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BIODIVERSITY RESEARCH

Modelling pink-footed goose (*Anser brachyrhynchus*) wintering distributions for the year 2050: potential effects of land-use change in Europe

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ABSTRACT

Feeding on farmland by overwintering populations of pink-footed geese (*Anser brachyrhynchus*) conflicts with agricultural interests in Northern Europe. In order to forecast the potential future of this conflict, we used generalized linear models to relate the presence and absence of pink-footed geese to variables describing the contemporary landscape, and predicted their future distributions in relation to two land-use scenarios for the year 2050. One future scenario represented a global, economically orientated world (A1) and the other represented a regional, environmentally concerned world (B2). The probability of goose occurrence increased within cropland and grassland, and could be explained by their proximity to coast, elevation, and the degree of habitat closure. Predictions to future scenarios revealed noticeable shifts in the suitability of goose habitat evident at the local and regional scale in response to future shifts in land use. In particular, as grasslands and croplands give way to unsuitable land-use types (e.g. woody biofuel crops, increased urbanization, and forest) under both future scenarios, our models predicted a decrease in habitat suitability for geese. If coupled with continued goose population expansion, we expect that the agricultural conflict will intensify under the A1 and particularly the B2 scenarios.

Keywords

Agricultural conflict, *Anser brachyrhynchus*, biofuel, future land-use scenario, species distribution model.

INTRODUCTION

Throughout Europe, expanding populations of migratory geese conflict with agriculture as they forage on pastures and arable land. This conflict has intensified in recent decades due to a combination of increased numbers of geese wintering and breeding in Europe (Madsen *et al*., 1999a) and their transition from feeding in natural habitats or extensively grazed areas to intensively farmed agricultural land (Owen, 1976; Black *et al*., 1991; van Roomen & Madsen, 1992; van Eerden *et al*., 1996; Fox *et al*., 2005; Tombre *et al*., 2005). So far, the management of the conflict has been a local or national affair (van Roomen & Madsen, 1992), although it has long been recognized that a sustainable solution calls for an internationally agreed management plan, as many migratory flyways span multiple countries (e.g. Owen, 1976).

One of the prerequisites for successful, long-term management of the conflict is to have an overview of the current site and habitat use by geese at the flyway level. Such an overview will allow us to identify important factors that define suitable habitat for goose species. This in turn will help us to predict future utilization of European landscapes by geese under land-use scenarios that reflect plausible climate and socioeconomic changes.

Species distribution models are well suited to meet this prerequisite, and in recent years have seen increased use. These tools relate field observations to environmental predictor variables, based on statistically or theoretically derived response surfaces, for prediction and inference (Guisan & Thuiller, 2005). Once these relationships are quantified and formulated, they can be cautiously used to predict distributions to other scenarios reflecting forecasted conditions. Since the development of finer-scale climate change scenarios in the past decade, numerous studies have applied species distribution models to extrapolate the likely impacts of global change on species' distributions (Bakkenes *et al*., 2002; Peterson *et al*., 2002; Thomas *et al*., 2004). They have also

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been used to forecast species' response to future land conversion (Thuiller *et al.*, 2006).

In this paper, we predict the future of goose-agriculture conflict at the international level using species distribution models. We use records that document the Svalbard breeding population of the pink-footed goose (*Anser brachyrhynchus*) while overwintering in Belgium, the Netherlands, and Denmark, and employ a robust modelling approach that relates the pattern of goose occurrence with explanatory variables. We also use existing fine-resolution land-use data that map contemporary land-use patterns, and a new set of equally fine-scale land-use scenarios for the year 2050. The future land-use scenarios are interpretations of a subset of the Intergovernmental Panel on Climate Change (IPCC) scenarios (Nakicenovic *et al.*, 2000). Both reflect changes due to increased urbanization and shifts in agricultural practices to accommodate new biofuel crops. The A1 scenario represents a global, economically orientated world with intensification of farming practice (including increased use of fertilizers and pesticides) and abandonment of agriculture in marginal areas. The B2 scenario represents a regionally orientated, environmentally concerned world in which farming practices are less intensive (e.g. with regard to fertilizers and pesticides), and agricultural land abandonment is less prevalent (Rounsevell *et al.*, 2005; Rounsevell *et al.*, 2006). These scenarios reflect contrasting socioeconomic development pathways and thus have different consequences for agricultural land use and potentially goose distributions.

METHODS

Study population

The Svalbard population of pink-footed geese visits its high Arctic summering areas from late May to mid-September, and migrates via stopover areas in mid-Norway to its wintering grounds in Denmark, the Netherlands, and Belgium. In autumn the geese are concentrated in Denmark and the Netherlands, and during November to mid-January, the majority stays in the Flemish polders in Belgium. During mid-January to mid-April, the population concentrates in west Denmark, and continue to staging areas in mid- and north Norway before migrating to Svalbard (Madsen *et al.*, 1999b). Prior to the 1980s, the west German coast was also used as a regular wintering site, but lately only small flocks occur there sporadically (Prokosch, 1984). The population has increased from 15,000 to 20,000 in the 1960s to more than 50,000 in the early 2000s (Fox *et al.*, 2005). So far, the population has increased continuously with no signs of density-dependent processes affecting the growth, but the proportion of successful breeding pairs and the average brood size have declined with increasing numbers (Trinder & Madsen, unpublished data).

