ECOGRAPHY

Research Article

Changing patterns of colonisation and persistence during the wolf recolonisation of the human-dominated Italian alpine region

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Ecography
2026: e08044
doi: 10.1002/ecog.08044
Subject Editor: Susanne Akesson
Editor-in-Chief: Dominique Gravel
Accepted April 10, 2026

Dynamic occupancy models are fundamental for understanding complex species recolonisation processes, as they allow the assessment of both colonisation and persistence probabilities over time. Using a dynamic occupancy model and a large-scale multi-year dataset on wolf presence collected in the Italian alpine region between 2014 and 2020, we analysed temporal trends in wolf colonisation and persistence probabilities in relation to environmental factors, prey availability and human-related characteristics. Our results demonstrate that wolf recolonisation is an ongoing and dynamic process in the Italian Alps, with colonisation probabilities increasing throughout the study period, particularly in the northeast of the study area. Although we detected a slight positive temporal trend in the effect of human density, wolves continue to preferentially colonise natural areas, despite a decreasing availability, as evidenced by the continued positive effects of forest cover, low natural vegetation and presence of wild ungulates. Persistence probabilities remained relatively high and constant on average,

but we noticed an increasingly negative effect of the presence of livestock pastures and densely populated areas. On the other hand, we noticed an increasingly positive effect of covariates associated with natural areas, such as forest cover, low natural vegetation and wild ungulate richness. This resulted in an increasingly contrasted spatial pattern in persistence probability throughout the region, likely reflecting conflict zones where wolves attempt to establish but struggle to survive. Overall, our study aligns with trends observed in other wolf populations across Europe, showing an expansion into new areas with different characteristics, highlighting potential areas of emerging conflict that warrant continued targeted monitoring. These patterns offer valuable insights for wolf conservation and management in human-dominated landscapes.

Keywords: *Canis lupus*, dynamic occupancy model, habitat saturation, human-dominated landscape, spatio-temporal dynamics, trends in recolonization

Introduction

Understanding the distribution of species and the processes underlying them is a major goal of conservation biology and ecology (Franklin 2013, Guisan et al. 2017). As important is understanding how these distributions and processes change over time (Planillo et al. 2024). By tracking the distribution of species over time and how they respond to management interventions, conservationists can evaluate whether conservation actions, such as habitat protection or reintroduction programs, are achieving their intended goals (Guisan et al. 2013, Chandler et al. 2015, Johnston et al. 2020) and thus inform adaptive management practices and conservation strategies for maximum impact (Martin et al. 2011).

In Europe, several large carnivore species have recolonised some or most of their historical range, often from refuge areas in remote and mountainous regions (Swenson et al. 1995, Linnell et al. 2010, Chapron et al. 2014, Nowak and Mysłajek 2016, Di Bernardi et al. 2025, Moqanaki et al. 2025). In doing so, they have demonstrated the ability to recolonise regions with moderate human densities and persist in landscapes influenced by human activities (Chapron et al. 2014). The recolonisation of the wolf *Canis lupus* in Italy is an example of this adaptability to various environments. Despite relatively high human densities, Italy has experienced one of the most important wolf recolonisations in Europe in the last decades (Cimatti et al. 2021). Here, wolf recolonisation began in the late 1970s from the south-centre of the peninsula, moving northward from the Apennines and towards the Alps (Fabbri et al. 2007). By 2020, the size of the wolf population in the Italian alpine region was estimated as between 816 and 1120 (95% credible interval; Marucco et al. 2023a, Boiani et al. 2024), and the population extended throughout the Alps and across central Europe (Valière et al. 2003, Fabbri et al. 2007, Kaczensky et al. 2024).

Wolves have been traditionally associated with forested habitats (Massolo and Meriggi 1998, Marucco 2009, Milanesi et al. 2017, Louvrier et al. 2018, Grilo et al. 2019, Rehman et al. 2021), rugged mountains (Milanesi et al. 2017, Grilo et al. 2019, Rehman et al. 2021) and areas with low human density (Massolo and Meriggi 1998, Marucco 2009, Milanesi et al. 2017). However, wolves are highly adaptable (Mech 1995) and exploit a broad prey base, with a marked preference for ungulates (Guimarães et al. 2022), which means they can persist in a wide range of environments, provided that food resources are sufficient (Llaneza et al. 2012). Recently several studies from different parts of Europe have pointed out the difficulty in identifying the drivers of future population expansion (Fechter and Storch 2014, Louvrier et al. 2018, Nakamura et al. 2023, Planillo et al. 2024), with wolves now being documented in habitats that were previously considered unsuitable (Zanni et al. 2023, Planillo et al. 2024).

