewilding of aurochs in Europe. Due to data availability Europe was defined as the countries in the European Union (EU), the Schengen area and the United Kingdom. The spatial scope of this research is illustrated in figure 1. Historically, the distribution of aurochs ranged over all of Europe and was most prevalent on this continent (van Vuure, 2005). According to Wright (2013), *Bos primigenius* played a pivotal role in shaping Europe's ecosystems. Also, it is hypothesized that the reintroduction of the wild ancestor of cattle can be crucial in maintaining biodiversity in parts of this continent (Ozkurt, n.d.). Considering the history, and cultural and ecological significance of aurochs on this continent, Europe is a highly relevant area to explore potential rewilding opportunities.



Figure 1: Map of countries included in this research

2.2 Research strategy

This research was divided into two phases: identifying where aurochs used to thrive in the past and subsequently exploring where they can be rewilded under current conditions for different scenarios. The research framework is portrayed in figure 2. The yellow boxes illustrate the first phase, while the orange boxes depict the second phase.

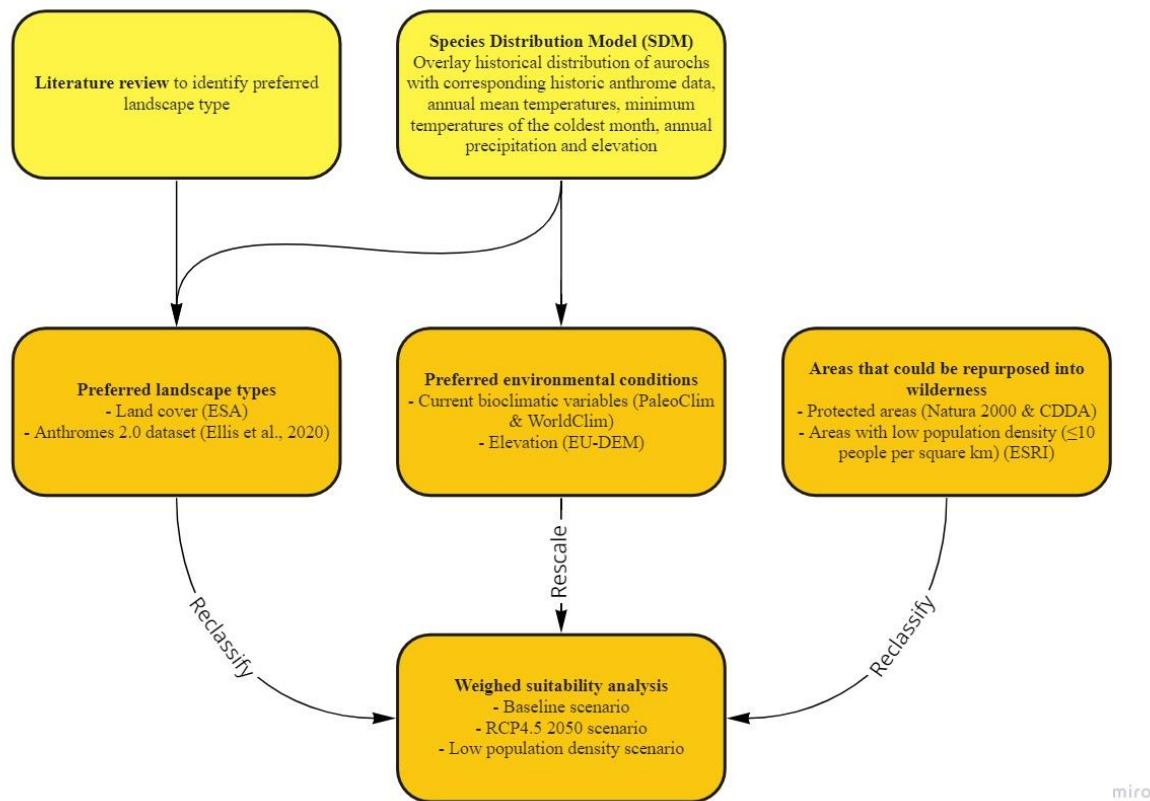


Figure 2: Research framework

2.2.1 Literature review

The first phase commenced with a literature review that was carried out to elucidate the habitat in which aurochs were able to flourish in the past. Landscape types, required space, temperature and elevation were considered when analyzing the literature.

2.2.2 Species Distribution Model (SDM)

Next, a Species Distribution Model (SDM) was used to determine under which bioclimatic conditions, elevations and anthromes in which aurochs were able to thrive in the past. SDMs compare observations of species occurrences with environmental estimates (Elith & Leathwick, 2009). According to Elith & Leathwick (2009), these models are utilized to get an understanding of the preference of species for certain conditions. Knowledge on these preferences can subsequently be used to predict distributions across landscapes (Elith & Leathwick, 2009). In the context of this research, archaeological bone finds of aurochs were compared with historic annual mean temperatures (bio_1), minimum temperatures of the coldest month (bio_6), annual precipitation (bio_12) and elevation. The overlay analyses were done in ArcGIS and the data was subsequently transported to Excel to be translated into graphs.

Also, historical aurochs' distributions were compared with corresponding historical anthrome data. This way, the influence of land use on aurochs could be demonstrated and its preference for certain anthromes clarified. Anthromes is a concept developed by Ellis & Ramankutty (2008), described as: "the characterization of terrestrial biomes based on global patterns of sustained, direct human interaction with ecosystems" (Ellis & Ramankutty, 2008). Conservationists have claimed that biodiversity conservation, including rewilding, should be extended to habitats directly influenced by humans (Martin et al., 2014). According to Martin et al. (2014), this deems the use of biomes, ecoregions and related

biogeographical frameworks as insufficient in analyzing rewilding efforts, as these frameworks reduce human influences to a single dimension of disturbance, while human influence come in many shapes and forms.

In ArcGIS the occurrences of aurochs' archaeological bone finds were divided in time slices according to the available data to which it was compared. Historical anthrome data is divided in 1000 year increments from 10,000 BCE to 1 CE and 100 year increments from 100 CE to 1700 CE, so the aurochs' occurrences were grouped in the same time slices accordingly. For the bioclimatic variables data could be found for the early-Holocene (11.7-8.326 ka BCE), mid-Holocene (8.326-4.2 ka BCE) and late-Holocene (4.2-0.3 ka BCE). Therefore, the aurochs' occurrences were grouped in these three periods. For elevation there was no temporal component included, as this research was based on the assumption that elevation has not changed significantly during the analyzed time period.

2.2.3 Weighted suitability analysis

The second phase consisted of a weighted suitability analysis done in ArcGIS, which was used to answer the main research question. A weighted suitability model contains multiple raster criteria layers with applied weights (Yalew et al., 2016). The criteria layers used in the weighted suitability analysis varied for the different scenarios, the utilized layers for the different scenarios are summarized in table A1 in the appendix. Due to time constraints no pairwise comparison method was used, so the applied weights were all set at 1. In the sensitivity analysis an experiment was done with different weights, based on the research by Leonardi et al. (2020). These results are outlined in figure A11 and table A8 in the appendix.

To describe the relative level of the criteria, a common scale is necessary (Valverde et al., 2016). In this research, the different raster criteria layers were reclassified and rescaled into suitability values ranging from 1 to 10, with 1 being least suitable and 10 being most suitable. The input for the reclassification and rescaling was based on the output of the first phase. Current land cover and anthrome maps were reclassified based on the results of the literature review and the overlay between historical aurochs distributions and corresponding historical anthrome data respectively. Areas in Europe that could be repurposed into wilderness consisted of mask layers, meaning that only the repurposable areas were taken into account in the analysis.

Present-day maps of bioclimatic variables and elevation were rescaled based on the outcome of the SDM. The resulting boxplots of the SDM illustrate the range of values in which aurochs were able to flourish in the past. These values were used as input for a Gaussian function, consisting of a lower threshold, upper threshold, midpoint and spread. The most suitable values were closest to the midpoint, becoming less suitable further away. The suitability value below the lower threshold and above the upper threshold were set at 0. Also, the spread was defined in such a way that the suitability trend perfectly fitted between the upper and lower threshold.

2.2.4 Sensitivity analysis

At last, a sensitivity analysis was done to explore the relationships between the output and inputs of the weighted suitability model (Chen et al., 2010). According to Chen et al. (2010), this gives an indication of the dependency of the model output on slight changes in the input criteria, testing the robustness of the outcome. A sensitivity analysis reduces uncertainty and is vital in calibrating and validating the weighted suitability model (Chen et al., 2010). The sensitivity analysis was done in ArcGIS by increasing the weight of the criteria by 0.25 for 9 runs. This was done for the following criteria: bio_1, bio_6, bio_12, elevation, land cover and anthromes.

2.3 Data collection

2.3.1 Aurochs archeological bone finds

A dataset compiled by Wright et al. (2016) was used for mapping the historical distribution of European aurochs occurrences. This dataset includes archeological sites of postcranial and cranial bone finds of European aurochs and domestic cattle from the Middle Pleistocene to the Medieval period (Wright et al., 2016). Whilst filtering on '*Bos primigenius*' 623 bone finds appeared in 64 distinct archeological sites in Europe. The dataset contains date ranges with an early and late estimation. Average of these early and late approximations was taken to ensure that data points would not be associated with several time slices.

2.3.2 Land cover

Land use maps with sustained human influence were taken from the Anthrome 2.0 dataset, which covers the period 10,000 BCE – 2015 CE (Ellis et al., 2020). Furthermore, a land cover map for 2015 CE was obtained from the European Space Agency (ESA) Climate Change Initiative (CCI), that classifies the Earth into 36 land cover types (Defourny et al., 2017). These types range from agriculture, forests, grasslands, urban and other categories.

2.3.3 Bioclimatic variables

Historic bioclimatic variables were obtained from the PaleoClim database (Brown et al., 2018). These variables are available for the early-Holocene (11.7-8.3 ka BCE), mid-Holocene (8.3-4.2 ka BCE) and late-Holocene (4.2-0.3 ka BCE). Current bioclimatic variables were also obtained from the PaleoClim database (Brown et al., 2018). The values are based on averages for the period 1979 – 2013. The future bioclimatic variables, used in the RCP4.5 2050 scenario, were gathered from the WorldClim v2.1 database (Fick & Hijmans, 2017). The following bioclimatic variables were used in this research, with the subsequently used abbreviation in brackets: Annual Mean Temperature [$^{\circ}\text{C} \times 10$] (bio_1), Min Temperature of Coldest Month [$^{\circ}\text{C} \times 10$] (bio_6) and Annual Precipitation [mm/year] (bio_12).