Goose distribution data

The goose distribution records were collected as part of a long-term monitoring program coordinated along the north-western European flyway. The population of pink-footed geese is closely monitored by teams of professional and amateur ornithologists in the winter range. These ornithologists visit foraging sites on a weekly basis during the winter months to count individuals and record neck-bands within the framework of a coordinated long-term study of the population (see http://pinkfoot.dmu.dk for details). We combined observations during the winter seasons 1999/2000 to 2003/2004 with detailed maps of the positions of flocks drawn by key national experts to describe the overall presence (and absence) of geese based on a (250 m × 250 m) grid (Fig. 1). Hence, for each 250 m × 250 m cell it was denoted whether geese were observed or not during the 4-year period. The distribution used for this analysis covers October to April, but for Denmark only January to April, because in autumn, geese are highly restricted in site use due to hunting (Madsen, 1984).

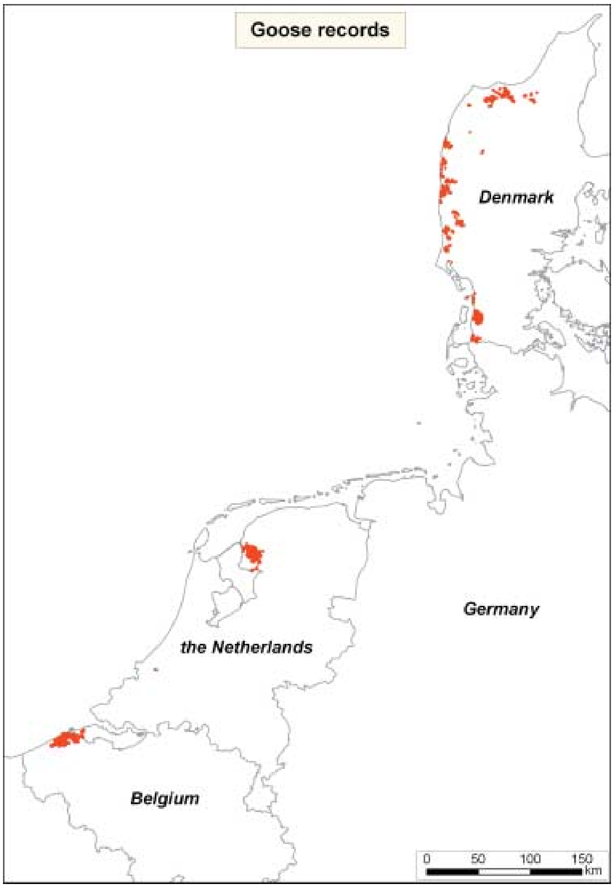

Figure 1 Known pink-footed goose-foraging areas (1999–2004) recorded in 250-m resolution pixels along the north-western European flyway.

Explanatory variables

Each of our predictor variables related to long-standing hypotheses explaining winter distribution of geese. These include foraging categories (cropland, grassland or non-foraging), degree of habitat closure, distance from coast, elevation, and a spatial autocovariate (see below).

Foraging categories

Geese are herbivores; during winter and spring, pink-footed geese feed on grassland (salt marshes, seminatural grasslands, and pastures), barley stubble (autumn), winter cereals, and newly sown fields (spring) (Madsen, 1984; Meire & Kuijken, 1991; Fox *et al.*, 2005). We thus derived a map of potential foraging categories (cropland, grassland and non-foraging areas) based on a reclassification of the EU Corine land-cover classification map (Büttner *et al.*, 2004), derived from 1999 to 2001 Landsat 7 Enhanced Thematic Mapper ETM + satellite imagery (http://dataservice.eea.europa.eu/dataservice/metadetails.asp?id=823). This data set maps 47 land-cover and land-use categories across Europe at 250 m resolution. We amalgamated these categories into one of the following broader ones: cropland, grassland (including salt marsh, pasture, and other seminatural grasslands), and non-foraging areas (including forest, urbanized areas, and others classes that are clearly not used by geese, e.g. bare ground).

Degree of habitat closure

Geese flock, and when searching for foraging areas appear attracted to locations where they see other geese congregated, presumably as these may be successful foraging areas without predators. In general, geese prefer fields with an open view to avoid predation by natural predators and humans. During winter, flocks of pink-footed geese rarely enter fields with a width (defined as the shortest distance between obstacles of open view or roads perpendicular to the centre of a field) of less than 500 m (Madsen, 1985b; Gill *et al.*, 1996; Larsen & Madsen, 2000; Courtens *et al.*, 2005). Due to decreased visibility of other geese and potential predators, we predicted that the probability of geese would decrease with degree of habitat closure and included this as a predictor in our models. We calculated the degree of habitat closure as the percentage of forest or urban landscapes within a radius of 750 m of a focal cell in the Corine land-cover grid.

Distance from coast

Pink-footed geese follow a migratory corridor along the coast of the North Sea. They roost in sheltered bays on the coast, lagoons, or adjacent freshwater lakes, and also in the grassland polders of Belgium. The geese are known to typically stay within 20 km from the roosts (Madsen, 1986), although longer flights are occasionally recorded. We thus included distance to coast (m) as a predictor. We extracted marine and inland coastlines from the Corine data set.

Elevation

Other studies have shown that elevation correlates with patterns of goose occurrence (e.g. Wisz *et al.*, 2008). Though it is not clear that geese respond to elevation *per se*, we expect that it correlates with some landscape components or soil quality features which may have implications for goose habitat selection. We used the USGS GTOP30 global digital elevation model (DEM) with a horizontal grid spacing of 30 arc seconds (approximately 1 km) (http://edc.usgs.gov/products/elevation/gtopo30/gtopo30.html).

