Integrated spatially-explicit models predict pervasive risks to recolonizing wolves in Scandinavia from human-driven mortality

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ABSTRACT

Human-driven wildlife mortality is caused by both indirect causes and direct persecution due to conflicts of interests. The wolf, a predator frequently at risk from human-wildlife conflict, is returning to areas where it was historically extirpated in Scandinavia (Sweden and Norway). The wolf is expanding via a management strategy that allows wolves to reproduce exclusively in a wolf breeding range (WBR) in the south-central region. We modelled wolf territory occurrence in the WBR and all of Scandinavia, accounting for biotic and anthropogenic variables, and we also modelled the occurrence of human-driven mortality (traffic collisions, culling and illegal killing). We integrated territory distribution and mortality models in a two-dimensional model estimating habitat suitability and mortality risk for wolves. Forest was the main variable driving territory occurrence, and mortality was a consequence of variables associated with traffic infrastructure, human population, prey densities, and wolf management levels. Only < 0.1% of the WBR was not characterized by these risks. Our results confirm that human-related conflicts resulting in wolf mortality occur wherever the species is present, which leads to actions to control the population expansion. Considering the adaptability of wolves and the presence of potential suitable habitat in Scandinavia, their survival and expansion will be dependent on changes in public attitudes about illegal killing, and a review of policies and management actions. Our framework can be used to assist management of human-wildlife conflicts of recolonizing wolves elsewhere, or of other species at high risk from human-induced mortality.

1. Introduction

Large carnivores are top-predators frequently perceived as a threat to human interests and are associated with multiple and pressing conservation dilemmas due to their predatory habits on game, livestock, pets, and even humans (Chapron and Treves, 2016; but see also Kuijper et al., 2016). Consequently, human-carnivore interactions result in complex, persistent, and often intractable concerns that require proactive conservation strategies (Bekoff, 2001). The wolf (*Canis lupus*) is probably the most striking example of a long-standing conflict that results in complex synergies of people's perceptions, social reactions, and political and management decisions (Miller et al., 2016) that has often resulted in the persecution and extinction of the species in many areas of its historic distribution range (Chapron et al., 2014).

After decades of conservation initiatives in Europe, the wolf is currently returning to areas of its original distribution range where it could potentially occupy a broad range of human-affected habitats

(Chapron et al., 2014). A specific case of the wolf return is that in the Scandinavian Peninsula, i.e. Sweden and Norway (hereafter Scandinavia). Although considered as functionally extinct in the early 1960s (Haglund, 1968; Wabakken et al., 2001), the number of established wolf territories of wolf pairs and families in the Scandinavian population was estimated as ~70 in winter 2015–16 (Wabakken et al., 2016). The wolf is currently under different legal statuses and management regimes that vary between and within the two countries. Sweden is an EU member; consequently, the management of the species is ruled by the Habitats Directive (92/43/ECC). Norway, as a non-EU member, is only a signatory of the Bern Convention (Boitani et al., 2015). In Sweden, wolves are only allowed to establish territories south of the reindeer husbandry area that ranges from central to northern regions; therefore, most wolves entering the reindeer husbandry area are promptly killed. In Norway, wolves are limited to the 'Norwegian wolf zone' in the south-eastern part of the country bordered by Sweden to the east and by the area of free-ranging domestic sheep to the west and

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north. The number of wolves in Norway is restricted to a population goal defined by a given number of reproducing packs per year. Therefore, today the wolf breeding range (hereafter WBR) bounds the distribution of the wolf population in Scandinavia to the southern-central region, which is geographically isolated from the closest neighboring Finnish-Russian population to the north-east. The rate of genetic exchange with the Finnish-Russian population to the north-east (Åkesson et al., 2016), and human-related mortality including illegal killing (hereafter poaching, Liberg et al., 2012, Milleret et al., 2017) are important for the dynamics, size, spatial distribution, and genetic viability of the population. Consequently, given the conflicts associated with the species, the population size and viability, there is a need to spatially identify the drivers of wolf territory occurrence in the WBR accounting for the geographic distribution of potential wolf-human related mortality risks, including those that result from management decisions (i.e. culling).

The association between wildlife species and environmental features is often studied using species distribution models (SDM), which are valuable to assist conservation and management strategies (Miller, 2010) and to predict population expansion/reduction (Guisan and Thuiller, 2005). Spatial analyses to model the occurrence of carnivore-related conflicts due to livestock attacks (Treves et al., 2011; Miller, 2015) or game hunting interests (Recio and Virgós, 2010) have been hitherto applied to varied species like canids and felids (Treves et al., 2004; Edge et al., 2011; Behdarband et al., 2014; Miller, 2015; but see also Recio and Virgós, 2010). However, the combination of SDM providing concise information on ecological drivers of species distribution, and of models on conservation threats (e.g. human-related threats), can be of relevance to tailor and refine analytical frameworks for decision-making in systems with manifold human-wildlife conflicts. Studies on brown bears (*Ursus arctos*) in Europe incorporated mortality data into occurrence models to identify sink and source habitats (by accounting for habitat heterogeneity in demographic performance, Naves et al., 2003), or by discarding demographic features but approximating sink-like and source-like areas (through the independent modelling of the occurrence of presences and mortality events, Falcucci et al., 2009). However, because the brown bear is an endangered large carnivore of low reproductive rate, highly impacted by habitat loss, direct persecution, distributed in metapopulations, and often below viable population sizes (Wiegard et al., 1998; Ciucci and Boitani, 2008), the species may not be representative for other large predators. Further applications of SDM accounting for assorted human-driven mortality data are still required for large carnivores of high adaptability, medium-to-high reproductive rate, and high capacity of rapid expansion at geographic scales, such as the wolf.

