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Research

Mapping and explaining wolf recolonization in France using dynamic occupancy models and opportunistic data

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While large carnivores are recovering in Europe, assessing their distributions can help to predict and mitigate conflicts with human activities. Because they are highly mobile, elusive and live at very low density, modeling their distributions presents several challenges due to 1) their imperfect detectability, 2) their dynamic ranges over time and 3) their monitoring at large scales consisting mainly of opportunistic data without a formal measure of the sampling effort.

Here, we focused on wolves *Canis lupus* that have been recolonizing France since the early 1990s. We evaluated the sampling effort a posteriori as the number of observers present per year in a cell based on their location and professional activities. We then assessed wolf range dynamics from 1994 to 2016, while accounting for species imperfect detection and time- and space-varying sampling effort using dynamic site-occupancy models.

Ignoring the effect of sampling effort on species detectability led to underestimating the number of occupied sites by more than 50% on average. Colonization appeared to be negatively influenced by the proportion of a site with an altitude higher than 2500 m and positively influenced by the number of observed occupied sites at short and long-distances, forest cover, farmland cover and mean altitude. The expansion rate, defined as the number of occupied sites in a given year divided by the number of occupied sites in the previous year, decreased over the first years of the study, then remained stable from 2000 to 2016. Our work shows that opportunistic data can be analyzed with species distribution models that control for imperfect detection, pending a quantification of sampling effort. Our approach has the potential for being used by decision-makers to target sites where large carnivores are likely to occur and mitigate conflicts.

Introduction

Large carnivores are often considered as key elements for maintaining ecosystems. Because of their high position in the trophic chain, their extinction can lead to trophic cascades and detrimental changes in species abundance and functioning of ecosystems (Ripple et al. 2014). Once widespread in Europe, many populations of large carnivores were extirpated over the last century, mainly due to interferences with human activities (Breitenmoser 1998, Ripple et al. 2014). Since the 1970s, all large carnivores have recovered, resulting in most of the European countries hosting at least one viable population of large predators (Chapron et al. 2014). Often used as a conservation success story, the recovery of large carnivores in human-dominated areas comes with challenges, including the question of whether there are any sufficiently large and functional areas left for viable populations (Packer et al. 2013). Another issue is how to coordinate management of these species at large scales, possibly across borders (Linnell and Boitani 2012, Bischof et al. 2015), in particular in the context of international treaties and directives (e.g. the European Habitats Directive).

In this context, mapping the distribution of a species can help to target potential area of presence and mitigate conflicts often associated with the recovery of large carnivores. Species distribution models (SDMs) have become important tools in the ecological, biogeographical and conservation fields (Guisan and Thuiller 2005). By correlating presence-only or presence–absence data of a species to environmental factors, SDMs provide an understanding of habitat preferences and predictions on future species distribution. This is especially relevant for species involved in conflicts, since predicting their future presence can help targeting contentious areas and guide management to reduce conflicts (Guillera-Arroita et al. 2015). However, the monitoring of large carnivores remains challenging to carry out in the field because these species live at low density and occupy wide areas (Woodroffe 2001). Therefore, assessing the distribution of these species comes with methodological challenges.

First, standard SDMs such as Maxent (Phillips et al. 2006) rely on the assumption that the focal species is detected everywhere it is present (Yackulic et al. 2013). Going undetected at a given site does not necessarily mean that this species is absent from that site, but rather that it may simply be missed for various reasons related to observer abilities, habitat characteristics or species level of activity (Kéry et al. 2010, Kéry 2011). Ignoring the issue of imperfect detection can result in false absences that lead to flawed inference in two ways: 1) the distribution maps are biased by underestimating actual presences (Kéry and Schaub 2011, Lahoz-Monfort et al. 2014); 2) there may be confusion in identifying the drivers of the species distribution when detection depends on environmental explanatory variables that are independent from the variables influencing the species' actual presence (Lahoz-Monfort et al. 2014). To cope with this first issue, single-season or static site-occupancy models were developed (Mackenzie et al. 2006) and have been widely used for carnivores (Long et al. 2010, Thorn et al. 2011, Sunarto et al. 2012). Based on spatial and temporal replicated sampling of the target species, these models allow making the distinction between non-detections and true absences via the estimation of species detectability.

Second, most SDMs are implicitly based on the ecological niche concept (Grinnell 1917, Hutchinson 1957) and therefore rely on two main hypotheses: 1) the species is present in areas where environmental conditions are the most favorable and 2) dispersal is not a limiting factor (Jeschke and Strayer 2006). However, expanding species are often absent from an area not because conditions are unfavorable but because they have not yet dispersed to this area, or because of geographical barriers or dispersal constraints (Araújo and Guisan 2006). Hence, static SDMs ignore important dynamic processes, which may lead to bias in the resulting distributions and should therefore not be used for prediction (Zurell et al. 2009, Yackulic et al. 2015). To deal with this second issue, occupancy models have been extended (Mackenzie et al. 2003, Royle and Kéry 2007) to account for the influence of dynamic processes such as colonization and extinction on the species range dynamics (Mackenzie et al. 2003). So-called multi-season or dynamic site-occupancy models are increasingly used to assess the range dynamics of expanding or invasive species (Bled et al. 2011, Broms et al. 2016a), but remain rarely applied to carnivores (Marcelli and Fusillo 2012, Miller et al. 2013).

Third, data collection is particularly costly if not unfeasible for elusive species that need wide areas due to the large presence area required for sampling. In this context, citizen science is considered as an efficient source of information to assess changes in a species distribution by covering wide areas (Schmeller et al. 2009). However, data from citizen science are often collected with protocols that do not control for variation in the sampling effort 1) in time: a site can be sampled by several observers during a given year and not the following year and 2) in space: given two sites where the species is present, if the sampling effort is lower in one site, this might lead to recording a false absence in this site (Kéry et al. 2010). As a consequence, if sampling effort is not controlled for, detectability can be estimated low, for instance at sites with no sampling effort, leading to biased estimates of the distribution area (Van Strien et al. 2013).

Static and dynamic occupancy models hold promise to analyze population trends from opportunistic data because the data collection process is formally incorporated (Isaac et al. 2014). However, to address the third issue and apply occupancy models to opportunistic data, one needs to differentiate between a site that was not sampled and a site that was sampled but the species was not detected. In the case of several species being monitored, the detection of a species in a site informs about the non-detection of other species because this site is known to have been sampled (Van Strien et al. 2013). This no longer holds for single-species settings, and the assumption is sometimes made that all sites where at least

one detection occurred are sampled throughout the whole duration of the study (Molinari-Jobin et al. 2012, Rich et al. 2013).

