Are historical land use patterns and chemical soil characteristics complementary for assessing the restoration potential of Nardus grassland?

Restoration potential of Nardus grassland

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ABSTRACT

Aims: Historical land use legacies and chemical soil characteristics both explain either directly or indirectly the habitat quality of Nardus grassland, which is protected under the European habitat directive. Yet the relative importance and complementarity of both sets of variables are generally unknown. This knowledge is also relevant for practical reasons, as historical land use variables can be used in desktop spatial analyses, whereas soil characteristics require field surveys to collect samples for laboratory analyses. To this end, we aim to disentangle the relative importance of historical land use legacies and soil chemistry for the Nardus grassland quality, and determine the potential of habitat suitability mapping for predicting potential restoration areas.

Location: Natura 2000 grasslands in Flanders (northern Belgium)

Methods: We compared the model performance of three generalized additive models (GAM), using either land use history metrics, soil chemistry, or both as explanatory variables, with the Nardus grassland indicator species count as response.

Results: All three models were able to predict areas suitable for at least 3 Nardus grassland indicator species with high sensitivity and specificity. However, minimum 4 indicator species are required for a favorable conservation status of Natura 2000 Nardus grasslands in Flanders. Using this threshold to detect high priority zones, the model based on historical land use variables resulted in a lower sensitivity than models which included soil chemistry.

Conclusions: We suggest a two-step approach, with an a priori desktop spatial analysis based on historical land use variables subdivided in a high priority zone and lower priority zone. If the targeted area for restoration or conservation can be found within the high priority zone, additional soil analysis are only required to help guide conservation and restoration measures. If additional sites are considered within the lower priority zone, a field survey to collect additional soil data is recommended.

KEYWORDS

Habitat distribution model, Historical land use, Soil chemistry, Vegetation science, Ecological restoration, Species-rich grassland, Natura 2000, Sensitivity, Specificity

INTRODUCTION

Targeted conservation and restoration of specific habitat types undergoing anthropogenic pressures require a thorough understanding of how global environmental changes affect ecosystem patterns (biotic) and processes (abiotic). Contemporary habitat conditions are mainly determined by historical land use change, which has been considerate in Europe (Goldewijk, 2001; van Vliet *et al.*, 2015). The effect of land use legacies and its importance for conservation has often been emphasized but has been rarely examined for specific ecosystems. However, this is essential to understand how land use legacies affect contemporary and potential natural vegetation (Perring et al., 2016). This is especially the case for species communities with a slow-growth strategy which are sensitive to land use intensification due to competitive pressures, such as species-rich Nardus grassland (syntaxonomic class *Nardetea strictae*; Van Daele et al., 2017).

Species-rich Nardus grassland occurs in 24 countries and 6 different bioregions in Europe on oligotrophic and acidic soils with a high siliceous fraction (Galvánek and Janák, 2008). Nardus grassland is a priority habitat for conservation and restoration in the European habitats directive (92/43/EEC; Convention on Biological Diversity 2014), as it is species-rich, of high cultural value, and has seriously declined in the past century (Critchley, Burke and Stevens, 2004). The main drivers of this decline are eutrophication, acidification, fragmentation, loss of traditional management practices and land abandonment (Soons *et al.*, 2005; Bobbink *et al.*, 2010; Stevens *et al.*, 2011). Reinstating the original management practices, i.e. mowing or grazing, is often insufficient and measures to restore the abiotic and biotic conditions can be necessary (Schelfhout *et al.*, 2017). However, ecological restoration can be very costly or can have negative side effects (Török *et al.*, 2011), and therefore careful selection of sites with a high restoration potential is essential (Burnside, Smith and Waite, 2002). For this purpose it is necessary to understand the factors that determine Nardus grassland habitat quality.

The habitat quality of acidic grasslands can be explained by chemical soil characteristics to a high degree (Janssens *et al.*, 1998; Kleijn *et al.*, 2008; Ceulemans *et al.*, 2013). Increased availability of N, P, K, often as a result of fertilization, stimulates biomass production, alters the feedback between aboveground and belowground communities and reduces the species richness of grasslands through competitive exclusion (Wardle, 2004; Crawley *et al.*, 2005; Leff *et al.*, 2015; Van Daele *et al.*, 2017). Furthermore, nitrogen deposition and the resulting acidification have been identified as important drivers of degradation (Bobbink *et al.*, 2010; Duprè *et al.*, 2010).

Whereas many studies have unraveled the relationship between soil chemistry and Nardus grassland species richness, historical land use patterns have received less attention. Yet historical land use determines present-day species richness of grasslands in many ways, either directly or indirectly by affecting other explanatory variables. Historical land use is a major determinant for the physico-chemical and biotic properties of the soil, and also for the composition of the soil seed bank (Cousins, 2009). Land use changes can cause habitat loss and reduce connectivity, thus reducing the metapopulation capacity (Hanski and Ovaskainen, 2002). However, grasslands can maintain a high diversity that reflects historical connectivity, even when they are currently isolated (Lindborg and Ove Erikksson, 2004; Auffret, Plue and Cousins, 2015). Furthermore, current species richness is not only determined by the continuity of Nardus grassland itself, but also by historical presence of land use types that can harbor Nardus grassland species, such as heathland, open woodland and forest edges (Van Calster *et al.*, 2008). For these reasons, the inclusion of land use legacies is considered to be essential to predict future ecosystem patterns and processes (Perring *et al.*, 2016).

Land use legacies can be quantified in distinct time slices represented by historical maps, and can be used to model the effects of the historical landscape configuration on the present-day distribution of species and communities (Guisan, Zimmermann and Thuiller, 2017). Application of the resulting statistical function on relevant spatially explicit variables, can generate a suitability map. Such a map displays the predicted suitability for target species or communities, and can be used to identify potential areas for conservation and ecological restoration (Ferrier and Guisan, 2006; De Keersmaeker *et al.*, 2014; Guisan, Zimmermann and Thuiller, 2017). A suitability map could be cost-effective, as it can be used in a desktop analysis, whereas many other explanatory variables, e.g. chemical soil characteristics, require a time-consuming field survey.

The aim of this study is to evaluate the statistical complementarity of historical land use variables and chemical soil characteristics in predicting the potential number of Nardus indicator species, as a proxy of Nardus grassland quality. To this end, we compare three models with either historical land use characteristics, chemical soil variables, or both as explanatory variables. The model with only historical land use characteristics offers the opportunity to construct a habitat suitability map, and we aimed to explore this pathway for a study area with a heterogeneous land use history.

METHODS

Study area

Our study area covered most of Flanders (Fig 1), the northern part of Belgium (13,500 km^2). Belgium has a temperate maritime climate with little regional variability, cool summers and moderate winters. The average temperature is 9.8°C with a minimum monthly average of 2.5°C in January and a maximum of 17.8°C in July. Average rainfall amounts to 925 mm/year (KMI, 2016). Sand and loamy sand are the most abundant soil textures in the north of Flanders, while the south of Flanders is mainly covered by silty loam and sandy loam. Polders and the coastal areas are generally characterized by the presence of clay and clay loam (Zomlot *et al.*, 2015). Species-rich Nardus grassland (habitat code 6230) is a threatened Natura 2000 habitat in Flanders that only covers 250-300 ha, and it is aimed to restore an additional 250 ha over the next years (INBO, 2016).