Considering the wolf in Scandinavia is restricted today by management actions to constrain its demography and distribution to the WBR, we first elaborated a SDM to identify the biotic and anthropogenic variables driving the spatial occurrence of wolf territories and to predict the potential distribution of wolf territories in the WBR. Second, we explored these predictions for all of Scandinavia assuming the hypothetical scenario where the species would be allowed to reproduce elsewhere under the same management strategy applied in the WBR. To devise a framework able to account for mortality risks, we also modelled the occurrence of human-caused mortality on wolves due to traffic, culling or poaching, and identified key habitat variables predicting each of these mortality causes. Although culling is based on management decisions, we aimed to explore possible associations between these mortality events and surrogates of likely conflict such as human, livestock, and ungulate presences. We then produced a final integrated two-dimensional model that combined information on the predicted occurrence of mortality causes and the produced SDM to identify heterogeneity in the potential suitability of habitats accounting for mortality risk levels. Because the wolf is a generalist species that was once broadly distributed in Scandinavia (Lönnberg, 1934), we predicted a potential broad distribution of wolf territories in the
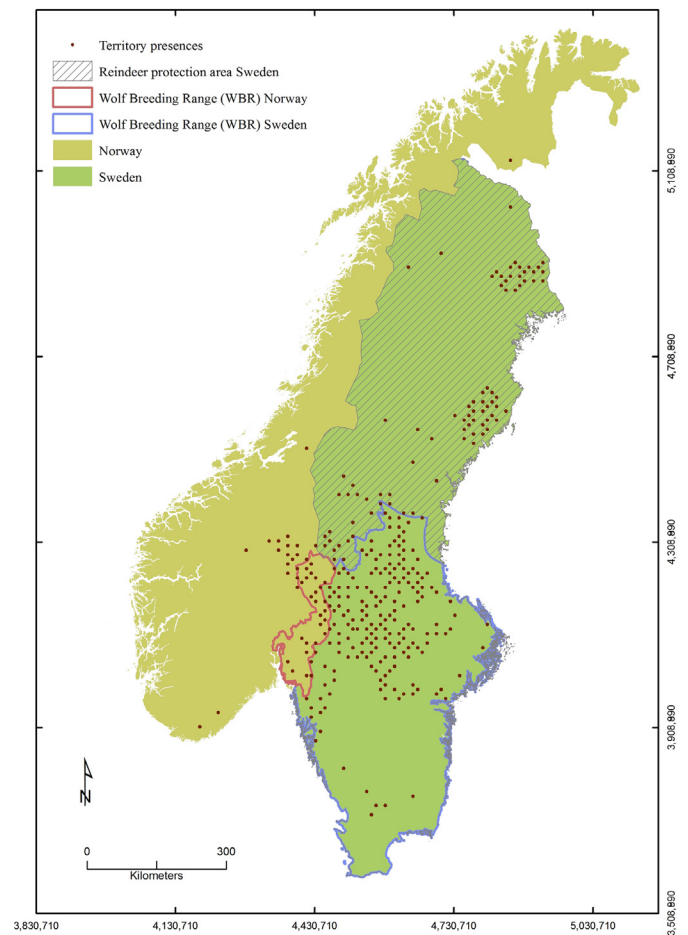

Fig. 1. Study area of the Scandinavian Peninsula including Sweden and Norway with the areas of the wolf breeding range (WBR) and the selected presences of wolf territories. The wolf is subject to different protection laws within the WBR in Sweden and Norway. Outside these areas wolves are generally killed through management actions.

southern parts of the WBR area and all over Scandinavia, a pattern highly shaped by human presence and persecution. Our framework can provide spatially-explicit predictions on wolf expansion and the potential distribution of wolf mortality risks under a conceptual case. This methodological framework can be applied in the management of wolf populations or other species worldwide at risk from human induced mortality.

2. Methods

2.1. Study area

We conducted research in the Scandinavian Peninsula over an area of 773,585 km² comprising Sweden and Norway (Fig. 1). The Scandes in the west-central area of Scandinavia is the only mountainous region in Sweden, otherwise mostly occupied by hills of boreal forest ridges and lakes in the north and an increasing proportion of arable land in the south. Norway is dominated by mountains, fjords, boreal forest, wherein valleys are often inhabited by humans with farming of domestic animals. About 75% of the total vegetation coverage is dominated by boreal coniferous forest, mainly Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*. An expanding widespread network of forest roads is used by forest exploitation. Extensive agriculture occurs mostly to the south, and semi-domesticated reindeer farming takes place in the northern half of the peninsula. Human population is mostly distributed and concentrated in sparse urban areas in the central and southern parts

of Scandinavia, whereas rural regions often have densities under 1 inhabitant/km^2 (SCB, Statistics Sweden, www.scb.se).

2.2. Wolf population in Scandinavia

The wolf is one of the large carnivore species of Scandinavia along with the brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*) and wolverine (*Gulo gulo*). The decline of the wolf population in Scandinavia during the 19th and 20th centuries due to persecution resulted in fewer than 10 individuals in the late 1960s (Haglund, 1968) followed by a recolonization in the 1980s with the arrival of two immigrant wolves (Wabakken et al., 2001). During the last 30 years, the population has shown a 10–15% average annual increase limited by culling and poaching (Liberg et al., 2011), and by an inbreeding depression relieved by the occasional arrival of new immigrant wolves from the Finnish-Russian populations (Åkesson et al., 2016). The current population is classified as vulnerable according to the species red list in Sweden (Westling, 2015), and as critically endangered in Norway (Henriksen and Hilmo, 2015).