Here, we considered grey wolves *Canis lupus* as a case study to illustrate the challenges in using opportunistic data and SDMs to infer the range dynamics of large carnivores. Wolves disappeared in most of the western European countries during the twentieth century (Promberger and Schröder 1993, Boitani 2010) except in Spain, Portugal and Italy (Boitani and Ciucci 1993). The species naturally recolonized the French Alps from the remaining Italian population (Valière et al. 2003, Fabbri et al. 2007). Because the species is protected by law while being a source of conflicts with sheepherding, its recolonization process needs to be carefully monitored.

Our main objective was to describe and determine the drivers of wolves' recolonization pattern in France between 1994 and 2016. To account for imperfect detection, we built a dynamic site-occupancy model (Mackenzie et al. 2006) and analyzed opportunistic data collected by a network of trained volunteers since 1992. To do so, we built a posteriori the sampling effort to account for biases in data collected through citizen science. To describe the recolonization process over time, we addressed two main questions: 1) what are the environmental and biological factors influencing colonization and extinction probabilities? 2) How can sampling effort be inferred a posteriori, i.e. after the data were collected, and to what extent does sampling effort correlate with detection probability?

Methods

Study species and area

The first wolf *Canis lupus* occurrence was detected in France in the early 1990s as a consequence of the Italian population's expansion (Valière et al. 2003, Ciucci et al. 2009). The species then spread outside the Alpine mountains to reach the Pyrenees and the Massif Central westward first in 1999, and the Vosges Mountains northward from 2011. The wolf is an opportunist species that can adapt its diet depending on available prey species (Poulle et al. 1997, Imbert et al. 2016). In areas with livestock farming, strong interactions between wolf presence and sheep breeding usually occur. The study area mostly covered eastern France and a major part of central France (Fig. 1).

Data collection

Wolf detection data were made of presence signs sampled all year long from 1992 to 2016 thanks to a network of professional and non-professional observers. The network size has increased from a few hundred people in 1994, up to 3138 wolf experts in 2016. Every observer is trained during a 3-d teaching course led by the French National Game and
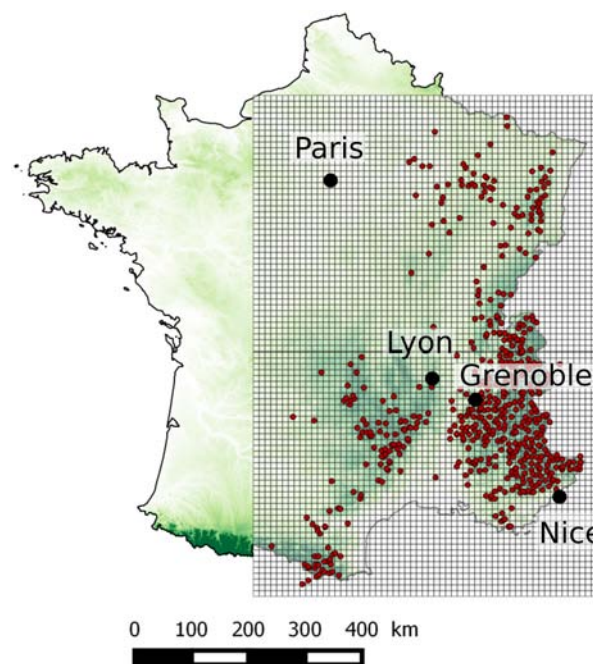

Figure 1. Maps of cumulated species detections (red dots) for the period 1994–2016. Sites were defined as 10×10 km cells within a grid covering all detections. Dark green areas represent mountainous areas with an altitude higher than 1500 m.

Wildlife Agency (ONCFS) to document signs of the species' presence (Duchamp et al. 2012). Presence signs went through a standardized control process combining genetic identification tools, and validation standards to prevent misidentification (Duchamp et al. 2012). For every presence sign, the date and location of collection were stored in a geo-referenced database. These data are considered opportunistic in the sense that monitoring occurs all year long in an extensive manner without explicitly quantifying the sampling effort.

Dynamic site occupancy models

To model the colonization dynamics of wolf, we used dynamic site-occupancy models (Mackenzie et al. 2003) where sampling units were defined as 10×10 km cells (European Commission 2006). Site occupancy models rely on the closure assumption which states that the ecological state of a site (whether it is occupied or not) remains unchanged through occasions (or surveys) j within a year k. Sites were monitored mainly in winter from December to March, the most favorable period to detect the species between the two peaks of dispersal events in spring and fall (Mech and Boitani 2010). We defined the secondary occasions j as December, January, February and March and $y_{i,j,k}$, the observed state of site i equal to 1 if at least one sign of presence was found at site i during occasion j in the year k (and 0 otherwise).

We considered a state-space formulation of the dynamic occupancy model (Royle and Kéry 2007) in which the model is viewed as the combination of 1) the ecological process that

involves the latent ecological state of a site, i.e. whether it is occupied or not; 2) the observation process that leads to the detections or non-detections by the observer conditional on the state of the system. The colonization probability $\gamma_{i,k}$ is the probability that an empty site i during year k becomes occupied during year $k + 1$, while the extinction probability $\varepsilon_{i,k}$ is the probability that an occupied site i during year k becomes empty during year $k + 1$. We define $z_{i,1}$ as the initial latent state of site i as being drawn from a Bernoulli distribution with the success probability being $\Psi_{i,1}$,

$$z_{i,1} \sim Bernoulli\,(\Psi_{i,1})$$

All other latent states $z_{i,k}$ for $k > 1$ are drawn from a Bernoulli distribution as

$$z_{i,k+1} \mid z_{i,k} \sim Bernoulli\,(z_{i,k}\,(1 - \varepsilon_{i,k}) + (1 - z_{i,k})\,\gamma_{i,k})$$

On top of the ecological process stands the observation process, in which the detections/non-detections are drawn from a Bernoulli distribution

$$y_{i,j,k} \mid z_{i,k} \sim Bernoulli(z_{i,k}\,p_{i,j,k})$$

where $p_{i,j,k}$ is the probability that the species is detected at site i for an occasion j during year k. The state-space formulation is appealing as it makes explicit the latent states $z_{i,k}$ that can be used to build distribution maps. We modelled detection probability with logistic regression using sampling effort, road density and months as covariates. We modelled colonization probability with logistic regression using forest cover, farming cover, rock cover, mean altitude, proportion of high altitude (> 2500 m), the number of observed occupied neighboring sites at short distance, the number of observed occupied neighboring sites at long distance and the distance to the nearest barrier (road or main river) as explanatory variables. Finally, we modelled extinction probability as a logistic function of 'year' as a continuous covariate. We describe these covariates below.