2.3.4 Elevation

A high-resolution (25m) Digital Elevation Model (DEM) of the European Union (EU-DEM) was used, developed by the Copernicus program for the year 2000 (Eurostat, 2014).

2.3.5 Protected areas

A map of protected areas in Europe was produced by merging Natura 2000 areas with the Common Database on Designated Areas (CDDA). The European Environment Agency (EEA) provided a map with all the Natura 2000 protected areas (European Environment Agency, 2021b). The CDDA protected areas were also obtained from EEA (European Environment Agency, 2021a).

2.3.6 Population density

A population density map was acquired from Socioeconomic Data and Applications Center (SEDAC) (CIESIN, 2018). This map provides estimates of population density in number of persons per square kilometer for the year 2015. These estimates are based on national censuses and population registers (Doxsey-Whitfield et al., 2015).

3. Results

3.1 Literature review

This section will shed light on the habitat that aurochs preferred, aiming to answer the sub-question: “What kind of habitats did aurochs occupy formerly?”. Whilst analyzing the literature close attention was paid to landscape types, required space, temperature and elevation. The literature provided numerous examples of landscape types that aurochs used to inhabit. For the other categories little information could be found. Ultimately, 14 sources provided information on the different categories. The findings on preferred landscape types are summarized in table 1 below.

The landscape types that aurochs preferred can be divided into optimal and suboptimal (refugee) habitats. Cromsigt et al. (2012) argue that many species can be considered refugees that have been limited to a suboptimal habitat due to human influence. Van Vuure (2005) hypothesizes that the process of extinction of aurochs was mainly driven by hunting and ousting by introducing domestic cattle into aurochs’ feeding grounds. Historic reconstructions of aurochs distributions could therefore be based on suboptimal conditions restricted by human influence (Cromsigt et al., 2012). It is very likely that aurochs had been living in suboptimal conditions long before their extinction (Cromsigt et al., 2012). Thus, a distinction will be made between living conditions that were optimal for the survival of this species and suboptimal conditions in which they were forced to live due to the presence of humans.

This research considers the optimal landscape types for aurochs to be open grasslands (mentioned 6 times) and grasslands bordering forests (mentioned 3 times). Hofman-Kamiska et al. (2019) demonstrate that aurochs often occupied open habitat and less forested areas. This is supported by Augustyn & Perzanowski (2021) who mention that aurochs have a higher preference towards open landscapes. What both papers have in common is that they illustrate that *Bos primigenius* was forced to live in more forested areas due to human ousting. Schulz-Kornas & Kaiser (2007) add to this that aurochs were displaced from its natural grasslands to forest borders by competition of domestic cattle and horses.

Suboptimal landscape types include wet forested landscapes (mentioned twice), riparian forests, floodplains, wetlands and fens (all mentioned once). Lynch & Hamilton (2008) carried out a stable isotope analysis to illustrate the co-existence of wild aurochs and domestic cattle in England. This study points out that aurochs preferred more forested and wetter habitats compared to cattle (Lynch et al., 2008). They compare the two bovine species in a time frame of significant human influence. It could thus be argued that these were suboptimal conditions. This claim is supported by van Vuure (2005), who hypothesizes that aurochs inhabited riparian forests and wetlands along lakes. In the same book, van Vuure (2005) contends that fens probably belonged to the most important refugee habitats of *Bos primigenius*.

Table 1: Preferred landscape type of the aurochs

Landscape type	Mentioned in literature	Optimal/suboptimal
Open grasslands	6	Optimal
Grasslands bordering forests	3	Optimal
Wet forested	2	Suboptimal
Riparian forests	1	Suboptimal
Floodplains	1	Suboptimal
Wetlands	1	Suboptimal
Fens	1	Suboptimal

In terms of preferred temperature and elevation, a research by Spassov (1992) illustrates that aurochs specialized towards a warmer climate. Zong (1985) attests that this keystone species preferred a temperate climate. The literature concurs that aurochs preferred to live in flat-grounds (mentioned twice) and lowlands (mentioned 3 times). Van Vuure (2005) claims that aurochs used to inhabit lowlands and lower mountainous regions. Hall (2008) adds to this that *Bos primigenius* could be found in low-lying areas with flat grounds. Nevertheless, it does not become sufficiently evident from the literature what the preferred temperatures and elevation was. Therefore, in the SDM these variables will be included to more accurately elucidate the preferred environmental conditions of this herbivore. Required space of aurochs is hardly mentioned in the literature. However, van Vuure (2005) indicates that one aurochs needs around 500 hectares of space, with herds generally consisting of 20 to 30 heads in winter. This research therefore assumes that the required space for a herd of 20 heads is 10,000 ha.

3.2 Species Distribution Model (SDM)

This section will formulate an answer on the sub-question: “Under which environmental conditions were aurochs able to thrive in the past?”

3.2.1 Aurochs occurrences

Figure 3 shows archeological bone finds of aurochs between the period 10,000 BCE and 1,400 CE. The different colors indicate the time period in which the occurrence can be dated back to. The dataset used did not contain archeological bone finds for Eastern Europe. Thus, showing a bias towards Western Europe in the map.

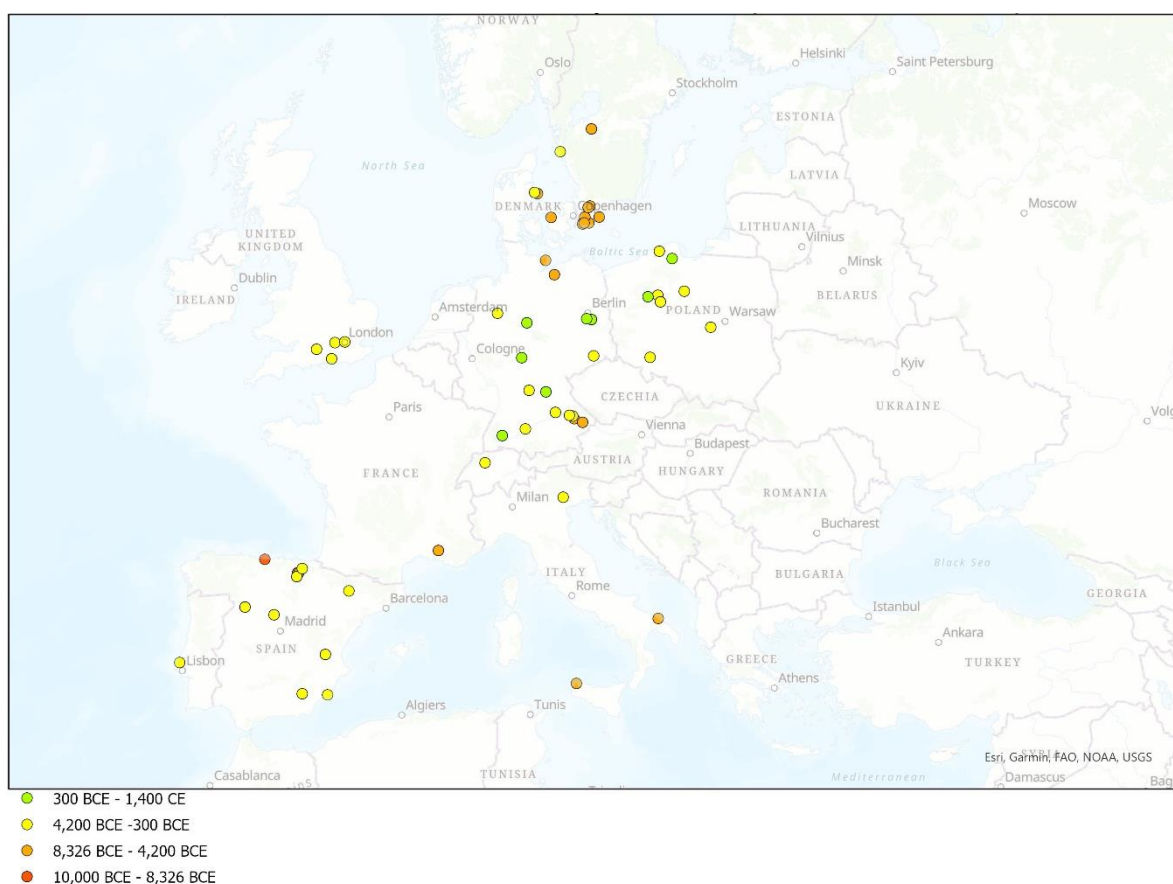


Figure 3: Aurochs occurrences between the period 10,000 BCE and 1,400 CE

3.2.2 Anthromes

Figure 4 depicts the anthromes covered by aurochs occurrences for (a) 10,000 BCE to 0 CE and (b) 0 CE to 1,400 CE. Most striking is the shift from aurochs mostly covering remote woodlands before 0 CE to more frequent occurrences in populated woodlands after 0 CE. As time progressed and human influence increased in Europe, aurochs moved from inhabited treeless, remote- and wild woodlands to populated- and residential woodlands. Residential and populated woodlands could thus be considered suboptimal conditions according to the refugee species theory devised by Cromsigt et al. (2012).