Response data

To model the potential habitat suitability for Nardus grassland we used a vegetation database with 1728 georeferenced surveys of Natura 2000 grassland habitat in Flanders (INBO, 2015). The dataset comprised the vegetation composition, sampled between 2001 and 2013 in plots with standard dimensions of 3 m * 3 m. The habitat quality of the Natura 2000 type 6230 is assessed by the number of Nardus grassland indicator species (Oosterlynck *et al.*, 2020). A total of 12 indicator species, representative for a favorable local conservation status in Flanders, were selected: *Galium saxatile, Nardus stricta, Polygala vulgaris, Potentilla erecta, Viola canina, Festuca ovina agg., Carex pallescens, Platanthera bifolia, Veronica officinalis, Carex panicea, Gentiana pneumnonanthe* and *Pedicularis sylvatica.* The count of these Nardus grassland indicator species in a vegetation plot was used as response variable.

From this vegetation database, we selected plots for which chemical soil variables (Olsen phosphorus, ammonium, nitrate, pH, total aluminum, exchangeable potassium and organic matter) were also available. To ensure all land use metrics could be determined, vegetation plots located within 1000 meter of the border of Flanders were removed. Plots with at least one indicator species were randomly selected, with a minimum neighborhood distance of 200 meters between plots, as determined by a threshold buffer, to avoid autocorrelation. The number of grassland plots without indicator species was limited to approximately 20% of the selection to reduce zero inflation, and these plots were randomly selected within 1000 meters proximity of plots with at least one indicator species. This procedure resulted in the selection of 225 Natura 2000 grassland plots, 52 of which contained no Nardus indicator species. The same procedure was used to obtain a validation dataset, used for the model only based on historical land use. This validation dataset contained 84 grassland plots of which 26 without indicator species.

Explanatory data

Chemical soil characteristics

Soil chemical properties were determined based on soil mixture samples (5 cores) collected in 2012 and 2013. Soil samples were air-dried at 40°C and after drying, crushed with a jaw crusher and sieved till 2mm. Samples for total analysis were further reduced till 100 µm with a ball mill. Olsen P values were determined by shaking 1 g dry soil for 30 min at 200 rpm with 0.5 M $NaHCO_3$ at pH 8.5 and subsequent colorimetric analysis of the extracts using the blue ammoniummolybdate method with ascorbic acid as reductor. Color in the extract was removed with 1M sulfuric acid. Concentrations of total aluminum (Al_{tot}) were measured with an inductive coupled plasma atomic emission spectrometer (ICP-AES; ISO 22036, 2008) after microwave digestion in a mixture of hydrochloric and phosphoric acid (3/1:v/v) for 10 min at 175°C. To measure exchangeable potassium, the soil sample was first mixed with a single extraction with dilute unbuffered silver-thiourea (AgTU) solution (0.01 M Ag + 0.1 M TU) and then measurements were performed with the ICP-AES (Silver Thiourea Method – BBI, 2014). Loss-on-ignition (LOI) was used to estimate % soil organic matter (SOM). To determine the percent LOI, a crucible with an air-dried subsample (40°C) was combusted at 550 °C for 4 h. The pH (pH-H_2O) was measured potentiometrically in a soil/water extract (1/5:m/m). Soil extractable nitrogen (NO_3^- and NH_4^+) was extracted from air-dried soil samples using a 1 M KCl solution and subsequent analyzed on a continuous flow analyzer. Nitrite and nitrate nitrogen were spectrophotometrically analyzed with sulphanilamide and N-(1-naphtyl)-ethylene-diamine dihydrochloride as a red-violet dye. Nitrate was reduced to nitrite before analysis. Ammonium nitrogen was spectrophotometrically measured with the adjusted Berthelot's reaction (ISO 11732, 1997).

Landscape and historical land use characteristics

We determined 48 nearest neighborhood (NN) variables of all selected Natura 2000 grassland plots, measured as the distances towards the edges of land use patches, displayed by six historical maps using ArcGIS 10.3.1 (Table 1). The map legends indicated that eight land use classes could be distinguished: heathland, grassland, arable land, orchard, forest, open water, marshland and buildup areas. The NN measurements could be either negative or positive, depending on whether the vegetation plot was located within or outside the land use patch, respectively (De Keersmaeker *et al.*, 2014). The metrics were not calculated on present-day land use, as we aimed to assess the restoration potential and predict potential Nardus grassland species richness. Furthermore, NN distances to unnavigable watercourses were determined as positive distance values to linear elements, e.g. to assess effects of nutrient and sediment deposition.

Potential collinearity between variables was assessed based on Pearson correlation coefficients, Ward clustering and the relationships between variables (Appendix S1, Table S1, Fig. S1-S5). If land use classes were highly correlated (r > 0.7) and clustered (Harrell, 2001; Dormann *et al.*, 2013), similarity between GAM response patterns were evaluated (see “Modelling and validation procedure”). Open water and marshland had little to no effect on the occurrence of Nardus grassland indicator species and both correlated land use classes were reclassified to a new water class. Similarly, orchards and arable land were reclassified as cultivated land (see Appendix S1 for a more in depth assessment). Measurements on maps from 1865 and 1920 were excluded from the analysis based on their similarity to the respective measurements on maps from 1890 and 1960, respectively. Finally 12 historical variables, and the NN to unnavigable watercourses, were selected for the modeling procedure. A principal component analysis of the selected variables displayed an appropriate spread of metrics over the four distinct time slices (Appendix S1, Fig. S6). All analyses were executed in R version 3.2.3 (R Development Core Team, 2015), using the package cluster version 2.0.6 (Maechler *et al.*, 2017).

Modelling and validation procedure

Based on the Moran's I index, the selected sample plots were randomly distributed and there was no indication that spatial autocorrelation was relevant for the modelling procedure (Moran's index = 0.1, z = 1.4, p = 0.15). Partial effects of the explanatory variables on the number of Nardus grassland indicator species were analyzed using a generalized additive model (GAM). Penalized regression splines were used to fit noisy observations in the GAM (k = 4). The NN measurements, expressed in km, were transformed using an inverse logit transformation to reduce the effect of outliers. Values beyond the measured NN observations were appointed the maximum rescaled value of 1 (equaling ca 5 km). The Nardus indicator species number per plot was identified as an over-dispersed count and was thus modelled with a quasi-Poisson distribution. Smoothed response shapes of predictor variables, when other land use classes were fixed at a 50 m distance, were used to illustrate partial effects of independent land use classes.