This may reflect a trend in the wolf recolonisation dynamics. During the early stage of recolonisation, wolves occupied remote and uninhabited areas (O'Neil et al. 2020, Kuijper et al. 2024, Planillo et al. 2024), but as the populations continued to grow (Boitani et al. 2022), dispersing individuals seemed to gradually occupy more anthropised habitats. In western Poland, for example, wolves started occupying habitats characterised by reduced forest cover and increased presence of anthropogenic structures (Nowak et al. 2017). In multiple places in Europe, recently formed wolf packs occupy regions in proximity to human settlements (Chapron et al. 2014). Wolf expansion in Italy seems to be no exception, as wolves now occupy most of the national territory (La Morgia 2022) and, especially in central and southern Italy, have ventured beyond areas considered undisturbed (Meriggi et al. 2020, Musto et al. 2021). In the Italian alpine region, where the wolf population is still considered as expanding (Marucco et al. 2023b), these dynamics at large scale are still unexplored, although recent observations seem to agree with the European trend.

In this study, we analysed data from the Italian alpine wolf population collected between 2014 and 2020 with a dynamic occupancy model (Mackenzie et al. 2006). Dynamic occupancy models are particularly useful for studying population recolonisation over time and have been applied to a wide range of data, from birds (Broms et al. 2016) to amphibians (Chandler et al. 2015). The dynamic nature of the model means that, in addition to detection and occupancy probabilities, pivotal parameters of the recolonisation process such as local persistence and colonisation probabilities can be quantified, together with their drivers (Broms et al. 2016). With this approach, our goal was to test 1) whether the wolf population expansion continued between 2014 and 2020, i.e. the number of occupied sites increased; 2) whether similar trends were found for the probabilities of colonisation and

persistence; and 3) whether the effect of landscape covariates influencing local persistence and colonisation probabilities changed over time. Specifically, we focused on the effect of three suites of variables, reflecting environmental conditions, prey availability and human disturbance.

Material and methods

Wolf data and study area

We used data from a large-scale wolf monitoring program that took place in the Italian alpine region between 2014 and 2021 (Fig. 1). Monitoring occurred during winter, from October to April of the next year. Given the high associated costs, monitoring was conducted in only four years during that period, in the winters of 2014/2015, 2015/2016, 2017/2018 and 2020/2021. For simplicity, we refer to these monitoring seasons as 2014, 2015, 2017 and 2020, respectively.

Data collection was mainly conducted systematically, i.e. wolf signs of presence were collected along pre-established transects (Supporting information). Trained personnel, including park rangers, local authorities and volunteers, walked these transects monthly and recorded wolf tracks, scats, pictures from camera traps, urine markings and other wolf signs, following standardized protocols to ensure data reliability (Marucco et al. 2020). The length of surveyed transects was recorded as a measure of sampling effort (2014 = 9492 km, 2015 = 9327 km, 2017 = 13 528 km, 2020 = 39 609 km). GPS tracks were recorded each time a transect was visited. Transects were mostly located in areas of known wolf presence, as they were originally established as a means to follow the local evolution of the wolf population. In addition, wolf presence data were also collected opportunistically throughout the entire region in the same season, whether by trained personnel on occasions other than systematic searches, or by members of the public, who collected signs of presence that could be verified by trained personnel. This means that wolf occurrence data was available for the entire Italian alpine region, albeit with varying sampling intensity. Each presence sign was associated with information about its location, date and an image to allow validation by an expert. To increase the reliability of the model, we used the SCALP criteria (Status and Conservation of the Alpine Lynx Population; Molinari-Jobin et al. 2012) and kept wolf observations categorised as C1 (clear evidence) and C2 (confirmed observation) only (Marucco et al. 2023b). In the end, the dataset consisted of 9725 wolf scats, 2172 snow-tracks and 3543 pictures from camera traps.

To allow for the analysis of these data with a dynamic occupancy model, we had to organise them into sites, primary and secondary occasions (Royle and Kéry 2007, Bailey et al. 2014). Sites represent the fundamental spatial unit of the model and