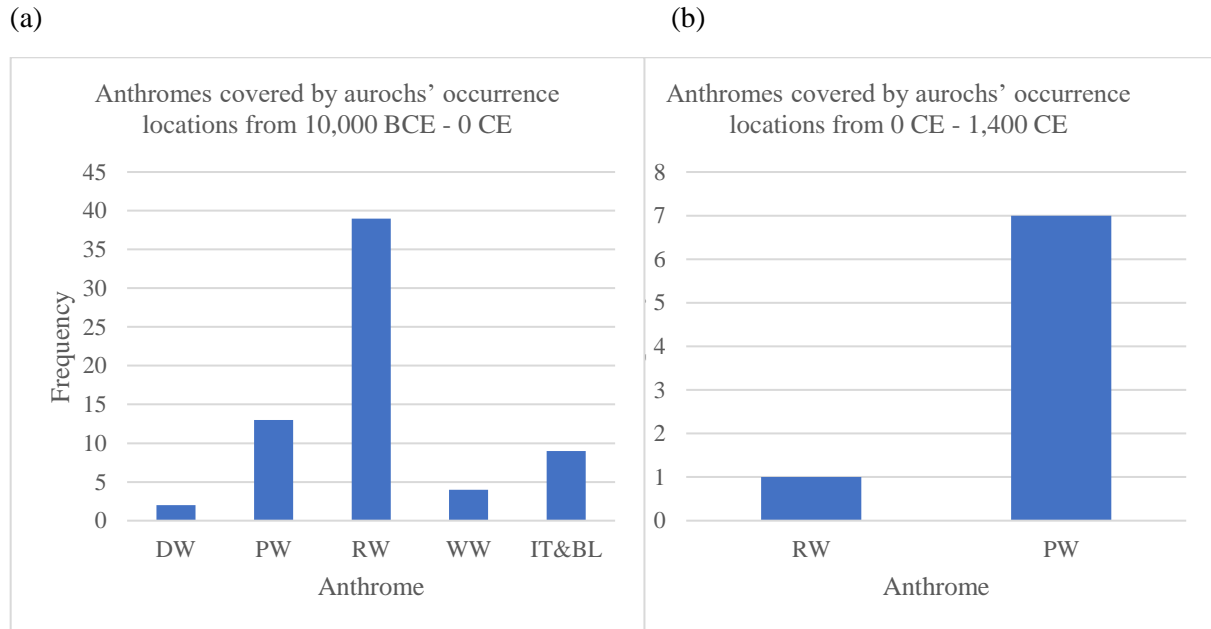


Figure 4: Anthromes covered by aurochs' occurrence locations from (a) 10,000 BCE to 0 CE (b) 0 CE to 1,400 CE

DW = Residential woodlands

PW = Populated woodlands

RW = Remote woodlands

WW = Wild woodlands

IT&BL = Inhabited treeless & barren lands

3.2.3 Bioclimatic variables

In figure 5 the range of climate conditions covered by aurochs' occurrences during the Holocene (11.7-0.3 ka BCE) are illustrated. Archeological bone finds of aurochs occurred in annual mean temperatures ranging from 5.5 to 17.9 °C, with an average of 9.5 °C. Minimum temperature of the coldest month in which aurochs were found range from -10.4 to 9.1 °C with an average of -3.8 °C. Annual precipitation covered by aurochs' occurrences range from 285 to 1303 mm/year with an average of 696 mm/year.

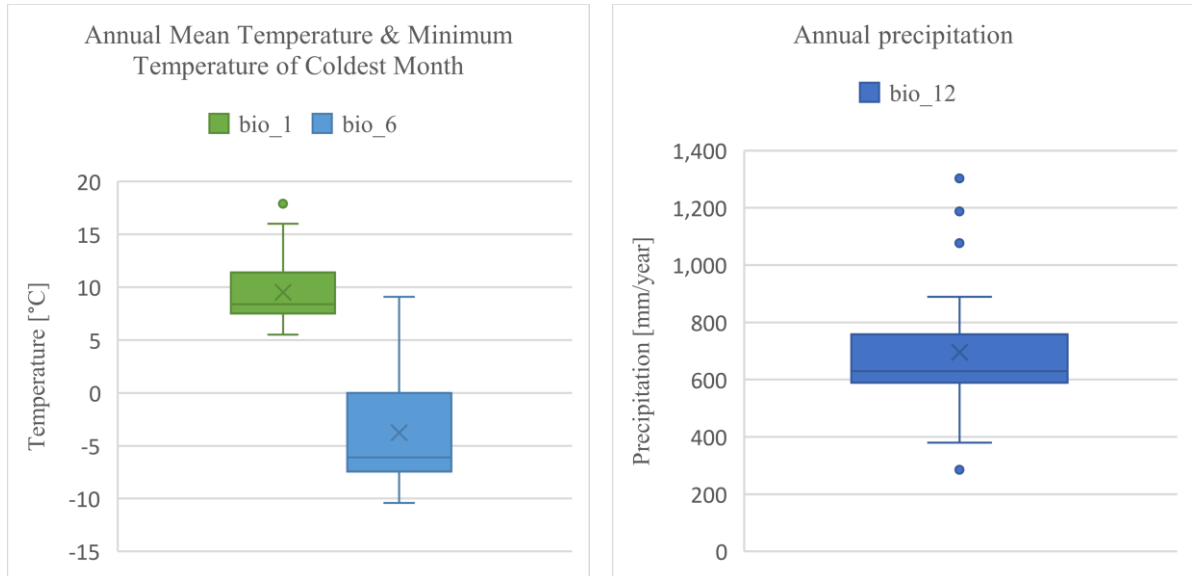


Figure 5: Range of climate conditions covered by aurochs' occurrence locations during the Holocene (11.7-0.3 ka BCE)

Bio_1 = Annual Mean Temperature [°C]

Bio_6 = Min Temperature of Coldest Month [°C]

Bio_12 = Annual Precipitation [mm/year]

3.2.4 Elevation

The range of elevation covered by aurochs' occurrences is portrayed in figure 6. Aurochs could be found on elevations ranging from -0.2 to 1030m, with an average of 206m. This is in line with the outcome of the literature review, that stated aurochs prefer lowlands, flatlands and lower mountainous regions.

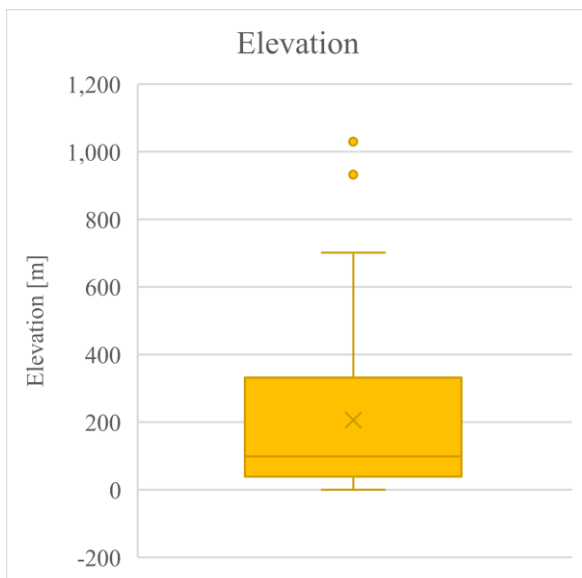


Figure 6: Range of elevation [m] covered by aurochs' occurrence locations

3.3 Weighted suitability analysis

3.3.1 Areas that can be repurposed into wilderness

This section will answer the sub-question: “Where in Europe can land be repurposed into wilderness?” Figure 7 reveals the areas with low population density (≤ 10 people per square km) in green and protected areas ($\geq 10,000$ ha) in blue in Europe. What stands out is that Northwestern- and Central Europe barely have any sparsely populated areas. The protected areas are spread quite evenly over the entire continent.

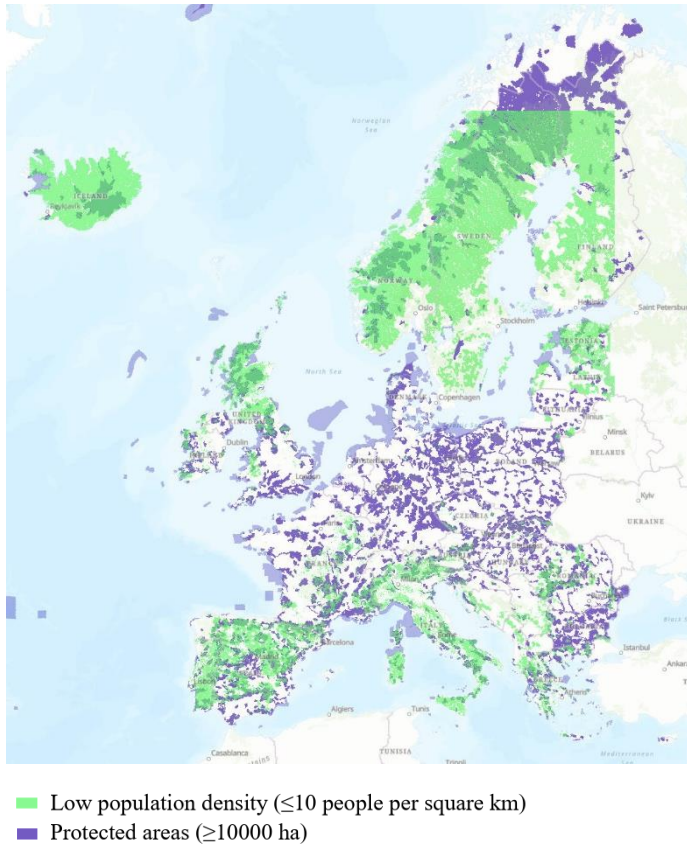


Figure 7: Areas in Europe that can be repurposed into wilderness

3.3.2 Protected areas scenario

Figure 8 depicts the weighted suitability analysis for the protected areas ($\geq 10,000$ ha) scenario. What becomes apparent is that most suitable areas can be found in Northwestern- and Central Europe, the Baltic states and the United Kingdom. Southern- and Northern Europe and the Alps are less suitable for rewilding of aurochs. In general, this scenario contains a substantial amount of suitable areas. Table 2 below illustrates that 54% of the area taken into account in the analysis have a high or very high suitability. This amounts to approximately 2,000,000 hectares of suitable land. For the protected areas scenario the separate suitability maps and used input for all the used criteria layers are summarized in tables A2-7 and figures A1-10 in the appendix. The separate criteria layers and input were only visualized for this scenario, as this was considered to be the baseline scenario.