The spatially explicit model (model 1), based on the 13 selected landscape variables, was compared to a hybrid model which additionally integrated 7 chemical soil variables (model 2), and to a model based on the soil chemical variables alone (model 3). Stepwise regression was used for each GAM with a backwards selection procedure using the mgcv package, version 1.8–22, in R (Wood, 2006, 2011). As a validation for model 1, the mean absolute error and root mean square error between simulated and observed values were calculated on the training and the validation datasets. The predictive capacity of the spatially explicit model (model 1) in delineating areas for conservation and restoration was assessed based on a 1000-fold cross-validation with a 30% validation partition to determine model performance. The model performance was assessed by the sensitivity, the specificity, the positive predicted value (PPV), the negative predictive value (NPV), the true skill statistic (TSS), and the accuracy. These metrics were determined based on a confusion matrix of the true positives (TP), the false positives (FP), the true negatives (TN), and the false negatives (FN). The sensitivity illustrated the ability of the model to correctly identify suitable areas ($Sensitivity = \frac{TP}{TP+FN} * 100$),while the specificity depicted the ability of the model to correctly identify unsuitable areas ($Specificity = \frac{TN}{FP+TN} * 100$). The positive predictive value (PPV) quantified the probability that predicted suitable areas were observed as suitable ($PPV = \frac{TP}{TP+FP} * 100$), while the negative predictive value (NPV) quantified the probability that predicted unsuitable areas were observed as unsuitable ($NPV = \frac{TN}{FN+TN} * 100$). The true Skill Statistic (TSS) places equal weight on the sensitivity and specificity, with values ranging between -1 and 1 ($\text{TSS} = \{\frac{TP}{TP+FN} + \frac{TN}{FP+TN}\} - 1$). The accuracy quantified the ratio of correct predictions relative to the total amount of total predictions ($Accuracy = \frac{TP+TN}{TP+TN+FN+FN} * 100$). To evaluate the relationship between model performance and the Nardus grassland indicator species threshold, we evaluated the relationship between the sensitivity and the specificity for thresholds ranging from 1 to 12 species with a precision of 1. The sensitivity and specificity (performance metric) was modelled with a general linear model:

$$glm(performance\ metric \sim threshold\ * \ metric\ type, family\ =\ quasibinomial)$$

with the performance metric as percentages, the threshold ranging from 1-12 predicted Nardus grassland indicator species, and the metric type as a binary factor. Habitat suitability mapping

We selected a compact test area of 2424 ha designated as a Natura 2000 area (Fig. 1) near the village of Malle, located in the Campine region with predominantly sandy soils. Relevant landscape characteristics (model 1) were determined in a 10 m * 10 m resolution grid, and the same grid extent and resolution was used to predict the potential number of Nardus grassland indicator species and its 95 % confidence interval. Habitat patches with a favorable conservation status require at least 4 indicator species (Oosterlynck *et al.*, 2020), and this threshold was used to delineate high priority zones for conservation and habitat restoration. Additionally, a lower priority zone was delineated based on a threshold of 3 up to 4 Nardus grassland indicator species, which coincided with the intersection of the sensitivity and specificity. To determine the ecological validity of the predictions, we calculated the proportion of Nardus grassland and other land use types in both the high priority zone and lower priority zone (INBO, 2016).

RESULTS

Model 1, using only historical landscape characteristics, explained 25.4% of the deviance in Nardus grassland indicator species occurrence. The root mean square error of the training data was 2 indicator species and was similar when applied to the validation data (1.8). The proximity of grassland in 1960 had the strongest negative effect on the occurrence of Nardus grassland indicator species (Table 2), up to approximately 500 m distance (Fig. 2). A similar but weaker effect was observed for grassland in 1890. The proximity of heathland in 1777 and forest in 1890 had a strong positive effect on the current number of Nardus grassland indicator species. The partial effect of cultivated areas in 1960 displayed a slight positive effect. The proximity of rivers had a slight negative effect up to approximately 750 m. With a threshold of at least 4 Nardus grassland indicator species, the specificity indicates that 89.9% of the observed unsuitable areas were predicted as unsuitable areas (Table 3). The negative predictive value indicated that predicted unsuitable areas had a 77.7% probability of being observed as unsuitable. However, sensitivity was much lower, as only 37.9% of the area containing at least 4 observed indicator species was predicted as potentially suitable according to model 1. The positive predicted value determined that there was a 61% probability that predicted suitable areas were also observed as suitable. With a threshold of 3 indicator species the sensitivity increased to 71.9%, which indicates a strong reduction of false negatives and an increased potential to identify observed suitable areas (Fig. 3). This is also reflected in the increased TSS of 0.44 for a threshold of 3 Nardus indicator species compared to a TSS of 0.28 with a threshold of 4 indicator species. This was the result of a steep reduction of the sensitivity compared to the increase in specificity at a threshold of 4 Nardus grassland indicator species (Fig. 3).Model 2 which included both landscape and soil chemical variables (Table 3) explained 52.2% deviance, 26.8% more than model 1. The partial effects of the soil variables in model 2 were all significant, and their inclusion made several landscape variables redundant (Table 2). NN distances on cultivated land in 1960, grassland in 1850 and rivers were removed during the backward selection procedure of model 2. The partial effect of NN from heathland in 1777 was retained, but not significant anymore. With a threshold of 4 Nardus grassland indicator species, the specificity of model 2 (89.3%) was similar to that of model 1. However, the sensitivity of the model containing both landscape and soil chemical variables equaled 62.1%, which is higher than the value of model 1 which was based on landscape variables alone (37.9%). With a threshold of 3 Nardus grassland indicator species the sensitivity was similar (75.3%) to model 1 which was based on landscape variables alone (71.9%). Even though the sensitivity intersected with the specificity at a threshold of 3 Nardus indicator species (Fig. 3), the overall true skill statistic was lower (0.48) compared to a threshold of 4 Nardus indicator species (0.51). This was the result of a less steep reduction of the sensitivity compared to the increase in specificity at a threshold of 4 Nardus grassland indicator species (Fig. 3).Model 3, only based on soil chemical variables, explained 45.3% deviance, which is slightly less than the hybrid model 2 but more than model 1 (Table 3). The concentration of total aluminum, organic matter, Olsen phosphorus, ammonium and exchangeable potassium were all significant explanatory variables of Nardus grassland species richness. Nitrogen oxide and pH were also included in model 2 and 3 but only had a slight effect (Table 2). When only biochemical variables were included (model 3), the specificity was lower (66.9%) with a threshold of 3 Nardus grassland indicator species compared to a threshold of 4 (86.8%). On the other hand, the sensitivity was higher with a threshold of minimum 3 (76.4%) species compared to a threshold of minimum 4 species (62.1%). Even though the sensitivity intersected with the specificity at a threshold of 3 Nardus indicator species, the overall true skill statistic was lower (0.43) compared to a threshold of 4 Nardus indicator species (0.49). This was the result of a less steep reduction of the sensitivity compared to the increase in specificity at a threshold of 4 Nardus grassland indicator species (Fig. 3).