In Scandinavia, the main prey species of wolves are moose (*Alces alces*) and roe deer (*Capreolus capreolus*) (Sand et al., 2008). Other potential prey species are the red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and wild boar (*Sus scrofa*). Small preys are a minor part of the wolf diet (Sand et al., 2012). Brown bears have been identified as an intraguild driver of space use by wolves (Ordiz et al., 2015).

2.3. Wolf territory presence and mortality data

For the SDM, we compiled data on wolf territories as minimum convex polygons (MCP) produced from annual monitoring campaigns between 1998 and 2015 (Liberg et al., 2012; [Dataset] Recio et al., 2018). These territories were areas repeatedly occupied by wolves with at least one scent-marking wolf during winter (as indicator of an established family, territorial pack, or other stationary individuals), or from VHF/GPS locations of radio-collared wolves (Liberg et al., 2012). We considered established territories of single individuals, pairs, and packs over Scandinavia. Because the sampling protocol is not systematic and unified for the entire peninsula, we based our analyses on presence-only data, which is the recommended approach for species of wide dispersal capabilities (Falcucci et al., 2013). Presence data referred to confirmed wolf territory presence, i.e. overlapping wolf territories (MCP) over 10 × 10 km grid-cells (N = 396 presences). To account for sampling differences and spatial autocorrelation, we selected and treated presences (Fig. 1) as described in [Dataset] Recio et al., 2018.

Wolf mortality records have been regularly collected since 1978 by government authorities, including traffic collisions. We used the locations of traffic mortality events reported from collisions involving cars or trains (N = 74, [Dataset] Recio et al., 2018) since 1999. Culling regulations refer to 1) permissions to kill a wolf due to protection/defense of livestock or pets when a threat is perceived or previous attacks have occurred (hereafter protective/defensive hunting), or 2) licensed hunting to target certain territories and individuals for population regulation purposes. Verified poaching events were mostly identified by radio-collared wolves that were killed while monitored (Liberg et al., 2012). We selected and treated the presences of each type of mortality events within 10 × 10 km grid-cells as described in [Dataset] Recio et al., 2018. The number of grid-cells with presence of wolf mortality varied between cases (N = 74, N = 35, N = 202, N = 100 for traffic, poaching, protective/defensive, and licensed hunting, respectively. [Dataset] Fig. 1 in Recio et al., 2018).

2.4. Habitat variables

We considered an initial set of variables (Table 1) extracted and quantified per each 10 × 10 km grid-cells using ArcGis 10.1 software

(Redlands, CA) to model the spatial distribution of wolves and wolf mortality, respectively. Full details about the variables and sources are provided in [Dataset] Recio et al., 2018. For the SDM, we used variables on natural landcover, anthropogenic landcover and infrastructures, human population density, surrogate estimations on the abundance of wolf prey in Scandinavia, and the distribution of the brown bear population (as shown in Boitani et al., 2015) as an interspecific competitor in Scandinavia (Ordiz et al., 2015). Anthropogenic landcover accounted in the SDM for the indirect impact of human transformation of the landscape on the occurrence of wolf territories, and included agricultural areas and other anthropogenic artificial surfaces. We also integrated the number of sheep farms per grid-cell to account for potential conflicts due to livestock attacks (Frank et al., 2015). Because main roads can have an impact on habitat fragmentation and secondary roads are used by wolves for daily movements (Zimmermann et al., 2014), we calculated the total density of both transport infrastructures (kilometers per grid-cell). We incorporated human population density (number of inhabitants/km^2) as surrogate of grade of humanization. A prey species index was calculated for each ungulate species (moose *Alces alces*, roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, and wildboar *Sus scrofa*) per grid-cell using the average number of animals shot per square kilometer between the 2012 and 2015 hunting season. Harvest size is related to the population density of moose and roe deer (Ueno et al., 2014; Mattisson et al., 2013), and we assumed this relationship for the rest of the ungulate species.

We employed some of the variables used for the SDM to model the occurrence of mortality due to traffic, poaching, protective-defensive hunting, and licensed hunting (Table 1). For the traffic mortality, we used the variables railway, main and secondary road density (kilometers per grid-cell), and human population density. To independently model poaching, protective/defensive hunting, and licensed hunting, we selected an initial set of explanatory variables depicting human presence and activities, and accessibility to wolf habitat. These variables (Table 1) included cover of agricultural areas, ship-farms, prey densities as a surrogate of their importance as game species for humans, main and secondary roads to account for human accessibility to wolf habitats, and the categorical binomial variable WBR in the poaching and culling models. The variable WBR accounted for possible differences on mortality within and outside of this area (Fig. 1), and was delineated by merging the area to the south of the reindeer husbandry area in Sweden with the 'Norwegian wolf zone'.

We conducted a combined correlation test (r < 0.7) and a variance inflation factor (VIF < 4) (Zurr et al., 2010) to select only variables of low multicollinearity in the initial models (Table 1). Correlation and multicollinearity occurred among the artificial surfaces and human population density, and between agricultural cover and number of sheep farms. Consequently, only human population density was incorporated in the model as a surrogate of human presence. We also discarded sheep farming in favor of agricultural cover because the later represent an agent of landscape modification and potential conflicts due to the presence of domestic animals and livestock.

