Environmental factors affecting the distributions of the native Eurasian beaver and the invasive North American beaver in Finland

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1. Introduction

Understanding environmental factors affecting species distributions is important when planning species' management. Furthermore, visual maps of suitable areas for the species are needed in order to make results transferable to conservation managers. For these purposes, species distribution modelling (SDM) has been a popular method in conservation planning in recent decades. SDMs aim to predict possible distribution of species based on environmental suitability (Elith et al. 2009, Guisan et al. 2013). Especially the possible distributions of rare or endangered and invasive species are often of interest. Invasive species are the greatest threat to biodiversity after habitat loss caused by humans (e.g. Yiming & Wilcove 2005) as for example, they may exclude native species with similar niches from the area. Information on suitable habitats and possible distributions can be applied e.g. when planning conservation and reintroductions of native species and control of invasive species.

The native Eurasian beaver (*Castor fiber*) was hunted to near extinction in Europe in the late 1800s, and only eight populations of the species survived in small refuges with approximately 1200 individuals in total (Nolet & Rosell 1998). In recent decades, the species has been reintroduced into several countries in Europe. Thus, knowledge on the factors affecting the distribution and suitable habitats for the native beaver is needed (see e.g. Smeraldo et al. 2017, Swinnen et al. 2017), especially in areas where the species lives close to the invasive North American beaver (*Castor canadensis*). The native Eurasian beaver and the invasive North American beaver are morphologically and ecologically similar and live in close contact in Finland and in Russian Karelia (Parker et al. 2012).

In Finland, the original Eurasian beaver population was hunted to extinction in the late 1800s, but the species was reintroduced in the 1930s with individuals from Norway (Granit 1900, Lahti & Helminen 1969). Simultaneously, North American beavers were brought from the United States, because at the time their species status was not known (Lahti & Helminen 1974). The population of the North American beaver grew rapidly especially in the lake district of eastern Finland, whereas the Eurasian beaver survived only in one place and the population grew slowly in western Finland. In the recent monitoring count of beavers, the number of active winter lodges was 3673 for the North American beaver and 1172 for the Eurasian beaver (Luke 2018). At present, the distributions of the two species are partly sympatric in the regions of Pirkanmaa and Etelä-Pohjanmaa in western Finland, as well as in western Lapland (Fig. 1; see also Alakoski et al. 2019). Because the Eurasian beaver did not survive after the original introductions in areas where both beaver species were present, it is assumed that the spread of the North American beaver is a threat for the Eurasian beaver (Liukko et al. 2015). The spread of the invasive beaver towards the distribution of the native beaver raises a conservation issue, because the native Eurasian beaver is classified as being near threatened in Finland (Hyvärinen et al. 2019) and its population size and distribution should increase. The North American beaver has larger litters, which may be the reason for a more rapid growth rate of the population and may give it the advantage when the species meet (Parker et al. 2012). Competition for resources, such as the best habitats, is inevitable between the two species with similar niches.

Both beaver species are semiaquatic, monogamous and territorial (Wilsson 1971, Nolet & Rosell 1994). Beavers use mainly deciduous trees for foraging, but sometimes also coniferous species are consumed (Danilov et al. 2011, Kauhala & Karvinen 2018), and mixed forests can be used as habitats (Kauhala & Turkia 2013, Kauhala & Karvinen 2018). Young trees with a diameter of <20 cm are often preferred as forage (e.g. Dvořák 2013). In summer, aquatic vegetation and terrestrial herbs are also commonly utilized (Danilov et al. 2011). In addition, agricultural fields might offer additional forage (Alakoski et al. 2019). Beavers have been found even in parks close to city centres (J. Raitaniemi, pers. com.) and within highly urbanized regions (Dewas et al. 2012). Recent studies on factors affecting the distribution for both beaver species in other countries have shown that close distance to a riverbank, willow (*Salix* spp.), poplar (*Populus* spp.), wetland vegetation (Swinnen et al. 2017), and woody wetland and shrub density (Francis et al. 2017) increase the habitat suitability for beavers. Previous studies on habitat use in Finland suggest that especially the most common deciduous tree species, birch (*Betula* spp.) is important forage for beavers (Kauhala & Karvinen 2018, Alakoski et al. 2019). Furthermore, the Eurasian beaver lives closer to agricultural areas than the North American beaver (Kauhala & Turkia 2013, Alakoski et al. 2019) and also utilizes small streams between cultivated fields, whereas the North American beaver lives in an area abundant in lakes.

Climate largely determines the possible ranges of species (White 2008, Jokinen et al. 2019). Because Finland is a long country (ca. 1300 km), climate conditions vary greatly between the south and north. Furthermore, the climate in western Finland is milder than that in eastern Finland. Warm temperatures in late autumn may lengthen the time when beavers can collect their winter food cache, whereas spring temperature indicates the time when the snow and ice will melt, and herbs start to grow and thus become available for the beavers. In addition, freezing winter temperatures decrease beavers' activity outside the lodge and they have to rely on their food cache. Thus, it is important to include climatic variables to SDMs (e.g. Bradie & Leung 2016, Jokinen et al. 2019) to be able to determine the relative role of different environmental factors affecting the distribution patterns of the species.

In this study, the aim was to model the environmental factors affecting the present distributions of the two species of beavers in Finland using citizen-science data on beaver observations and environmental variables. We used the Maxent software package for species distribution modelling (Phillips et al. 2018) and investigated whether predictions on suitable habitats change when the species are modelled separately or together. We predicted, based on earlier studies (e.g. Alakoski et al. 2019), that 1) beavers live in areas with abundant riparian areas and the Eurasian beaver uses smaller aquatic habitats than the North American beaver; 2) both species favour deciduous trees in their habitats, but their most favoured tree species may differ; 3) young and herb rich forests are preferred; 4) proximity to agricultural areas might differ between the two species' (potential) habitat; 5) urban areas and large human population size might exclude beavers from otherwise potential areas; and 6) climate may have a different role in the models, because it differs between the two species' present ranges. Finally, we produced maps on available habitats suitable for beavers in Finland. This information can be used to develop effective conservation strategies, e.g. planning the best reintroduction sites for the native Eurasian beaver.

2. Material and methods

2.1 Study area

The landscape in Finland is dominated by bodies of water and industrial coniferous and mixed forests, where scots pine (*Pinus sylvestris*) is the most dominant species, along with Norway spruce (*Picea abies*), downy birch (*Betula pubescens*) and silver birch (*B. pendula*) as common species. Agricultural areas and denser human populations are found mainly in southwestern and southern Finland (for details, see Alakoski et al. 2019). We were interested in the potential habitats of beavers in the whole of Finland. However, as a semi-aquatic species, an aquatic habitat is essential for beavers and thus we expected that suitable habitats could only be found close to waterways and water areas. The distribution of the Eurasian beaver is restricted to southwestern Finland and western Lapland, whereas the North American beaver is found over a larger area mainly in eastern Finland (Fig. 1). The present ranges of the two species were used as areas for background samples (e.g. Elith et al. 2010), but the model was transferred to the whole watercourse area of Finland (excluding the archipelago) in order to predict distribution based on the availability of suitable habitats.

2.2 Data for beavers

We used the data of the Finnish Wildlife Agency on beaver observations with exact coordinates from August 2017 to August 2018, including beaver lodges (Eurasian (E) 169; North American (NA) 179), dams (E 41; NA 53), feeding sites (E 50; NA 59) and other sightings and sounds (E 107; NA 197). The data was collected mostly with a mobile app OmaRiista, where citizens can give information about their hunting bag/catch and wildlife observations directly on a digital map. Hunters usually report beaver lodges in the autumn while hunting moose (*Alces alces*). Beaver species was assumed on the basis of the history of beavers in Finland (see Brommer et al. 2017), from DNA analyses and skull morphometry from hunted beavers in the area of sympatry, as well as from DNA analyses from wood chips collected at the base of trees felled by beavers (Kauhala & Timonen 2016). In practise, most of the data was from beaver locations without verified species identification. However, available data for individuals identified by their species (259 DNA samples and 129 skulls) indicate that the Eurasian and North American beavers live in separate areas in Finland, but there are also areas of sympatry (Fig. 1; Kauhala & Karvinen 2018, Alakoski et al. 2019, Iso-Touru et al. 2020, Sjöberg & Belova 2020). Thus, we are confident that most observations that lacked species recognition could be identified based on the location of the observation (the same approach was used by e.g. Brommer et al. 2017 and Alakoski et al. 2019, see also Iso-Touru et al. 2020). However, we admit that a few misidentifications can occur in the data especially near and within the areas where the ranges of the Eurasian and the North American beaver meet in Finland, but this should not affect the results on habitat suitability as both species have data from these sympatric areas.

Altogether there were 367 observations for the Eurasian beaver and 488 for the North American beaver. However, Maxent used a total of 229, 263 and 488 observations for the Eurasian beaver, the North American beaver and the species together, respectively. That is, Maxent did not use observations that lacked data for one or more of the environmental variables and which were not located within a 50-meter riparian habitat (92 % of the original observations occurred within 50 meters of a watercourse). We modelled the habitat suitability of the beaver species separately, because we were interested in possible differences between the native and invasive species' habitats. We also modelled the two species together, because the habitat use of the beaver species may potentially not much differ (Parker et al. 2012). The local abundance of the two beaver species in Finland results mainly from their reintroduction history (e.g. Brommer et al. 2017), i.e. both species are most abundant close to the sites where they were successfully introduced. Therefore, the environment in the present ranges does not necessarily describe accurately the conditions that are optimum for each species. Instead the model combining both species includes larger area potentially suitable for both species (Fig. 1).