Sampling effort

Monitoring the range expansion of wolves at the country level prevented us from implementing any standardized experimental sampling design. Instead, the presence signs were sampled in an opportunistic way and the sites were defined a posteriori. We adopted an original approach to infer the non-detections based on the available qualitative information on the observers. When entering the network, observers attended a 3-d training session to learn how to identify the species and how it is monitored (Duchamp et al. 2012). During these training sessions, we recorded the observers' personal and professional address, socio-professional category and entry date into the network. The entry and exit dates (whenever known) were used to quantify how many observers were present in the network each year. If necessary, we updated their socio-professional category. We calculated a circular buffer for the prospection area for each observer based on a radius specific to his/her socio-professional category and

a center located at his/her address (Supplementary material Appendix 1 Table A1). For instance, for an observer belonging to the category 1 (departmental authority) whose address was located in the French Department number 39, his/her prospection area would be 4999 km², which is the size of the Department (Supplementary material Appendix 1 Fig. A1 and Table A2). For this observer, a circular buffer was built with a radius calculated as

$$Radius = \sqrt{\frac{prospection\ area}{\pi}}$$

For each 10×10 km cell, we then calculated the number of observers monitoring the species per year, i.e. the sampling effort, by summing the number of prospection areas overlapping the cell (Supplementary material Appendix 1 Fig. A2). Sites with a sampling effort equal to zero were not prospected by observers. To avoid estimating a detection probability at sites that were not prospected, we set the detection probability to zero when the sampling effort was null at these sites. When at least one observer was found in a cell in a given year, we considered that sampling occurred. We expected that the sampling effort had a positive effect on the detection parameter. We performed a sensitivity analysis to assess how a change in the construction of the sampling effort influenced the model parameter estimates (Supplementary material Appendix 1 Fig. A3).

Other covariates

Keeping in mind that wolves can adapt to a large range of different habitats, we incorporated proxies of variables that might shape the wolf distribution (Table 1). Using the CORINE Land Cover® database (U.E – SOeS, Corine Land Cover 2006), we defined three covariates to characterize the landscape of the study area: forest cover, farming cover and rock cover. Forest cover may structure the ungulate distribution (i.e. prey species). As a consequence, we expected that forest cover would have a positive effect on colonization, and rock cover would have a negative effect on colonization. Farmland cover was defined as a covariate including pastures areas which can be used by livestock, a possible prey to wolves and a proxy for rural landscape under human influence. Altitude may also have an influence on colonization (Llaneza et al. 2012, Falcucci et al. 2013). We used the IGN BD_ALTI® database (250 m resolution) to calculate the mean altitude of each site as well as the proportion of altitude higher than 2500 m. We predicted a site with a high proportion of high-altitude (> 2500 m high) would be less attractive for the species as ungulate species might be less abundant above this limit.

Dispersal capacity is a key factor to explain the dynamic of wolf colonization (Boyd and Pletscher 1999, Kojola et al. 2006, Ciucci et al. 2009). Because cells occupied by established packs may act as a source of dispersers at short and long-distance (Yackulic et al. 2012), the neighborhood of an unoccupied cell may influence its colonization probability

Table 1. Description and expected effects of covariates used to describe the occupancy dynamics of wolf in France.

Covariate	Abbreviation	Parameter	Description	Expected effect	Reference
Forest cover	Forest	Colonisation (γ)	Percentage of mixt, coniferous or deciduous forests cover	+	Oakleaf et al. 2006, Fechter and Storch 2014
Farmland cover	Agr	Colonisation (γ)	Percentage of pasture lands and other farming activities cover	+/–	Glenz et al. 2001
Rock cover	Rock	Colonisation (γ)	Percentage of rock cover	–	
High altitude	Halt	Colonisation (γ)	Proportion of altitude higher than 2500 m	–	Glenz et al. 2001
Altitude	Alt	Colonisation (γ)	Mean altitude	+/–	Llaneza et al. 2012 Falcucci et al. 2013
Distance to the closest barrier	Dbarr	Colonisation (γ)	Minimal distance between a highway or one of the five main rivers in France	–	Falcucci et al. 2013
Short distance occupied neighboring cells	SDAC	Colonisation (γ)	Proportion of observed occupied contiguous cells	+	Bled et al. 2011
Long distance occupied neighboring cells	LDAC	Colonisation (γ)	Proportion of observed occupied cells within a 150 km radius without the contiguous cells	+	
Year (continuous)	Trend-year	Extinction (ε)	Year as a linear effect	–	Marucco 2009
Sampling effort	SEff	Detection (p)	Number of observers per site per year	+	
Road density	Rdens	Detection (p)	Percentage of site covered by roads	+	
Month-survey	survey	Detection (p)	Occasion of survey (categorical)	+/–	Marucco 2009

(Veran et al. 2016). In that spirit, the presence of individuals at short and long-distance could be accounted for by using conditional autoregressive models and auto-logistic models (Bled et al. 2013). However, due to the computational burden and convergence issues, we could not implement this approach here. We therefore defined two covariates that consisted of the observed number of contiguous observed occupied cells at both short and long-distances around the focal cell. The short-distance covariate was defined as the number of observed occupied cells directly contiguous to the focal cell i.e. situated within a distance of 10 km. The limit for the long-distance parameter was set to avoid a dilution effect due to the small number of observed occupied cells at very long-distances but large enough to account for most long-distance observed occupied cells that could play a role in the colonization probability. Based on observations of wolf dispersal in the western Italian Alps (Marucco and McIntire 2010), we set this limit at 150 km around the focal cell. We expected a positive effect of these two covariates on the probability of a site to be colonized.

Because dispersal could be driven by the presence of physical barriers (Wabakken et al. 2001, Blanco et al. 2005), we defined a landscape covariate depicting the distance from the center of the site to the closest barrier defined as highways or rivers (U.E – SOeS, Corine Land Cover 2006). We expected this covariate to impact colonization negatively.

In the first few years after sites become newly colonized, extinction probability is expected to be high as long as only isolated individuals use them. Once a pack has settled, pack persistence is the rule for wolves when other packs are present in the surrounding areas (Mech and Boitani 2010). Pack splitting may rise from various sources including harvest or poaching of alpha pairs (Gehring et al. 2003, Brainerd et al.