2.5. Modelling procedures

We modelled independently the potential distribution of wolves and mortality events using a maximum entropy approach with Maxent software (Elith et al., 2011). Maxent is a machine learning method widely employed to predict species distribution using presence-only data that consists of testing presence data versus background locations of unknown presence representing the available environmental conditions in a study area (Elith et al., 2011). Maxent is low sensitive to the number of presence locations to produce accurate models that outperform other methods (Merow et al., 2013). Maximum entropy approaches stem from applications in varied research areas (e.g. signal processing, image reconstruction, or astronomy) to make predictions using incomplete data by estimating the most dispersed, or closest to

Table 1

Summary of the model inputs and outputs for the spatial distribution model (SDM) on the probability of wolf territories and mortality occurrence using Maxent. The information includes: 1) the initial variables considered and the final variables and regularization values of the most plausible model after model selection procedures; 2) the percentage of contribution of the final variables, permutation importance and the type of effect on the probability of occurrence of wolf territories or mortality events; and 3) predictive capability of each model estimated using the area under the curve (AUC) for both the training and test data (WBR: wolf breeding range area).

Model	Initial variables	Final regularization (λ)	Training AUC	Test AUC	Final variables	% Contribution	Permutation importance	Overall effect on occurrences
SDM	Forest, natural non-forest, agriculture, human population density, main roads, secondary roads, moose, roe deer, red deer, fallow deer, wild boar, bears	2	0.82	0.83	Forest	69.4	60.9	(+)
					Moose	9.4	13.1	(+) up to 2/3 of the moose density
					Human population density	9.3	3.0	(−)
					Natural non-forest	7.9	12.1	(+)
					Roe deer	2.6	5.0	(+)
					Secondary roads	1.5	5.8	Greater at intermediate values
Traffic mortality	Main roads, secondary roads, human population density	4	0.86	0.84	Secondary roads	58.0	73.9	(+)
					Railways	42.0	26.1	(+)
Protective-defensive	Agriculture, main roads, secondary roads, moose, roe deer, red deer, fallow deer, wild boar, WBR	4	0.77	0.77	Moose	62.1	39.1	(+) at low values, then (−)
					Roe deer	26.5	30.9	(+) at lowest values, then (−)
					Secondary Roads	11.4	30.0	(+)
Licensed hunting	Agriculture, main roads, secondary roads, moose, roe deer, red deer, fallow deer, wild boar, WBR	4	0.91	0.93	Secondary roads	22.7	27.9	(+) at intermediate values
					Moose	22.4	24.6	(+) at intermediate values
					Roe deer	19.0	17.8	(+) at lowest values, then (−)
					Agriculture	7.3	10.3	(−)
Poaching	Agriculture, main roads, secondary roads, moose, roe deer, red deer, fallow deer, wild boar, WBR	4	Mean AUC = 0.90		WBR	65.9	52.0	Highest in the WBR
					Agriculture	18.8	32.8	(−)
					Secondary roads	15.9	15.2	Greater at intermediate values

uniform probability distribution (Merow et al., 2013). Accordingly, we extended the application of Maxent beyond SDMs to model and predict the potential distribution of the different wolf mortalities.

For recolonizing species, SDMs are influenced by the definition of the available area of expansion because they are not in equilibrium with the environment and consequently, the definition of availability is often subjective except for the case of species limited by geographic boundaries (Gallien et al., 2012; Falcucci et al., 2013). Our study area was mostly bounded by sea; in addition, we also assumed that humans are the only regulating "predator" of wolves holding the species to potentially occupy almost the entire Scandinavia (Liberg et al., 2012). To ensure that the range of values of the variables identified from the model as an ecological optimum in the entire study area was represented by the training datasets, we conducted a multivariate environmental similarity surface (MESS) analysis in Maxent for each model (Elith et al., 2011).

Maxent integrates the possibility to fit complex response curves by selecting several feature classes (linear, squared, product, hinge, and threshold) (Merow et al., 2013). However, it is considered that the marginalized response curves for each predictor are enough to define a final model (Merow et al., 2013). Consequently, we discarded product features in Maxent input settings to facilitate output interpretations, and reduced the number of features because no evidence of predictor interactions existed. Regularization parameters in Maxent settings reduce model overfitting by ensuring the model satisfies the empirically measured constraints instead of a precise fitting, and by discarding features of the model. Maxent provides a default value of regularization but considering a range of values is recommended (Elith et al., 2011; Merow et al., 2013). Hence, we applied a set of seven regularization values ($\lambda_1 = 0.5$, $\lambda_2 = 1$, $\lambda_3 = 2$, $\lambda_4 = 4$, $\lambda_5 = 8$, $\lambda_6 = 16$, $\lambda_7 = 32$) (Halvorsen et al., 2016) independently in the SDM and mortality model procedures.

Except for the poaching dataset that consisted of only 35 locations, we split each presence dataset of territories and mortalities in 80% and 20% to train and test the model, respectively. We then run models accounting for the seven regularization values independently in the SDM and mortality model procedures. We modelled complexity through a step-selection procedure from each initial model using ENMs tools based on AICc values (Warren and Seifert, 2011) as described in Appendix A. The best model selected was computed using a cumulative output in Maxent, which depicts the relative probability of occurrence at that location plus all others with lower or equal probabilities, rescaled to range between 0 and 100 (Elith et al., 2011). This final run for each model also included each 20% leave-out dataset to test for predictive capacity, except for poaching due to the afore mentioned reduced number of presences. For this case, we conducted a cross-validation that leaves consecutively one-sample-out during 35 iterations and used the rest of the data as training. We measured model predictive accuracy using the area under the curve (AUC) of the receiver characteristic (ROC) curve of the training and test data as reported by Maxent (Elith et al., 2011).