2.3 Environmental variables

Variables used for the habitat suitability models were: aquatic habitat type, length of shoreline in the area, volumes of birch (*Betula bendula*, *B. pubescens*, *B. nana*), spruce, pine, aspen (*Populus tremula*), willow (*Salix* spp.), grey alder (*Alnus incana*) and black alder (*Alnus glutinosa*), forest age, site fertility, distances to agricultural fields and urban areas, human population size and average temperatures for late autumn, winter and early spring (Fig. 2). All explanatory variables were analysed in ArcMap (ESRI 2011) and they were computed from a 50-meter riparian habitat (description below in aquatic habitat) covering the whole country. The grid cell size for all explanatory variables was transformed to 16 m x 16 m, which was the highest accuracy of a variable, before importing to Maxent.

2.3.1 Aquatic habitat

We added waterways (streams < 20 m) and water areas (rivers > 20 m and lakes) from the data of the National Land Survey of Finland (topographic map 1:100 000) (Maanmittauslaitos 2/2015). The Euclidean distance to waterways and water areas (both as polylines and merged together) was computed with a maximum distance of 50 meters, which is a typical maximum foraging distance for beavers (e.g. Müller-

Schwarze 2011). All variables were computed from this 50-meter riparian habitat. The aquatic habitat type was also used as an explanatory variable according to the classes of the National Land Survey of Finland (excluding sea water, which did not occur in the data), except lakes were divided into four classes according to their size. Therefore, there were ten aquatic habitat type classes: 1) streams <2 m, 2) streams 2−5 m, 3) streams 5−20 m, 4) >20 m rivers, 5) canals, 6) reservoirs, 7) lakes ≤ 1 ha, 8) lakes ≤ 10 ha, 9) lakes ≤ 100 ha, and 10) lakes >100 ha. In addition, length of shoreline in meters was computed with the merged polylines of waterways and water areas in a grid cell of 20 km x 20 km covering the whole area of Finland. The original beaver observations could occur anywhere inside the grid cell. Twenty km was selected as the axis length, because it is a reported maximum dispersal distance of beavers in one year (Hartman 1995).

2.3.2 Forest

We used the 2015 forest inventory data of the Finnish Forest Research Institute (Luke 2017; resolution 16 m x 16 m) to obtain volumes of birch, other deciduous trees, spruce and pine, forest age and site fertility (Tomppo et al. 2008). Volumes (as cubic meters per hectare) of birch, other deciduous trees (including aspen, alder spp., European mountain ash or rowan (*Sorbus aucuparia*) and the goat willow (*Salix caprea*)), spruce and pine were used to describe the forest growing stock (Ylitalo 2013). A combined variable of “deciduous trees” was computed as the sum of the birch and other deciduous trees. However, in the 16-meter resolution thematic map other deciduous tree species than birch (spp.) were not separated. Thus, the abundances of aspen, willow trees, grey alder and black alder (m^3/ha) were calculated by dividing the volume of other deciduous trees into species-specific proportions on the basis of geostatistical interpolation of the National Forest Inventory sample plot tree data. The abundance data of species-specific volumes of other deciduous species were computed with a resolution of 1 km x 1 km (for further information see Jokinen et al. 2019). Thus, these tree species volumes do not represent actual tree abundance in the riparian area pixels but rather a relative abundance of these species at the landscape level.

Forest age is the weighted average age of the growing stock in a forest stand in classes of one year. Site fertility is based on classification of the forests by vegetation zones into ten classes according to their fertility and wood production capacity (site fertility index: rank of 1, high to 8–10, low fertility). These classes are: 1) herb rich forest, 2) herb rich heath forest, 3) mesic forest, 4) sub-xeric forest, 5) xeric forest, 6) barren forest, 7) rocky and sandy soils/alluvial land, 8) summit and fjeld land with single coniferous trees, 9) mountain birch dominated fjelds and 10) open fjelds. Classes 1−6 are classified as forest, class 7 can be forest land, poorly productive forest land or unproductive land. Classes 8−10 occur in Northern Finland and are either poorly productive forest land or unproductive land.

2.3.3 Human influence

A raster of distance to agricultural fields was calculated with the Euclidean distance tool in GIS for the Corine land cover data for Finland for year 2012 (20 m x 20 m per grid cell; SYKE 2/2015) classes 2111−2441. Similarly, the Euclidean distance to urban artificial areas (classes 1111−1331: including urban fabric; industrial, commercial and transport units; mine, dump and construction sites) was computed. For the local human population size, we used the 2017 population size in each municipality (Statistics Finland; www.stat.fi).

2.3.4 Climate

To describe the areal climatic conditions, the average monthly air temperatures for the ten previous years from October 2007 to April 2017 were derived from the data of the Finnish Meteorological Institute (fmi.fi:11.10.2018): the average temperatures from October to November (late autumn), December to February (winter) and March to April (early spring) were computed. Twenty-two observation stations distributed evenly in Finland that offered persistent weather data were used to measure the weather variables in this study. The average temperatures were extrapolated with the spline tool in GIS from the selected measurement points to describe areal temperature variation in Finland.

2.4 Species distribution models

We selected the Maximum entropy modelling software, Maxent (Phillips et al. 2006, Phillips & Dudik 2008) as it models species distributions using presence-only records. It compares the environmental data at the species locations to that of background samples in the environment (e.g. Phillips et al. 2006, Phillips & Dudik 2008, Elith et al. 2011, Merow et al. 2013). Maxent uses a machine learning method and aims to find the distribution that is most spread out, or closest to uniform, while taking into account the most contributing environmental variables at known species locations. Maxent chooses the distribution that maximizes the similarity between the environmental characteristics at the species locations and that of the whole environment. The maps of suitable habitats can be visualized in GIS and edited to find potential patterns of interest. The model performance in Maxent can be evaluated with the area under the receiving operating character (ROC) curve (AUC) (e.g. Jokinen et al. 2019). In their standard definitions, AUC and ROC describe the probability that the presences are discriminated from the absences (e.g. Jiménez-Valverde 2012, Yackulic et al. 2013). AUC values of replicated runs in Maxent indicate the model performance with presences against background samples, which can also include actual presence locations in addition to pseudo-absences, instead of real absences for which AUC is usually used (Merow et al. 2013). AUC values tend to be higher in Maxent for species with narrow ranges, but this does not necessarily mean that the models are better (Phillips 2017).

We aimed to create a model that can be utilized in conservation planning, that is, produce as good distribution maps as possible. For this intention Merow et al. (2013) argued that the aim should be to predict where the species occur, at the expense of complex response curves and potential over-fitting. Therefore, we (i) included all the known environmental variables that could affect the beavers' distribution to create distribution maps. However, we also wanted to interpret the importance of different predictors. Thus (ii), we built a simplified version of our model (see below) which creates response curves that are more readily interpreted (Merow et al. 2013). That is, the more parsimonious models also reduce correlating variables. Finally, (iii), because forage is an important factor in the habitat of beavers, we created a model including only the resource factors (tree and forest type variables) to investigate which contribute most to distribution. Thus, in the end, we created in total three models and analysed the two species both separately and together (3*3 = 9 models).

We established most of the settings in Maxent according to Young et al. (2011), except we used Maxent's "raw output": Maxent first makes an estimate of the ratio $f_1(z)/f(z)$, scaled to sum to one, between the conditional density of the covariates at the presence sites and the unconditional density of the covariates at the study area; thus giving an estimate of the relative suitability of one site vs another (Elith et al. 2010, Guillera-Arroita et al. 2014). The original raw output is suitable for e.g. territorial animals, because it does not make assumptions about prevalence as the logistic outputs do (Merow et al. 2013, Phillips et al. 2017). To account for the bias in surveying effort, a background sample area was made from the riparian area of the municipalities where the species' observations were made (different areas for the two species in their separate models and combined area for the model with both species together). This was added as a "bias file". To evaluate the models' performance the random test percentage was set to 25 percent and the model was run 15 times. We created response curves to see the variables' effect and did Jackknife tests to measure variable importance.

2.4.1 The full model (i)

The response variable was the observations of the beaver locations. A total of 172 and 198 presence records were used for model training and 57 and 65 for model testing (i.e. random test percentage 25; Young et al. 2011), for the Eurasian beaver and the North American beaver, respectively. With both species, 366 presence records were used for training and 122 for testing. The explanatory variables (N=17) were: aquatic habitat type, length of shoreline, volume of aspen, willow, grey alder, black alder, birch, spruce and pine, forest age, site fertility index, distance to agricultural fields and urban areas, human population size and average temperatures for late autumn, winter and early spring. All explanatory variables were from a 50-meter riparian zone and they were continuous, except for aquatic habitat type and site fertility, which were categorical.

2.4.2 The model with the most important environmental variables (ii)

We made a more parsimonious model with only the most important factors (Appendix A & B). The importance of the environmental variables was considered based on their percentage contribution to the model, the three Jackknife tests on model training and test gain, and AUC on the test data. However, environmental factors can be divided into three groups: limiting factors which control ecophysiology (e.g. temperature), disturbance factors which describe perturbations in the environment (e.g. anthropogenic disturbance), and resource factors (e.g. vegetation), which are the supplies needed by the organisms to survive (Guisan & Thuiller 2005). Bradie and Leung (2016) suggest using all these groups in the Maxent models. All climate variables were important but based on their response curves, they seemed to affect similarly. Because of their correlative nature, we kept only the best fitted climate variable in the model. For both the species together and for the Eurasian beaver, the mean winter temperature had the greatest contribution to the model. For the North American beaver, the mean autumn temperature had the greatest contribution of all the climate factors, but the differences were small. Therefore, we included the mean winter temperature in all the models, to be able to compare the results between species. For the resource factors (forage), we added a combined variable “deciduous trees” to account for all possible forage. Thus, for the Eurasian beaver, the North American beaver and both species together (three separate analyses; N=229, 263 and 488, respectively), we created models including five explanatory variables: aquatic habitat type, mean winter temperature, human population size, agriculture and deciduous trees.

2.4.3 The model with the resource factors (iii)

For the Eurasian beaver, the North American beaver and the species together (N=232, 271 and 503, respectively), we created models that describe the availability of food resources for beavers. We included seven tree and forest type variables: birch, aspen, grey alder, black alder, willow, forest age and site fertility.