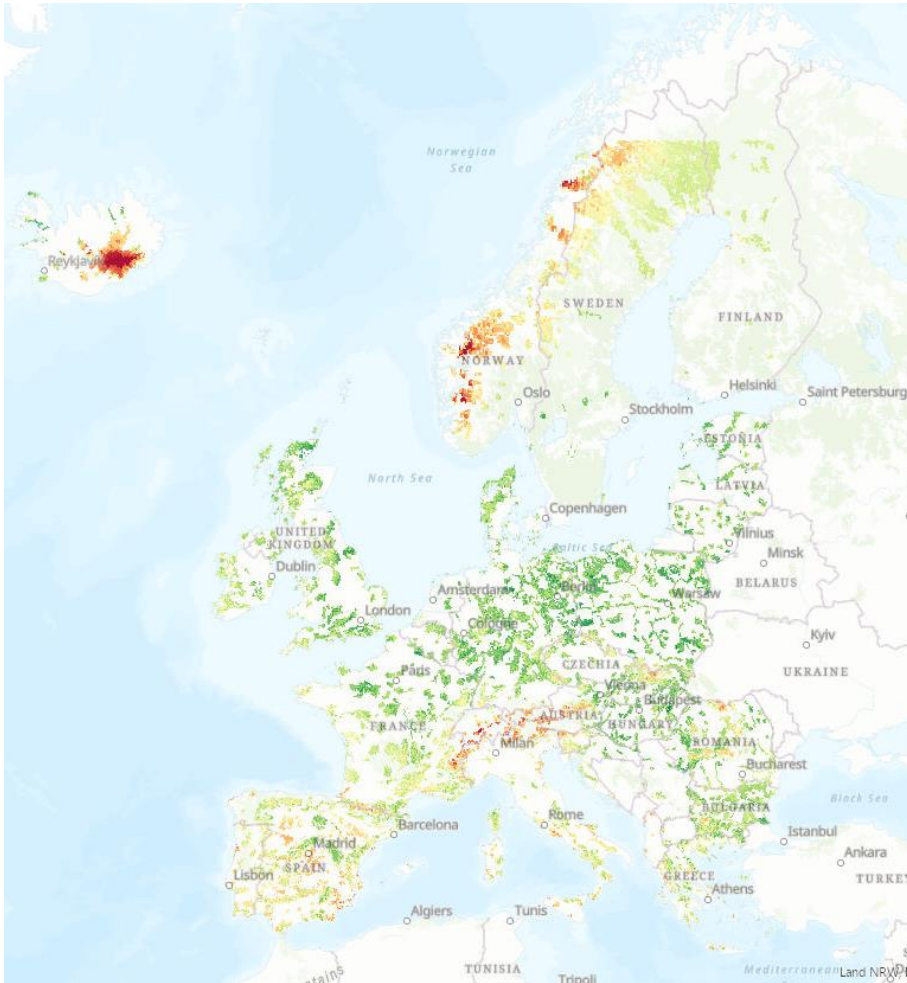


Figure 8: Weighted suitability analysis map for the protected areas scenario

Table 2: Percentage from the total analyzed area and its size in hectares for different suitability classes in the protected areas scenario

Suitability	Percentage from the total analyzed area	Area in hectares
Very high (10–8)	8%	292800
High (8–6)	46%	1714600
Moderate (6–4)	35%	1289400
Low (4–2)	10%	384200
Very low (2–0)	1%	50300

3.3.3 Low population density scenario

Figure 9 portrays the weighted suitability analysis map for the low population density scenario. The Northern United Kingdom, parts of Scandinavia and Baltic states are most suitable for rewilding in this scenario. Table 3 indicates that the share of highly or very highly suitable areas is 39% of the total analyzed area.

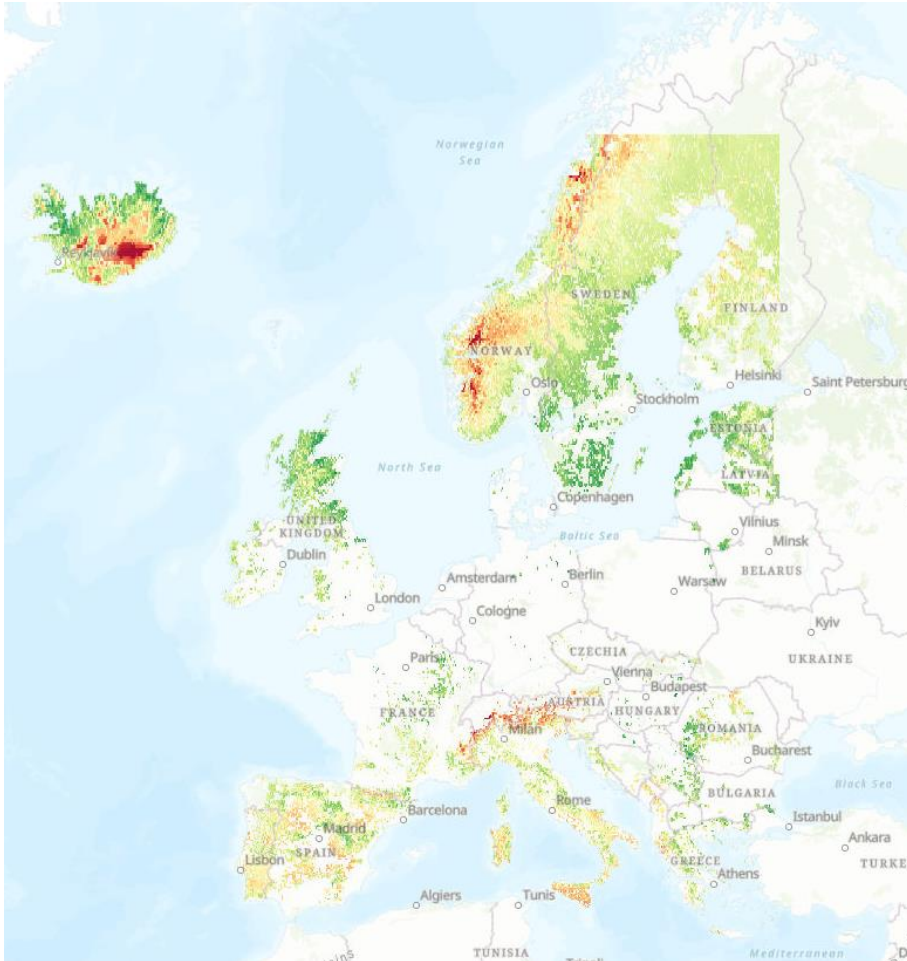


Figure 9: Weighted suitability analysis map for the low population density (≤ 10 people per square km) scenario

Table 3: Percentage from the total analyzed area and its size in hectares for different suitability classes in the low population density scenario

Suitability	Percentage from the total analyzed area	Area in hectares
Very high (10–8)	5%	149900
High (8–6)	34%	1041400
Moderate (6–4)	48%	1489300
Low (4–2)	11%	348900
Very low (2–0)	2%	52500

3.3.4 RCP4.5 2050 scenario

In this section, the sub-question: “Will the identified suitable rewilding areas still be suitable in the face of climate change?” will be tackled. Figure 10 illustrates the weighted suitability analysis map for the RCP4.5 2050 scenario. Interestingly, most suitable areas can be found in Northwestern- and Central Europe, the Baltic states and the United Kingdom. Southern- and Northern Europe and the Alps are less suitable for rewilding of aurochs in this scenario. Table 4 reveals that 41% of the analyzed area has a high or very high suitability. This adds up to nearly 1,500,000 hectares of suitable land.

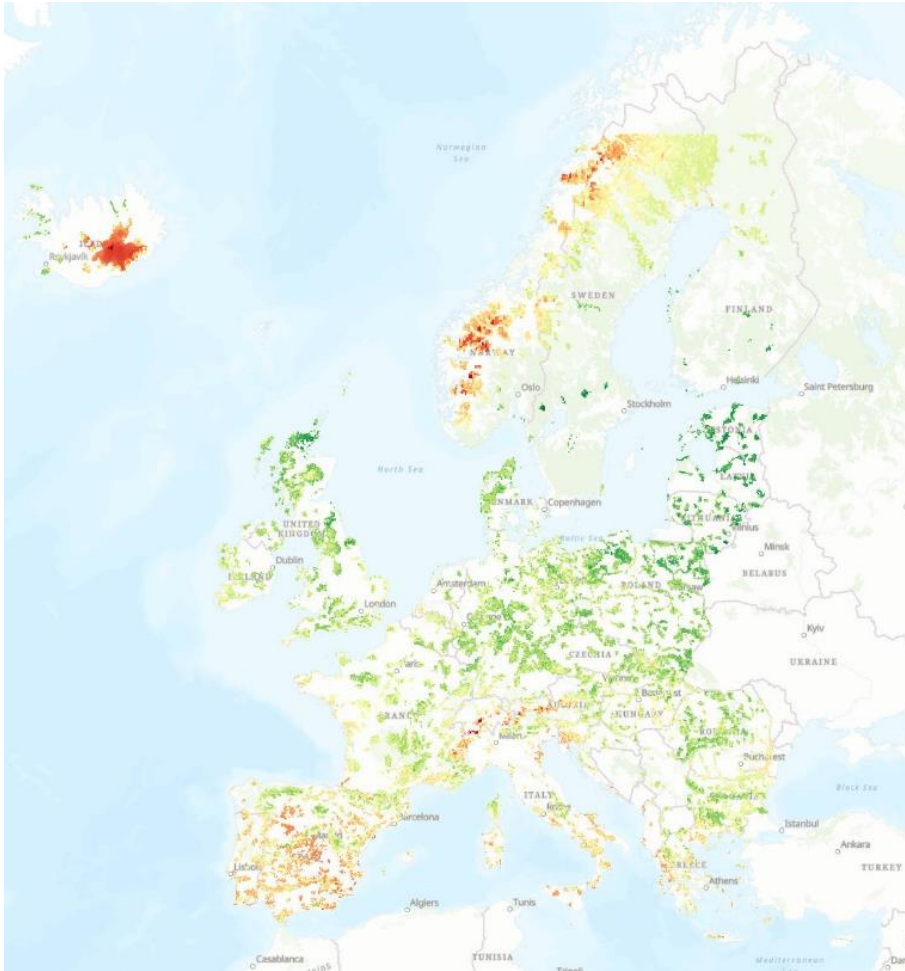


Figure 10: Weighted suitability analysis map for the RCP4.5 2050 scenario

Table 4: Percentage from the total analyzed area and its size in hectares for different suitability classes in the RCP4.5 2050 scenario

Suitability	Percentage from the total analyzed area	Area in hectares
Very high (10–8)	4%	135700
High (8–6)	37%	1380400
Moderate (6–4)	44%	1650300
Low (4–2)	14%	520500
Very low (2–0)	1%	44200

3.3.5 Sensitivity analysis

In figure 11 the sensitivity analysis is visualized for the different criteria layers used in the protected areas scenario. It reveals that the environmental conditions layers are quite stable despite a slight variation in degree of change. The land cover and anthrome criteria layers seem most sensitive to weight changes. With a significant increase in low and moderate suitable areas and substantial decrease in highly suitable areas when increasing the weight of these criteria. In general, the very low and very high suitability areas remain relatively stable for all the criteria, while highly and moderately suitable areas are subject to the biggest amount of change for most criteria. Areas of low suitability increase slightly for all criteria when increasing the weight. All in all, the outcome of the weighted suitability analysis could be considered robust according to this sensitivity analysis