Application of model 1 to the test area (Fig. 3) revealed that the predicted indicator species number ranged from 1.2 to 5.2 indicator species (Fig. 4), with a confidence interval (CI) ranging from ± 1.4 to 2.4. (Fig. 4). Based on the projected suitability in the test area, there was a conservation and restoration potential of 106.1 ha (5.5% of the total test area) in the high priority zone with at least 4 predicted indicator species, of which 4.3% is currently covered by Nardus grassland. For the area covered by Nardus grassland according to the contemporary NARA land use map (Poelmans and Van Daele, 2014), model 1 predicted an average of 3.6 ± 0.6 (mean ± SD) indicator species. The rest of the high priority zone was covered by heathland (2.1%), forest (78.5%), pasture (9.3%), cultivated land (3.0%), urban area (2.5%) and water (0.2%). A total of 403.3 ha was delineated in the lower priority zone and had a predicted Nardus grassland indicator species count between 3 and 4 according to model 1. This area was covered by heathland (7.3%), forest (70%), pasture (10.2%), cultivated land (6.8%), urban area (5.1%) and water (0.6%) according to the contemporary NARA land use map (Poelmans and Van Daele, 2014).

DISCUSSION

Spatio-temporal metrics in suitability modelling

Habitat suitability models are widely used to quantify a community's realized niche and predict the likelihood of occurrence in unsurveyed areas. Although it is accepted that some explanatory variables are not integrated and that not all niches are colonized (Guisan, Zimmermann and Thuiller, 2017), factors explaining the plant community niche have to be predominantly integrated in the model (Elith *et al.*, 2006; Öster *et al.*, 2009). To predict the potential suitability for plant communities in time, e.g. as a tool for ecological restoration, it could be a viable strategy to focus on past land use and omit present day landscape variables for suitability modelling (De Keersmaeker *et al.*, 2014).

Historical connectivity and past management explain current diversity patterns in semi-natural grasslands (Lindborg and Ove Erikksson, 2004; Gustavsson, Lennartsson and Emanuelsson, 2007; Cousins, 2009). However, the past distribution of habitat types and the characteristic plant communities are generally not depicted in historical maps. Furthermore, detailed qualitative information on management history (e.g. fertilization) are mostly lacking. Each map unit of a specific time slice has a distinct suitability or impact, explained by drivers such as seed bank survival (Bekker, Verweij and Smith, 1997) and soil chemistry (Kleijn *et al.*, 2008). This complicates the application of mechanistic incidence function models (IFM) that are developed for patch and meta population dynamics, but require information about patch occupancy and connectivity which are not available for our study (Hanski, 1994). By contrast, the use of NN metrics can encompass proxies for connectivity and environmental quality, which can be adequate for suitability modelling. NN measurements can yield accurate results, when they are used for species sensitive to the landscape matrix (Fagan and Calabrese, 2006) or for species with remnant population dynamics, e.g. ancient forest species (De Keersmaeker et al. 2014). The latter could also apply for grassland specialists, that disperse step wise and decrease linear with the distance from their remnant habitat source (Cousins & Lindborg 2008). An additional advantage of the NN metrics that we applied, is that the negative values within and positive values outside land use patches can deal with positional errors of historical maps (De Keersmaeker et al. 2014). Furthermore, this approach can account for habitat edge effects or soil gradients that could explain the presence of Nardus grassland species, e.g. near forest edges, or near field islets on loamy soil (De Graaf *et al.*, 2009).

Impact of land use legacies on Nardus habitat quality

A substantial amount of plots with a high count of Nardus grassland indicator species were located within or near forests in 1890. Several of these indicator species can occur in forests or forest edges (Eriksson, 1996; Cousins and Eriksson, 2002; Gustavsson, Lennartsson and Emanuelsson, 2007; Cousins and Aggemyr, 2008; Van Calster *et al.*, 2008). These species generally have a transient seed bank and emerge from the seed bank when the light conditions change due to disturbances, e.g. forest clearing (Hermy, 2015). Before the late 19th century, forests were intensively managed (e.g. grazed) and thus included more species that are presently classified as grassland or heathland species (Olff *et al.*, 1999; Van Calster *et al.*, 2008; Hermy, 2015). Furthermore, grasslands converted to forest in the 19th century are unlikely to contain high nutrient concentrations and thus exhibit suitable physicochemical properties for species-rich Nardus grasslands (Johansson *et al.*, 2008), as opposed to sites continuously managed as grassland that have most likely received fertilization in the 20th century. Consecutive short interval cutting, e.g. during the first (1914-1918) and second World War (1940-1945) and mowed or grazed firebreaks could explain survival of these species in forest environments (De Keersmaeker *et al.*, 2011).

A large amount of grassland points, with a high number of Nardus grassland indicator species, was heathland in 1777 or occurred in its vicinity. Species-rich Nardus grasslands are often closely related to heathland and they can occur together as a mosaic (Galvánek and Janák, 2008). Nardus grassland and heathland both indicate little or no fertilization, but heathland predominantly occurs on acidic sandy soil, whereas Nardus grassland is restricted to soils with a pH > 5, e.g. loamy outcrops (Roem and Berendse, 2000). Both can occur together as a mosaic and it is therefore likely that historical map units described Nardus grassland as heathland.

Arable land use legacies limit dispersal and establishment and thus reduce the potential for successful restoration of species-rich grassland communities (Öster *et al.*, 2009; Ceulemans *et al.*, 2014), yet the suitability model indicated an increase of Nardus species near areas cultivated in 1960. Former arable fields could indicate extensively managed old field islets or verges with remnants of species-rich communities (Cousins & Lindborg, 2008; Cousins, 2006) and are often located on productive sites with slightly higher loam and clay fractions (Cousins, 2009), suitable for Nardus grasslands (Roem and Berendse, 2000).

Grassland management in 1960 clearly had a detrimental effect on the Nardus grassland species number. Between 1958 and 1990 livestock production caused an increase of manure input in Flanders (van Wesemael *et al.*, 2010), which attributed to a high phosphorus surplus on agricultural land in Belgium (Eurostat, 2009). This surplus causes a phosphorus accumulation in the soil and can also affect surrounding land, e.g. by surface runoff (Smith *et al.*, 1998). Increased phosphorus levels are highly unfavorable for Nardus grassland conservation and restoration (Schelfhout *et al.*, 2017).

Are historical land use patterns complementary to soil analyses?