For a spatially-explicit identification of the habitat suitability for wolf territories accounting for wolf mortality, each category of the SDM map was corrected for mortality occurrence using the produced final models. We considered this correction as a realistic interpretation of the probability of territory occurrence associated with habitat suitability and of mortality risks compromising wolf survival. For instance, a high suitability area will have the highest probability of wolf territory occurrence; however, if a high probability of mortality is identified in that area, the risk of failing in the successful establishment and/or survival of individuals within a territory could also be high. Accordingly, we defined the risk of mortality as the categorical level of threat compromising the survival of the members of wolf territories and classified through the interaction of the probabilities of wolf habitat suitability and of mortality occurrence (Table 2). We adapted the method described by Falcucci et al. (2009) to integrate the resulting SDM map with: 1) the traffic mortality map; 2) an ensemble of the predictive

maps of the occurrence of the different wolf hunting mortality causes; and 3) an ensemble of the predictive maps of all the mortality causes (traffic and wolf hunting). To integrate the SDM and the mortality models, we classified the probability values of the SDM and mortality maps into four discrete categories obtained by splitting data per quartile value (Falcucci et al., 2009). In the SDM, the first quartile contained the lowest probability of occurrence values depicting very low or unsuitable areas for the species, and the fourth quartile indicated a high suitability. Similarly, the probability of mortality occurrence for each mortality cause resulted from very low or no mortality to high probability of mortality. The ensemble of mortality models consisted of taking the maximum category rank of mortality for each grid-cell among the categorical mortality maps. Irrespective of demographic information, Falcucci et al. (2009) considered the nomenclature of sink-like and source-like to combine different categories of bear occurrence and mortality. To avoid confusion with demographic performance not specific to our analyses, we only referred in our classification to suitability (i.e. habitat suitability), and mortality risk categories (where higher probabilities of mortality impoverish the different categories of habitat suitability, Table 2).

3. Results

3.1. Distribution model of wolf territories

The results for the SDM on wolves are summarized in Table 1, the resulting predictive map in Fig. 2a, and the graph outputs in Appendix B. Forest cover had the highest contribution (69.4%) to the model and showed a positive relationship with the occurrence of wolf territories. The variables natural non-forest, densities of moose, roe deer, and humans, as well as secondary roads contributed less to the model (< 14% each). A visual analysis of the MESS outputs of Maxent revealed that for the entire Scandinavia, the values of each variable considered in the model were within the range of the values of the training dataset. The model predictive performance was good (AUC = 0.82) according to Baldwin (2009) classification.

3.2. Mortality occurrence modelling

The results for the mortality models are summarized in Table 1, the predictive maps in Fig. 2b-2d, and the graph outputs in Appendix B. The most plausible model on traffic mortality included the density of secondary roads (58.0%) and railways (42.0%). The occurrence of traffic mortality increased with the abundance of these infrastructures. The model prediction capability was good (AUC = 0.84).

The variables with the highest contribution to the final model on protective-defensive culling were moose (62.1%), deer density (26.5%), and secondary roads (11.4%). The highest mortality caused by protective-defensive culling occurs at low densities of moose and roe deer, and at an increased density of secondary roads. The predictive performance of the model using test data was good (AUC = 0.77). The final model for licensed hunting showed secondary roads as the variable with the highest contribution to the model (51.3%), followed by moose density (22.4%), roe deer density (19%) and agricultural cover (7.3%). Contrary to protective-defensive mortality, the abundance of secondary roads showed that the highest occurrence of wolves killed under licensed hunting was at an intermediate density of secondary roads. The occurrence of wolves killed increased at low-to-medium density of moose. Low densities of roe deer were positively related to wolf mortality but showed a negative relationship at higher densities. The predictive performance of the model using test data was good (AUC = 0.88).

The variable with the highest contribution to the final model on the wolf mortality caused by poaching was the factor WBR (65.9%), i.e. poaching occurrence was highest in the WBR area. Poaching was negatively associated with cover of agricultural areas, and increased with

Table 2

Contingency table to integrate maps on the wolf territory suitability in Scandinavia extracted from the species distribution model (SDM) map, and the mortality risk categories. Medium to high probabilities of mortality occurrence pose a risk that impoverishes the different categories of habitat suitability.

		Suitability			
		1	2	3	4
		(Unsuitable-very low)	(Low)	(Medium)	(High)
Mortality occurrence	1 (None- very low)	Unlikely territory occurrence	Low suitability	Medium suitability	High suitability
	2 (low)				
	3 (Medium)	Unlikely territory occurrence	Low risk	Medium risk	High risk
	4 (High)				

density of secondary roads at low values but showed a nearly constant effect at high densities. The predictive performance of the model was very good (AUC = 0.90, Baldwin, 2009). Visual analyses on the MESS outputs from Maxent yielded positive values for all the mortality models, which indicated that the values of the variables of each mortality model across the entire geographical area were within the range of values of the training datasets.

3.3. Integrating territory and mortality occurrence

The two-dimensional integration of the suitability map and the occurrence of traffic mortality (Fig. 3) revealed that 86.4% of the WBR, and 44.2% of the total area of Scandinavia poses a risk for wolf mortality due to traffic (cars and trains) collisions (Fig. 4). The SDM map combined with the ensemble maps on all mortality events except traffic mortality resulted in a total risk area of eventual wolf mortality due to

culling or poaching of 85.1% for the WBR area and 53.3% for Scandinavia. The integrated SDM and mortality map identified a total risk of mortality area of 87.3% of the WBR and 54.3% of the total Scandinavia. A total of 44.5% and 24.9% of the WBR area showed high risk and medium risk, respectively. A total of 24.1% and 20.3% of the entire Scandinavia had a high risk and medium risk for wolves, respectively. Only 0.9% of the WBR and 31.7% of Scandinavia remained suitable land out of the categories of risk for the occurrence of wolf territories. The integrated two-dimensional map also acknowledged an area of unlikely territory occurrence due to unsuitable or very low suitable habitat of 12.6% of the WBR, and 24.1% of Scandinavia (Fig. 4).