2.4.4 Maps of suitable habitats

Habitat suitability maps were created for the full model with the raw output's point-wise averages of the 15 output grids in GIS. To be able to compare the suitable areas, the figure categories for the Eurasian beaver, the North American beaver and both species together were scaled similarly, i.e. the category breaks were the same. Three scales were used to describe the habitats - the least suitable, those with medium suitability and the most suitable, in order to find potential patterns of interest, which were evaluated visually. The cell size was increased by 100 to 1600 m x 1600 m, using the mean of the input cell values, to form more continuous and easily interpreted maps. It should be noted that these scales do not describe unsuitable habitats or absolutely the best habitats and no thresholds were used.

In addition, we created similar maps with the results of the resource model (model iii) to find out where the habitat is the most suitable when climate, aquatic type and disturbance factors are not taken into account. We also made maps with a higher resolution where the habitats for the Eurasian beaver were limited to the riparian area of streams and rivers >2 m, and areas where the human population size was <10 000. These maps could be applied in planning reintroductions for the Eurasian beaver.

3. Results

3.1 The full model and the reduced model

The full model (model i) with 17 variables indicated a good model performance with mean training data AUC values of 0.94, 0.86 and 0.87 for the Eurasian beaver, the North American beaver and both species together, respectively. The reduced model (ii) with five variables had AUC values of 0.93, 0.84 and 0.87 for the Eurasian beaver, the North American beaver and both species together, respectively.

For the Eurasian beaver, the aquatic habitat type made the greatest contribution to the full model (model i; 45.3 %) and the reduced model (model ii; 51.6 %), followed by the mean winter temperature (14.9 % and 20.9 %, respectively), human population size (12.5 % and 14.7 %, respectively) and agriculture (9.2 % and 10.7 %, respectively). The contributions of the other explanatory variables were less than 4 %.

Similarly, for the North American beaver, the aquatic habitat type made the greatest contribution to the full model (71.5 %) and the reduced model (81.9 %), followed by the autumn temperature (5.3 %) and aspen (5.0 %) in the full model and the mean winter temperature (11.6 %) in the reduced model. Other variables contributed by less than 4 %. In addition, for both beaver species together, the aquatic habitat type made the greatest contribution to the full model (55.2 %) and to the reduced model (58.1 %), followed by the mean winter temperature (24 % and 31.5 %, respectively). The contributions of the other explanatory variables were less than 6 %. The aquatic habitat type was the environmental variable that in all the models produced the highest gain when used in isolation, and, when omitted, produced the most reduction in gain. For variable contributions in each model and Jackknife tests see Appendix A & B.

According to the response curves for the aquatic habitat type (reduced model, Fig. 3), streams (5−20 m) and rivers (>20 m) were the most suitable for the Eurasian beaver. In addition to streams (5−20 m), lakes (1−10 ha) were the most suitable for the North American beaver and the species together. Small streams (<2 m) and large lakes (>100 ha) were the least suitable for both species separately and together. The response to the winter temperature was not linear for the beavers: an optimum mean temperature for the Eurasian beaver was between −3 and −2°C and for the North American beaver approximately −6°C. In addition, a small human population size and the vicinity of agriculture predicted the best habitat suitability for the Eurasian beaver (Fig. 3).

3.2 The model with the resource factors

The model (iii) with only the resource variables had AUC values of 0.79, 0.68, 0.74 for the Eurasian beaver, the North American beaver and both species together, indicating that resource factors alone do not explain distribution as well as the full model. Aspen made the greatest contribution to the models with 42.4 %, 52.6 % and 63.5 %, respectively. For the Eurasian beaver and the species together, birch had the second most contribution with 17 % and 15.4 %, respectively, whereas for the North American beaver, grey alder was the second most important with a 22.1 % contribution. In addition, forest age (11.9 %) and site fertility (10.5 %) contributed to the model for the Eurasian beaver. Other variables contributed by less than 10 % in all models.

From the most important resource variables, the abundance of birch (Eurasian beaver and both species together), and grey alder and aspen (North American beaver) increased the habitat suitability (Fig. 4). For the Eurasian beaver, approximately 2.5 m^3/ha of aspen predicted the most suitable habitat, and for both species together areas with approximately 6.5 or >15 m^3/ha of aspen were most suitable. In addition, for the Eurasian beaver young and herb rich (heath) forests were most suitable (Fig 4.).

3.3 Habitat suitability maps

Habitat suitability maps based on the full model can be seen in Fig. 5. The most suitable habitats for the Eurasian beaver occur mostly in south-western Finland, whereas for the North American beaver the most suitable areas occur mostly in south-eastern Finland. The resource models' results show that the most suitable habitats occur more abundantly for the Eurasian beaver. In the models with both species together there is a larger area of suitable habitats than in the species-specific models (Fig. 5).

4. Discussion

We observed that the main contributors for the distribution of beavers in Finland were the presence of suitable aquatic habitat types and the climate. These variables together seemed to mainly determine where beavers could be located. Moreover, we observed that the resource variables, especially aspen, birch and grey alder, affected the habitat suitability of the two species differently. However, the observed differences partly reflect the differences in the present distribution areas of the two species. Thus, the habitat suitability maps based on the combined data for both species may also be used to indicate potential areas for the native Eurasian beaver in Finland.

4.1 Environmental characteristics best explaining the habitat suitability

Aquatic habitat type best explained the riparian habitat suitability for beavers. Both species preferred medium sized lakes and medium to large streams and rivers. The suitability of wider streams and rivers is in accordance with earlier studies of the Eurasian beaver. Ruys et al. (2011) reported that colonizing beavers selected the widest possible waterways in France, with a mean width of 59 m. These rivers offer a constant water level and a water depth of >50 cm, which is the minimum required level for beaver settlement (Müller-Schwartze 2011). In contrast, in Norway where the beaver populations are near the carrying capacity, beavers selected narrower sections of the river to achieve easier access to both sides of the riverbank (Pinto et al. 2009). However, beaver lodges did not occur along the narrowest rivers surveyed in Sweden (Hartman 1996). It should be noted that in our raw data from the riparian area for both species together (N=723), streams <2 m were the second most used aquatic habitat. The difference between the observed use of the smallest streams in our data and the model predictions imply that the smallest streams were only used in Finland because they are abundant in the environment. Contrary to Brommer et al. (2017), the length of shoreline in the landscape did not make a large contribution in our models. The small contribution of shoreline length perhaps reflects the good dispersal abilities of beavers.

Furthermore, climate, indicated here by the winter or autumn temperature, was an important factor explaining habitat suitability and the distribution of beavers. The optimum mean winter temperature for the Eurasian beaver was between −3 and −2°C and for the North American beaver approximately −6°C. The observed difference between the species may, at least partly, result from difference in distribution due to different introduction histories. Indeed, in the model for both species together, the response to mean winter temperature was more linear, indicating a preference for areas with a warmer winter temperature. A warm winter temperature likely reflects a generally warmer climate and a shorter winter in the area, which means a longer activity period when beavers can collect winter food caches. Furthermore, a warm climate also means an early spring (growing season) and thus better food resources for beavers. Warm temperatures may also have a positive effect on energy balance and foraging time during winter because energy requirements of beavers are unlikely to be met solely by their winter food cache (Dyck & Macarthur 1993). The North American beaver's preference for colder areas may also indicate the importance of snow cover which gives shelter from cold and predators. A 40 cm thick snow cover keeps the temperature inside the lodge up to 38°C above the lowest air temperatures outside (Stephenson 1969). Furthermore, beavers have adapted to cold by also decreasing their activity outside the lodge during extended periods of cold weather (e.g. Lancia et al. 1982).

Human disturbance and agriculture also explained the present distribution of the Eurasian beaver. Habitat suitability was highest immediately next to agriculture and at a very small human population size. However, despite of the preference for low human population size beavers can occur in human dominated areas (see e.g. Dewas et al. 2012). In areas where beavers are not hunted, they may live close to large human populations. Human population and agriculture are more abundant in the range of the Eurasian beaver and thus affected its distribution and habitat use, observed also in earlier studies (Kauhala & Turkia 2013, Alakoski et al. 2019).

The abundance of trees, site fertility and forest age contributed surprisingly little to the habitat suitability. Gorshkov and Gorshkov (2011) found that beavers' foraging preferences were largely determined by the availability of different tree species in the riparian zone, suggesting that the role of individual tree species for beaver distribution may indeed be hard to detect. However, the combined variable for deciduous trees did not much contribute to our models either. Nolet and Rosell (1994) found that forage may not need to be abundant in a small area in the riparian zone but could be more scattered in a larger area. This may partly explain the small contribution of abundance of forage near beaver observations in the present study. However, for aspen, grey and black alder, and willow trees we used data for relative abundances in a larger area. We did not have data for shrubby willows, which might be utilized as forage as they are often abundant in riparian habitats. Based on earlier analysis of these data (Alakoski et al. 2019) birch is more abundant near the lodges (within core areas) than within the rest of the territory. Thus, at least for birch, the models should have overestimated the role of birch for distribution, which furthermore highlights the unexpectedly low contribution of resource variables in our full model.

4.2 Resource factors explaining habitat suitability

Abundance of aspen was the most important factor from the used resource factors (abundance of trees, site fertility and forest age) in our models. For the North American beaver, the response to aspen abundance was clearly linearly positive, but for the Eurasian beaver the optimal value did not need to be the highest abundance of aspen. That is, in a model with the other resource variables, unexpectedly, a relatively low abundance of aspen (approximately 2.5 m^3/ha) predicted the best habitat suitability. However, when aspen was treated alone, a higher abundance of aspen also predicted a high habitat suitability for the Eurasian beaver. The nonlinear response curve in the previous model version may result from a correlation with some other (resource) variable. Furthermore, aspen is relatively rare in the present range of the Eurasian beaver (Fig. 2a), which is not necessarily the most optimum habitat for beavers. Based on earlier studies on beavers' foraging behaviour aspen is often reported to be the most preferred species for beavers (Danilov et al. 2011) and birch has been found to be important in Finland (Kauhala & Karvinen 2018, Alakoski et al. 2019). In addition, in line with our results, Danilov & Kan'shiev (1983) found that the North American beaver utilized grey alder more often than the Eurasian beaver when the two species lived in the same area, although not in a similar habitat. Probably all deciduous species can increase the habitat suitability for beavers, but their importance depends on the species' local abundance and composition.