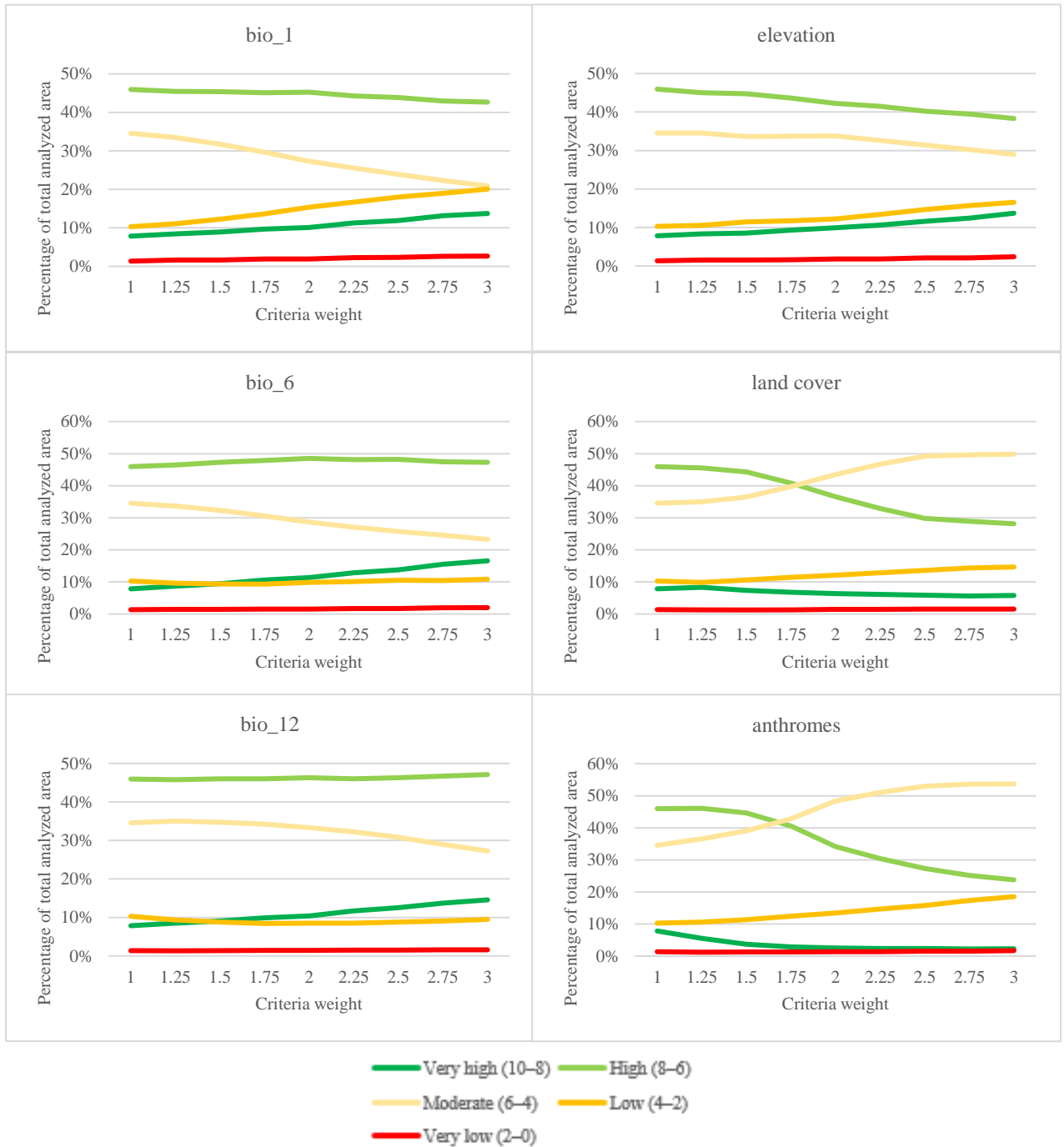


Figure 11: Sensitivity analysis for the different criteria in the weighted suitability model

4. Discussion

4.1 Comparison of scenarios

As the results pointed out, the protected areas scenario had the highest amount of highly or very highly suitable areas. There was a drop in the share of these suitability classes for the low population density scenario. The difference with the protected areas scenario is that this scenario takes areas into account with low population density instead of protected areas. What stands out is the lack of sparsely populated areas in Northwestern- and Central Europe, where the environmental conditions and land cover seem to be most suitable for the reintroduction of aurochs, as seen in the protected areas scenario (figure 8). Table 3 indicates that this leads to a lower share of highly and very highly suitable areas in the low population density scenario, with 39% compared to 54% in the protected areas scenario.

The RCP4.5 2050 scenario is similar to the protected areas scenario, but instead of current bioclimatic variables the analysis was carried out with future bioclimatic variables for the year 2050 under the RCP4.5 scenario. Most striking is the overall shift to less suitable areas compared with the protected areas scenario. With Southern- and Northern Europe becoming even more unsuitable and the highly and very highly suitable areas in Northwestern- and Central Europe slightly shifting to more moderate suitability. This also becomes apparent in table 4, that reveals that highly and very highly suitable areas decreased from 54% to 41%. This results in a loss of around 500,000 hectares of suitable rewilding areas in the face of climate change.

4.2 Limitations

In theory, rewilding is accompanied with numerous potential ecological benefits. Yet, empirical evidence on successful rewilding projects is still lacking (Svenning et al., 2016). Even though there have been several rewilding projects, like Oostvaardersplassen in the Netherlands and Pleistocene Park in Siberia, no quantitative data has been produced as of yet on megafauna reintroductions (Rubenstein & Rubenstein, 2016).

A limitation of using anthromes in this analysis is that there is a compromise in detail when classifying an area according to its land use and global population density estimates (Ellis et al., 2010). According to Ellis et al. (2010), these kind of trade-offs are predispositions of global classification systems. Consequently, an area can be allocated to a certain anthrome, while the difference between being allocated to another anthrome is negligible.

Moreover, the SDM analysis could be a bit misleading, as it only used presence data of aurochs occurrences (Cromsigt et al., 2012). As a result, the historically occupied habitat by aurochs represents the most suitable habitat for this species. Cromsigt et al. (2012) argues this is not always the case, as *Bos primigenius* could have been limited to a suboptimal habitat due to human influence. Distinction between optimal and suboptimal conditions for aurochs was made in the literature review, but this was not done in the SDM for the environmental variables. This means that the outcome of the SDM does not directly reflect environmental suitability of Europe for the aurochs. Nevertheless, the comparison of historical bioclimatic variables with aurochs occurrences was done for the Holocene, during a time where human influence was relatively small. Therefore, despite the inaccuracies of the SDM, it still gives a broad overview of aurochs' preferences for certain environmental conditions.

Furthermore, there should be ethical considerations with respect to rewilding if the aim is to provide tourism (Thulin & Röcklinsberg, 2020). Thulin & Röcklinsberg (2020) assert that the main goal of rewilding should be the conservation and restoration of ecosystems. Rewilding should not feed the paradigm of human dominion over nature that has shaped our relationship in the west with the natural world in the past, but transcend this view by taking a step back as humans and letting nature run its course (Monbiot, 2013).

4.3 Future research

Due to uncertainties and limitations in this research, future research is necessary. This research could be enriched by using more criteria. It would for instance be interesting to carry out the SDM with a Net Primary Productivity (NPP) variable. This way, an empirical estimate could be given for the landscape type that aurochs used to inhabit, as forests on average have a substantially higher NPP than grasslands (Scurlock & Olson, 2013). Regrettably, no database could be found that contained historical NPP values for Europe.

The low population density scenario was used to simulate farmland that could be abandoned in the future. According to Pereira & Navarro (2015), farmland in Europe is diminishing, as many people are flocking to cities. Ceausu et al (2015) state that rewilding has been proposed as an approach to manage farmland abandonment. This scenario could be more grounded by analyzing where in Europe farmland will be abandoned, not merely on the basis of sparsely populated areas.

5. Conclusion

The aurochs has had a significant influence on the shape of Europe's ecological and cultural landscape. Further, it is hypothesized that the extinction of this keystone species may have contributed to global warming and the coextinction of other species, illuminating its potential as a species to rewild areas in Europe. Therefore, this research aimed to answer the following research question: "What are suitable areas in Europe for the rewilding of aurochs?"

It can be concluded that Northwestern- and Central Europe contain the biggest share of suitable areas to rewild aurochs with, also in the face of climate change. *Bos primigenius* could be reintroduced in protected areas ($\geq 10,000$ ha) in these regions. When considering rewilding aurochs in sparsely populated areas, the Northern United Kingdom and parts of Scandinavia and the Baltic states emerge as most suitable areas. Despite limitations of this research, it can be useful to inform policymakers on where to rewild aurochs. This way, the cultural and ecological value of this megafauna species could be restored on the European continent, potentially contributing to the mitigation of climate change.