4. Discussion

Our study provides a novel framework for modelling wolf territory habitat suitability and mortality occurrences. We integrate both biotic
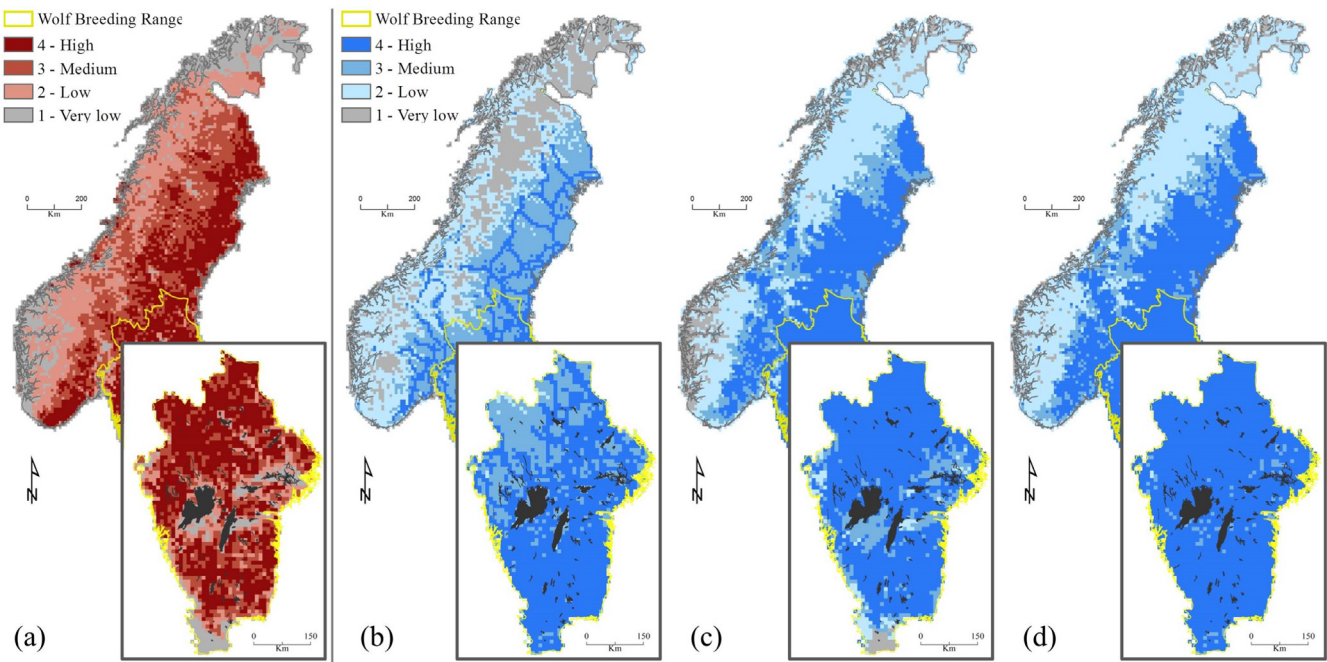

Fig. 2. Predictive maps across Scandinavia and the wolf breeding range (WBR) to the south showing: (a) species distribution model (SDM) map on suitability/occurrence of wolf territories, (b) probability of mortality occurrence caused by traffic (train, vehicles) collisions, (c) human killing of wolves produced after assembling the predictive maps on culling (protective-defensive and licensed hunting maps) and poaching occurrence, and (d) results after assembling the maps on the probability of mortality occurrence due to traffic, culling and poaching.
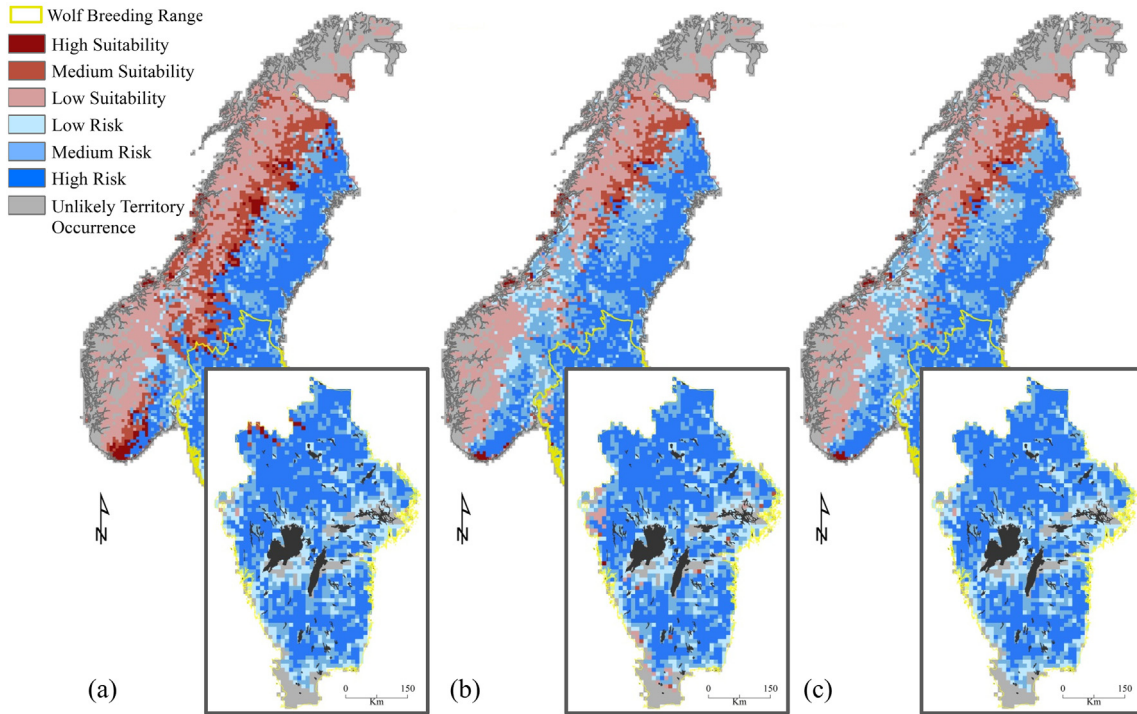
Fig. 3. Maps on suitability and mortality risk resulting from the two-dimensional integration of the SDM model/map with (a) the traffic collision occurrence model/map, (b) the ensemble killing mortality (culling and poaching) occurrence model/map, and (c) the ensemble model/map on all mortalities.