4.3 Potential suitable habitats for the species on a map

In the species-specific models, most of the potentially suitable habitats for the Eurasian beaver occur in south-western Finland, where the species' present range mostly occurs, whereas the least suitable habitats occur in northern and eastern Finland. Our predictive maps can be used to identify areas which are highly suitable, but presently are not inhabited by beavers. Such areas that could be used as reintroduction sites for the Eurasian beaver occur north and south-east from the present distribution of the species (Figs. 1 and 5a). In addition, small highly suitable areas also occur sporadically in other parts of the country (see also below the potential suitable habitats with the model with both species).

The most suitable habitats for the North American beaver seem to occur in southern and central Finland, but also occurring mostly in the species' present range (Fig. 5b). The least suitable areas occur in northern and south-western Finland. Based on the species-specific models the present range of the Eurasian beaver seems to be of low suitability for the North American beaver. However, this result partly depends on the background area used in the species-specific models, i.e. the present distribution of each species. In other words, we do not know if the habitat use of the two species would be similar in Finland if they were sympatric. According to Danilov et al. (2011b), when occupying a similar habitat, no noteworthy differences in construction activity, landscape use or diet seemed to exist between the Eurasian and the North American beaver. Additionally, Parker et al. (2012) concluded that niche overlap is virtually complete between the species, although knowledge on sympatric populations of the species is limited. For Maxent models, it is well known that the selection of background area influences model performance (VanDerWal et al. 2009). This at least partly explains the varying results we obtained with species-specific models and models with the species combined.

Thus, the models with both species combined might best predict the potential location of suitable habitats for beavers in Finland. Based on the full model of combined data, suitable habitats for beavers occur in most of southern and central Finland, and in north-western Finland, whereas the least suitable areas occur mostly in northern Finland (Fig. 5c). When taking into account only the resource factors, suitable habitats occur in most of Finland, except in a small area in north-eastern Finland. This fits the present knowledge of multiple beaver occurrences in Northern Finland better than the full model which mainly base on the occurrence of aquatic habitat types and climate. In species-specific models, when the habitat suitability maps were created based only on the resource model (i.e. forage availability), there seemed to be more suitable habitats for the Eurasian beaver, but less for the North American beaver. The most suitable areas especially for the Eurasian beaver differ greatly from those created with the full model, whereas for the North American beaver they occur in the same areas but follow more the abundance of aspen and grey alder (Figs. 2 and 5). It should be noted, that when using background data instead of true absences, AUC-values are not recommended for comparing model fit, and a model with a lower AUC-value could predict a potential distribution better than a model with a higher value, which could approximate the realized distribution more (Jiménez-Valverde 2012). Moreover, beavers are flexible in their habitat use and could therefore colonise areas outside our predicted suitable habitats. However, highly suitable areas for beavers in Finland can be seen on the maps in Fig. 5.

4.4 Management implications and conclusions

Overall, the limiting factors (aquatic habitat type and climate) and disturbance factors (agriculture and human population size) mainly predicted the habitat suitability for beavers, whereas the resource factors (forage trees) contributed only little. Indeed, climate and bathymetry or topography are often found to be the most important factors in Maxent-models (Bradie & Leung 2016), although the relative importance of different environmental variables also depends on the spatial scale of the studies (Elith & Leathwick 2009). However, when planning species conservation and mapping suitable habitats for e.g. reintroductions, adequate resources should also be available. Deciduous tree abundance (in Finland especially birch and aspen) in the riparian zone should be taken into account when estimating suitable habitats for the Eurasian beaver. In addition, terrestrial and aquatic herbs (Danilov et al. 2011) should be present and the quality of the aquatic habitat, e.g. bank slope (Hartman 1994) might be important. We did not have data for these smaller scale environmental variables, and at least the water depth should be taken into account, as beavers are reported to need a minimum water depth of 50 cm (Müller-Schwartze 2011), which our result on the importance of wider streams might also indicate. Nevertheless, the large-scale environmental factors used in this study can be utilized in planning e.g. areas for reintroductions; however, the quality of the site should be checked in the field.

Our study can be used to improve conservation planning of the Eurasian beaver and highlight the importance of also including other variables than resource variables when modelling the distribution of species. Naturally, at the territory level it is essential to have enough forage, but the favoured tree species may be related to their availability in the local environment. However, ultimately what determines distribution of beavers in Finland depends on the location of suitable aquatic habitats, climate, and human influence, including hunting. Since the environmental requirements of the beaver species are more or less similar, management of beaver populations in Finland should include eradication of the invasive beaver from areas where it is intruding on the range of the native beaver.

Species distribution models can be a valuable tool in species management and conservation, and collaboration between researchers and decision makers is advisable (Guisan et al. 2013, Jokinen et al. 2019). However, the limitations of the models should be considered when making recommendations based on the SDMs (Yackulic et al. 2013). These models rely heavily on the available data on species occurrences and evaluate the habitat suitability according to the habitat at the present species locations. Because of this, sufficient data on the species' occurrences is needed. For this citizen-science data is a valuable resource, because ecological surveys that cover large areas may otherwise be too time and cost consuming. In addition, as suggested in this study, the history of the species may play an important role in where the species occurs; this is reflected in the habitat available in the present environment of the species. Therefore, studies on habitat suitability with data from different environments could offer more comprehensive information in order for decision makers to make better management plans.

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References

Alakoski, R., Kauhala, K. & Selonen, V. (2019). Differences in habitat use between the native Eurasian beaver and the invasive North American beaver in Finland. *Biol. Invasions,* 21, 1601. https://doi-org.ezproxy.utu.fi/10.1007/s10530-019-01919-9

Brommer, J. E., Alakoski, R., Selonen, V. & Kauhala, K. (2017). Population dynamics of two beaver species in Finland inferred from citizen- science census data. *Ecosphere,* 8(9), e01947. https://doi.org/10.1002/ecs2.1947

Bradie, J. & Leung, B. (2017). A quantitative synthesis of the importance of variables used in MaxEnt species distribution models. *J. Biogeogr.,* 44, 1344–1361. doi:10.1111/jbi.12894

Danilov, P., Kanshiev, V. & Fyodorov, F. (2011). Characteristics of North American and Eurasian beaver ecology in Karelia. –In: Sjöberg, G. & Ball, J. P. (eds.), Restoring the Eurasian beaver: 50 years of experience. Pensoft, Sofia–Moscow. pp. 55–72.

Danilov, P., Kanshiev, V. & Fyodorov, F. (2011b). History of beavers in eastern Fennoscandia from the neolithic to the 21st century. –In: Sjöberg, G. & Ball, J. P. (eds.), Restoring the Eurasian beaver: 50 years of experience. Pensoft, Sofia–Moscow. pp. 55–72.

Dewas M, Herr J, Schley L, Angst C, Manet B, Landry P & Catusse M (2012). Recovery and status of native and introduced beavers *Castor fiber* and *Castor canadensis* in France and neighboring countries. *Mammal Rev.,* 42, 144–165.

Dvořák, J. (2013). Diet preference of Eurasian beaver (*Castor fiber* L., 1758) in the environment of Oderské vrchy and its influence on the tree species composition of river bank stands. *Acta Universitatis Agriculturae Et Silviculturae Mendelianae Brunensis*, https://doi.org/10.11118/actaun201361061637

Dyck, A. P. & MacArthur, R. A. (1993). Daily energy requirements of beaver (*Castor canadensis*) in a simulated winter microhabitat. *Can. J. Zool.,* 71, 2131–2135.

Elith, J. & Leathwick, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.,* 40, 677–697

Elith, J., Phillips, S. J., Hastie, T., Dudíc, M., Chee, Y. E. & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.,* 17, 43–57. doi:10.1111/j.1472-4642.2010.00725.x

ESRI. (2011). ArcGIS desktop. Release 10. Environmental Systems Research Institute, Redlands, California, USA.

Francis, R. A., Taylor, J. D., Dibble, E., Strickland, B., Petro, V. M., Easterwood, C. & Wang, G. (2017). Restricted cross-scale habitat selection by American beavers. *Curr. Zool.,* 63, 703–710. https://doi.org/10.1093/cz/zox059

Gorshkov, D. & Gorskhov, Y. (2011). Feeding strategy of beavers in Tatarstan Republic. In: Sjöberg, G., Ball, J.P. (eds.) Restoring the European Beaver: 50 Years of Experience. Pensoft, Sofia-Moscow.

Granit, A. W. (1990). Bävern i Finland. *Tidskrift för Jägare och Fiskare* 8, 45–55.

Guillera- Arroita, G., Lahoz- Monfort, J. J. & Elith, J. (2014). Maxent is not a presence–absence method: a comment on Thibaud *et al.*. *Methods Ecol. Evol.,* 5, 1192-1197. doi:10.1111/2041-210X.12252

Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.,* 8, 993–1009.

Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis I., Sutcliffe, P. R., Tulloch, A. I. T. , Regan, T. J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T. G., Rhodes, J. R., Maggini, R., Setterfield, S. A., Elith, J., Schwartz, M. W., Wintle, B. A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M. R., Possingham, H. P., Buckley, Y. M. & Arita, H. (2013). Predicting species distributions for conservation decisions. *Ecol. Lett.,* 16, 142–1435.

Hartman G. (1994). Ecological studies of a reintroduced beaver (*Castor fiber*) population. SLU/Repro Uppsala.

