Agent-based models predict patterns and identify constraints of large carnivore recolonizations, a case study of wolves in Scandinavia

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ABSTRACT

Large carnivores are recolonizing areas of their historical range in Europe. This process has strong implications for conservation and management related to human-wildlife conflicts. Analyses and modelling of the observed mechanisms of spatial expansion can predict recolonization patterns under human influences. We demonstrate how spatially-explicit, agent-based models can assist to identify and predict how humans impact shape large carnivore recolonizations. Using detailed data obtained through long-term surveillance of wolf territories, we identified the mechanisms of recolonization and predicted the spatio-temporal patterns of expansion of the wolf in the Scandinavian Peninsula. We disentangled the observed mechanisms of expansion to develop WolVES (Wolf Virtual Expansion Simulator), an agent-based model software. We applied the model to investigate in silico the observed lack of wolf recolonization into the suitable but densely human-populated area of southern Sweden and projected the expansion into the future. We tested the impact of traffic barriers and territory termination (wolf mortality most likely due to culling and poaching) on the observed recolonization in the south. Simulations identified that traffic infrastructures impacted only at configurations of insurmountable barriers unlikely to occur in Scandinavia, while low rates of territory termination had a major impact on the recolonization. Simulating until 2030 predicts that wolves will not colonize southern Sweden, which highlights the complexities of this process in areas of increased human-influence. The capability of simulators to test hypotheses and discriminate constraints of future population development makes them a valuable tool for ecologists, managers, and decision-makers involved in regional and transboundary conservation challenges of large carnivore recolonizations.

1. Introduction

Global habitat destruction has diminished the roaming capability of animals (Tucker et al., 2018) and particularly of wide-ranging species such as the terrestrial large carnivores (Ripple et al., 2014). The expanded habitat requirements of large carnivores and direct persecution arising from people's emotional and economic concerns (Heberlein, 2012; van Eeden et al., 2020) have historically resulted in the decline and range contraction of their populations (Chapron et al., 2014; Ripple et al., 2014). However, large carnivores are currently returning to areas of their former distribution range where they were extirpated, leading to the reignition and intensification of long-standing conflicts with humans (Chapron et al., 2014). Improved methods to identify where

and when large carnivores will recolonize using the observed patterns of expansion would enable the anticipation of conflicts and assist decision-making with regard to management and conservation policies that will impact large carnivore population recoveries and range expansions (Louvrier et al., 2018; Miller, 2015; Recio et al., 2018; Ronnenberg et al., 2017).

In this study, we developed and demonstrated a spatial modelling approach to identify and simulate how humans and the availability of suitable habitat shape the expansion and distribution of a large carnivore, the wolf (*Canis lupus*), across broad geographic areas. The wolf is an symbolic large carnivore linked to long-standing conflicts with humans and is currently recolonizing regions of Europe and North America (Chapron et al., 2014; Mech, 2017). Though the human-

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dominated landscapes of Europe still provide sufficient space and suitable habitat for large carnivore recolonizations (Milanesi et al., 2016), wolf expansion is in some countries and regions much restricted and thus, populations remain endangered (Kojola et al., 2018). This may be a consequence of human attitudes against wolf presence resulting in harvest and poaching (Fritts et al., 2003; Kuijper et al., 2016; Liberg et al., 2012a; Suutarinen, 2019) and to the widespread human modification of landscapes that has created extensive networks of traffic barrier infrastructures and intensively managed forest and agricultural lands. Although the wolf is a generalist capable of adapting easily to humans and anthropic landscapes (Fritts et al., 2003; Recio et al., 2018; Ronnenberg et al., 2017), these human factors may hamper the dispersal and expansion of wolf populations although species distribution models based on environmental variables predict much widespead habitat for the species (Eriksson and Dalerum, 2018; Recio et al., 2018).

We focused on a case study of wolf recolonization in the Scandinavian Peninsula (hereafter referred to as Scandinavia, including Sweden and Norway), which bares management challenges common to other species and regions. Thus, our research is a representative of the management issues of large carnivores in human-dominated areas worldwide. The recolonization pattern of wolves in Scandinavia is shaped by management policies addressing the mitigation of human-wildlife conflicts and the conservation of nature. Particularly, the land uses and conservation interests in northern and southern Scandinavia impact in wolf management policies. Northern Scandinavia is reindeer (*Rangifer tarandus*) husbandry/herding area, while the southernmost parts have a higher human population and more intensive land use, which in both areas creates a negative attitude to wolf recolonization. Furthermore, there exists a pervasive pressure on wolf populations from poaching (Liberg et al., 2012a, 2020). To guide management decision-making, the wolf recolonization in Scandinavia has been studied from different angles, including extensive monitoring (Liberg et al., 2012b), habitat suitability models (based on landscape, prey, and anthropogenic variables) (Eriksson and Dalerum, 2018; Karlsson et al., 2007; Recio et al., 2018), and risk mapping for wolf survival (Recio et al., 2018). These studies identified most of Scandinavia, including the southern areas, as suitable habitat for wolf recolonization. However, because habitat modelling cannot consider the behavioural responses that shape wolf expansion (e.g. dispersal), these approaches failed to predict the extremely weak recolonization process in the south of Scandinavia where few attempts of establishment have occurred. Agent-based models (ABM) are a useful modelling technique as they provide spatially-explicit predictions and detailed mechanistic understanding of the expansion and recolonization of wildlife species (O'Sullivan and Perry, 2013; Railsback and Grimm, 2019). These models are useful in supporting decision-making in environmental and conservation management (Kelle et al., 2013; Singer and Graham, 2012). Moreover, ABM are well suited to analyse the population-dynamics of large mammals because the empirical monitoring of these species often focuses on the behaviour of single individuals or family groups.