and anthropogenic variables to identify risk gradients of human-caused wolf mortality. Wolves could potentially occupy almost any area of the WBR in Southern Scandinavia, and generally most of Scandinavia. However, a high probability of human-caused mortality accompanies wolves in their potential distribution. This is shown by our results with < 0.1% of the WBR classified into suitable areas not linked with risks, although in a potential habitat that combines low suitability with non-to-low human-driven mortality. Even though this conclusion re-affirms a well-known intrinsic consequence of the longstanding human-wolf conflict (Heberlein, 2012), this reality is illustrated here with a comprehensive spatially-explicit approach to identify the different gradients of habitat quality over a geographic range attending to human-driven mortality on wolves. Incorporating the distribution of mortality occurrence in our research complemented our SDM results by modelling the causes of human-driven mortality that shape the expansion of a wolf population. Mortality causes most usually emerge from the human-wolf conflict, which often results in measures and

preventive actions to control wolf population density and distribution wherever the species is present. The pervasive risk of human-driven mortality on wolves in the WBR is primarily caused by culling and poaching, and secondly, by traffic collisions in an area that contains a high density of transport infrastructures in Scandinavia. Reducing the potential high traffic mortality in the WBR requires the introduction of measures to reduce collisions in specifically identified areas of risk (Beckmann et al., 2010). Conversely, culling and poaching ultimately result from human-driven decisions that are expected to emerge from assorted human-wolf conflicts, yet the WBR contains most of the human population in Scandinavia.

Our SDM results suggest that wolf territories most likely occur in areas with high coverage of natural landscape, primarily forests and secondly natural non-forested areas, all with low human population density (see also Karlsson et al., 2007, and Chapron et al., 2014). Although prey and anthropogenic variables showed a smaller contribution to our model (see also Ordiz et al., 2015), prey density might still
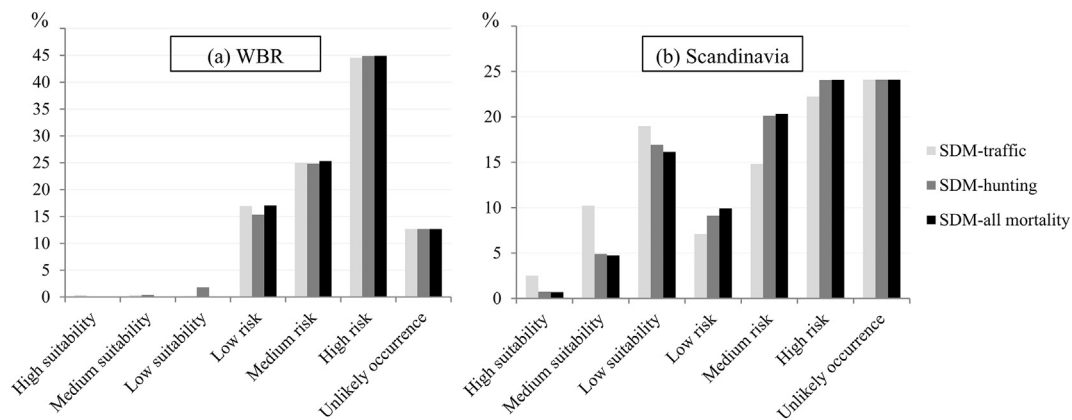

Fig. 4. Percentages of the area covering the different suitability and risk categories in the wolf breeding range (WBR) in: (a) Southern Scandinavia, and (b) total Scandinavia. Categories were produced from an integrated two-dimensional model of the spatial distribution model on wolves (SDM) with the different mortality occurrence models (traffic, licensed hunting, protective-defensive, poaching, and all mortality).

have important implications in shaping wolf population distribution and space use. Roe deer density is inversely correlated with territory size (Mattisson et al., 2013); consequently, large areas hosting high densities of roe deer or other alternative ungulates might host more wolf territories. Conversely, moose density is unrelated to wolf territory size (Mattisson et al., 2013), notwithstanding the moose is the most important prey in the current wolf distribution (Sand et al., 2008). Our results suggest that moose density is not a limiting resource for wolf territory occurrence since the moose is broadly distributed and highly available all over Scandinavia (Sandström et al., 2013). Red deer, fallow deer, and wild boar are currently confined to the southern parts of Scandinavia lacking in most of the current wolf distribution, and hitherto, these prey species are not significant for wolves (Zimmermann et al., 2014). Research is required to identify the implications of these prey species in terms of biomass consumption and territory size once the wolf population would have expanded over its entire distribution range. Our models could not infer an effect of interspecific competition with bears on wolf territory occurrence, which contrast with the previously observed impact of bears in the expansion of wolves in Scandinavia (Ordiz et al., 2015). This possible discrepancy requires caution because it might be a consequence of the grain, scale, and the different predictor we employed.