Spatial autocovariate (SAC)

Spatial autocorrelation is common with environmental and ecological data, and arises when the values of data-points are similar to those nearby (Augustin *et al.*, 1996). Such spatial dependence of data can lead to invalid parameter estimates in a model. It also can overestimate the variation of the dependent variable that is explained by the predictor variables independent of this phenomenon. To evaluate and control for spatial autocorrelation, we computed a spatial autocovariate (SAC) and included these in our generalized additive models (GAM) (see below). We computed SAC using the method described in Augustin *et al.* (1996) for completely sampled grids (see equation 1 in that paper), as follows:

$$SAC = \frac{\sum_{j=1}^{k_i} w_{ij} y_j}{\sum_{j=1}^{k_i} w_{ij}}$$

where SAC is the autocovariate term that is a weighted average of the number of occupied cells among a set of k_i nearest neighbours of cell i. The weight given to cell j is $w_{ij} = 1/h_{ij}$, where h_{ij} is the Euclidean distance between squares i and j (Augustin *et al.*, 1996). Values range from 0 to 1. Cells with values closer to 1 are more highly correlated to its neighbouring cells than cells with a value closer to zero. We computed SAC for the eight cells immediately surrounding each focal cell (the Queen's case).

Spatial extent of our analysis and selection of absence records

We restricted our analysis area to the parts of Belgium, Denmark, and the Netherlands that did not extend beyond the environmental range of our 7,409 250-m resolution goose occurrence records. Fifty-two goose records coincided within grid cells classified as non-foraging areas (presumably within forage patches too small to be mapped at 250-m resolution). Thus, we confined the extent of our analysis within 30 km of the coast, below 30 m of elevation, below 70% habitat closure, and all three forage classes (cropland, grassland, and non-foraging). In order to obtain a representative sample of the vast area in which geese were absent for our model, 50,000 real absence records were selected randomly from within the study area in Belgium, the Netherlands, and Denmark. This represented approximately 6.7 times the number of presence records.

Statistical analyses

We modelled the probability of occurrence of pink-footed geese using GAMs (Crawley, 2002) with a binomial error structure, a logic link, and case weights to balance the number of presences and absences. First, we identified the most parsimonious number of smoothing parameters for each continuous predictor (distance to coast, elevation, and degree of habitat closure) individually using Akaike Information Criteria (AIC) and Bayesian Information Criteria (BIC). Both criteria confirmed that each continuous predictor required two smoothing degrees of freedom.

We then performed two GAM selection experiments. The first experiment included all explanatory variables mentioned above, but not the spatial autocovariate (SAC). The second experiment included all explanatory variables plus the SAC.

Because the model is based on presence records and a random sample of a vast number of real absence records, the resulting GAM-based prediction is not a calculation of probability of occurrence, *per se*, as the input data are not representative of the frequency of occurrence of geese in the region. However, predictions from the model allow us to rank the suitability of locations in the study area, and this practice is widely used (see Elith *et al.*, 2006 for a discussion). Moreover, a recent study evaluating absence data selection strategies for presence only data has shown that selecting large numbers of absences yields robust estimates for ranking the suitability of sites (Phillips *et al*. unpublished data).

Model evaluation

We evaluated model explanatory power using proportion of deviance explained and model discriminatory power, using both Area Under the Receiver Operating Characteristic Curve (ROC), and max kappa. These evaluators have been widely used to evaluate classification accuracy of species distribution model (e.g. Guisan & Zimmerman, 2000; Elith *et al.*, 2006).

Spatial prediction

Models that incorporate a SAC are not expected to be applicable to other situations in space and/or time, because the spatial arrangement of species and environmental gradients might differ between current and future scenarios (Guisan & Thuiller, 2005). Using a SAC for prediction could only predict high probability of occurrence in locations within the limited neighbourhood of the existing goose-foraging areas and low probabilities everywhere else. This is a clear limitation for predicting future suitable areas for a species that is known to adopt new foraging areas along their flyway. As we wish to identify the new locations geese may colonize under future climate scenarios, we used the GAM that excluded the spatial autocovariate to make spatial predictions. For the future scenarios, we substituted the contemporary predictors derived from Corine (2000) (foraging classes and degree of habitat closure) for those derived from AI and B2 scenarios. Predictions made outside the range of values upon which a model was trained often yield unrealistic predictions (Thuiller *et al.*, 2004). After we confirmed that predicted probability of occurrence in both non-foraging areas and areas with high habitat closure (> 70%) were realistic (i.e. near zero), we predicted the model to Belgium, the Netherlands, Denmark, and Germany within 30 km of the coast and below 30 m elevation, even if the degree of habitat closure exceeded the range of the presence records in the training data (69%). We calculated the predicted probability values using the 'predict' function in R, and mapped them in ArcGIS 9.2. We then converted the continuous probability surfaces to binary predictions (presence–absence maps) using the model's max kappa threshold value (Guisan & Thuiller, 2005), which optimized the fit of the contemporary prediction to the occurrence data.

Future land-use scenarios

European land-use change scenario maps for the year 2050 were developed in a previous study (Ewert *et al.*, 2005; Rounsevell *et al.*, 2005; Schroter *et al.*, 2005; Rounsevell *et al.*, 2006). These maps give land-use shares (as percentages) for each cell on a 10′ longitude/latitude grid and are based on an interpretation of the four storylines of the IPCC Special Report on Emissions Scenarios (SRES) (Nakicenovic *et al.*, 2000) designated A1, A2, B1, and B2. The A1 scenario is global and economically orientated. The A2 scenario is also economically orientated, but more regional in focus. The B1 scenario is global, but at the same time reflects an environmentally concerned world and the B2 scenario while also environmentally concerned represents a regionalized world. These global storylines were translated into relevant land-use change drivers such as population increase, increase in food demand, etc. at the European scale. The land class types are urban, cropland, grassland, forest, bioenergy crops ('liquid', 'non-woody', and 'woody') and surplus (i.e. abandoned agricultural land). For some land-use types, it was necessary to identify distinct regional trends in driving forces based on countries or country groups (or both). The regional trends also differ between scenarios (Rounsevell *et al.*, 2006).