Chemical soil characteristics (model 3) explained 45.3% of the deviance in the Nardus grassland indicator species count. This was considerably better than the deviance explained by the historical land use patterns in model 1 (25.4%). There was a clear redundancy of several historical land use variables when chemical soil variables were included into a hybrid modelling procedure (model 2). In spite of this, three historical land use variables (NN to heathland in 1777, to forest in 1890, and to grassland in 1960) were retained into the final hybrid model and these variables further increased the proportion of deviance explained to 52.2% (Table 3). However, when predictions were reclassified into potential areas for conservation and ecological restoration based on a threshold of minimum 3 Nardus grassland indicator species, all three models performed equally well (Table 3). When the threshold was increased to a minimum of 4 indicator species, the sensitivity of the model based on historical land use variables (37.9%) was below the sensitivity of the model with additionally included biochemical variables (62.1%) due to the high amount of false negatives. This indicates that the model based on historical land use variables alone included a considerable number of sites with more than 4 observed indicator species into the lower priority area with 3 up to 4 predicted indicator species. However, observed unsuitable areas with less than 4 observed Nardus grassland indicator species were accurately predicted, as indicated by the high specificity (89.9%). Furthermore, most (77.7%) of the predicted unsuitable areas were also observed as unsuitable, as indicated by the high negative predictive value. This highlights the potential of a priori spatial desktop analyses on a scale impossible to cover by soil sampling. The Nardus grassland habitat suitability map can be used to delineate suitable areas for restoration, for prospection of relics, but also to identify least cost paths for restoring connectivity between habitat patches. Furthermore, the habitat suitability map based on historical land use variables can be an effective and unbiased guidance for additional field surveys, e.g. to collect soil samples that are required to pinpoint sites with the highest restoration potential. In the high priority zone, suitable for at least 4 Nardus grassland indicator species, additional soil analyses can increase the positive predictive value (from 61% up to 70.7%) and accuracy (from 74.7 up to 81.3%) of the model prediction. Furthermore, insight in the soil chemistry can help guide conservation and restoration measures and increase the chance of success (Ceulemans *et al.*, 2014; Van Daele *et al.*, 2017). When the Natura 2000 surface area and habitat quality objectives cannot be met within the high priority zone, soil samples in the lower priority zone (with a potential for 3 up to 4 indicator species) are recommended to detect sites with a high potential, missed as a consequence of the low sensitivity of model 1. High priority zones for conservation and restoration, based on historical land use, covered 5.5% in our test area. Whereas soil sampling in the total test area (2424 ha) is out of reach, targeted sampling of selected sites in the high and lower priority zone can be feasible.

CONCLUSION

This research unraveled the intricate relationship between historical land use legacies, soil chemistry, and the contemporary habitat quality of Nardus grassland, a specialized oligotrophic plant community. Furthermore, these relationships have proven useful to predict the potential habitat quality. The comparison of three statistical models, based on historical land use variables, soil chemistry variables, and both, illustrated the potential of a two-step approach for the prospection of sites for conservation and restoration of species-rich Nardus grassland. Historical land use variables alone can generate a map which discerns a high priority zone with high accuracy but relatively low sensitivity, and a lower priority zone with a high and balanced overall accuracy. In case the targeted area for conservation or restoration cannot be found in the high priority zone, a field survey to collect soil samples in the lower priority zone is the successive step. Soil sampling is recommended to further increase the overall accuracy of the high priority zones and necessary to detect additional sites with high potential in the lower priority zones when the targeted surface area cannot be allocated within the high priority zone. As a conclusion, consulting the habitat suitability map based on historical land use can considerably reduce the search area for additional time-consuming soil sampling. Finally, this research approach could prove valuable for the allocation of conservation and restoration actions for other specialized habitat types, of which the quality is explained by soil chemistry and historical land use patterns.

ACKNOWLEDGEMENTS

We would like to thank the Research Institute for Nature and Forest (INBO) for the facilitation of historical maps and the grassland dataset. Furthermore, we are grateful for the cooperation of the Forest and Nature lab (Ghent university) and the Plant Ecology and Nature Conservation Group (Wageningen University). This research was made possible by the Research Foundation Flanders (application number G050215N).

AUTHOR CONTRIBUTIONS

Conceived the experiment: LdK, FVD; Data selection: FVD, MR; Spatio-temporal analysis: FVD, Shrinkage procedure and model building: FVD, TO, HVC; Writing of the paper: FVD; Revisions and suggested refinements: JVR, KV, LdK, MR, TO

DATA AVAILABILITY STATEMENT

Training data for the three GAM models, raster datasets of the prediction and confidence interval of the test area, and the three GAM models which can be used to predict the Nardus grassland indicator species count can be found in a Dryad Digital Repository: 10.5061/dryad.xsj3tx9h1

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Table 1: Overview of the used cartographic material and vegetation database.

Name of the historical map	Year of origin	Original scale
Ferraris atlas	1771- 1778	1:11 520
Cadastral map	1845-1855	1:20 000
Carte du dépôt de la guerre et topographie	1865	1:20 000
Carte du dépôt de la guerre et topographie	1890	1:20 000
Carte du dépôt de la guerre	1920	1:20 000
Military geographical institute	1960	1:25 000
FlaVen grassland database	2012 -2013	

Table 2 Parametric coefficients of the intercepts and smooth terms generated by the GAM models based on historical land use (model 1), historical land use and soil chemistry (model 2), and soil chemistry alone (model 3). First part of the landscape smooth term variable name indicates the specific land use and the year indicates the date of the map used to define the nearest neighborhood measures. First part of the Soil Chemistry smooth term variable name indicates the chemical element and the second part indicates the specification. P Olson is the bio-available phosphorus, Al total is the total available aluminum content, K AgTU is the exchangeable potassium, OM LOI is the organic matter content, N NH_4 is the ammonium content, N NOx is the nitric oxide content, and pH H2O is the soil acidity. NI (Not Integrated) are terms removed by the selection procedure for Model 2.

	Model 1			Model 2			Model 3		
Intercept	Estimate	T-value	p-value	Estimate	T-value	p-value	Estimate	T-value	p-value
	0.802	12.87	< 0.001	0.432	3.606	< 0.001	0.448	3.63	< 0.001
Smooth terms	edf	F-value	p-value	edf	F-value	p-value	edf	F-value	p-value
Landscape									
Cultivated 1960	0.892	2.08	0.007	NI	NI	NI			
Forest 1890	1.923	1.782	0.049	2.829	3.564	0.01			
Grassland 1850	0.858	2.347	0.003	NI	NI	NI			
Grassland 1960	2.015	2.99	0.007	1.986	2.763	0.011			
Heathland 1777	0.996	2.172	0.006	0.692	0.73	0.069			
Rivers	1.738	1.56	0.058	NI	NI	NI			
Soil chemistry									
P Olsen				1.614	2.994	0.005	1.889	4.856	< 0.001
Al total				2.839	7.408	< 0.001	2.743	8.533	< 0.001
K AgTU				1.017	6.277	< 0.001	0.946	4.399	< 0.001
OM LOI				2.817	7.947	< 0.001	2.669	5.589	< 0.001
N NH_4				2.71	4.344	0.003	2.715	4.476	0.003
N NO_x				0.773	1.435	0.018	0.829	1.7	0.013
pH H_2O				2.908	3.824	0.008	2.776	2.228	0.067

Table 3 Performance of the three GAM models. The amount of grasslands used to construct the model is depicted as N, the corrected goodness-of-fit is indicated as R² adjusted, the deviance explained is the proportion of the null deviance explained by the model, the GCV is the minimized generalized cross-validation score of the fitted GAM, and the scale estimate depicts scaled deviance. These parameters were determined during model fitting. The specificity depicts the ability of the model to correctly identify observed unsuitable areas, while the sensitivity depicts the ability of the model to correctly identify observed suitable areas. The positive predictive value (PPV) quantifies the probability that predicted suitable areas have been observed as suitable, while the negative predictive value (NPV) quantifies the probability that predicted unsuitable areas have been observed as unsuitable. The true Skill Statistic (TSS) places equal weight on the sensitivity and specificity and ranges between -1 and 1. The accuracy quantifies the ratio of correct predictions relative to the total amount of predictions. These performance metrics were determined post-hoc based on a threshold of minimum 3 and 4predicted Nardus indicator species respectively, out of a total of 12 listed by Oosterlynck et al. 2020.