2008) leading to a locally extinct site. Within the distribution of an actively expanding population, extinct sites might be recovered by surrounding individuals, either by dispersers or by neighboring packs. We therefore expected extinction probability to decrease over time.

Finally, in addition to sampling effort, we considered the potential effect of road densities on the species detectability, first through facilitation of site accessibility for the observers and second, because cross roads can be used as marking sites (Barja et al. 2004), which can lead to a higher detectability. Because presence signs rely partly on track records in the snow, we considered month as a categorical variable to account for the variation in detection conditions due to weather variations across the survey months (Marucco 2009).

Last, we considered the initial occupancy probability as constant since only two sites were occupied in the first year of the study, which was not enough to assess the effects of covariates on this parameter.

Model fitting, selection and validation

We performed covariate selection using stochastic search variable selection (SSVS; George and McCulloch 1993, O'Hara and Sillanpää 2009). In brief, SSVS builds a model that includes all covariate combinations as special cases. In practice, this is achieved by adding binary indicator variables, α_p equals 1 or 0, which allows the estimation of the regression parameter β_p or excludes it by setting it to a constant (Supplementary material Appendix 1 Table C1). In a Bayesian framework, we explored the model space generated by excluding or including covariates. The priors for regression parameters β_p were written as $(1 - w)$ Normal(0,0.0001) $+ w$ Normal(0,1) with $w \sim$ Bernoulli(0.5) therefore assuming a

priori that each covariate had a 50-50 chance of being present in the model. We checked that the model space was well sampled by the SSVS and that we did not get stuck in a particular set of models. We used three different initial model configurations (with all covariates vs without any of the covariates vs a few covariates picked at random in the set of all covariates). We did not explore different priors as mixing and convergence were satisfying. Prior to model selection, we ran a Spearman test to check for correlations among covariates.

We used Markov chain Monte Carlo (MCMC) simulations and parameter estimation. We ran three MCMC chains with a burn-in period of 2500 iterations followed by 10 000 iterations on which we based our inference. We used posterior medians and 95% credible intervals to summarize parameter posterior distributions. To assess the effect of a covariate on a parameter, we set the other covariates to their mean value. We checked convergence visually by inspecting the chains and by checking that the R-hat statistic was below 1.1 (Gelman and Shirley 2011). We finally produced distribution maps of the latent states by using a posteriori means of the $z_{i,k}$ from the best model. To assess the fit of our final model, we used the posterior predictive checking approach (Gelman et al. 1996) that has recently been applied to occupancy models (Broms et al. 2016b) (Supplementary material Appendix 1 Fig. B1).

Data deposition

Data available from the Dryad Digital Repository: <http:// dx.doi.org/10.5061/dryad.g9s1d> (Louvrier et al. 2017).

Results

The effect of covariates on detectability and the dynamic of occupancy

The model best supported by the data had detection as a function of sampling effort, road density and occasion (month) and colonization as a function of forest cover, farmland cover, mean altitude, proportion of high-altitude and the number of observed occupied cells at a short and long-distance neighborhood (Supplementary material Appendix 1 Table C1). This model appeared to fit the data adequately well (Supplementary material Appendix 1 Fig. B1).

Initial occupancy probability was low, as expected since few sites were detected as occupied at the beginning of the study (Supplementary material Appendix 1 Table C2).

As predicted, forest cover had a positive influence on the probability that a site became colonized. The proportion of farmland cover within a cell also appeared to have a positive influence on this probability. Below 1500 m of mean altitude, the probability that a site became colonized was close to zero, whereas above this limit the probability reached up to 0.07 (0.05; 0.11) (Fig. 2). This probability decreased with the high-altitude proportion in a site. Over time, the number of observed occupied neighboring cells increased at both short and long-distance (Supplementary material Appendix 1 Fig. D1). If all of the 8 neighboring cells were observed as occupied, the probability that the target cell became colonized was 0.48 (0.32; 0.58) compared to a colonization probability of 0.11 (0.08; 0.15) if the target site had only 0 to 2 contiguous neighboring cells observed occupied. As this number increased, the probability that a site became colonized increased accordingly (Fig. 2).

Sites located within the Alps had the highest number of observed occupied sites at both short and long-distance. Colonization probability was the highest in this area (Fig. 3). The highest part of the Alps (i.e. sites with the greatest proportions of high-altitude) remained with a low colonization probability (Supplementary material Appendix 1 Fig. D2). Overall, this probability remained higher than zero in mountainous areas and increased with time as the number of occupied sites increased (Fig. 3).

Finally, and as expected, detection probability varied according to the survey month with the lowest mean value of 0.17 (0.16; 0.18) in December and the highest value of 0.25 (0.24; 0.26) in January (Fig. 4). As expected, detection probability increased when the number of observers per site increased but, in contrast with what we expected, decreased with increasing road density. The sensitivity analysis showed weak effects of variations in the prospection areas used to build the sampling effort, except for the number of observed occupied sites at long distance (Supplementary material Apendix 1 Fig. A3).

Distribution map

From 1994 to 2016, 10 918 presence signs were recorded by the network and used in our analysis. The species was initially spotted in 2 cells in 1994 and was detected in 188 cells in 2016 (around 70-fold increase, see top panel in Fig. 5). This led to an apparent occupancy (proportion of occupied sites on the total number of sites in the study area) varying from 0.001 in 1994 to 0.047 in 2016.

Accounting for both sampling effort and imperfect detection, we estimated the number of occupied sites as up to 10 (1; 19) in 1994 and up to 211 (195; 227) in 2016 (top panel in Fig. 5). Overall, the estimates were higher than the naïve estimates of occupancy. When we ignored the sampling effort in the detection process, we found an estimated number of occupied sites equal to 2 (1; 4) in 1994 and up to 192 (180; 204) in 2016. Most discrepancies between the two models (accounting for vs. ignoring the sampling effort) were found at the early stage of the colonization process when the network of observers was implemented mainly in eastern France (compare bottom left and right panels in Fig. 5; see also Supplementary material Appendix 1 Fig. D3). Accounting for the sampling effort allowed us to infer the species presence on sites that were not prospected or prospected with a low sampling effort (top panel in Fig. 5).