These scenarios were downscaled to the spatial resolution of the Corine (2000) land-cover map (i.e. 250 m) and this process is described in (Dendoncker *et al.*, 2006). 'Downscaling' refers to the representation of data originally only available at coarse resolution at a finer resolution. Briefly, the statistical downscaling method was based on a spatial multinomial logistic regression model that uses the observed fine resolution (250 m) land-use data of the Corine map. The model provided initial probability maps of land-use presence for each land-use class. These probabilities were then updated using the land-use quantities given by the scenarios at the 10′ level and an iterative procedure based on Bayes' theorem. The land-use class with the highest probability of occurrence was then represented on the downscaled maps for the year 2050; a single land-use class was therefore attributed to each pixel. This statistical approach allows the uncertainties arising from the downscaling methodology to be given by the probability distributions. In order to match the Corine land-cover categories used in goose models, 'liquid' bioenergy crops (e.g. oilseed rape or Colza) were reclassified as cropland, while 'non-woody' and 'woody' bioenergy crops (e.g. willow plantations) were reclassified with other forest within the 'non-foraging' land-use category.

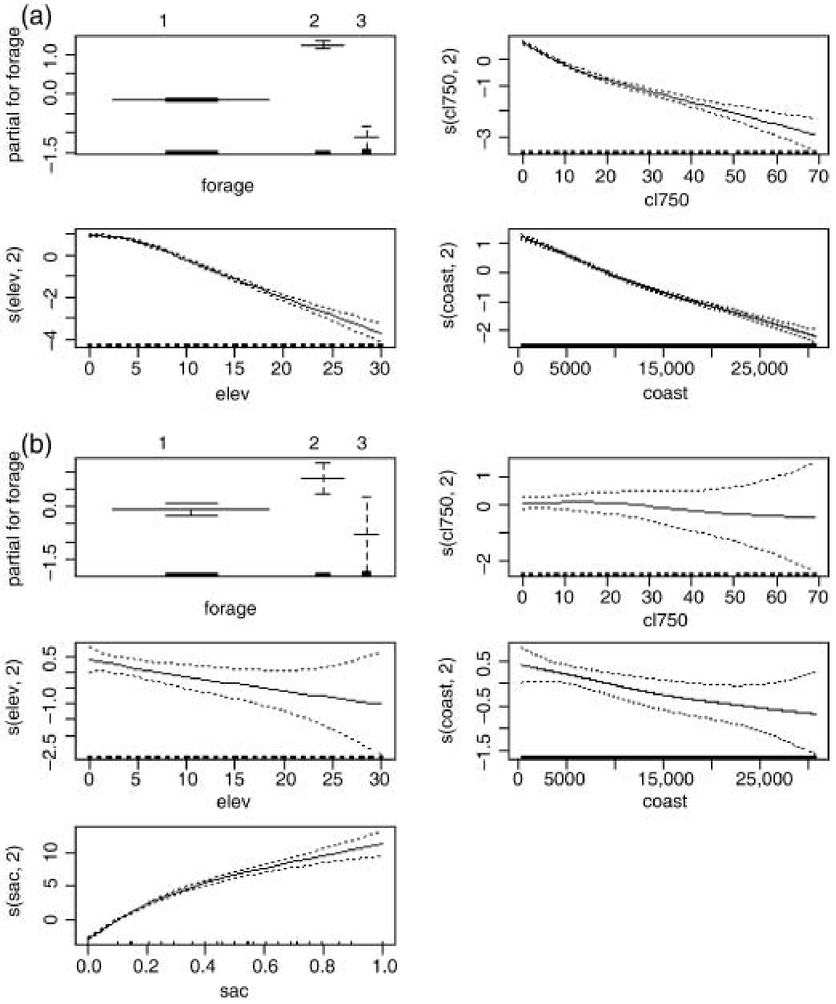

Figure 2 The most parsimonious Generalized Additive Model (GAM) included the forage cover categorical predictor, and two smoothing degrees of freedom for the continuous variables (elevation and distance to coast and a spatial autocovariate (SAC)). Contrary to model selection by Akaike Information Criteria, under Bayesian Information Criteria model selection degree of habitat closure at 750 m was not included when SAC was included. The *Y* axis is a transformation of the probability of occurrence of geese; higher values correspond to higher probability. Dashed lines represent 95% confidence intervals for the fitted relationship. Foraging category 1 = 'cropland'; 2 = 'grassland'; 3 = 'non-foraging' as derived from the Corine 2000 land-cover map. elev = elevation (m), coast = distance to coast (m), SAC = spatial autocovariate. (a) GAM excluding the SAC. (b) GAM including the SAC.

RESULTS

Goose distribution generalized linear model (GLM)

GAM experiment 1

The most parsimonious GAM (without spatial autocovariate) incorporated all of the predictors: the categorical variable 'foraging class', habitat closure, distance to coast (coast), and elevation. Response curves were generally consistent with theoretical predictions (Fig. 2a). The probability of occurrence of geese had a decreasing relationship to habitat closure, distance to coast, and elevation. Probabilities were highest in the 'grass' forage cover category, lowest in the 'non-foraging' category, and intermediate for croplands. D2 was 0.33, indicating a respectable fit to the data. ROC area = 0.84 which indicates a useful model with good discriminatory power and max kappa was 0.38, indicating a model that predicts presences and absences better than random.