		Model 1	Model 2	Model 3
Performance metrics	Threshold	Land use history	Land use history and soil chemistry	Soil chemistry
N	/	225	225	225
R-sq. (adj.)	/	0.231	0.491	0.389
Deviance explained (%)	/	25.4	52.2	45.3
GCV	/	1.911	1.37	1.484
Scale estimate	/	1.781	1.264	1.355
Specificity (%)	3	72.1	72.8	66.9
Sensitivity (%)	3	71.9	75.3	76.4
NPV (%)	3	79.7	81.8	81.2
PPV (%)	3	62.7	64.4	60.2
TSS	3	0.44	0.48	0.43
Accuracy (%)	3	72	73.8	70.7
Specificity (%)	4	89.9	89.3	86.8
Sensitivity (%)	4	37.9	62.1	62.1
NPV (%)	4	77.7	85	84.7
PPV (%)	4	61	70.7	66.1
TSS	4	0.28	0.51	0.49
Accuracy (%)	4	74.7	81.3	79.6

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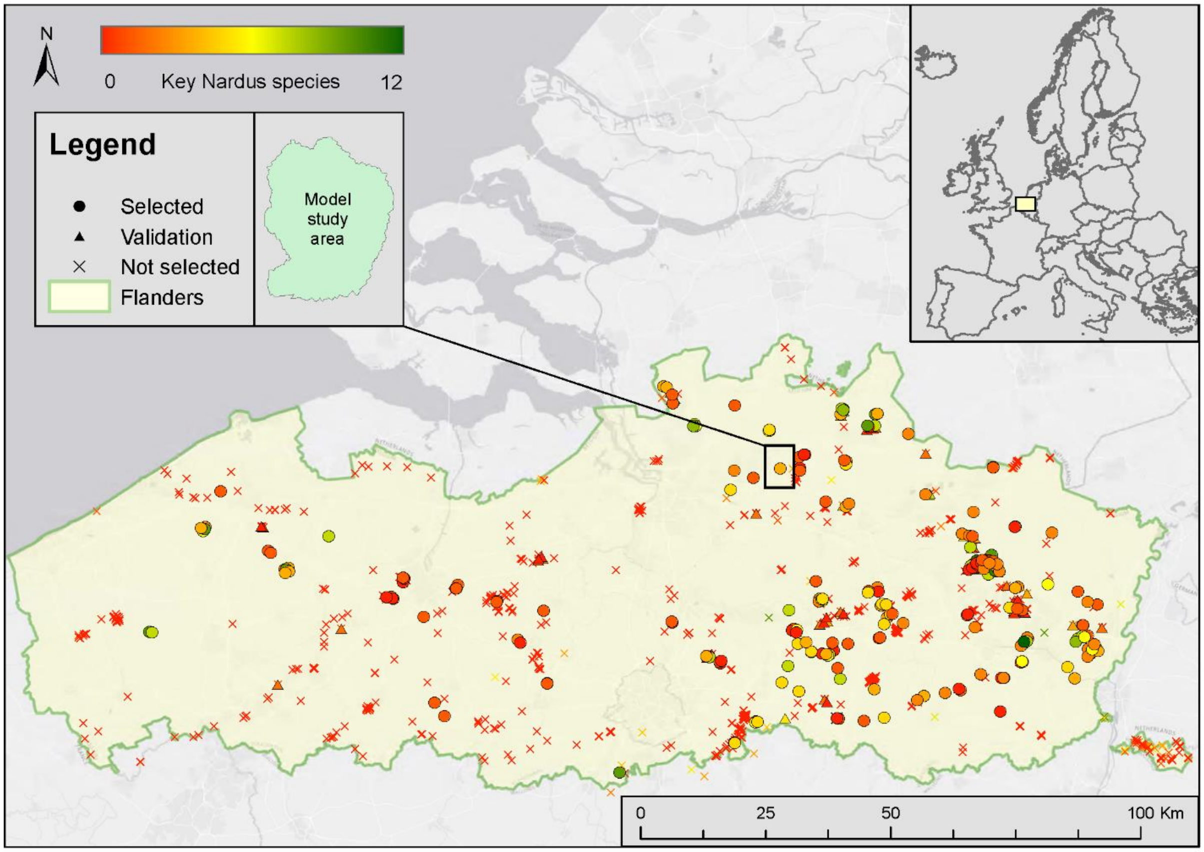

Figure 1: Study area with the indicated spatially explicit database of semi-natural grasslands in Flanders (INBO, 2015). The color ramp indicates the number of Nardus grassland indicator species (0-12) that were sampled in the vegetation survey. The grasslands that were used in the spatially explicit model (225) are indicated with circles, the grasslands used in the validation (84) are indicated with triangles and the small crosses indicate grasslands that did not fulfil the selection criteria.