Hartman, G. (1995). Patterns of spread of a reintroduced beaver *Castor fiber* population in Sweden. *Wildl. Biol*., 1, 97–103. doi:10.2981/wlb.1995.0015

Hartman, G. (1996). Habitat selection by European beaver (*Castor fiber*) colonizing a boreal landscape. *J. Zool*., 240, 317–325.

Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A. & Liukko, U.-M. (eds.) (2019). The 2019 Red List of Finnish Species. Ympäristöministeriö & Suomen ympäristökeskus. Helsinki. 704 p.

Iso-Touru, T., Huitu, O., Tapio, M., Kučinskienė, J., Ulevičius, A., Bukelskis, E., Tirronen, K., Fyodorov, F., Panchenko, D., Saarma, U., Valdmann, H. & Kauhala, K. (2020). Low genetic polymorphism in the re-introduced Eurasian beavers in Finland: implications for conservation. *Mammal Res*., 65: 331–338.

Jiménez- Valverde, A. (2012). Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Glob. Ecol*., 21, 498–507. doi:10.1111/j.1466-8238.2011.00683.x

Jokinen, M., Hanski, I. K., Numminen, E., Valkama, J. & Selonen, V. (2019). Promoting species protection with predictive modelling: Effects of habitat, predators and climate on the occurrence of the Siberian flying squirrel. *Biol. Cons.,* 230, 37–46.

Kauhala, K. & Karvinen, J. (2018). Majavien elinympäristönkäyttö maastokartoitusten ja metsästäjien lähettämien pesäkoordinaattien perusteella (Summary: Habitat use of beavers based on mapping in the field and lodge coordinates from hunters). *Suomen Riista,* 64, 21–34.

Kauhala, K. & Timonen, P. (2016). Mitä majavien kallot kertovat (Summary: What do beaver skulls reveal)? *Suomen Riista* 62, 7–18.

Kauhala, K. & Turkia, T. (2013). Majavien elinympäristönkäyttö: alkuperäislajin ja vieraslajin alustavaa vertailua (Summary: Habitat use of beavers: preliminary comparison between a native and alien specis). *Suomen Riista,* 59, 20–33.

Lahti, S., Helminen, M. (1969). Suomen majavien istutushistoriasta ja Kannan levinneisyys 1960-luvulla (Summary: History of reintroductions and present population status of the beaver in Finland). *Suomen Riista,* 21, 67–75.

Lahti, S. & Helminen, M. (1974). The beaver *Castor fiber* (L.) and *C. canadensis* (Kuhl) in Finland. – *Acta Theriol*., 19, 177–189.

Liukko, U-M., Henttonen, H., Hanski, IK, Kauhala, K., Kojola, I., Kyheröinen, E-M, Pitkänen, J. (2016). The 2015 Red List of Finnish Mammal Species. Ympäristöministeriö and Suomen ympäristökeskus. 34 p.

Luke (2015). http://kartta.luke.fi/

Maanmittauslaitos (2/2015). https://tiedostopalvelu.maanmittauslaitos.fi/tp/kartta

Merow, C., Smith, M. J. & Silander, J. A. (2013). A practical guide to MaxEnt for modelling species' distributions: what it does, and why inputs and settings matter. *Ecography*, 36, 1058–1069. doi:10.1111/j.1600-0587.2013.07872.x

Müller-Schwartze D. (2011). The beaver. Its life and impact. Cornell University Press.

Nolet, B. A. & Rosell, F. (1994). Territoriality and time budgets in beavers during sequential settlement. *Can. J. Zool.,* 72, 1227–1237.

Nolet, B. & Rosell, F. (1998). Comeback of the beaver Castor fiber: an overview of old and new conservation problems. *Biol. Cons.,* 83, 165–173.

Parker, H., Nummi, P., Hartman, G. & Rosell, F. (2012). Invasive North American beaver *Castor canadensis* in Eurasia: a review of potential consequences and a strategy for eradication. *Wildl. Biol.,* 18, 354–365.

Phillips, S. J., Anderson, R. P. & Schapire, R. E. (2006). Maximum entropy modelling of species geographic distributions. *Ecological Modelling*, 3–4, 231–259, ISSN 0304-3800. https://doi.org/10.1016/j.ecolmodel.2005.03.026.

Phillips, S. J. (2017). A Brief Tutorial on Maxent. Available from url: http://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed on 2019-10-15

Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E. & Blair, M. E. (2017). Opening the black box: an open- source release of Maxent. *Ecography*, 40, 887-893. doi:10.1111/ecog.03049

Phillips, S. J., Dudík, M. & Schapire, R. E. (2018). [Internet] Maxent software for modelling species niches and distributions (Version 3.4.1). Available from url: http://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed on 2018-9-5.

Pinto B., Santos M. J. & Rosell F. (2009). Habitat selection of the Eurasian beaver (*Castor fiber*) near its carrying capacity: an example from Norway. *Can. J. Zool.,* 87, 317–325. doi:10.1139/Z09-015.

Ruys, T., Lorvelec, O., Marre A. & Bernez, I. (2011). River management and habitat characteristics of three sympatric aquatic rodents: common muskrat, coypu and European beaver. *Eur. J. Wildl. Res*. 57, 851. https://doi.org/10.1007/s10344-011-0497-y

Sjöberg, G. & Belova, O. (eds.) (2020). Beaver as a renewable resource. A beaver dam handbook for the Baltic Sea region. Interreg for Baltic Sea Region, WAMBAF. European Regional Development Fund.

Smeraldo, S., Di Febbraro, M., Ćirović, D., Bosso, L., Trbojević, I. & Russo, D. (2017). Species distribution models as a tool to predict range expansion after reintroduction: A case study on Eurasian beavers (*Castor fiber*). *J. Nat. Conserv.,* 37, 11–20.

Stephenson, A. (1969). Temperatures within a Beaver Lodge in Winter. *J. Mammal.,* 50, 134–136. doi:10.2307/1378645

Stringer, A. P., Blake, D. & Genney, D. R. (2018). *Eur. J. Wildl. Res.,* 64, 41. https://doi-org.ezproxy.utu.fi/10.1007/s10344-018-1195-9

Swinnen, K. R. R., Strubbe, D., Matthysen, E. & Leirs, H. (2017). Reintroduced Eurasian beavers (Castor fiber): colonization and range expansion across human-dominated landscapes. *Biodivers. Conserv.,* 26, 1863. https://doi.org/10.1007/s10531-017-1333-9

Tomppo E., Haakana M., Katila M., Peräsaari J. 2008. Multi-source national forest inventory – methods and applications. Managing Forest Ecosystems 18. Springer.

VanDerWal, J., Shoo, L.P., Graham, C. & Williams S.E. (2009) Selecting pseudo-absence data for presence-only distribution modelling: How far should you stray from what you know? *Ecol. Modell*., 220, 589–594. https://doi.org/10.1016/j.ecolmodel.2008.11.010

White, T. C. R. (2008). The role of food, weather and climate in limiting the abundance of animals. *Biol. Rev.,* 83, 227–248.

Wilsson L. (1971). Observations and experiments on the ethology of the European beaver (*Castor fiber* L.). *Viltrevy,* 8, 115–306.

Yackulic, C.B., Chandler, R., Zipkin, E.F., Royle, J.A., Nichols, J.D., Campbell Grant, E.H. and Veran, S. (2013). Presence- only modelling using MAXENT: when can we trust the inferences? Methods Ecol Evol, 4, 236–243. doi:10.1111/2041-210x.12004

Yiming, L. & Wilcove, D. S. (2005). Threats to Vertebrate Species in China and the United States. *BioScience,* 55, 147–153.

Ylitalo E., editor (2013). Finnish Statistical yearbook of forestry 2013. Finnish Forest Research Institute, Vammalan Kirjapaino, Sastamala, Finland.

Fig.1 The present distribution of the Eurasian and North American beavers in Finland based on the monitoring count in 2017 and species determination using skull morphometry and DNA analyses. Green = Eurasian beaver, brown = North American beaver, points = DNA analysis, squares = observations. (see also http://riistahavainnot.fi/pienriista/majavatiheys)

Fig.2 Examples of environmental variables in GIS. A) Abundance of aspen (m^3/ha in 1 km x 1 km), b) abundance of birch (m^3/ha in 16 m x 16 m), c) abundance of grey alder (m^3/ha in 1 km x 1 km), d) human population size in municipalities, e) mean winter temperature (°C) and f) distance to agricultural areas (m)

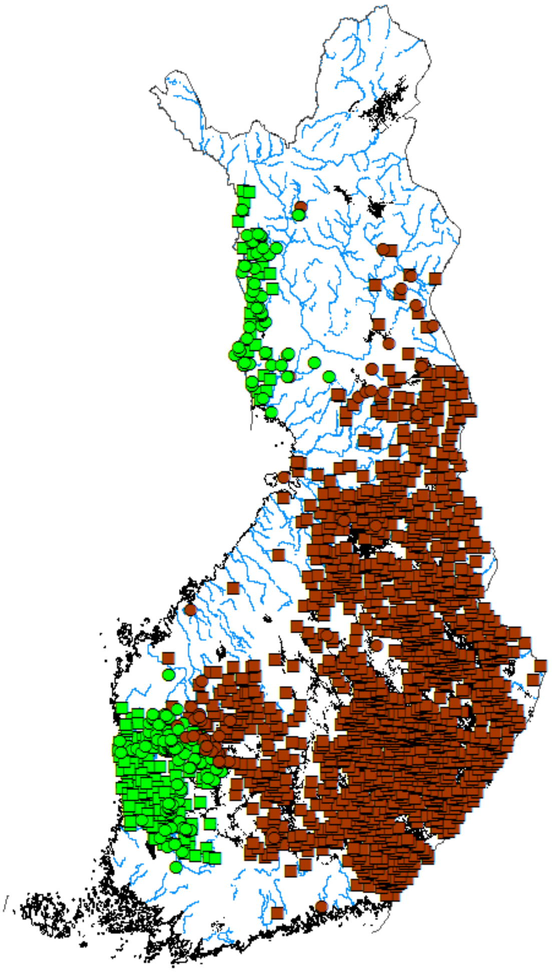
Fig.3 Response curves on how the most contributing environmental variables in the reduced model (model ii in main text) affect the Maxent prediction on habitat suitability as each variable is varied, keeping all other environmental variables at their average sample value. First column indicates the Eurasian beaver, the second column's first two figures the North American beaver and last two both species together. In the bar charts the red colour indicates the average estimate of the 15 model runs, blue indicates the highest estimate, and light blue the lowest estimate. In the line charts, red line indicates the average of the 15 runs and blue colour indicates the variation in the model estimates