Our results showed that in 1994 the species was found only in the southern Alps, and then actively colonized
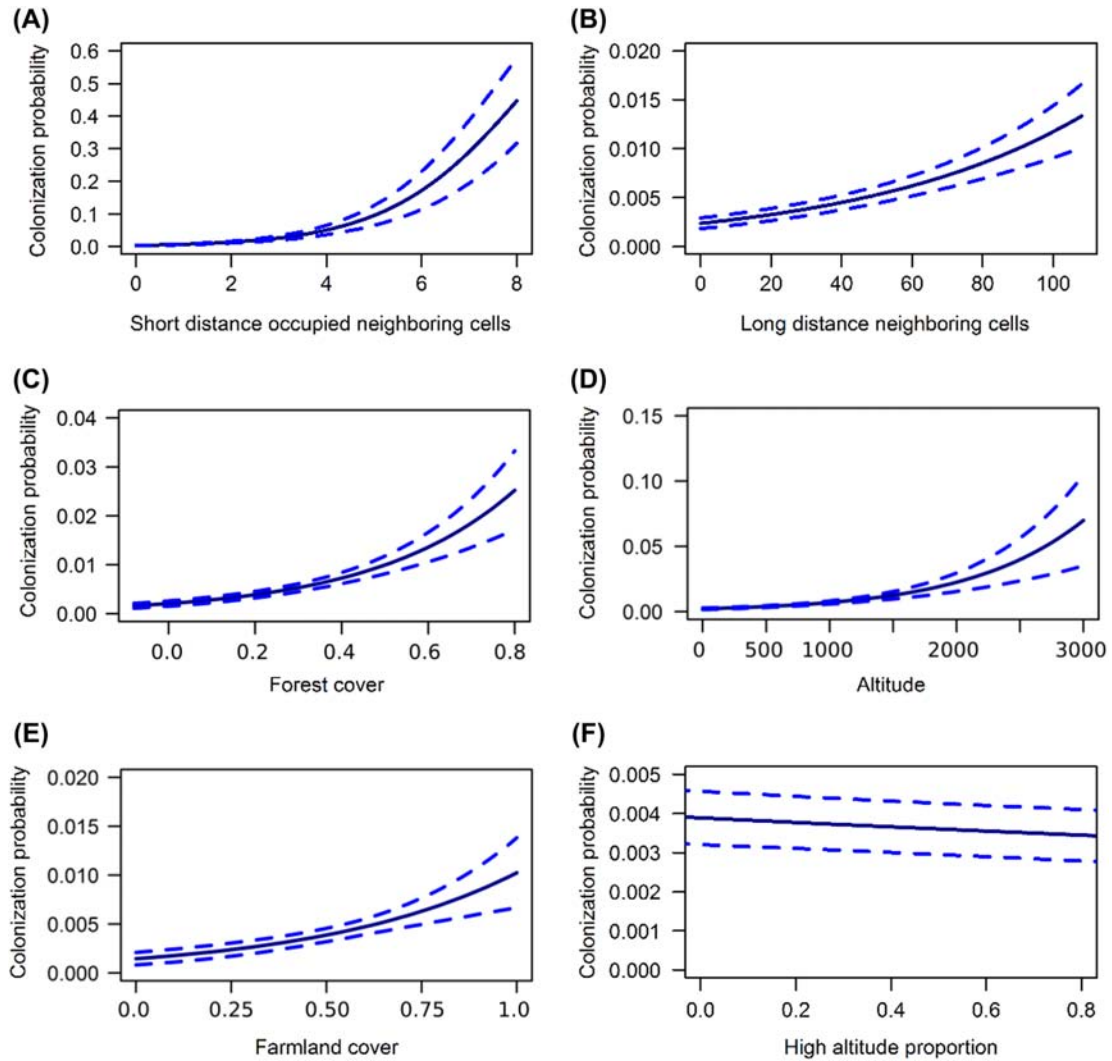
Figure 2. Relationship between the estimated colonization probability and (A) short-distance occupied neighboring cells, (B) long-distance occupied neighboring cells, (C) proportion of forest cover, (D) altitude, (E) proportion of farmland cover, and (F) site proportion of altitude higher than 2500 m.

towards the northern Alps at the beginning of the 2000s. The colonization process started to reach the Pyrenees and Massif Central area in early 2000, and the Vosges area in the very north-eastern part of France, at the beginning of the 2010s, indicating that the French wolf population is still in a phase of expansion west and northward from the alpine range. This led to an average expansion rate (i.e. number of occupied sites divided by the number of occupied sites the previous year) of 112% (100%; 128%) (Fig. 6). This expansion rate first decreased over time, from 225% (118%; 600%) at the early stage of the wolf colonization in 1994 to 103% (91%; 117%) in 2000 due to low number of occupied cells, then stabilized at 107% (98%; 117%) on average per year demonstrating that the population is still in an expanding phase mainly thanks to the colonization outside of the alpine range.

The model did not predict absence in places where presence signs were found (Fig. 7). Sites with high occupancy probability were mainly close to the sites where the species had been previously detected, mostly due to the effect of short-distance neighbors. Some sites had a high probability of being occupied (> 0.75), however the uncertainty associated with those predictions was also high (standard deviation [SD] > 0.30). We found sites with high probability of occupancy (> 0.75) with low uncertainty (SD < 0.20), and some of those sites were observed as occupied in the following year because the model propagates information backwards in time and so z_k is informed directly by z_{k+1}.