We identified from an extensive wolf monitoring program (Liberg et al., 2012b) the observed environmental mechanisms that shape wolf territory expansion in Scandinavia and incorporated them into a spatially-explicit ABM. In the process of territory expansion (i.e. the recolonization of unoccupied areas by new wolf territories), we considered ecological conditions including food availability and habitat suitability, assumed mortality from human actions (such as culling and poaching), and traffic infrastructure. With the model, we explored the spatial dynamics of potential wolf recolonizations in Scandinavia and predicted the wolf expansion pattern up to 2030. Furthermore, we evaluated by testing competing hypotheses, the mechanisms that could constrain the wolf expansion to the south of Scandinavia. Particularly, we investigated in silico how the presence of movement barriers (i.e. traffic infrastructure that may be crossed but not circumnavigated - Beyer et al., 2016), and the termination of wolf territories (i.e. mainly caused by killing of wolves) have impacted and will impact the population expansion towards the south of Scandinavia. Thus, we firstly hypothesized that wolf territory settlement is hindered in the south due to a low permeability caused by a high density of traffic barriers (highways and railways), which are a relevant source of mortality and a barrier to the movements of carnivores (Selva et al., 2015). Second, we hypothesized that on top of the barrier effects, wolf territories in the south will continue disappearing soon after their establishment due to legal culling or poaching (Miller et al., 2016; Milleret et al., 2016). Knowledge of the future wolf range can support conservation and management policies to mitigate human-wolf conflicts. Considering our modelling approach as a basis, we aim to provide a valuable research initiative applicable to other territorial large carnivore species expanding into human-dominated landscapes.

2. Methods

2.1. The wolf in Scandinavia

The wolf was considered as functionally extinct in Scandinavia in 1966 due to human persecution (Wabakken et al., 2001). With a current population of ~400 individuals (Wabakken et al., 2018), the species is classified as vulnerable in Sweden (SLU Artdatabanken, 2020) and critically endangered in Norway (Henriksen et al., 2015). It is assumed more rapid recolonization and population growth is constrained by management (culling), illegal killing (poaching), and inbreeding depression (Åkesson et al., 2016; Liberg et al., 2012a; Wabakken et al., 2001). Location and persistence of wolf territories are surveyed thoroughly every year and an ample number of individuals are tracked using GPS-collars (Åkesson et al., 2016; Bischof et al., 2019; Wabakken et al., 2018).

To lessen conflicts, wolf culling occurs under different management regimes that ultimately determine where the species can subsist or be killed. In Sweden, wolves are protected under the Habitat Directive 92/43/ECC, which is binding EU legislation. However, to safeguard the cultural heritage of the Sami population and their traditional land use of reindeer husbandry/herding, wolves are culled and territories are not allowed to establish in the area covering central to northern Sweden. In Norway (a non-EU member), a "wolf-zone" (17,000 km^2, ~5% of the country) was created in the south-east region bordering Sweden; out of the zone, free-ranging sheep and semi-domestic reindeer husbandry/herding occurs so dispersing or newly established wolves are culled. Consequently, under this management in Scandinavia, wolf territories can only establish in a wolf breeding range (WBR) that covers south-central Sweden and the Norwegian "wolf-zone" (Fig. 1, see also Recio et al., 2018). Thus, the WBR concentrates the presence of wolf territories in Scandinavia. Similarly to North America (Stenglein et al., 2015, 2018), the wolf density in Scandinavia is modified by a spatially varying risk of mortality associated with the presence of humans and their activities. Additionally, this management regime also reduces gene flow from the large source populations in Finland and Russia (Åkesson et al., 2016). In summary, the population can only continue expanding in the remnant areas in the northern part of the WBR (NWBR), or towards the southern part of the WBR in Sweden (SWBR).