GLM experiment 2

The spatial autocovariate had a significant relationship to the residuals from the most parsimonious model in GAM experiment 1 ($P < 0.001$), confirming the presence of spatial autocorrelation in our data. When we built a second GAM which included a SAC, the most parsimonious model (based on AIC) included an intercept, the SAC, and all of the predictor variables. However, according to BIC the most parsimonious model included all these predictors except for the habitat closure predictor. The response shapes of predictors in the SAC-based GAM experiment were broadly similar to the first GAM experiment which excluded SAC (Fig. 2b). However, confidence intervals surrounding fitted relationships were wider after controlling for the effects of spatial autocorrelation (Fig. 2b). ROC area was 0.99, indicating a model with nearly perfect discriminatory power.

Future land-use scenarios

Depending on the existing levels of agriculture, urbanization, or conservation areas, each country was estimated to experience different levels of land conversion in response to shifting land-use policy. In general, the differences between Corine (2000) and the B2 scenario were most extreme, but substantial changes between Corine and A1 were also observed in some countries (see Appendix S1 in Supplementary Material).

All scenarios suggest that the Netherlands, and particularly Germany, will experience the most dramatic changes in cropland,

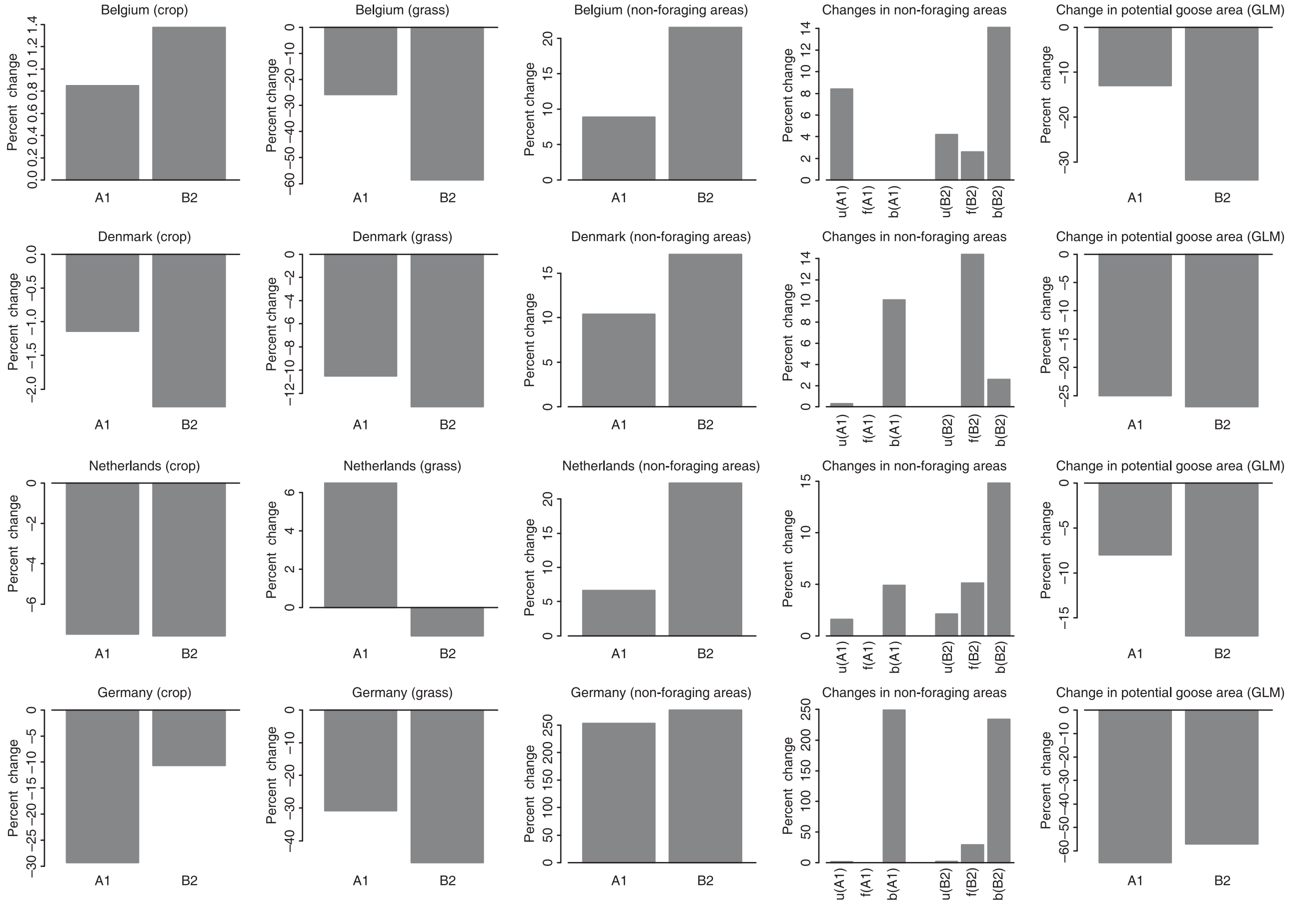

Figure 3 Histograms indicating the percentage change from Corine (2000) per country according to the two future scenarios. A1 relates to a global economic orientated world with intensification of farming practice. B2 represents a regionally orientated environmentally concerned world (Diniz & Hawkins, 2003). u = new urbanization, f = new forested areas and abandoned agricultural land (which is expected to return to forest if left unmanaged), and b = new woody biofuel plantations.

while Belgium and Denmark will experience more modest changes. In Germany, the amount of croplands would change far less under the B2 scenario than the A1 (See Fig. S1 in Supplementary Material and Fig. 3). In the Netherlands, similar levels of croplands will be converted under the two scenarios, with only slightly more lost under B2 than in A1.