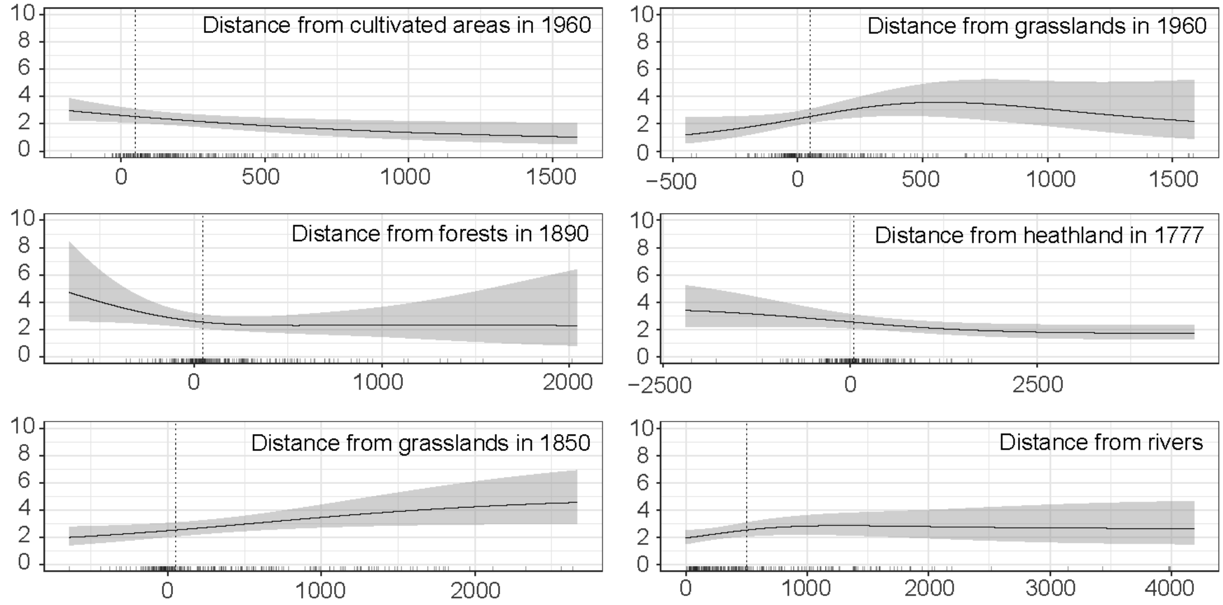

Figure 2: Estimated partial effects of the 6 landscape variables used in GAM model 1. The x-axis depicts the modelled distance from the land use in meters and the density tick marks indicate the values of the observations. The x-axis labels are positioned in the top right of each plot. The 95% confidence interval is indicated by the grey area. The dotted lines indicates the reference value (50 meters) used to construct the 2d plots.

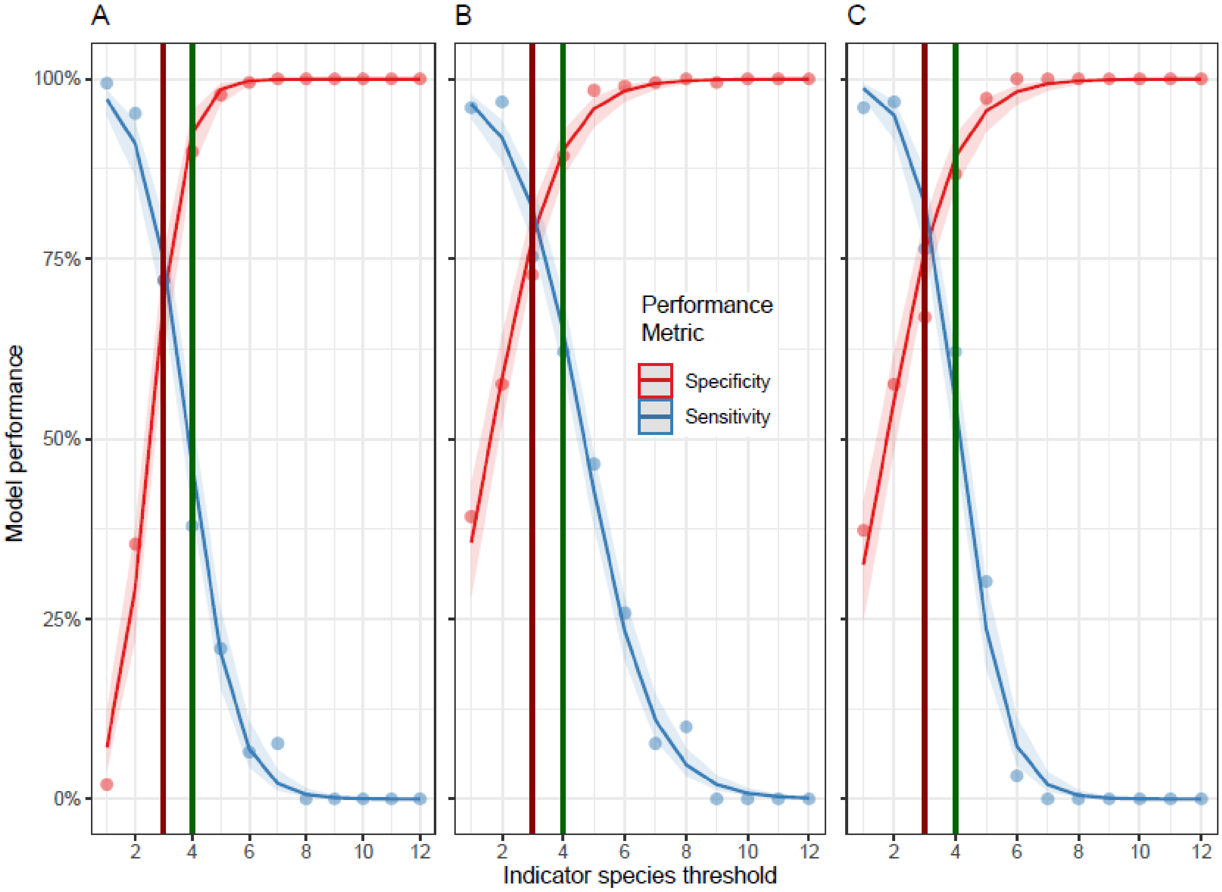

Figure 3: Evaluation of the model performance based on the threshold used for delineating the potential areas for conservation and ecological restoration (Fig. 5). Panel A depicts the first model which was based on the historical land use data, panel B depicts the second model which was based on the combined historical land use and soil chemical data, and panel C depicts the third model which was based on the soil chemical data alone. Sensitivity (blue) represents the proportion of correctly predicted observed suitable areas by a model at a specific threshold. Specificity (red) represents the proportion of correctly predicted observed unsuitable areas by a model at a specific threshold. The vertical dark green line indicates a threshold of 3 predicted Nardus grassland indicator species, which coincides with the optimum between sensitivity and specificity. The vertical dark green line indicates a threshold of 4 predicted Nardus grassland indicator species, which coincides with the minimum amount of Nardus grassland indicator species required to obtain a favorable conservation status in Flanders (Oosterlynck *et al.*, 2020).