2.2. Study area

Our study area comprised mainland Sweden and Norway (Fig. 1). The human population is mostly concentrated in the central and southern parts of the WBR, where an increasing proportion of agricultural land and the highest densities of road and railway infrastructure also occur. We split the WBR in NWBR and SWBR, where the SWBR was the subarea to the south of the large lakes in Sweden (Fig. 1). This division allowed us to test our questions on the observed lack of recolonization in southern Sweden despite the presence of apparently suitable habitat. Outside of the WBR (OWBR) covers the rest of Scandinavia.
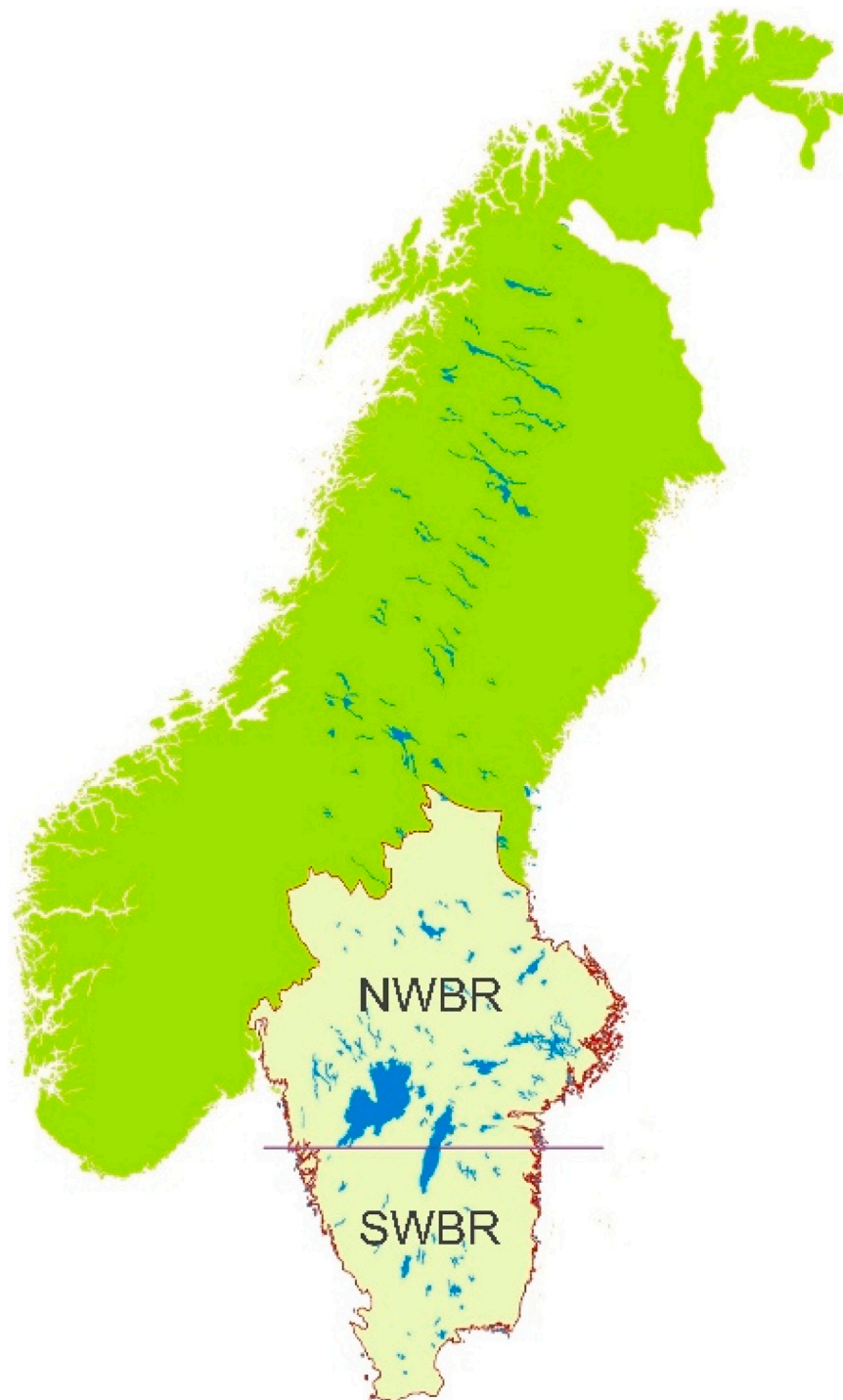
Fig. 1. Study area in the Scandinavian Peninsula. The area bounded in red indicates the wolf breeding range (WBR) where we focused our research. We divided the WBR into northern (NWBR) and southern (SWBR) parts (see horizontal line) to test our hypotheses on the recolonization of the SWBR by wolves. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.3. Agent-based model framework

Agent-based models are constructed bottom-up to analyse the spatial and temporal patterns of population-dynamics at large-scales arising from the behaviour of entities/agents of interest and their interactions (e.g. individual animals, groups, territories) at small-scales (O'Sullivan and Perry, 2013; Railsback and Grimm, 2019). The information at small-scales is represented by mathematical rules that describe the probable behaviour of the agents in response to the environment following ecologically driven rules. The agents adjust their behaviour according to their own current state, the environment, and/or other agents (Railsback and Grimm, 2019). Ultimately, the projections in the simulations reveal the spatial and temporal patterns of population-dynamics at large-scales. Therefore, ABMs can address the complexity inherent in ecological processes and assist decision-making in conservation management and strategy.

Using an ABM approach, we developed the spatially-explicit model environment WolVES (Wolf Virtual Expansion Simulator) to simulate the spatial expansion of wolf territories based on data from extensive monitoring of the Scandinavian wolf population (Liberg et al., 2012b).

Table 1

Parameters of the agent-based model (ABM) for the expansion of wolf territories in Scandinavia.

Parameter	Variable name[a]	Value[b]	Calibration range[c]	Source
Territories				
Initial number of territories		17/60		Reports (Liberg et al., 2012a, b; Wabakken et al., 1999, 2015)
Initial year		1998/2014		
Territory in/out of WBR		From raster		Recio et al., 2018
Territory size	T_{size}	Eq. (1)		Mattisson et al., 2013
Territory creation				
Mean probability of territory creation	MTC		0–1	Empirical approximated by calibration
Distance to original territory		Exponential distribution ($\mu = 101.8$ km)		Empirically calculated (Liberg et al., 2012a, and O. Liberg personal communication)
Infrastructures presence (roads and railways)		From raster		
Territory establishment				
Habitat suitability of territory to settle	ST		0–100	Recio et al., 2018
Ungulate (roe deer) density		From raster		Mattisson et al., 2013; Recio et al., 2018
Probability of territory to disappear				
Probability of territory to disappear (WBR)	Td-WBR		0–1	Empirical (Table A3). Weibull distribution
Trend in probability of territory to disappear (WBR)	tpd-WBR		0–1.50	″
Mean probability of a territory to disappear (NWBR)	Td_NWBR		0–1 (0.18–0.26 by 0.01)	Calibrated. Weibull distribution.
Trend in probability of territory to disappear (NWBR)	tpd_NWBR		0–1.70	″
Probability of a territory to disappear (SWBR)	Td_SWBR		0–1 (0.4–0.8 by 0.1)	Calibrated. Normal distribution
Probability of terminating a territory out of the (WBR)			0–1	Empirical. Normal distribution
Traffic infrastructure				
Roads and railway		From raster		
Probability of crossing	Pc	0.6	(0.4–0.7 by 0.1)	Calibrated

[a] Refers to the variable names as used in the text.