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7. Appendix

Table A1: Layers used in the different scenarios, before standardization

Protected areas scenario	Low population density scenario	RCP4.5 2050 scenario
Land cover map, for 2015 CE	Land cover map, for 2015 CE	Land cover map, for 2015 CE
Anthrome map, for 2000 CE	Anthrome map, for 2000 CE	Anthrome map, for 2000 CE
Annual mean temperature map, averages for period 1979-2013 CE	Annual mean temperature map, averages for period 1979-2013 CE	Annual mean temperature map, for 2050 CE in RCP4.5 scenario
Minimum temperature of coldest month map, averages for period 1979-2013 CE	Minimum temperature of coldest month map, averages for period 1979-2013 CE	Minimum temperature of coldest month map, for 2050 CE in RCP4.5 scenario
Annual precipitation map, averages for period 1979-2013 CE	Annual precipitation map, averages for period 1979-2013 CE	Annual precipitation map, for 2050 CE in RCP4.5 scenario
Elevation map, for 2000 CE	Elevation map, for 2000 CE	Elevation map, for 2000 CE
Protected areas ($\geq 10,000$ ha) map, for 2021 CE	Population density (≤ 10 people per square km) map, for 2015 CE	Protected areas ($\geq 10,000$ ha) map, for 2021 CE

Table A2: Reclassification land cover (suitability scale 1 to 10)

Land cover	Suitability
Urban	1
Croplands	1
Mosaic croplands/herbaceous	2
Bare	2
Sparse vegetation	4
Tree cover closed	4
Tree cover closed to open	5
Tree cover open	6
Marshes/fens	6
Mosaic trees/herbaceous	6
Mosaic herbaceous/trees	8
Shrublands	8
Grasslands	10

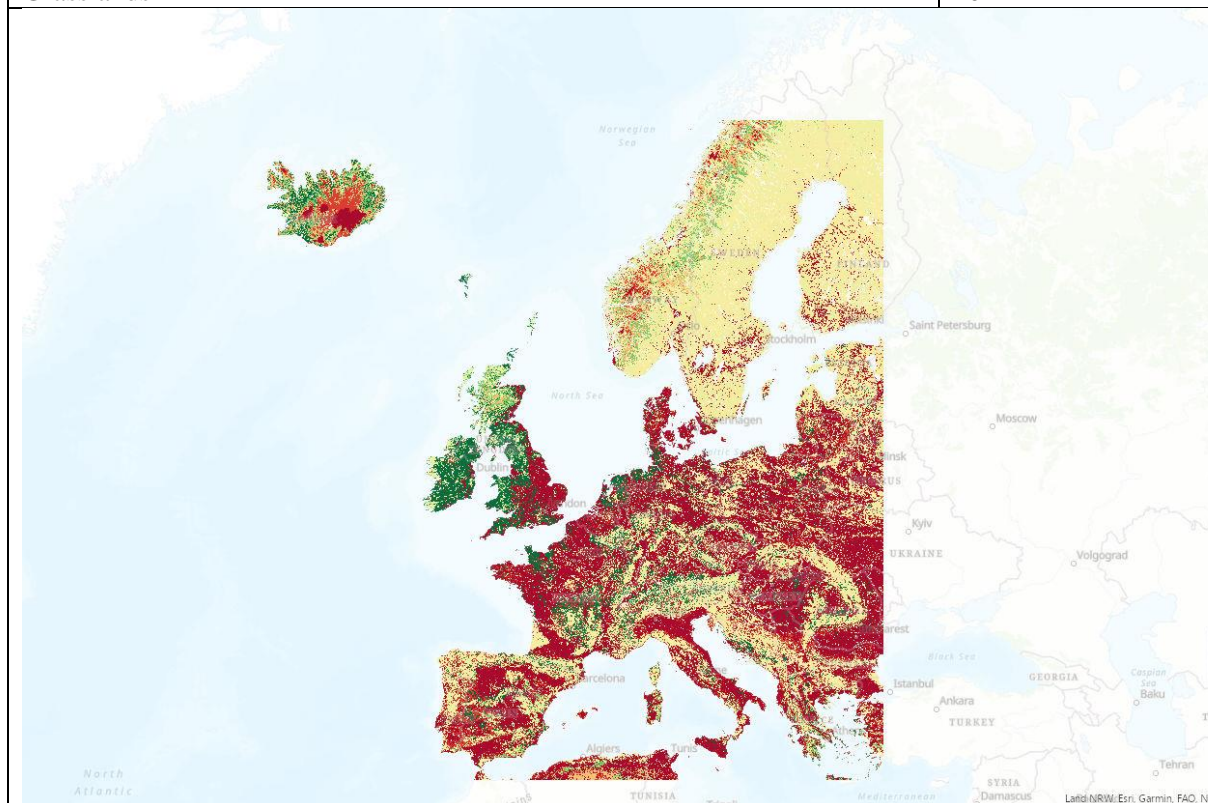


Figure A1: Suitability map land cover

Table A3: Reclassification anthromes (suitability scale 1 to 10)

Anthromes	Suitability
Ice	1
Dense settlements	1
Villages	1
Croplands	1
Remote croplands	2
Residential rangelands	4
Residential woodlands	4
Populated rangelands	6
Populated woodlands	6
Inhabited treeless & barren	8
Wild treeless & barren	8
Remote rangelands	10
Remote woodlands	10
Wild woodlands	10

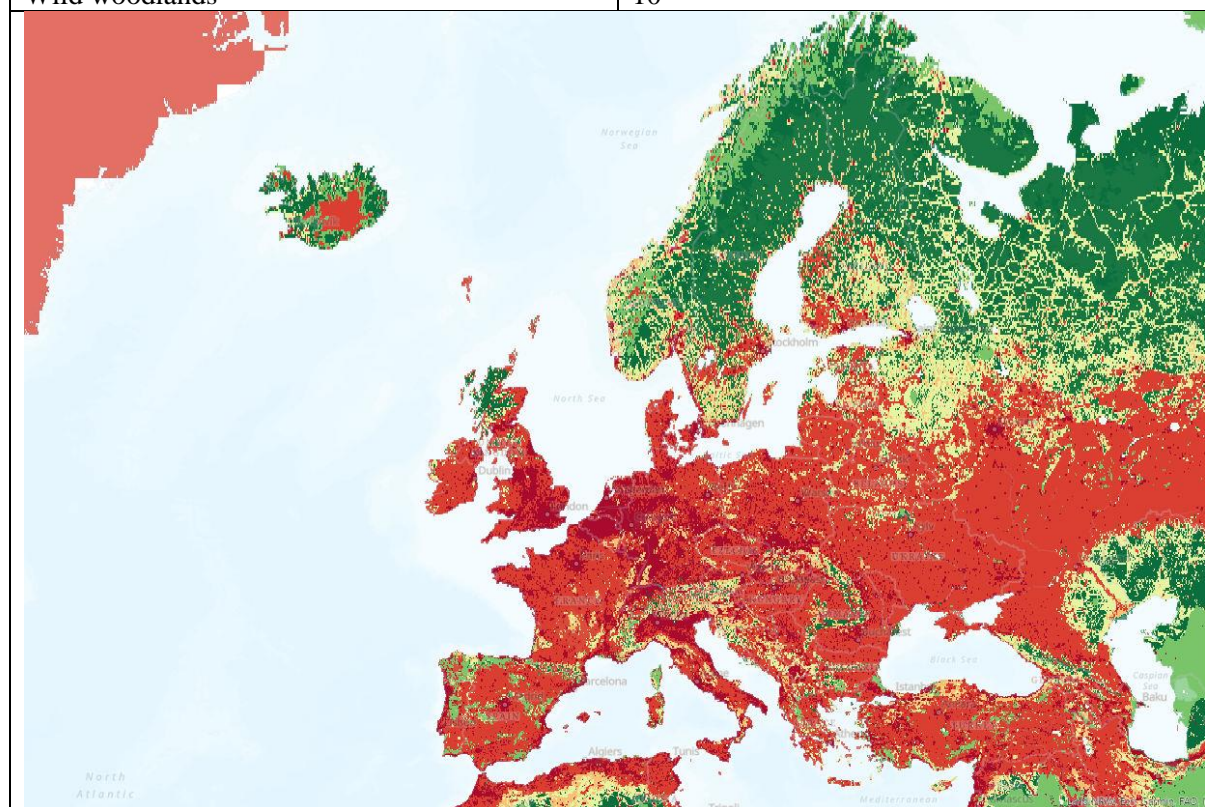


Figure A2: Suitability map anthromes

Table A4: Input for rescale by function bio_1

Gaussian function	Value
Midpoint	95.07692308
Spread	0.0008
Lower threshold	55
Value below threshold	0
Upper threshold	179
Value above threshold	0