Fig.4 Response curves on how the most contributing environmental variables in the resource model (model iii in main text) affect the Maxent prediction on habitat suitability as each variable is varied, keeping all other environmental variables at their average sample value. First column for the Eurasian beaver, second column's first two figures for the North American beaver and last two for both species together. In the bar charts the red colour indicates the average estimate of the 15 model runs, blue indicates the highest estimate, and light blue the lowest estimate. In the line charts, red line indicates the average of the 15 runs and blue colour indicates the variation in the model estimates

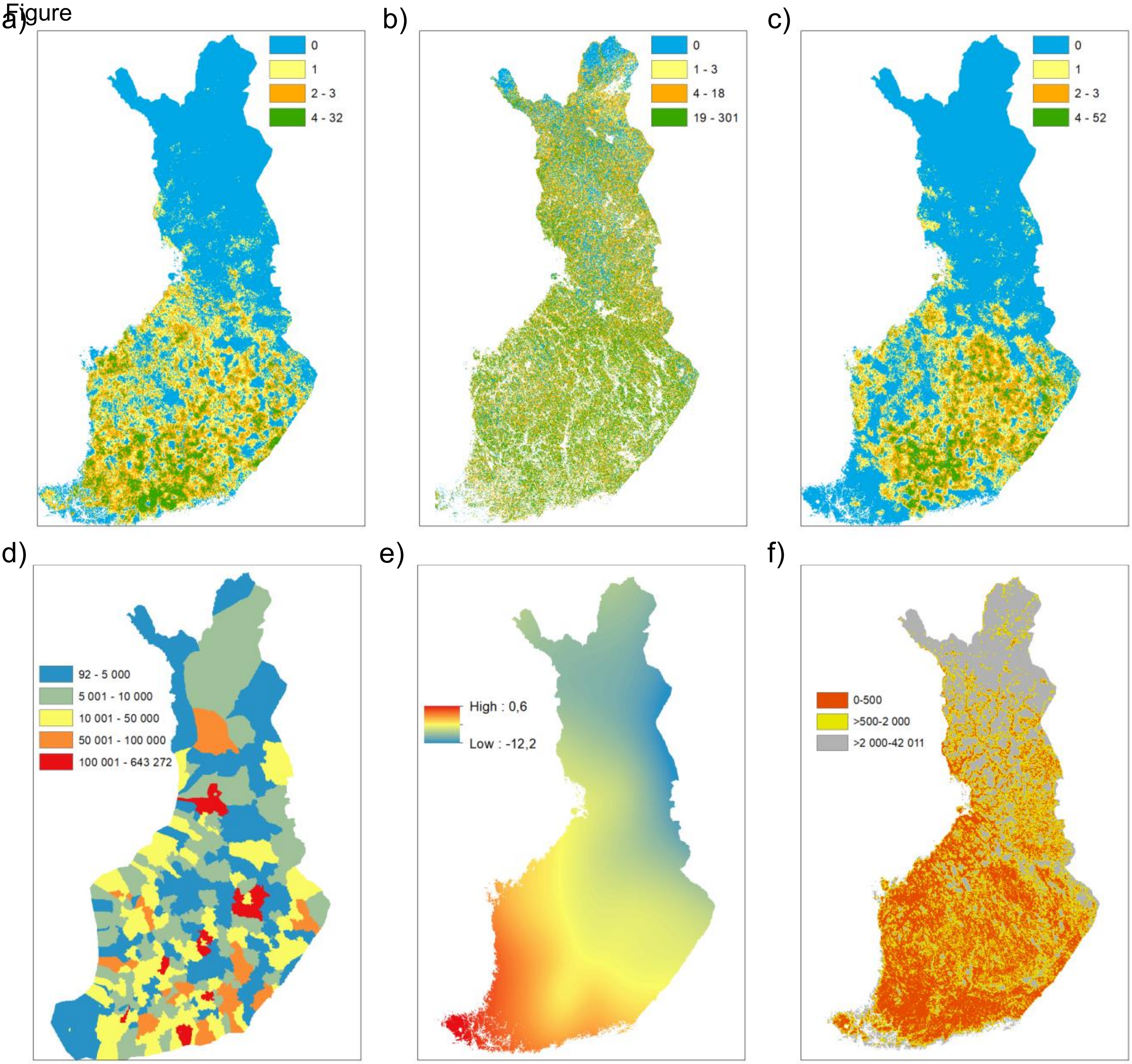
Fig.5 Maps of potential suitable habitats for the Eurasian beaver (a, d), the North American beaver (b, e) and both species modelled together (c, f). Red = most suitable habitat, yellow = medium habitat and blue = least suitable habitat. Maps produced using the averages of raw output of the full model (a–c), and the resource model (d–f), i.e. with tree species, site fertility and forest age

Fig.6 Example of suitable habitats (cell size 100 m x 100 m) based on the resource model's results for the Eurasian beaver, limited to streams and rivers with a width of >2 m in municipalities with less than 10 000 people. The area was selected so that it also included medium and most suitable habitats based on the full model's results

Figure



Figure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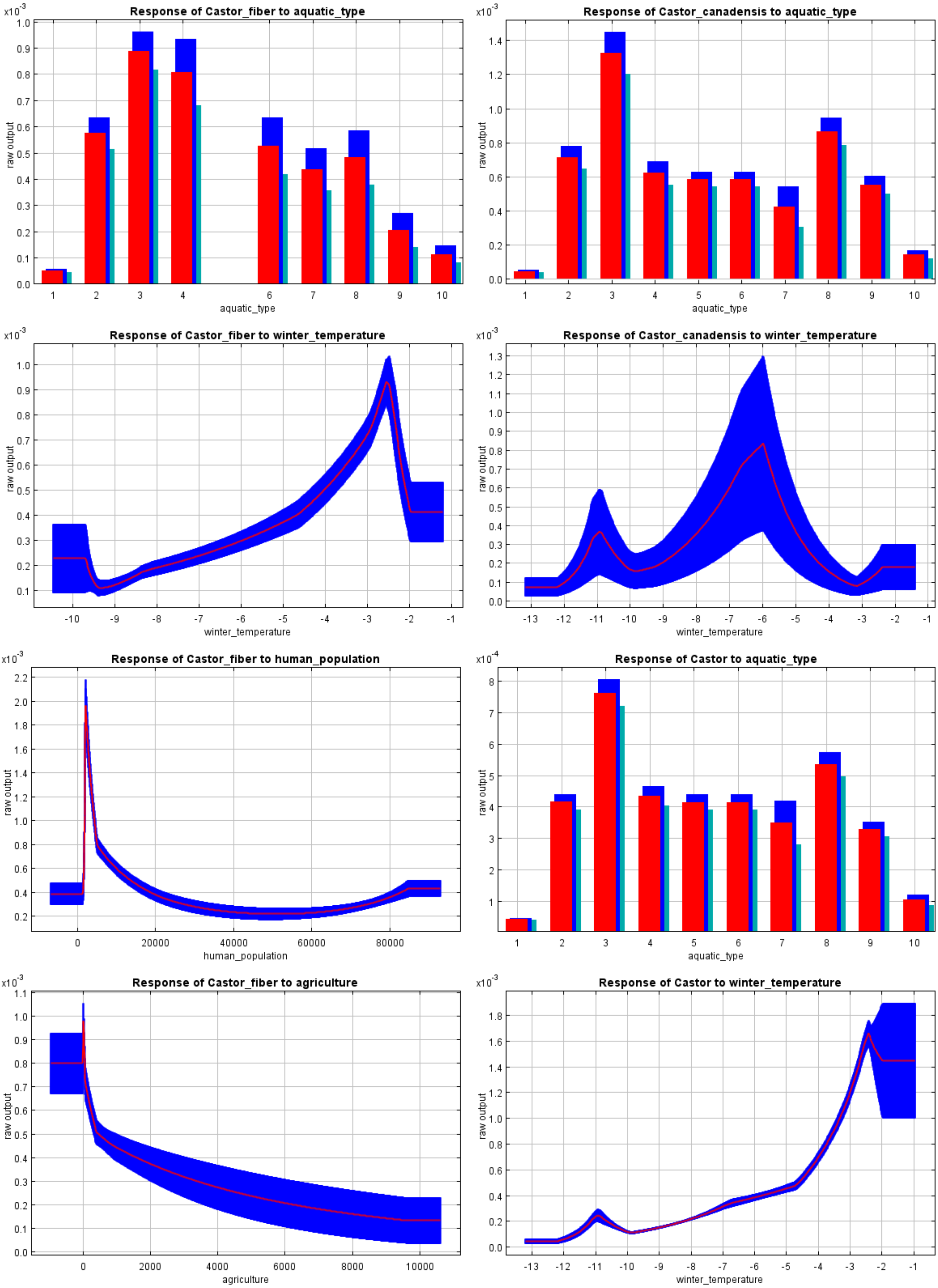
0
1
2 - 3
4 - 32
b)
0
1 - 3
4 - 18
19 - 301
c)
0
1
2 - 3
4 - 52
d)
92 - 5 000
5 001 - 10 000
10 001 - 50 000
50 001 - 100 000
100 001 - 643 272
e)
High : 0,6
Low : -12,2
f)
0-500
>500-2 000
>2 000-42 011