[b] Variable values of the model to simulate the observed expansion between 1998 and 2014.

[c] The initial range from which parameters were calibrated. WBR depicts wolf breeding range, NWBR – northern part of the wolf breeding range, SWBR – southern part of the wolf breeding range.

Table 2

Outcomes of the agent-based model (ABM) on the expansion of wolf territories in Scandinavia and descriptions. WBR depicts wolf breeding range, NWBR - north of the wolf breeding range, SWBR - south of the wolf breeding range.

Model outcome	Description
Territories in Scandinavia	
Total created	Total number of territories created during the simulation in Scandinavia
Total disappeared	Total number of disappeared territories during the simulation in Scandinavia
In the current year in Scandinavia	Total number of territories in the current year of the simulation
In the current year in the WBR	Total number of territories created in the WBR during the current year
In the current year outside the WBR	Total number of territories created out of the WBR during the current year
Territories in the WBR	
Total created in the NWBR	Total number of territories created in the north of the WBR
Total created in the SWBR	Total number of territories created in the south of the WBR
In the current year in the NWBR	Total number of territories created in the NWBR during the current year of the simulation
In the current year in the SWBR	Total number of territories created in the SWBR during the current year of the simulation

WolVES software was designed as a versatile tool to support research and management and was implemented in the programming environment NetLogo v6.0.1 (Wilensky, 1999). We provide a detailed model description following the ODD (Overview, Design, and Details) protocol (Grimm et al., 2020) in the supporting information. A compilation of the parameters and values used in WolVES is included in Table 1. A compilation of the model outcome produced by WolVES is shown in Table 2. Operational and updated installation versions of WolVES and user manual can be downloaded at wolves.marianorecio.com.

We applied WolVES to predict the expansion of wolves in the WBR until the year 2030 from monitored recolonization patterns between 1998 and 2014. Each year counted from winter to winter, e.g. 2014 ranged from the winter of this year until that of 2015. We further tested the human impact caused by traffic infrastructure and killing of wolves on the population expansion in the NWBR and SWBR. For this purpose, we modelled in yearly time steps the cycle of wolf territories in three stages: the search for a suitable site to establish a new territory, the establishment of the territory, and the termination of the territory.

We modelled the wolf population at the aggregated level of wolf territories (as individual entities or agents in our ABM approach). The wolves are social animals; thus, cooperative behaviours determine spatial dynamics. Therefore, we argue that demographic processes at the organisational level of individual wolves can be aggregated at the level of wolf territories to model wolf expansion. Moreover, wolf territory is the organisational level annually surveyed and managed by the authorities (Liberg et al., 2012b). Using the same organisational level in

WolVES allows tying the model to available data and enhances its practical use and ease of application for management. The model uses a 10×10 km spatial resolution, as this is fine enough to resolve wolf territories that range in size 250–1800 km² (Mattisson et al., 2013).

The search for new sites to create a territory considered the probability to create a new territory, movement to the new site (accounting for barriers and distance) and the habitat suitability at the new site. The annual probability of an existing territory to create a new territory was estimated from the compiled annual monitoring data (Liberg et al., 2012b). Movement could be restricted by barriers such as waterbodies or traffic infrastructure (highways and railroads) (Cozzi et al., 2013; Selva et al., 2015; Smith et al., 2015). Traffic infrastructure influences wolf dispersals and population distribution with more territories in areas with low density of roads (Zimmermann et al., 2014). We used information on major roads extracted from the National Road Database (NVDB) (Swedish Transport Administration, status 2014). The distance of potential new sites to the original territory was exponentially distributed around the mean distance 101.8 km, following our empirical findings from analyzing the distance between territories and their natal territories. Site suitability was taken from a habitat suitability model (Recio et al., 2018) that was calculated from landcover, prey, and anthropogenic variables. We ignored wolf immigration from Russia and Finland via the OWBR, because outside the WBR most wolves are killed (Åkesson et al., 2016).

Because wolves can live almost everywhere in Scandinavia (Eriksson and Dalerum, 2018; Recio et al., 2018), we assumed wolf preference for potential new territories was ranked by habitat suitability and the avoidance of intraspecific competition. Therefore, territory establishment at a site depended on habitat suitability (Recio et al., 2018), food availability and intra-specific competition. The new territory could only include suitable areas that were not part of another wolf territory, because wolf individuals, pairs, and packs actively defend territories using scent-marks (Peters and Mech, 1975). Territory size depends on the availability of roe deer (*Capreolus capreolus*) (Mattisson et al., 2013). We estimated the density of roe deer from harvest data to range between 0.1 and 8 roe deer/km² in the study area (Mattisson et al., 2013; Recio et al., 2018).

We assumed that legal harvest and poaching were the dominant mortality causes leading to territory termination (Liberg et al., 2012a, 2020). Termination of an existing territory depended on its age (since establishment) and the local management regime. Age dependence was modelled according to empirical life tables (Table A1). Culling rates followed different management policies in the OWBR and WBR.