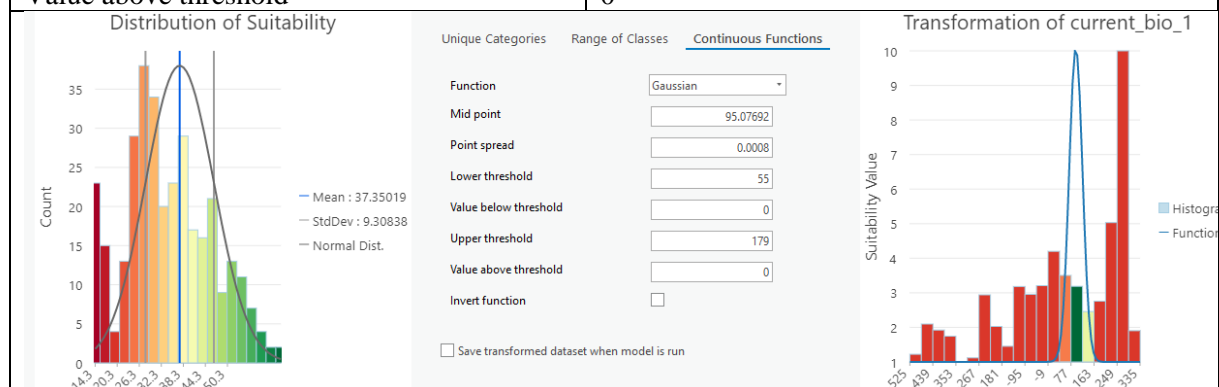


Figure A3: Input for rescale by function bio_1 on ArcGIS

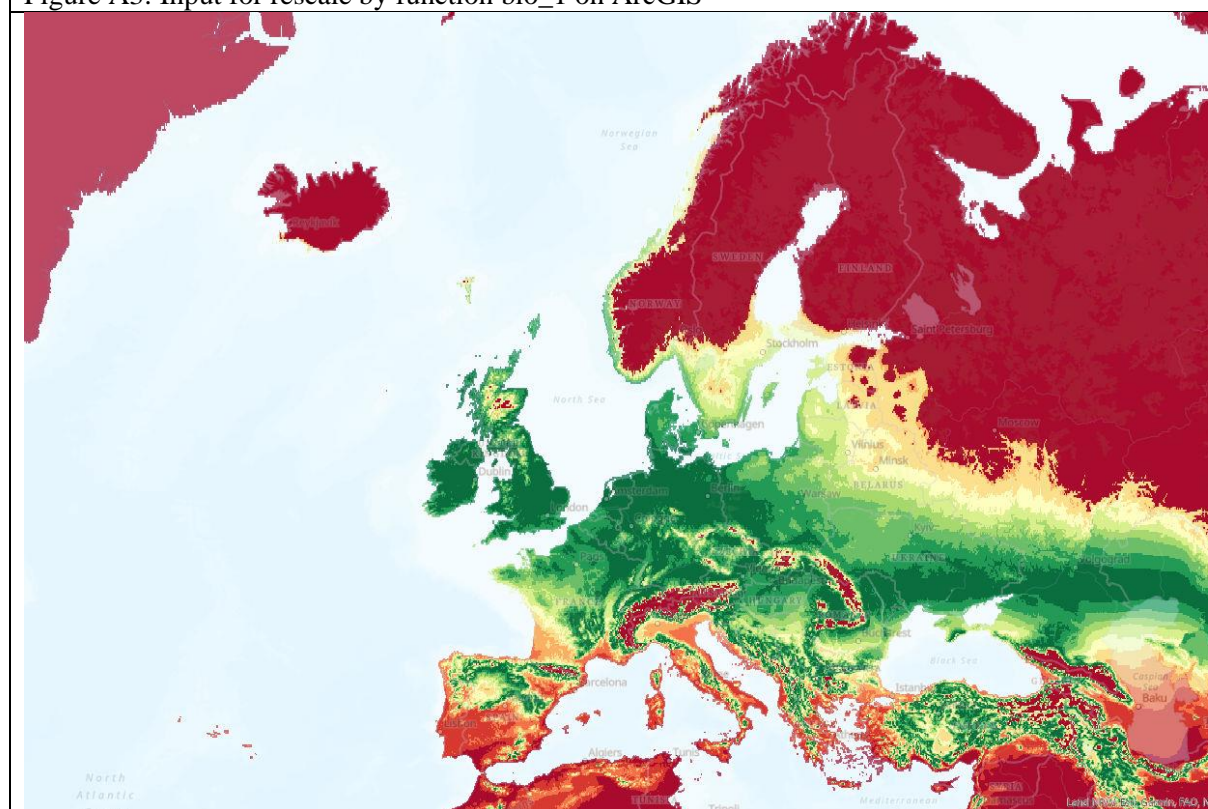


Figure A4: Suitability map bio_1

Table A5: Input for rescale by function bio_6

Gaussian function	Value
Midpoint	-37.73076923
Spread	0.0001
Lower threshold	-104
Value below threshold	0
Upper threshold	91
Value above threshold	0

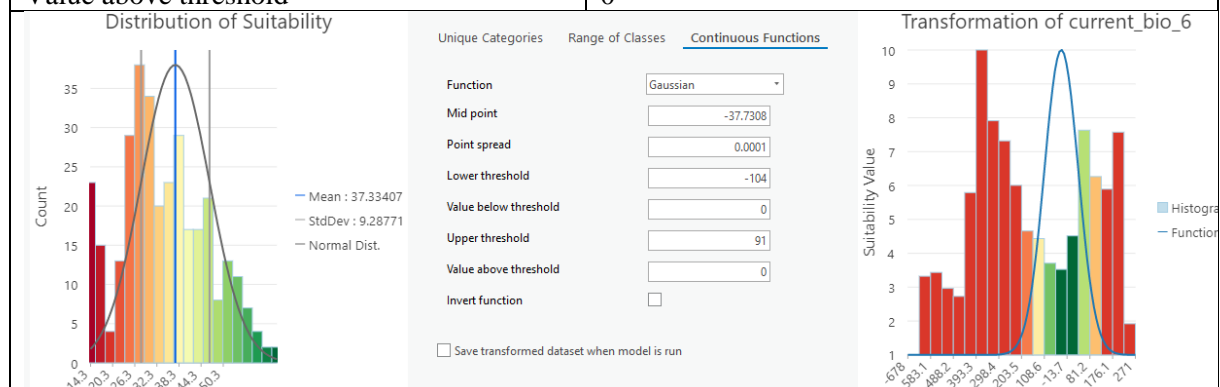


Figure A5: Input for rescale by function bio_6 on ArcGIS

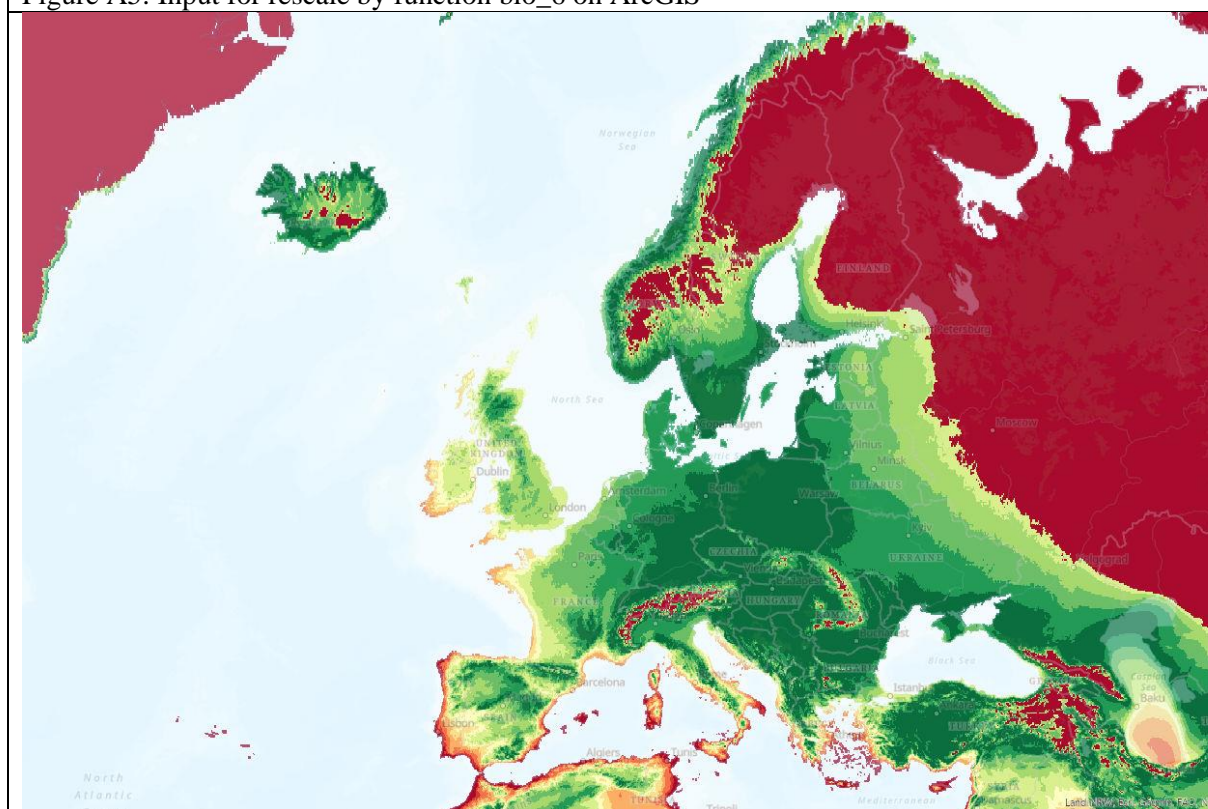


Figure A6: Suitability map bio_6

Table A6: Input for rescale by function bio_12

Gaussian function	Value
Midpoint	695.6730769
Spread	0.00001
Lower threshold	285
Value below threshold	0
Upper threshold	1303
Value above threshold	0