Discussion

Determining favorable areas is often accomplished by building distribution maps using habitat suitability models (Mladenoff et al. 1999) or occupancy models (Marucco
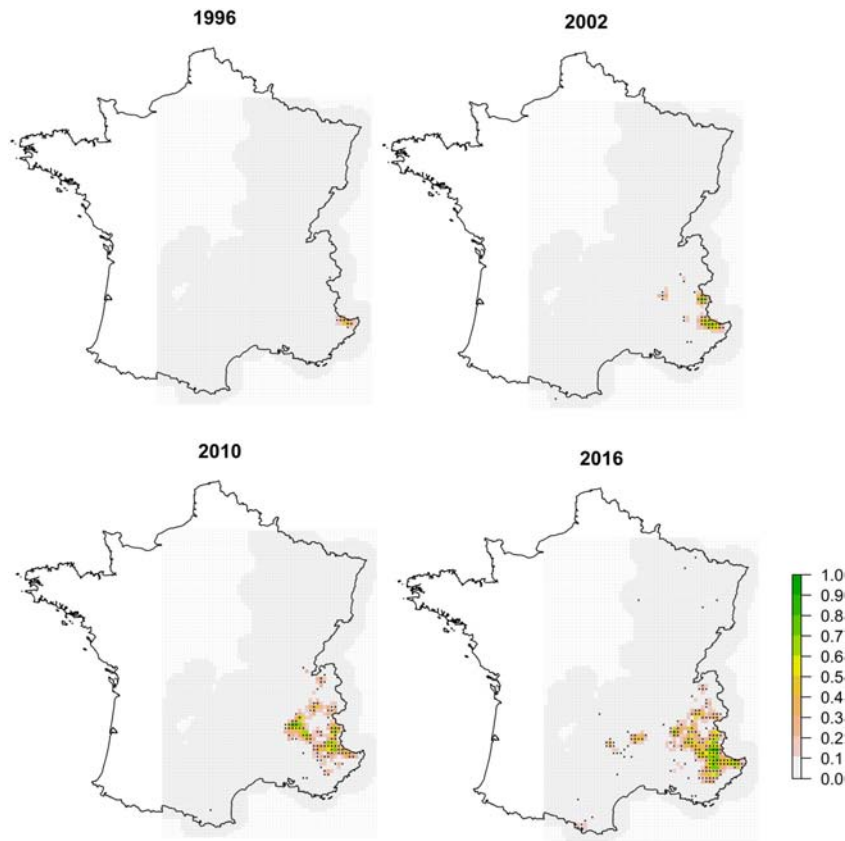
Figure 3. Maps of estimated colonization probability between 1995 and 1996, 2001 and 2002, 2009 and 2010, 2015 and 2016 from the best model (Table 2). Black dots represent detections made in 1995, 2001, 2009, and 2015.

2009). However, these studies often rely on a static relationship between the species of interest and its environment (Jedrzejewski et al. 2008). Here, we used dynamic site-occupancy models and brought new insights on the processes governing the dynamic of recolonization of a keystone carnivore species. By controlling for species detectability and heterogeneous sampling effort, our approach can be used to assess the distribution dynamics of any species based on opportunistic data, pending relevant information is gathered on the people collecting the data.

Model assumptions

Site occupancy models rely on several assumptions that need to be discussed (Mackenzie et al. 2003, 2006). First, the species should not be detected when absent from a site (i.e. no false positives). This is unlikely to happen in our case since we did not account for presence signs that were rejected because they did not fulfill the standardized criteria used to avoid species misidentification (Duchamp et al. 2012). If doubts persist about the occurrence of false positives, this assumption could be relaxed by using site-occupancy models that account for misidentifications (Miller et al. 2011, Rich et al. 2013).

Second, detection histories of all sampling units are assumed to be independent. However, detection histories were likely dependent in space because of a non-homogeneous spatial sampling effort inherent to opportunistic data. We partly accounted for this non-independence by quantifying the sampling effort. Furthermore, by accounting for the number of observed occupied neighboring cells, we made the detection history of a focal cell dependent partly on the detection histories of the neighboring cells. If the source of dependence is unknown, spatial autocorrelation can be modeled using geostatistical tools on occupancy or extinction/colonization parameters and also on detection (Bled et al. 2013).

Third, the status of a site should not change during primary occasions – the closure assumption (Rota et al. 2009). We used the data provided within the winter period from November to March as a primary occasion because it corresponds to the most stable period in the social organization of the packs. If movements or mortality occurred inside or outside of the sampling sites, it is likely, in our study, that the probability of occupancy in a given time interval did not depend on the occupancy status of a site in the previous time interval (Mackenzie and Royle 2005). In this situation of so-called random temporary emigration, the bias in parameter estimates is minimal, but occupancy should be interpreted as use of the sampling area rather than the proportion of area occupied by the species (Mackenzie et al. 2004).

Fourth, there should be no unmodelled heterogeneity in the model parameters. Regarding the detection probability,
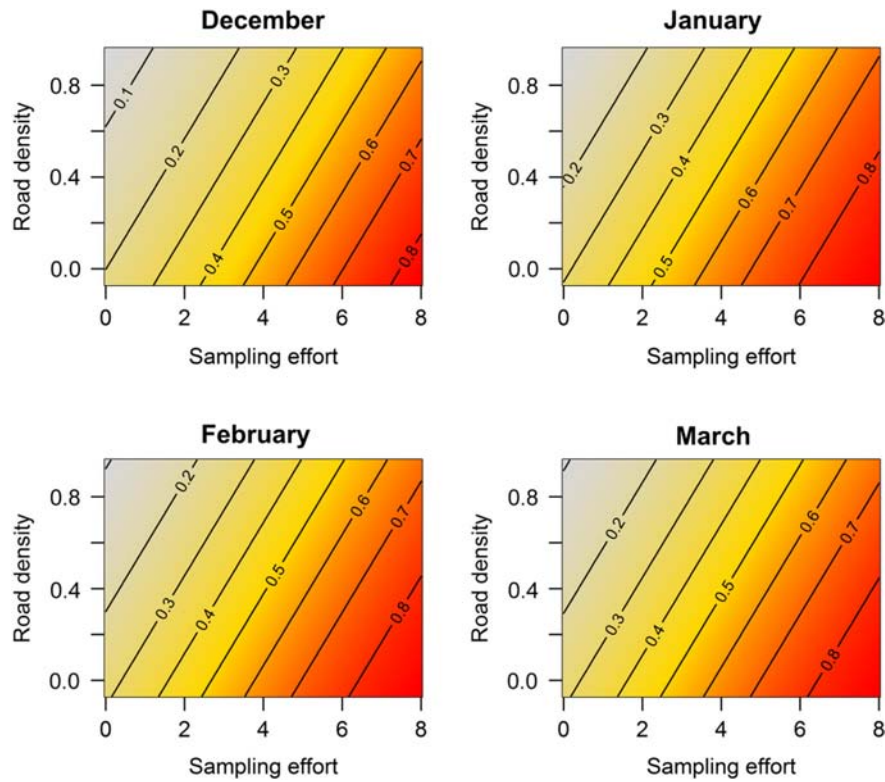
Figure 4. Joint effects of road density, standardized sampling effort and occasion (month) on the species detection probability.
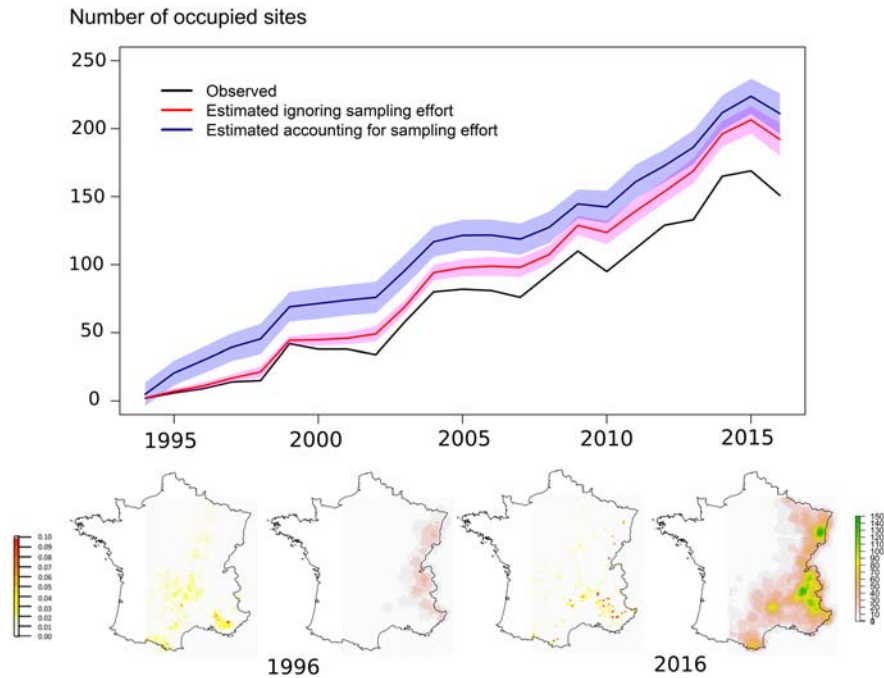