2.4. Model calibration

We calibrated the model to the observed wolf territory expansion in the NWBR from 1998 to 2014. We focused on the NWBR because most wolf territories occur there, are less affected by human intervention, and because leaving out the SWBR made our hypothesis testing independent from the model calibration.

For the purpose of model calibration, we aimed to fit two metrics of wolf expansion: 1) the absolute difference between the observed and simulated total number of territories created during the period 1998–2014 in the NWBR ($N = 227$ territories), and 2) the difference between the observed and simulated total cumulative territory age of all the territories in the NWBR in the same period ($N = 724$). We varied the parameters mean territory creation, habitat suitability threshold, and the Weibull probability distribution parameters for the territory termination in NWBR (i.e. the probability *Td* and the trend *tdp*). A detailed explanation of the parameters is provided in the Supplementary Information (section Model Calibration) and in Table 3. To account for parameter interactions, we sampled the parameter space in a full-factorial design applying the Netlogo's built-in parameter sampling tool BehaviourSpace. A sensitivity test (Fig. A4) was conducted in the package RNetlogo in R software (Thiele et al., 2012) to

Table 3

Range of values in the probability of crossing (pc) and the probability of territory termination (m) to the South of the wolf breeding range that best approximated the spatial descriptors obtained from replicated simulations (for each probability value) to the observed descriptors. Axis x contains the spatial descriptors used in the ellipsoid (Fig. A4) for the different values of pc and m, respectively. These descriptors consisted of the mean location (μ) of the population distribution, angle of the 1st elliptical standard deviation with the North (α), and the length of the x and y axis of the ellipse. Axis y contains the range of values that maximized the fitness of the test, i.e. the values that best approximated to those of the ellipsis calculated from the location of real territories. The shaded cells indicate the values in that maximized the fitness and were the most common for all the spatial descriptors. The dark grey bars represent the range of fitness values for pc, and light grey bars for m. The probability values of 0.6 for both, m and pc were the values that fitted all the spatial descriptors.

Values	μ-m	μ-pc	α-m	α-pc	x-m	x-pc	y-m	y-pc
0.8			×			×		
0.7		×	×		×	×		
0.6	×	×	×	×	×	×	×	×
0.5	×		×	×	×		×	×
0.4			×		×			×
0.3					×			×

assess how small changes around the most optimal calibrated parameters modified the model fitness.

2.5. Evaludation of model reliability

We evaludated reliability of the calibrated model (see Augusiak et al., 2014 for the concept of "evaludation" in ABM applications) by testing its ability to reproduce empirically monitored patterns of wolf expansion in the WBR from 1998 to 2014. As recorded in annual monitoring reports (Liberg et al., 2012b), the wolf recolonization started from the center of the NWBR and radiated outwards. We converted all the territories created in the WBR up to 2014 to centroid points and computed, using the R package *aespace*, the mean center of the population distribution in the WBR, and the 1st Elliptical Standard Deviation. The latter, characterized by the descriptors length of its major and minor axis and the angle of the ellipse with the North (Fig. A6). These three spatial descriptors resolved the spatial territory distribution at a finer scale than number of wolf territories, which was used for model calibration. Moreover, this pattern is at a higher resolution than the geographic regions that are addressed in the model purposes. Therefore, these spatial descriptors are suitable to independently evaluate the emerging properties of the model concerning the spatial distribution of wolf territories. We then assessed which parameter values the outputs from repeated simulations were the closest to those calculated from the monitoring reports, and thus, best characterized the shape of the wolf territory distribution.

2.6. Simulation experiments for hypothesis testing

We applied the calibrated model as a baseline for simulations. To investigate how traffic infrastructure influences wolf territory expansion and colonization in the SWBR, we assumed highways and railways are barriers to wolf movement and territory integrity because they can be fenced and the traffic volume might dissuade animals to cross (Selva et al., 2015). While holding the rest of the calibrated parameters unchanged, we enabled the probability of crossing in the calibrated model to range from 0 to 1 in steps of 0.1. Furthermore, we impeded territory termination in the SWBR to exclude this confounding factor.

To investigate how a high mortality in the SWBR limits wolf expansion, we assessed the impact of territory disappearance by shifting the probability of territory termination in the SWBR from 0 to 1 in steps of 0.1 while holding the other calibrated values unchanged. Further, we

omitted all traffic infrastructures in these simulations to remove any confounding influences caused by barriers.

We ran repeated simulations ($N = 99$) for each configuration of parameters. Then, we compared the number of wolf territories produced in the simulations for the NWBR and SWBR in the period 1998–2014 with the total extracted from the annual monitoring surveys ($N = 227$ and 7 for the NWBR and SWBR, respectively).

We used the parameter values of the calibrated model and the best fitting probability of crossing and territory termination in SWBR to simulate the process of wolf territory expansion for the period 2015–2030. This simulation extrapolated observed expansion patterns under the current management regime into the future. We also ran a simulation scheme where we assumed the same territory termination in the SWBR as it is observed currently in the NWBR. This simulation attempted to identify the future recolonization if the same territory termination of NWBR were applied to SWBR. Both simulations started with the territory distribution observed in 2014. To analyse the expansion of territories by 2030 in the SWBR, we conducted 999 simulations to assess the total number of territories created in the WBR and calculated the variance of model outputs.

3. Results

3.1. Model calibration

The best fitting model had the following parameter values: mean territory creation = 0.83; habitat suitability threshold = 5; mean territory termination (Td) in NWBR = 0.22; trend of territory termination (tdp) in NWBR = 1.13. Changes in these calibrated parameter around these selected values resulted in minor changes in fitness (Fig. A4).