The amount of grasslands was estimated to shift dramatically under the B2 scenario in Belgium, Denmark, and Germany. The scenarios projected that 60% and 40% of the Belgian and German grasslands (respectively) in our study area will be converted to non-foraging areas due to increased urbanization, possible afforestation of abandoned land, and the proliferation of woody biofuel plantations, all of which are unsuitable for geese (Fig. 3). Grassland loss could exceed 10% under A1 and 12% under B2 in Denmark. However, in the Netherlands grasslands increase under A1, but decrease under B2.

The changes in grassland conversion are also reflected in the increase in non-foraging areas, particularly under the B2 scenarios. Most notably, non-foraging areas were predicted to more than double in Germany, and increase by 40% in the Netherlands. The amount of croplands was estimated to decrease in the future scenarios in all countries except for the A1 scenario in Denmark.

Goose predictions to future land-use scenarios

As expected, areas predicted to be highly suitable under the present day scenario inherited quite lower probabilities of occurrence in the future if the land use changed from grassland or cropland to non-foraging areas. By converting the probability of occurrence maps to binary predictions using the max kappa threshold of 0.65, we found that the area suitable for geese decreased in each country in each scenario (Table 1, Figs 3 and 4). More goose habitat was lost under the B2 scenario in Belgium, Denmark, and the Netherlands than under A1, but in Germany slightly more was lost under the A1 scenario (Table 1, see Fig. S1, Figs 4 and 5).

DISCUSSION

The shape of our response curves support many long-standing hypotheses concerning habitat use by geese. We found that

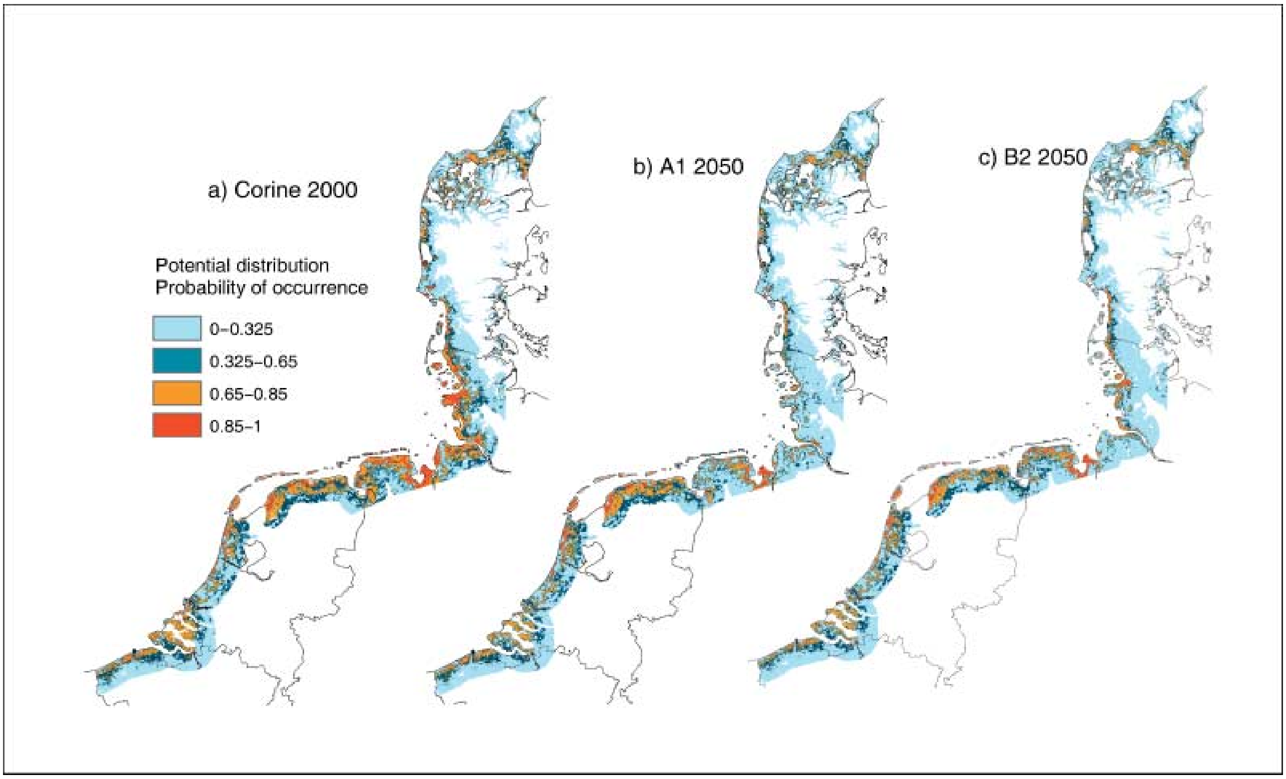

Figure 4 Spatial predictions of probability of occurrence of pink-footed geese based on the Generalized Additive Model (GAM) that included all predictors except the spatial autocovariate term (a) using contemporary predictors, including those derived from the Corine (2000) land-cover map; (b) using future predictors, including those derived from the A1 scenario; and (c)using future predictors including those derived from the B2 scenario. Pixels with probability of occurrence exceeding the max kappa threshold = 0.65 are presented in warm colours (orange increasing to red). The max kappa threshold optimized the fit of the probabilistic predictions to the goose presence–absence data when trained on contemporary predictors.