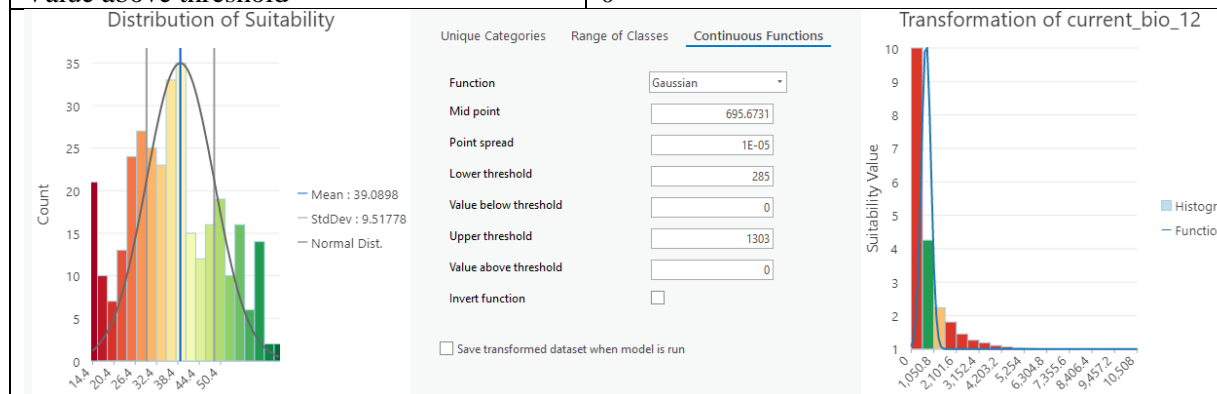


Figure A7: Input for rescale by function bio_12 on ArcGIS

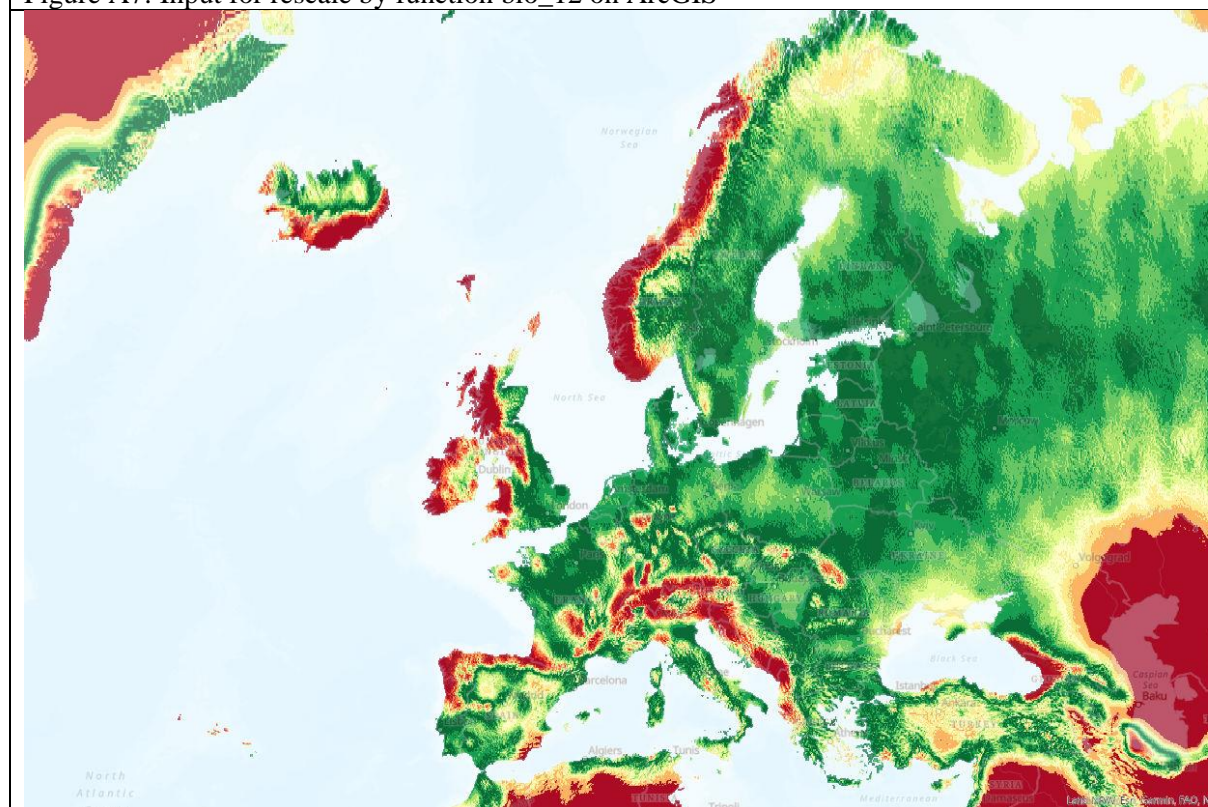


Figure A8: Suitability map bio_12

Table A7: Input for rescale by function elevation

Gaussian function	Value
Midpoint	205.9742636
Spread	0.00001
Lower threshold	0
Value below threshold	0
Upper threshold	1030
Value above threshold	0

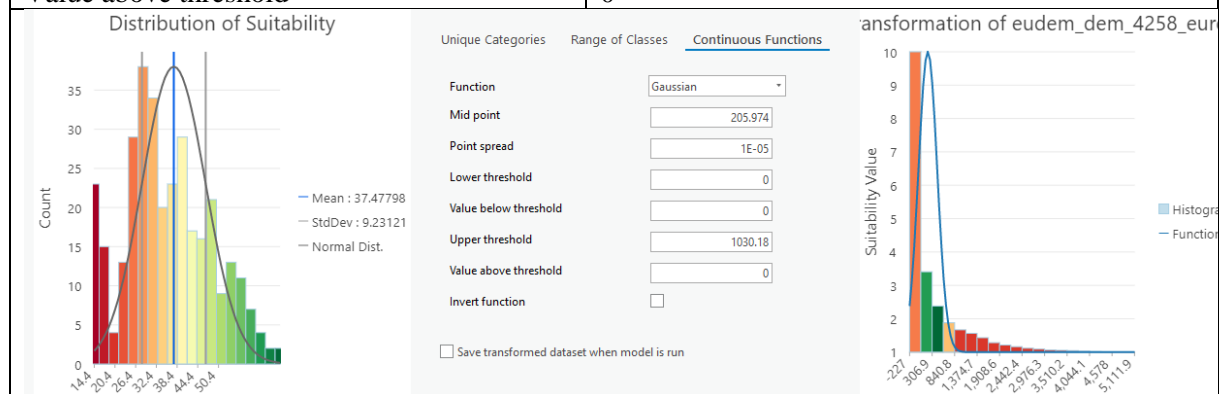


Figure A9: Input for rescale by function elevation on ArcGIS

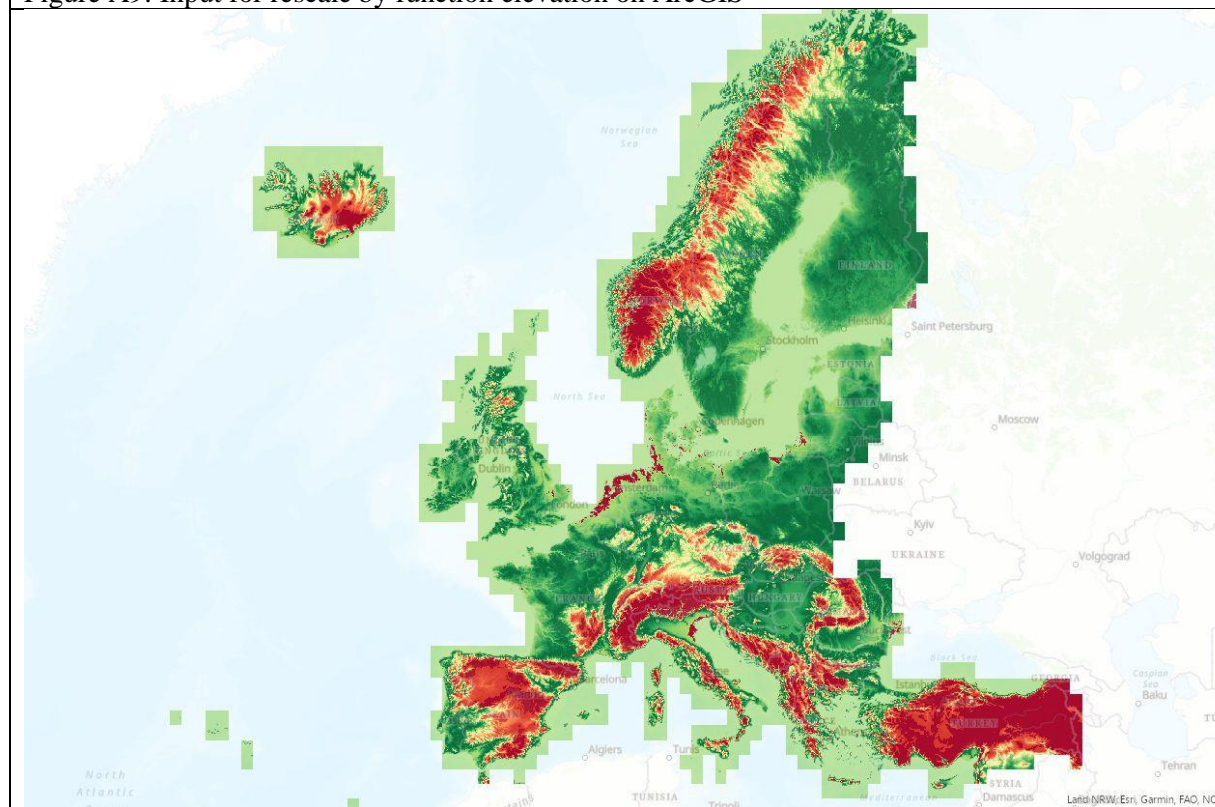


Figure A10: Suitability map elevation

Table A8: Weights applied to the different criteria in the suitability analysis, based on the research by Leonardi et al. (2020)

Criteria	Weight
Bio_1	2.25
Bio_6	7
Bio_12	1.75
Elevation	2
Land cover	3
Anthrome	1
Protected areas	1

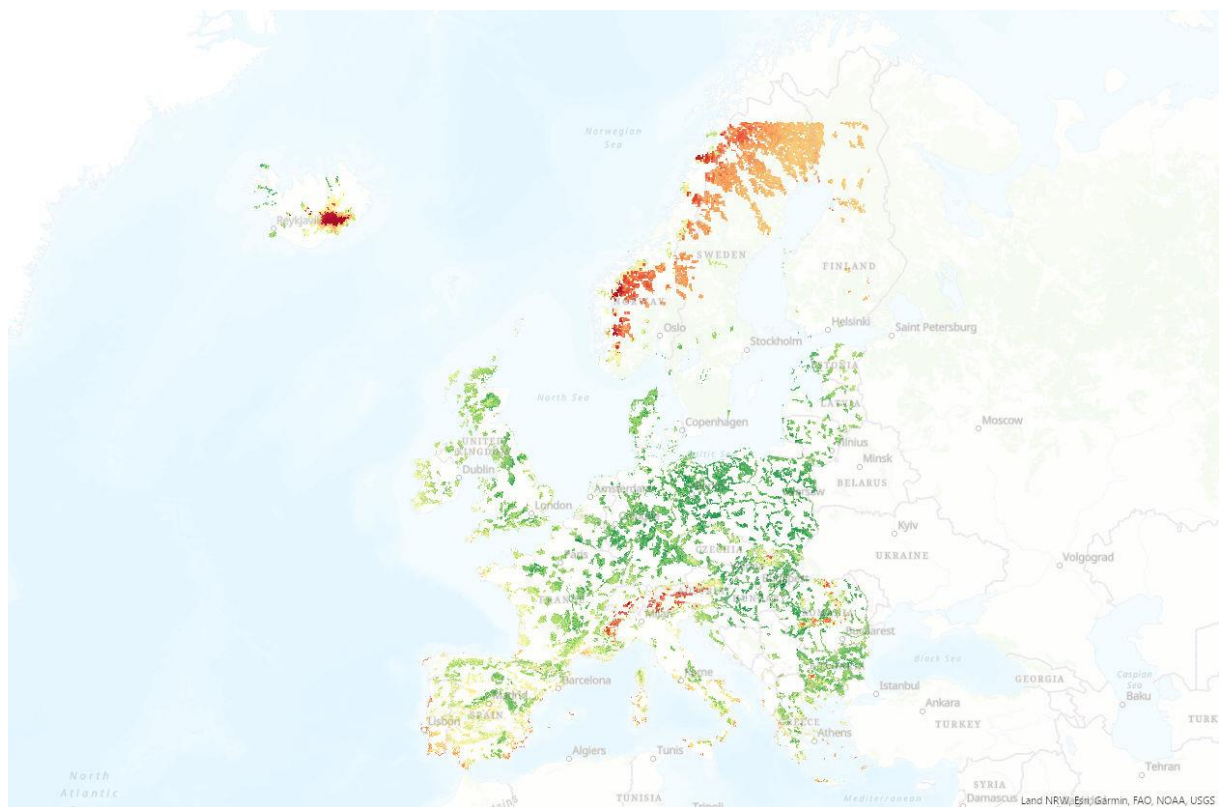


Figure A11: Sensitivity analysis for the weighted suitability analysis in the protected areas scenario, using the weights from table 3