Changes in the probability of crossing traffic barriers resulted in minimal changes in the total number of territories in the NWBR, except at values of a low probability of crossing, i.e. close to zero. Conversely, low to intermediate values of the probability of crossing strongly limited the expansion into SWBR (Fig. 2). A Kruskal-Wallis (chi-squared = 691.62, df = 10, p-value < 0.0001), and a Post-hoc Dunn test (Tables A4-A6) confirmed the significant differences between high and low probability of crossing simulations shown in Fig. 2. The calibrated value for the probability of crossing was 0.6.

Increasing the probability of territory termination in the SWBR reduced the total number of territories created there (Fig. 2; a Kruskal-Wallis test confirmed the significant impact of the parameter: chi-square = 666.46, df = 10, p-value < 0.0001). This impact was mostly due to significant differences (Tables A1-A3) between the lowest probabilities of termination (0–0.3) the and highest values. The calibrated value for the probability of territory termination in SWBR was 0.6.

3.2. Evaluation of model reliability

Our results confirmed that the simulations using the calibrated model maximized the fitness of the outputs approximating the median and the descriptors of the 1st Elliptical Standard Deviation better than other values of the model parameters (Table 3). Therefore, the calibrated model reproduced the observed spatial layout of wolf territories in the WBR well.

3.3. Simulation experiments for hypothesis testing

Simulations using the calibrated model revealed that only a minor part of the SWBR is likely to be colonized by 2030 (Fig. 3). The number of territories in the year of 2030 was: NWBR ± SD = 148.08 ± 7.80, SWBR ± SD = 7.9 ± 3.50. However, simulations applying the same probability of territory termination in the SWBR as in the NWBR but keeping the probability of crossing constant at 0.6 revealed no changes for the NWBR (NWBR ± SD = 149.90 ± 7.49), but it resulted in four
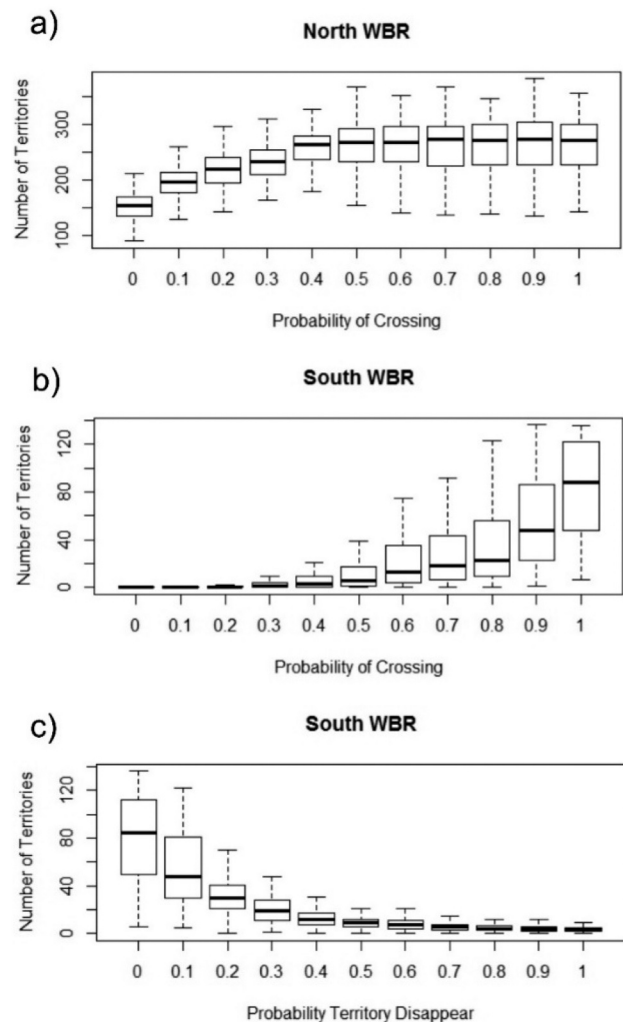

Fig. 2. Impact of changes in the probability of crossing (0–1) as barrier effect for wolf territory expansion that impacts on the number of territories created in the NWBR (a) and SWBR (b), while setting the probability of territory disappearance in the SWBR to 0. Impact of changes in the probability of territory disappearance in the SWBR on the number of territories created in this area while setting the probability of crossing = 1 (i.e. no effect) (c).

times more territories in the SWBR (SWBR ± SD = 32.15 ± 13.73) by 2030 (Fig. 3).

4. Discussion

The expansion of the wolf is a useful example of large carnivore recolonizations and of the pervasive conflicts with humans associated with these species. The wolf recolonization of Scandinavia is an illustrative example of this process (Gangaas et al., 2013; Ordiz et al., 2017; Recio et al., 2018). Using a spatially-explicit ABM approach we demonstrated that, assuming similar survival in the SWBR as observed in the NWBR, a significantly larger number of wolf territories should have already been established in the SWBR. However, this has not been the case, and our simulations reveal that although the number of territories will continue increasing in the NWBR, the recolonization of the SWBR will not likely occur in the next 10 years. This is despite the large areas of apparently suitable habitat are available (Eriksson and Dalerum, 2018; Recio et al., 2018) albeit with higher density human populations and transport infrastructure.