We found that the density of secondary roads and railways were the main causes of traffic mortality on wolves. Main road presence could be irrelevant for territory occurrence at the scale considered and compared to other resources required/avoided by wolves in each sampling unit. Wolves may avoid establishing in close proximity to main roads only at a small scale of perceptual range. Conversely, secondary roads can be paved with speed limits > 70 km/h, which could jeopardize wolves when they select this resource for movement efficiency within territories (Zimmermann et al., 2014). Secondary roads contributed to the final models on licensed hunting and protective-defensive culling, with the highest probability of mortality occurring at medium densities of secondary roads. For licensed hunting, this pattern might result from a similar trend in the association of secondary roads with the wolf territory occurrence as determined by the SDM, but also because licensed hunting operations are logistically facilitated in more accessible areas. The observed association between protective-defensive mortality and low densities of moose and roe deer, both important game species in Scandinavia, requires further research to unveil whether this trend is related to actions influenced by game management decisions. Agricultural landcover was negatively related to wolf mortality in the final licensed hunting model, probably because wolf territories mostly occur in forest and natural-vegetated areas, and wolf hunting is typically conducted in these habitats where wolf territories have existed for some time.

In Scandinavia, poaching is chiefly cryptic and represents approximately half of wolf mortality (Liberg et al., 2012). Poaching of large carnivores is mostly avoided in proximity to human exploitations to minimize the risk of being discovered (Rauset et al., 2016), which is supported by our findings with the highest poaching occurrence in the WBR but outside of agricultural areas. Considering the presence of wolves is perceived as undesirable by part of the public, our results on poaching might also be construed as a spatial illustration of the resistance to conservation laws governing the species' management (Heberlein, 2012). This interpretation could be supported by the evidence from previous research that warned about the increased poaching rate on different large carnivores observed even in protected areas of Scandinavia managed as national parks (Rauset et al., 2016). Arguably, caution is required given the small sample size of our poaching data and because it referred mostly to poaching cases on wolves equipped with radio-collars that, otherwise, would have remained undetected.

Our conclusions from the WBR could be applied to the entire Scandinavia if the permanent establishment of wolf territories would be permitted elsewhere. However, because dispersing individuals are generally killed outside the WBR, our results in these areas make our estimations highly hypothetical. Additionally, our presence dataset concentrated most of the data in the core of the WBR, and although we used a bias raster in Maxent that weighted sparse afield presences (Recio et al., 2018), we acknowledge that a broader distribution of wolf territories presences might result in more accurate predictions in remote areas to the WBR. Consequently, our estimations need to be taken with caution for regions such as those of west Norway, or a strip of land of medium suitability in the north of Scandinavia that might seem, at first glance, appealing for connectivity considerations. However, this strip of land in the north of Scandinavia does suggest that further efforts and legal reinforcement to consider wolf persistence in the reindeer husbandry area could facilitate population connectivity and gene flow with eastern wolf populations. Regarding western Norway, the SDM map showed large areas of low probability of territory occurrence that resulted in areas of a priori no-risk for wolves in the ensemble map. Nevertheless, although the model variables over these areas were within the range of the values existing in the training points (as confirmed by MESS analyses), the configuration of these variables (e.g. landscape and prey density) shaping the habitat in these regions (usually mountainous, less forested, and with the presence of fjords) is conspicuously different to the conditions found in the areas where the wolf is currently present. However, due to the high plasticity of the wolf, it could be claimed that these areas might also be broadly occupied by the species despite the low suitability identified by our models.

In conclusion, our spatially-explicit models show a potential distribution of the wolf over almost the entire WBR. However, these areas are also associated with pervasive mortality risk that often lead to culling and poaching actions. Although there are suitable areas of wolf habitat, there are no such areas having both, high suitability and no or low human-driven mortality of wolves in the WBR of Scandinavia. Consequently, considering the adaptability of wolves, their survival and expansion in Scandinavia will be secondarily enabled by environmental variables, but primarily driven by human actions. These actions will require general changes in public attitudes (poaching is likely occurring through the entire Scandinavia), law enforcement, and changes in management. Integrated wolf distribution models accounting for the distribution of mortality events can be interpreted as a spatially-explicit prediction of inherent problems associated with the long-standing conflict linked to the species, as also found in other regions where the wolf returned naturally, was reintroduced, or was planned to be reintroduced (Fritts et al., 2003; Musiani and Paquet, 2004; Nielsen et al., 2007). The analytical (variable analysis level) and visual (mapping level) characteristics of the method using Maxent make it a valuable informative tool for management and conservation. Probabilistic integrated maps require relatively few data on locations of species presence and mortality; thus, they can be readily produced to delineate, plan, prioritize and modulate management actions in identified areas of conservation/management interest for wolves. Estimations on the distribution of mortality risks of wolves or other conflictual predators can be used to foresee the need for specific decision-making and strategies in their management, including anticipated responses to poaching, identifying areas of expected low and random spatial occupancy due to high mortality risk, and taking proactive management actions where wolf occupancy is most expected. Our framework and findings can underpin further investigations accounting for the mechanistic drivers of expansion and conflict regarding demography, dispersal, or societal factors of relevance (Behr et al., 2017). Through the study case of wolves in Scandinavia, we further develop a novel methodological approach (Falcucci et al., 2009) that could be used to advance the conservation of other conflict-prone species worldwide.

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