Figure



Response of Castor_fiber to aquatic_type

Response of Castor_canadensis to aquatic_type

Response of Castor_fiber to winter_temperature

Response of Castor_canadensis to winter_temperature

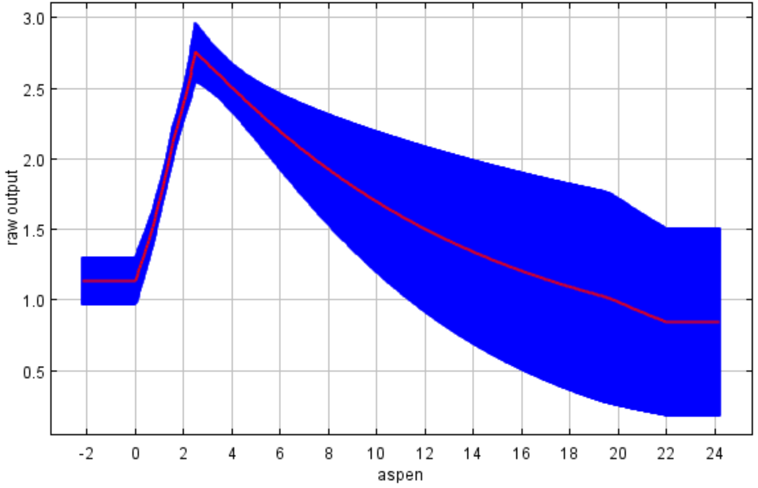
Response of Castor_fiber to human_population

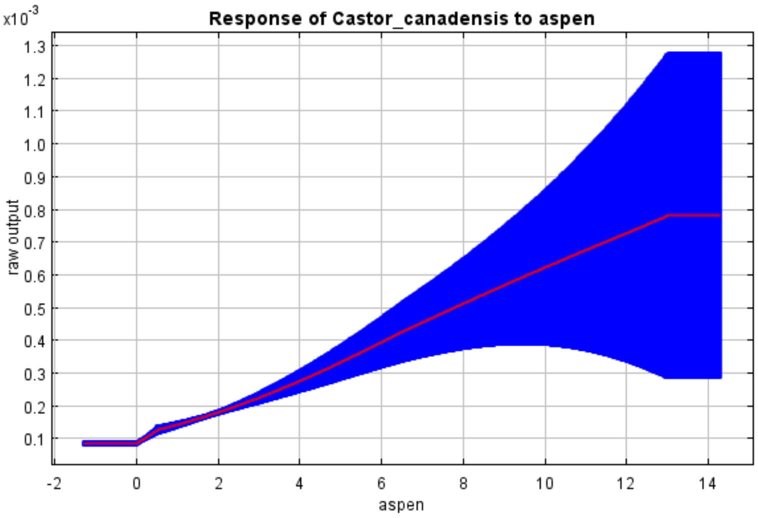
Response of Castor to aquatic_type

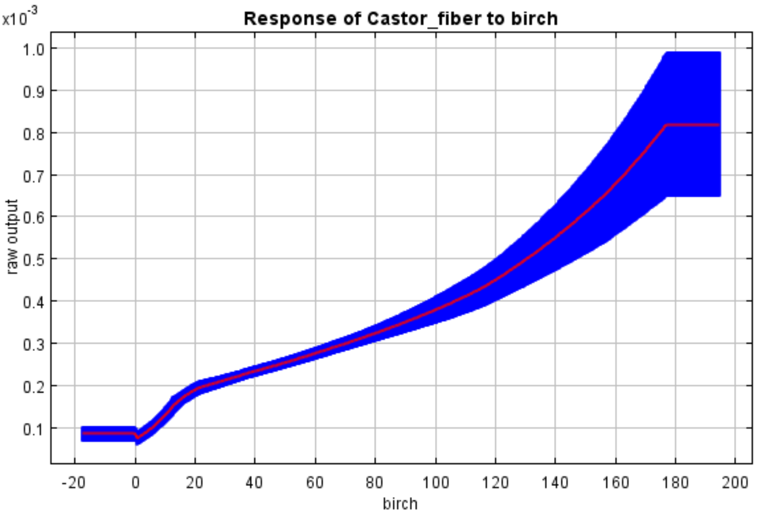
Response of Castor_fiber to agriculture

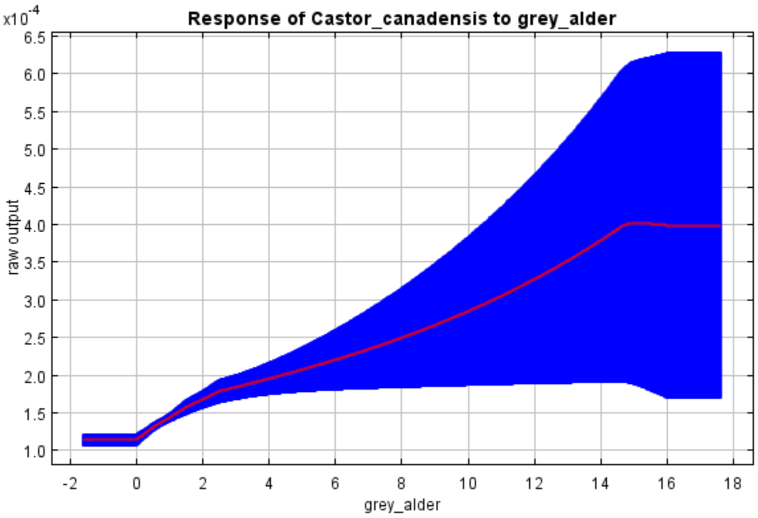
Response of Castor to winter_temperature