In our simulations, the infrastructures acting as barriers impacted wolf territory expansion and settlement, particularly at low
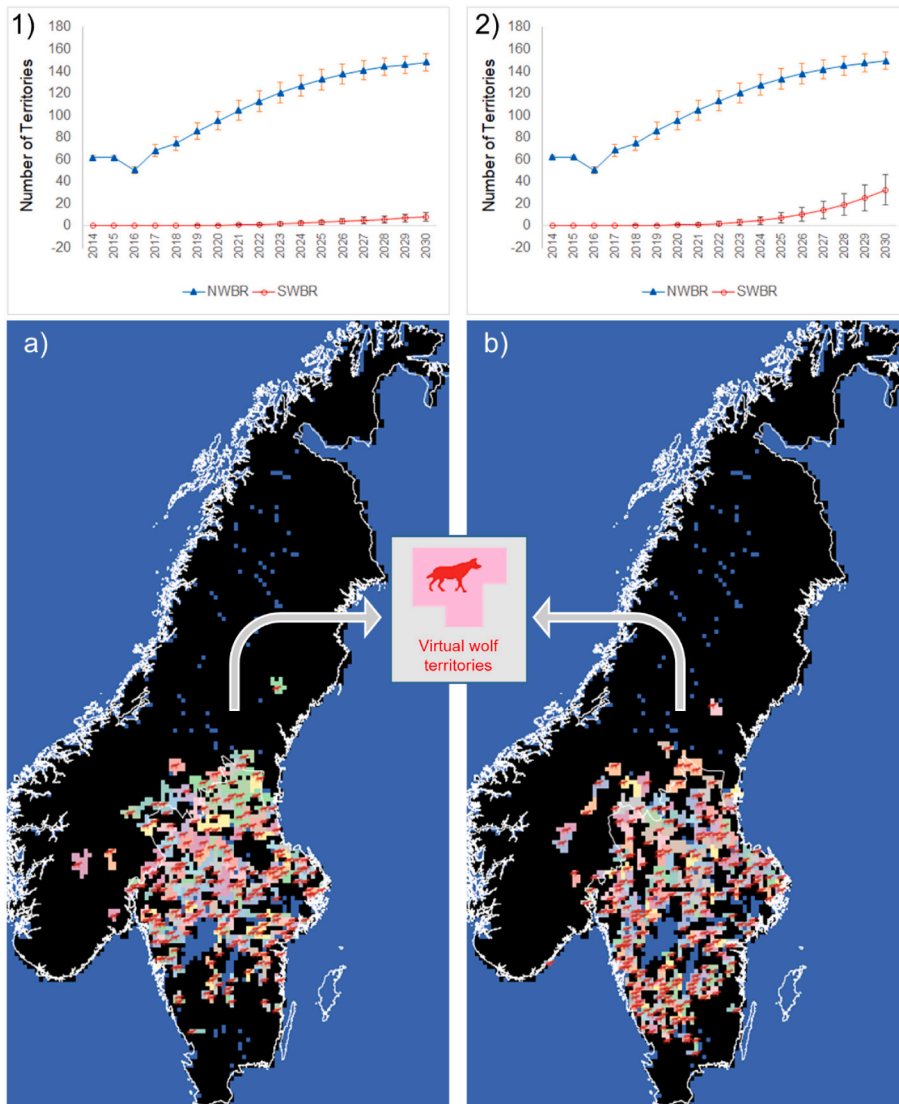
Fig. 3. Simulations in the period 2015–2030 executing 999 repetitions for each of the following configurations: (1) the calibrated values for the probability of territory termination in the NWBR and SWBR, respectively (left column in the graph); (2) the calibrated values used for the NWBR applied to the entire WBR (right column in the graph). The graphs (1) and (2) depict time series with the average number of territories per year (± standard deviations) calculated from the 999 simulations executed. Compared to scenario 2, scenario 1 produces lower numbers of territories in the SWBR. This reveals the current probability of territory termination in the SWBR that is higher than the expected for the entire WBR and thus, it is a major factor driving the future expansion of wolf territories in this region. Figures (a) and (b) are examples of single replications extracted from simulations (1) and (2), respectively. A set of adjacent similarly coloured grid cells represents a territory. The wolf symbol indicates the initial/centroid cell of the territory.

probabilities of crossing that represent hypothetical extreme cases of fenced infrastructures with high traffic densities that are currently scarce and unlikely to exist in the near future in Scandinavia. Wolves in Scandinavia have shown a tolerance to moving through landscapes that, in principle, could be considered inhospitable to the species (Åkesson et al., 2016; Wabakken et al., 2007). Therefore, roads may have limited impact on the wolf expansion in the SWBR. Initiatives to develop and spread infrastructure network should consider measures to facilitate movements of wildlife and reduce the risk of collisions (Milanesi et al., 2016; Selva et al., 2015). Crossing structures paired with suitable fencing and the preservation of areas free from traffic infrastructure (Selva et al., 2015; Smith et al., 2015) can help to ensure the movements of established carnivore species within home-ranges and increase the dispersal of young individuals. These actions will ultimately support wolf population connectivity and increase the viability of the wolf population in the SWBR.