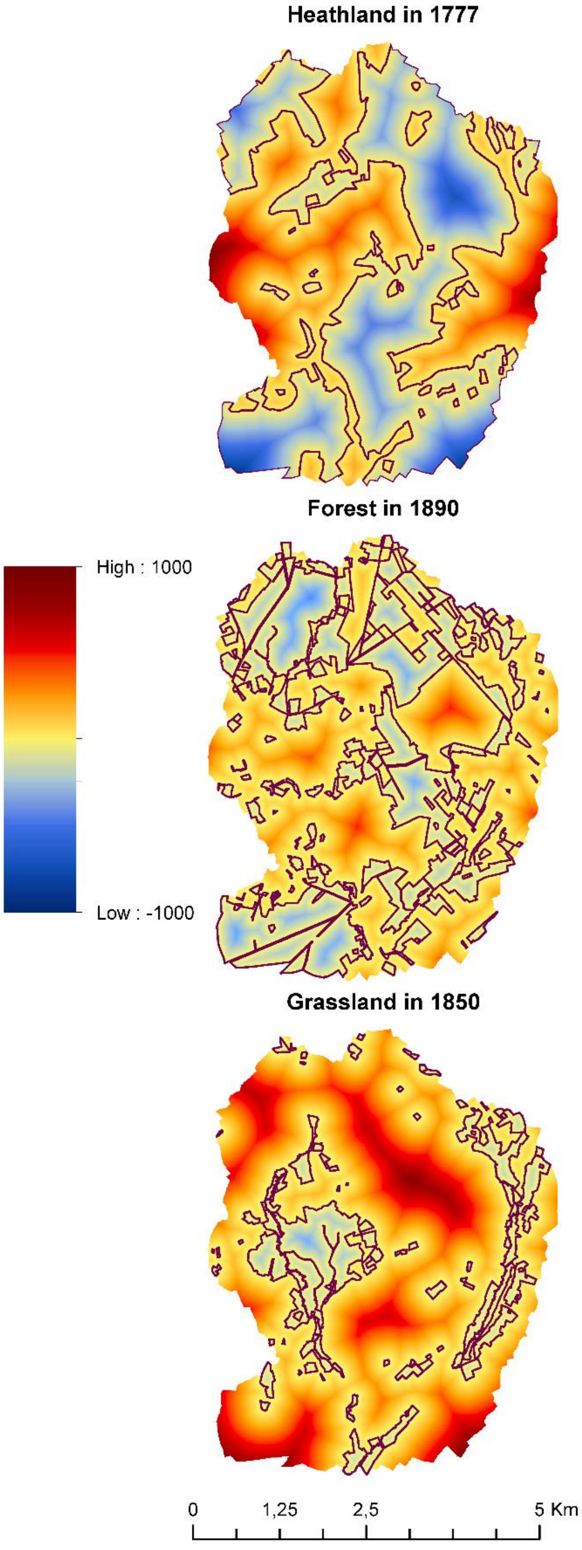

Figure 4: Nearest neighborhood distances in the test area, towards 5 selected land use classes on 4 time slices, and to rivers (colored blue). Negative values indicate a position inside a land use class. All rasters (6) were used to model the potential number of Nardus indicator species.

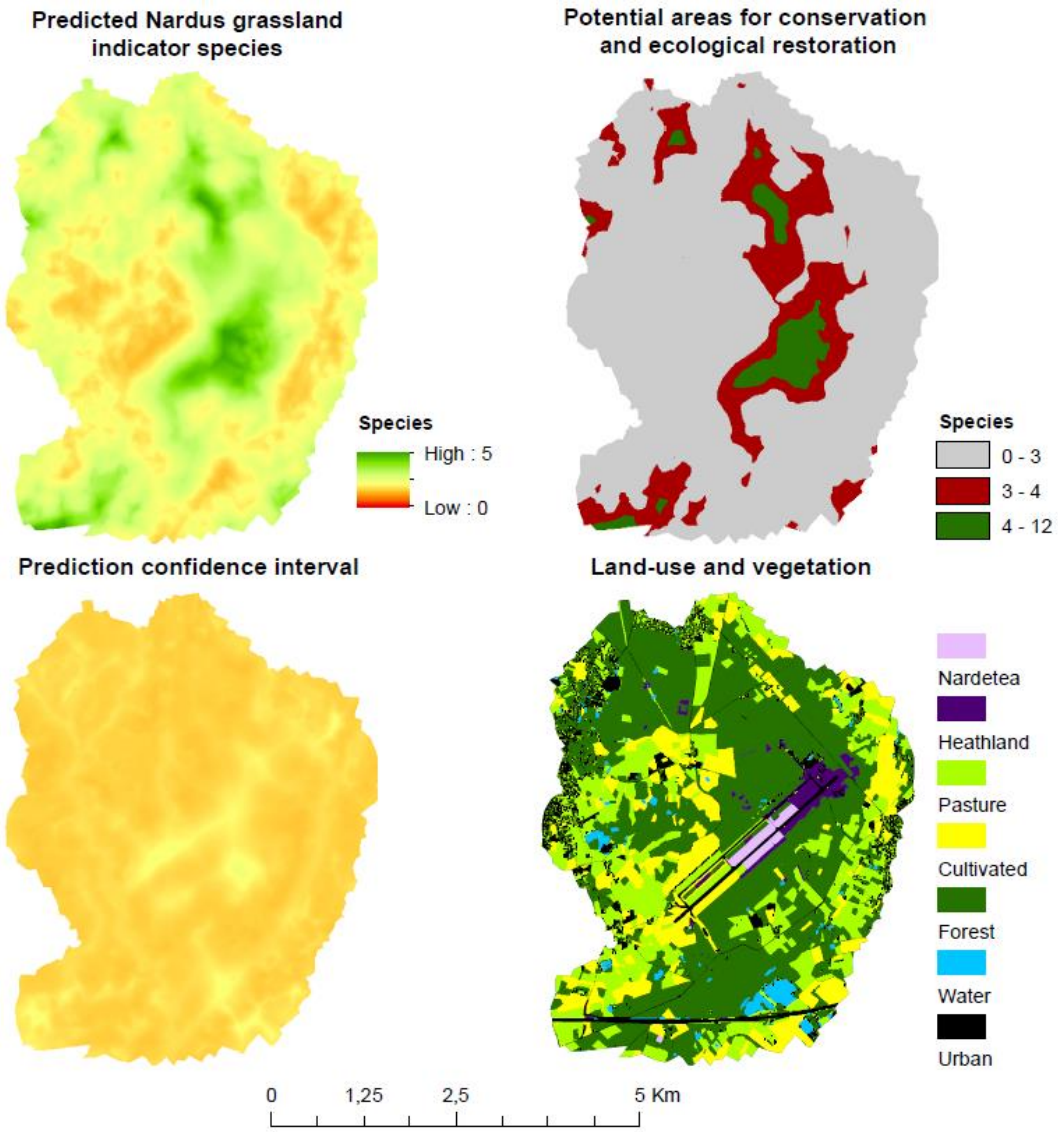

Figure 5: Spatial patterns of the predicted number of Nardus grassland indicator species in the test area (upper left) and its 95% confidence interval (lower left), potential areas for conservation and ecological restoration (upper right), and a contemporary land use and vegetation map of the test area (lower right). Potential areas for conservation and ecological restoration (upper right) were subdivided in a lower priority zone (3 up to 4 predicted Nardus grassland indicator species, indicated in dark red) and a high priority zone (≥ 4 predicted Nardus grassland indicator species, indicated in dark green). The lower priority zone requires additional soil analyses to verify which areas have the potential to develop a favorable conservation status with a minimum of 4 Nardus grassland indicator species (Oosterlynck *et al.*, 2020)*. The land use was based on the NARA land use map of 2014* (Poelmans and Van Daele, 2014) *and vegetation (Nardetea and Heathland) was determined based on Natura 2000 habitat types* (INBO, 2016).

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- Appendix S1: Detailed description of the variable selection procedure