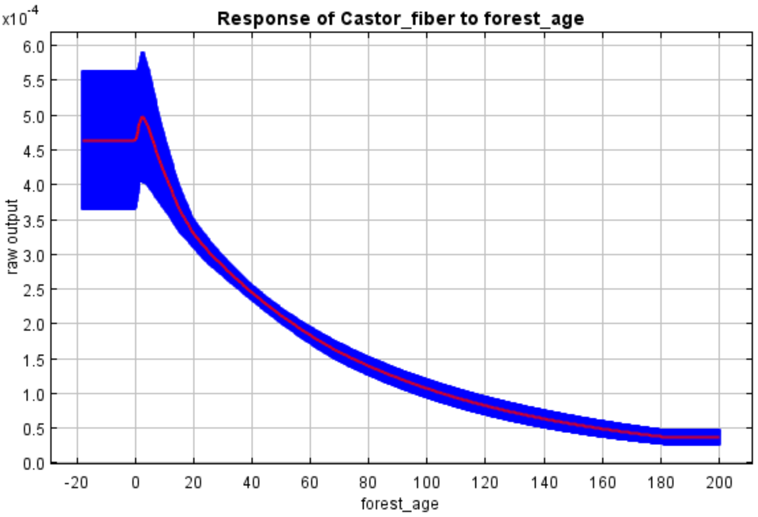
Figure

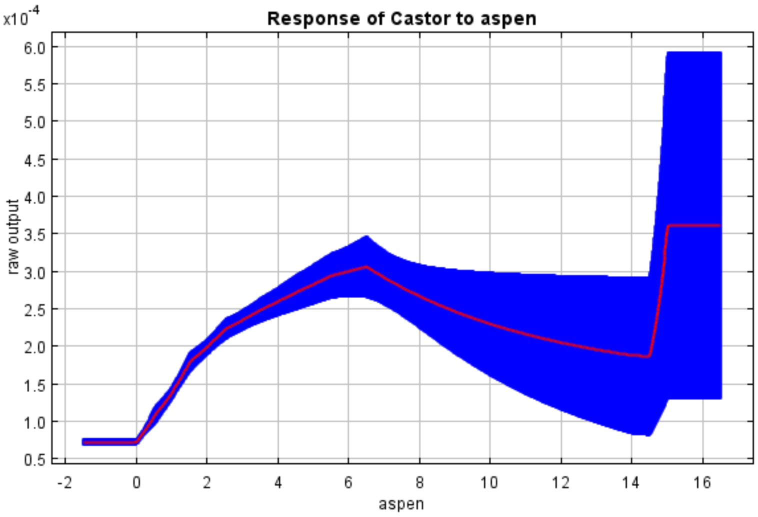

Response of Castor_fiber to aspen

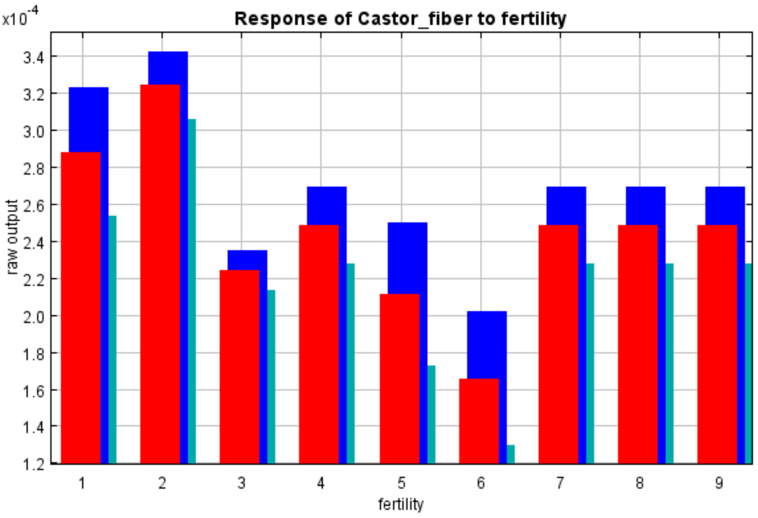

Response of Castor_canadensis to aspen

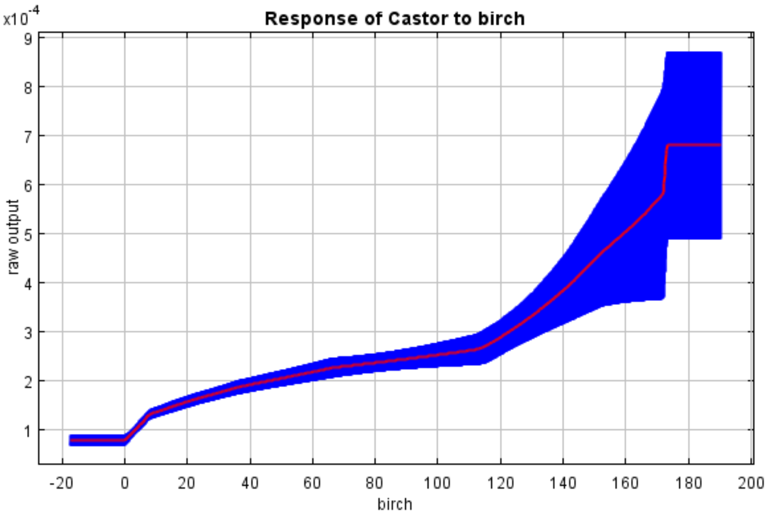

Response of Castor_fiber to birch


Response of Castor_canadensis to grey_alder

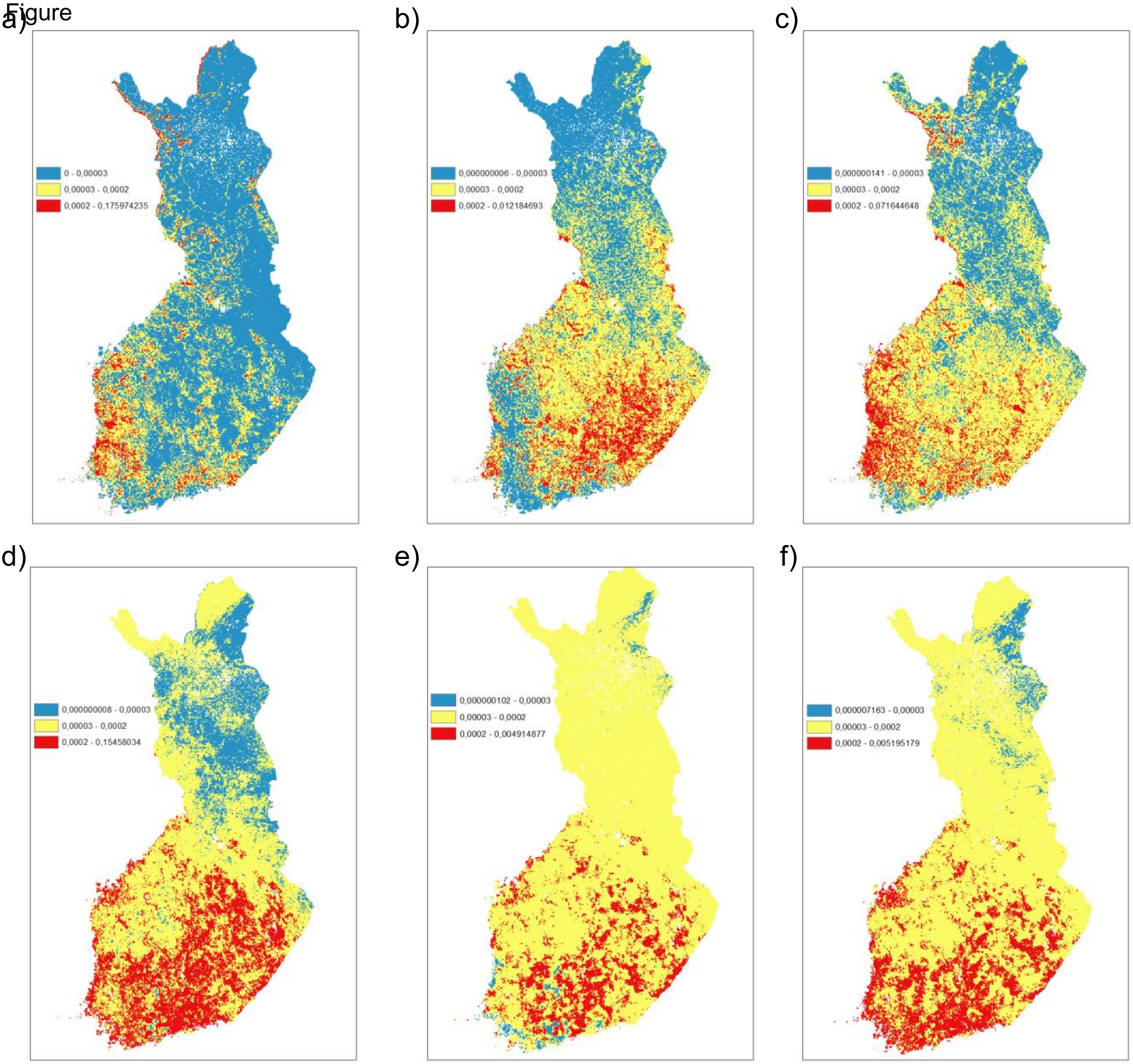

Response of Castor_fiber to forest_age


Response of Castor to aspen

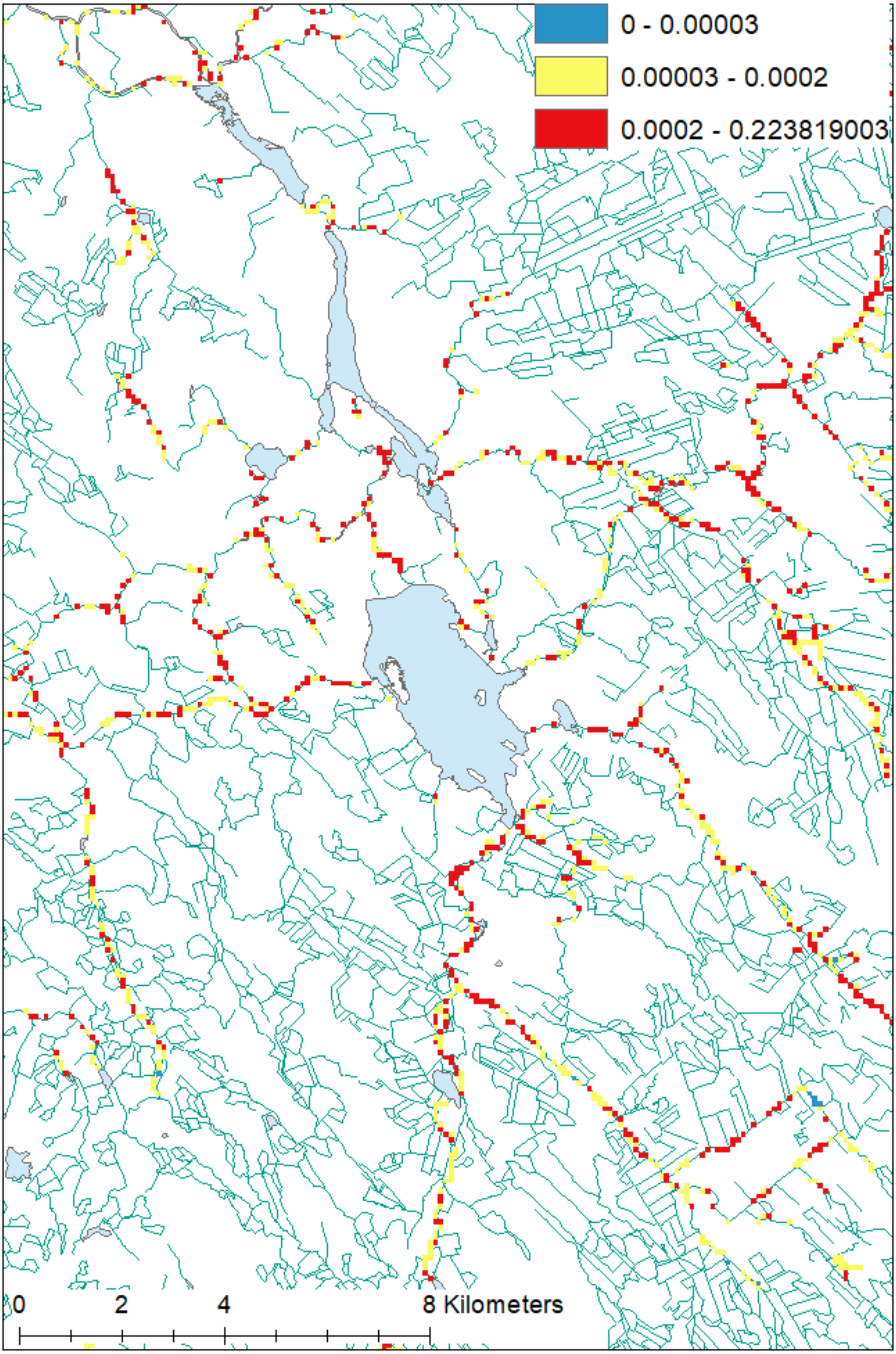

Response of Castor_fiber to fertility


Response of Castor to birch

Figure


a)
0 - 0,00003
0,00003 - 0,0002
0,0002 - 0,175974235
b)
0,000000006 - 0,00003
0,00003 - 0,0002
0,0002 - 0,012184693
c)
0,000000141 - 0,00003
0,00003 - 0,0002
0,0002 - 0,071644648
d)
0,000000008 - 0,00003
0,00003 - 0,0002
0,0002 - 0,15458034
e)
0,000000102 - 0,00003
0,00003 - 0,0002
0,0002 - 0,004914877
f)
0,000007163 - 0,00003
0,00003 - 0,0002
0,0002 - 0,005195179

Figure


0 - 0.00003
0.00003 - 0.0002
0.0002 - 0.223819003
0
2
4
8 Kilometers