Table 1 Potential goose area in each country as predicted by the most parsimonious GAM model (based on contemporary data and exluding spatial autocovariate) under 3 different land use conditions. Corine 2000 is a European land cover map for the year 2000. A1 and B2 are future land use scenarios for the year 2050.

	Potential goose area (km^2)		
Country	Corine 2000	A1	B2
Denmark	1526	1152	1119
Belgium	276	239	183
Netherlands	2865	2623	2371
Germany	3768	1336	1604

grasslands are the most suitable forage category for the geese, which is in keeping with their natural habitat. Croplands were found to be important too, in line with field studies that have shown an increase in use of winter and spring cereal fields by geese (Therkildsen & Madsen, 2000; Fox *et al.*, 2005; Kuijken *et al.*, 2005). Distance to coast and elevation were also selected as important predictors, which was also supported by previous work on this species' Svalbard breeding grounds (Wisz *et al.*, 2008; Jensen *et al.*, 2008). If a spatial autocovariate is selected in a model, it may explain a substantial portion of the species' occurrence pattern. If so, other variables that are selected in addition to the spatial autocovariate will relate to the less autocorrelated aspects of the distribution, and it has been posited that these factors may act at finer spatial scales (Diniz & Hawkins, 2003).When the spatial autocovariate was included, the confidence intervals on the habitat closure variable widened dramatically, and though model selection with AIC indicated it was an important predictor, BIC model selection did not confirm this. There may be an ecological explanation why habitat closure lost unique explanatory power after the SAC was included in the model. Geese flock and are attracted to locations where they see other geese foraging. Consequently, places with high densities of geese will obviously be highly spatially autocorrelated, and features that interfere with goose visibility (such as forests and other structures that increase habitat closure) will have little additional explanatory ability when SAC is included as a predictor. In the absence of an SAC for future predictions, we expect that the most parsimonious GAM that excluded the SAC but included habitat closure among other selected predictors will be useful to predict future potential foraging areas,

AUCs exceeding 0.75 are considered sufficiently accurate to be used in conservation and management (Pearce & Ferrier, 2000),

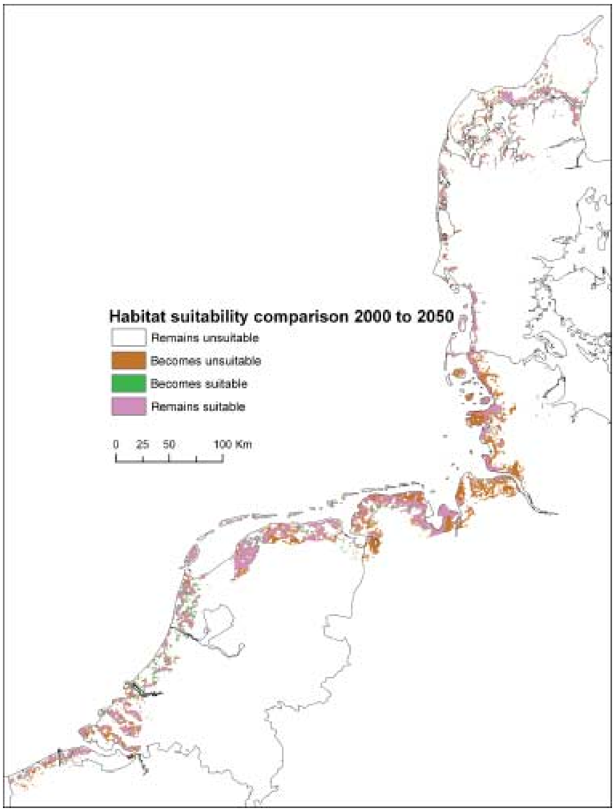

Figure 5 Comparison of contemporary potential pink-footed goose habitat (based on a GAM that included variables derived from Corine, 2000) to that estimated under the B2 future scenario. Differences between A1 and B2 predictions are reported in Table 1.

while an AUC of 0.9 indicates excellent classification accuracy according to Swets (1988). Our model had an AUC of 0.84. AUCs from other studies may be higher because they did not restrict the study area to the environmental range of the presence data, which would challenge the algorithm to discriminate presence and absence locations within a more environmentally homogenous data set. Our absence records and our study area were restricted within the environmental range of the presence records. If we had included locations well outside the range of presence records in our evaluation data set, we would have expected much higher AUCs, but may have represented goose distributions less accurately within the narrower area where the model is most needed for management.

The GAMs for the present distribution of pink-footed geese predicted large potential areas outside the observed distribution in 2000–04. This discrepancy can be explained by several factors. First, there may still be room for many more pink-footed geese which have not yet filled out the potential space. Support for this comes from historical and more recent information from Belgium and Denmark, confirming that pink-footed geese have expanded their ranges dramatically during the last 30–40 years. Over the past 40 years, geese have been drawn to the Flemish Polders in Belgium in response to a hunting ban, but probably also triggered by adverse winter weather further north in some years (Kuijken *et al.*, 2005). Pink-footed geese are currently expanding their range in the northern part of Denmark, and the area occupied has more than doubled from the early 1980s to 2000–04 (Madsen, 1986 and this study). They have colonized some of the northern areas predicted as suitable by our contemporary prediction (Fig. 4) since 2004, and numbers have increased from a few hundred to over 8000 individuals. The expansions are probably a result of the increase in population size as well as relocation from Germany, especially since the 1980s.