Figure 5. Up: number of 10×10 km cells observed (black), estimated occupied ignoring sampling effort (red) and estimated occupied accounting for sampling effort (blue) for each year from 1994 to 2016. Also displayed is the 95% credible interval for both estimates of the sampling effort. Down: maps of differences between estimates of occupancy from the model accounting for sampling effort and the one ignoring sampling effort. Dark red sites are sites that appeared estimated occupied by the model accounting for sampling effort but did not appear occupied once ignoring sampling effort. Both maps are associated with maps of the sampling effort on their right, for the years 1996 and 2016.
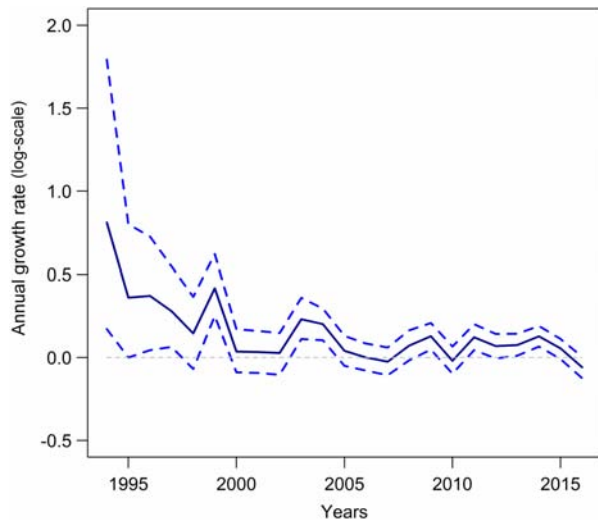
Figure 6. Growth rate (i.e. number of sites divided by the total number of sites the previous year) given for each year from 1994 to 2016, on a log scale.

some heterogeneity might remain due to a difference of detection in the presence signs, e.g. tracks vs hair (Graves et al. 2011). This was unlikely to occur in our study because

the vast majority of presence signs are tracks. Regarding the colonization parameter, even though we had data on the number of killed preys during the hunting season, we did not have information on wild prey density at such a large scale. Therefore, we used characteristics of their habitats as a proxy for their presence (Jedrzejewski et al. 2008).

Besides the usual assumptions of occupancy models, we also had to deal with opportunistic data that are collected through non-standardized sampling protocols. To cope with opportunistic data, we defined a grid of spatial units that was overlaid on the map of detections/non-detections. We used 10×10 km cells as sampling units, a choice we made in agreement with what was recommended by the European Union (European Commission 2006) and also shown to be the best tradeoff between the species territory size and sensitivity of the distribution to the size and shape of the unit cell (Marboutin et al. 2010). The average wolves' territory size vary between 100 and 400 km² in western and central Europe (Ciucci et al. 1997, Mech and Boitani 2010, Duchamp et al. 2012). Although these cells might not entirely cover wolves territories, Latham et al. (2014) studied the effect of grid size to assess wolf's occupancy and found that taking a large grid size may not be appropriate for areas with moderate to high wolf density as it can overestimate occupancy rate. On the other hand, if the size of the sampling unit is too small, then
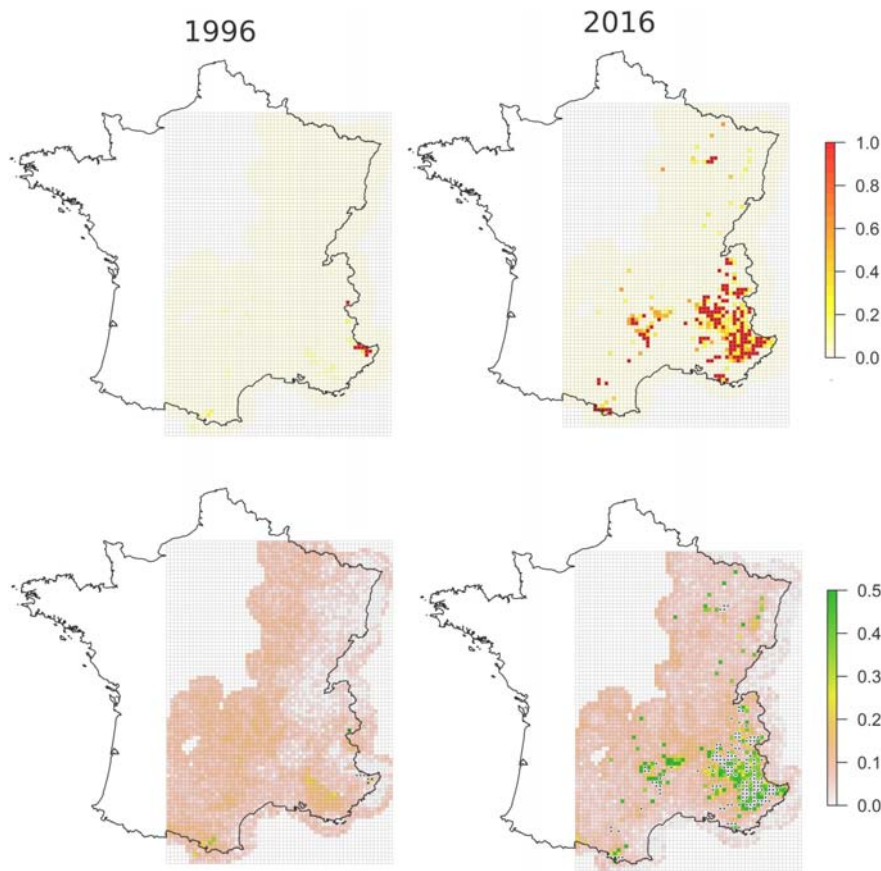

Figure 7. Maps of estimated occupancy (top) and associated standard deviation (bottom) for years 1996 and 2016. Black dots represent detections made in 1996 and 2016.

there is a risk of having very few detections within a year, which would make the estimation of the detection probability difficult.