Wolf territory termination strongly limited the recolonization of the species in the SWBR at any increment in the probability of territory termination in our simulations, suggesting that territory termination is the major factor limiting wolf population expansion in this area. The spatial expansion of a large carnivore like the wolf will come with pervasive risks for the species wherever it expands in Scandinavia (Recio et al., 2018). Considering that human-wolf conflicts are often a consequence of people's perceptions and attitudes against the species

(Fritts et al., 2003; Heberlein, 2012; van Eeden et al., 2020), conservation and management programs require monitoring human attitudes and actions against the species in areas like the SWBR. This part of Scandinavia hosts a higher density of both people and small-scale infrastructure (forest gravel roads) than the NWBR, and legal protective harvest (a permission to kill wolves to protect livestock or pets when a threat is perceived or previous attacks occurred) and poaching are likely the main impacting factors leading to the lack of wolf territories in this area. In fact, poaching has been identified as a strong impeding factor for the wolf restoration in Scandinavia (Liberg et al., 2012b, 2020) and Finland (Suutarinen and Kojola, 2018). Because of the cryptic nature of this illegal activity, the number of wolves that disappear is likely much higher than the actual number of identified kills (Liberg et al., 2020). This suggests that part of the discrepancy in the expansion observed in our model between the NWBR and SWBR might be a consequence of a much higher territory termination in the SWBR due to poaching. An additional factor of attention for the wolf expansion towards the SWBR is the increasing north-to-south gradient for seroprevalence of the sarcoptic mange. Although this factor has been identified as of little effect on the recovery of the Scandinavian wolf population (Fuchs et al., 2016), it could be a source of additional mortality in this area.

Our approach and findings using ABM could apply to other instances of large carnivore recolonization. Such as in Europe where the

absence of many species and of the ancient adaptations of human activities to coexist with them have fostered new and more relaxed husbandry and hunting practices (Chapron et al., 2014). There, conflicts caused by livestock and game animal loss (real and perceived) reignite, which severely lighten and escalate social sensibilities and pressures against the return of wolves and other large carnivores. These pressures often sway people and authorities to adopt different tolerances regarding poaching, culling, or retaliatory killing (van Eeden et al., 2020). Therefore, despite the availability of space and suitable habitat for large carnivores in Europe, their capability to roam, settle, and coexist with people remains impeded by direct persecution and likely to a lesser extent by physical barriers (e.g. transport infrastructures). Both these factors can contribute to the observed global decline in terrestrial mammalian movements (Tucker et al., 2018).

Previous approaches have used ABM for assessing the persistence of population of tigers (*Panthera tigris*) in conservation areas (Imron et al., 2011), the settlement and expansion of reintroduced brown bears (*Ursus arctos*) (Wiegand et al., 2004) and Eurasian lynx (*Lynx lynx*) (Kramer-Schadt et al., 2005), or for exploratory modelling on wolves to identify human-caused mortality in the USA (Stenglein et al., 2015). A previous application of ABM studying wolf recolonizations in Europe aimed to characterize potential expansion into Austria where it is absent (only non-territorial dispersers have been observed); therefore, observed patterns of expansion were not available for the model calibration (Crook and Paulus, 2016). Conversely, our approach implemented in WolVES benefitted from much empirical data on wolf populations collected in exhaustive collaborative surveys and surveillance transboundary programs between Sweden and Norway. This dataset enabled the incorporation of observed mechanisms in the model and the ability to calibrate it using on-going recolonization data. In a broader context, these valuable and rich datasets highlight the importance of exhaustive planning programs and policies at multiple levels to gather the most complete information possible on the expansion of conflict species such as large carnivores.

The recovery of large carnivores and their persistence under a co-existence model in the recolonized areas would also imply the return and restoration of their ecological functionality (Boitani and Linnell, 2015). Predictions to determine the impact and changes caused by this restoration in space and time would be of great importance. Therefore, further approaches using ABM to predict multiple ecosystem changes related to the presence of large carnivores would benefit from the integration of different interactive and/or synergic processes. This can include the integration of pervasive human impacts (Recio et al., 2018) with sub-models on ecological processes (e.g. predation, impact on herbivory, intra and interspecific interactions, parasitism and diseases) occurring at different spatial scales. Incorporating information from the social sciences, such as the local public opinions on the tolerance for large carnivores, could advance towards more realistic simulations to identify hot-spots of conflicts and retaliatory poaching.

Our spatially-explicit approach developed in the software WolVES and based on ABM aimed to contribute to the advances on these techniques for large carnivore recolonization. Models based in ABM are powerful tools that enable a virtual recreation of the observed expansion pattern of a wildlife species and to extrapolate it into future scenarios with the same or other alternative conditions. Similar approaches can assist decision-making in the conservation and management of wildlife species elsewhere as long as suitable empirical information on population growth and geographical expansion is available.

This study demonstrates how ABMs combined with extensive empirical data on species ecology can assist decision-makers in predicting future scenarios of wolf recolonization while identifying constraints to it. Our models discriminated human-caused mortality is a more important constraint to wolf recolonization in southern Sweden than increased infrastructure. For conflictive species of high expansion capabilities such as large carnivores, it is required to collect long-term

demographic and behavioural data at regional and transboundary levels to extrapolate observed expansion patterns into the future and to address predictions. Therefore, increasing collaborations between modellers, population ecologists, and conservation managers at local and transboundary levels is necessary. Through this multidisciplinary approach, relevant ecological processes of conservation and management importance can be identified at early stages.

CRediT authorship contribution statement

Mariano R. Recio: Conceptualization, Methodology, Formal Analysis, Validation, Software, Writing-Original draft, Writing-Reviieweing & Editing. **Alexander Singer:** Methodology, Formal Analysis, Validation, Software, Writing-Original draft, Writing-Reviieweing & Editing. **Petter Wabakken:** Resources, writing-Original draft. **Håkan Sand:** Resources, Conceptualization, Writing-Original draft, Writing-Reviieweing & Editing.

Declaration of competing interest

The authors declare no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108752.

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