Second, although geese are highly mobile, can sample many areas, and have adopted many new foraging areas in the past decades, they have a tendency towards site-faithfulness, usually returning to the same sites year after year. This leads to a clustered distribution, which may delay the colonization of new areas that may have suitable habitat. The traditional migratory habits of the geese may be part of the explanation why they do not use the German coast at present. Formerly, they migrated along the German coast and exploited several sites (Prokosch, 1984). For unknown reasons, they abandoned the sites and have in recent decades completely bypassed Germany, migrating directly from Denmark across the German Bight to the Netherlands and *vice versa*. In consequence, it may take a long time for the geese to return to the German sites, because they no longer sample that region.

Third, some of the potential sites may actually not be suitable, but our explanatory variables are insufficient to show this. The resolution of our analysis (250 m) was limited by the Corine land-cover data set. More detailed variables mapping road networks, physical landscape elements, and a finer-grained habitat classification may have modified the picture. For example, many wind farms have recently been built along the west coast of Germany, and these will prevent the geese from exploiting large areas (Kruckenberg & Jaene, 1999). Data mapping the distributions of wind farms are not readily available, so it was not possible to include these features in our analysis. Furthermore, our species distribution models do not account for biotic interactions with other species, such as competitors. The winter range used by the pink-footed geese overlaps with other goose species which have a preference for the same habitat types, and they co-occur in many areas. Interspecific competition for resources among geese has been shown to result in a local segregation of species (Madsen, 1985a; Kuijken *et al.*, 2005), and in some cases, resource depletion results in the displacement of one of them (Madsen, 2001).

Geese require roost sites adjacent to their foraging areas, but we did not include distance to potential roost sites as a predictor variable in our models. In Denmark, geese roost in marine and inland coastal areas up to 30 km from their foraging areas (Madsen, 1986). However, in the Flemish polders where foxes are absent and hunting is banned, pink-footed geese spend the night on grasslands, even though suitable open water is available for roosting within 20 km (Kuijken *et al.*, 2005). Our study area was restricted to within 30 km of marine and inland coasts. If we assume that pinkfeet can, if necessary, resort to using coastal areas for roosting throughout their wintering range, we can conclude that some sort of roost site was within reach of our potential foraging areas.

Future projections of species distributions have inherent limitations and must be interpreted with caution. First, data representing present-day distributions can only be sampled from the existing realized niche. If biotic interactions, such as intraspecific and interspecific competition, should shift in the future, predictions based on a current sample may no longer be realistic (Davis *et al*., 1998). Although we can evaluate the robustness of a model in a present-day scenario, we have no way of assessing the reliability of a model in a future scenario. Second, our predictions assume that geese have the opportunity to colonize all suitable habitat that is available. As stated above, this need not always be the case. Third, human attitude to the geese may alter their behaviour and site use. For example, in Norway, farmers have increasingly scared geese off their farmlands to alleviate the goose damage to pastures. Consequently, geese have become much more wary and have changed their migration habits (Klaassen *et al*., 2006). Finally, as stated above, predictions made outside the environmental range of occurrence records are often unreliable (Thuiller *et al*., 2004), and our predictions were restricted within the extremes of distance from coast and elevation for our goose-foraging records. Over the past 30 years we have observed that the population has gradually expanded its site use coinciding with the population increase (Fox *et al*., 2005). However, we have no way to predict how pink-footed geese might switch to use habitat outside their current range of environmental extremes along their north-west European flyway, such as if they expand their range into areas outside the present flyway corridor, or start to utilize new roosts and fields in areas beyond 30 km of any coast.

The land-use scenarios for 2050 illustrate that habitats preferred by geese (i.e. grassland and croplands) will decrease. In the Netherlands, Germany, and Denmark, grasslands are projected to reduce substantially. Most notably, under the B2 scenario the Netherlands and Germany could lose up to 50% of its grasslands, while Belgium could lose at least 60%. If the reduction in grassland is substituted with croplands, the areas may still be suitable for geese. However, if they are replaced by 'woody' biofuels, forest, or urban areas, goose habitat will be reduced.

At the scale of the entire flyway the overall change in goose distributions may not seem particularly striking. However, focusing on regional and local scales reveals substantial changes that could lead to intensified agricultural conflicts with economic consequences. Goose populations may come under pressure as a result of future land-use changes in some regions, especially under the B2 scenario. We expect that these effects will be particularly pronounced where distributions of pink-footed geese come in contact with competing goose species. For example, in Belgium 34% of potential goose habitat may be lost under B2 land-use changes. White-fronted geese (*Anser albifrons*) also occur in Belgium, have also undergone a population increase, and have rather similar habitat requirements to pink- footed geese (Madsen *et al*., 1999a). Competition with this species for suitable habitat could further exacerbate agricultural conflict in coming decades.

In the context of previous work in the arctic breeding grounds (Jensen *et al*., 2008), our results highlight the complex, dynamic nature of goose distributions in relation to habitat. As conditions on the Arctic breeding grounds ameliorate with climatic warming, density-dependent mechanisms that regulate population size on the breeding grounds may relax through prolonged breeding seasons and improved access to more nesting areas (Jensen *et al*., 2008). While survivorship and fecundity on the breeding range are enhanced, the goose–agriculture conflict can be expected to continue and will probably intensify (Trinder & Madsen, unpublished data). Extensive conversion of grassland and cropland on the wintering range to urban areas, 'woody' biofuel plantations, or forest could further exacerbate the conflict at key locations, and may foment a new version of density-dependent population regulation along the flyway.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Reclassification of Corine land cover 2000 for modelling goose-foraging areas. Grasslands include salt marsh, pasture, and other seminatural grasslands. Croplands include only those crop types used by geese for foraging. Non-foraging areas include urbanized areas, natural and anthropogenically derived forest types, and croplands that are unsuitable for geese.

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