Last, we assumed that observers were prospecting homogeneously inside the prospection area we assigned to them. This assumption may have been violated for two reasons. First, an observer might prospect more intensively near the center of the prospecting area, because it was defined as a home or work location, or near places where she/he already found presence signs (Duchamp et al. 2012). We also assumed that observers were prospecting homogeneously in time. However, observers may show different patterns in sampling frequency and some might not be prospecting during the months of winter. Finally, we assumed that once entered in the network, observers did not leave it unless we had information indicating the contrary such as a change of job or social status. Consequently, we might have overestimated the number of observers actually prospecting in the network. We therefore recommend recording carefully the activity of observers within the network to get a realistic picture of the actual sampling effort (Beirne and Lambin 2013).

Effects of environmental covariates

We used road density as a proxy of human presence and found a negative influence on the detection probability. When defining the road density covariate, we accounted for all types of roads (except highways). Because many observers from the network are wildlife professionals (Duchamp et al. 2012), main roads may not be used and accessibility to a site may consist mostly in dirt and forest roads or pathways. The negative influence could be explained by the fact that wolves tend to avoid roads (Whittington et al. 2005), therefore there might be fewer presence marks at sites with high road density. As expected, we found that detection probability increased when sampling effort increased, therefore highlighting the importance to account for imperfect detection when it is likely to be inhomogeneous in time and space. Finally, detection varied according to the month of the survey, which can be explained by the variability in snow conditions in the study area.

We found that colonization was mainly influenced by the number of observed occupied neighbors at short and long-distances, showing that dispersal and competition for space with other packs is a key factor of the dynamic of occupancy. These results corroborate those of Adams et al. (2008) who showed that dispersal was the main component explaining wolf population dynamics. Several long-distance dispersal events have been documented across the alpine area (Wolf Alpine Group 2014) and in France (Duchamp et al. unpubl.). Further studies explicitly modeling dispersal processes could help to better predict wolves colonization by accounting for factors that could enhance or slow down the dispersal rate for instance (Broms et al. 2016a).

We found that mean altitude had a positive effect on colonization probability. Wolves are highly flexible and can live in various areas from maize cultures to high mountains (Kaczensky et al. 2013). Starting from central Italy (Lucchini et al. 2002, Fabbri et al. 2007), wolves reached the alpine range via the natural Apennine mountain corridor. Therefore, the effect of mean altitude may be related to the history of the wolves' natural recovery process. However, we also found a negative effect of the proportion of altitude higher than 2500 m, i.e. the higher the proportion of high-altitude, the less likely a site was to become colonized. Above 2500 m, vegetation turns to sparse vegetation with rocky covers and snow. In contrast, more forest cover associated with lower altitudes (<2500 m) increased the probability that a site become colonized mainly because these habitats' structure and composition are much more suitable to the presence of key prey species (Darmon et al. 2012). To a lesser extent, the effect of farmland cover was also found to have a positive influence on the colonization probability. Although pasture areas host domestic preys (Meriggi and Lovari 1996) and may influence wolf colonization, the farmland covariate refers to rural exploited landscapes usually located down the valleys or lowlands. As wolf recovery is increasing over time, dispersers do not have other choices than to fulfill free available space to colonize. The overlap between human range activities and wolf settlement then increases as the recovering process is going on. The inclusion of more explicit covariates related to pastoral activity, such as the number of sheep in space, may provide a better understanding of the interaction between domestic prey and wolf presence, but these were not available to us.

Trends in wolf recolonization

Colonization patterns have been studied during recent decades (Wabakken et al. 2001). It appears that in Scandinavia, wolves were showing a colonization process that is typical of species with high dispersal capacities and pre-saturation dispersal (Swenson et al. 1998). This process is characterized by single long leaps forward and as a consequence, the colonization front is less well defined (Hartman 1994) compared to a stepping stone dispersal strategy. Wolves seem to follow a similar pattern in France (Fig. 6). This biological trait used by wolves is mainly known as a mechanism to avoid competition with other packs (Hayes and Harestad 2000). Once the area becomes saturated, dispersers may settle at unoccupied sites at long distance with higher risks of mortality due to an Allee effect (Hurford et al. 2006, Sanderson et al. 2013) or demographic stochasticity (Vucetich et al. 1997). In line with Marescot et al. (2011) who estimated a positive rate of increase in abundance, we demonstrated that the spatial dynamic mechanism of the wolves' natural recovery is still going on, particularly outside the alpine range both northward and westward. However, this recovery appeared to slow down, mainly due to areas becoming saturated within the alpine range associated with the natural barrier along the Rhône valley slowing down dispersal and/or a recent increase in official wolf controls. We may expect an increase in occupancy once few new packs have settled apart the alpine range.

We used dynamic occupancy models to assess the current and dynamic distribution of a species that is expanding since it returned; there is a temptation to aim at forecasting its future distribution. However, we emphasize the difficulty of achieving this objective because we could not incorporate the drivers that may appear relevant to explain future colonization events. For instance, now that wolves have settled in the alpine range and continue to expand, they are likely to encounter new environments such as lowlands in the next few years, a landscape that may drive future colonization. Consequently, use of our model as a predictive tool should be considered in an adaptive framework, i.e. by updating the management rules and the distribution maps every year during the active colonization phase.

The outcomes of our analyses have important consequences for managing animal species because their conservation status must be assessed partly through trends in their distributions (see art. 1 of the Habitats Fauna Flora European Directive). Dynamic occupancy models are therefore relevant tools to the decision-making process by providing maps and spatio-temporal trends. In the case of the wolf, these models can help in focusing the prevention of damage to livestock (Miller 2015). The identification of areas where the species may or may not occur along with the surrounding uncertainty may be used to target specific sites and determine priorities for implementing mitigation measures.

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