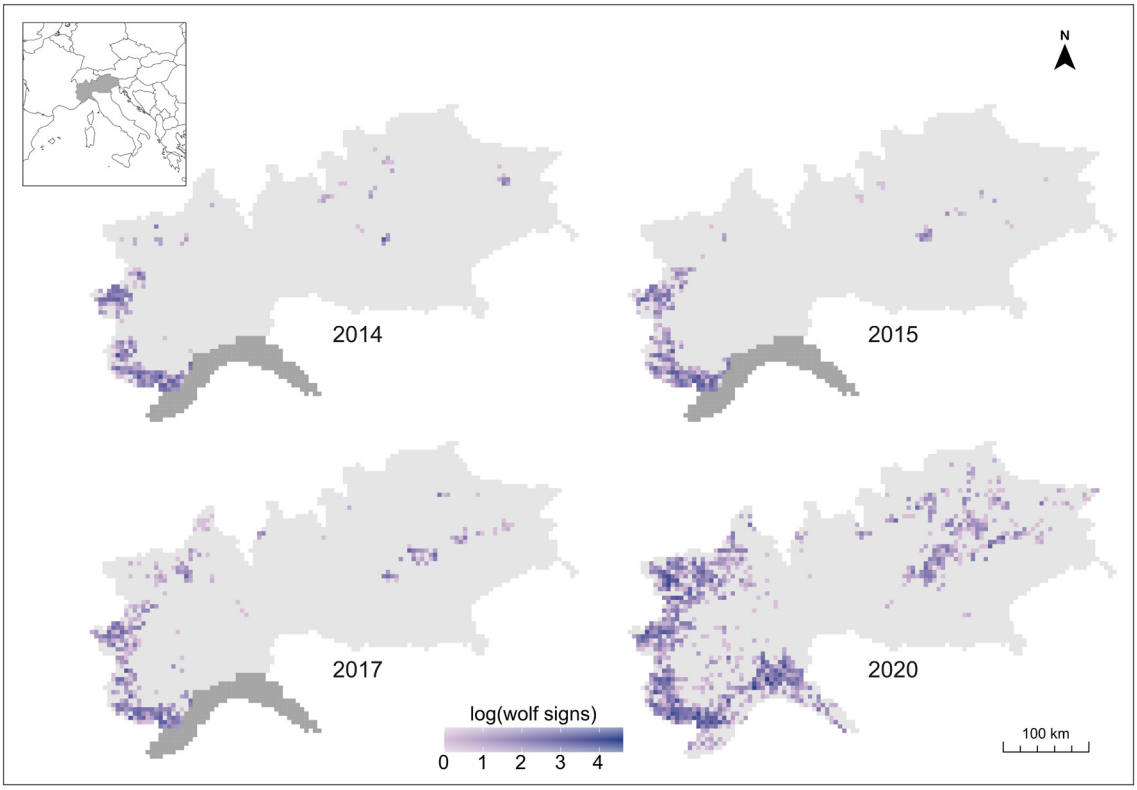

Figure 1. Number of wolf presence signs per 5 × 5 km grid cell collected in the Italian alpine region study area (grey area in the upper left corner) for each monitoring season between 2014 and 2020. Dark grey cells in the years 2014, 2015 and 2017 represent areas that were either not sampled or where data were unavailable for this analysis and were thus considered not sampled neither systematically nor opportunistically.

correspond to the different locations where wolves can be detected/non-detected. In our model, sites were defined as the 3917 grid cells of size 5 × 5 km overlapping the Italian alpine region (Fig. 1). Following Nakamura et al. (2023), we used a 5 × 5 km grid to define sites as it was deemed appropriate for detecting changes in wolf spatial use at the local level. Primary occasions correspond to the main temporal unit of the model, between which the occupancy state can change; while secondary occasions, nested within primary occasions, correspond to different detection occasions during which occupancy is assumed to be constant. In our case, primary occasions corresponded to monitoring seasons (one per year), and secondary occasions to months within each monitoring season (seven, from October to April). The dataset included in the analysis thus consisted of binary detection histories, 0 indicating no wolf detection and 1 indicating at least one observation, for each combination of site, month and year. Although the dataset spans seven calendar years (2014–2020), wolf presence signs were collected during four of those seven primary occasions only (dynamic occupancy model section).

Dynamic occupancy model

Dynamic, or multi-season, occupancy models are hierarchical models that estimate the probability that a given area (a 'site') is occupied by a species, as well as the probabilities that unoccupied sites become occupied (local colonization), and occupied sites remain occupied (local persistence) over time. Importantly, these models account for imperfect detection by modelling not only the ecological process (occupancy dynamics) but also the observation process (detection/non-detection), as these two processes lead to the observed data jointly (MacKenzie et al. 2003, Royle and Kéry 2007, Kéry et al. 2013, Broms et al. 2016, MacKenzie et al. 2017). The main parameters of the ecological process, initial occupancy, local colonisation and local persistence probabilities, can all be expressed as functions of multiple covariates. This allows testing for and quantifying their influence on the different processes and ultimately helps explain the variability in wolf occurrence throughout the landscape.

Spatial covariates

Here, we considered multiple covariates, which can be broadly categorised as reflecting 1) environmental conditions, 2) prey availability and 3) human disturbance.

1. Environmental covariates consisted of forest cover (forest), calculated as the percentage of each site covered by forests, including both broad-leaved and evergreen forests, and cover of short vegetation (shortveg), the percentage of each site covered by lower natural vegetation (heathland, transitional shrubland and natural grassland). Both covariates were extracted from the Corine Land Cover layer (Copernicus Land Monitoring Service 2018, EEA). Both forest and short vegetation covers have been positively correlated with wolf presence in previous studies (Oakleaf et al. 2006, Marucco 2009, Louvrier et al. 2018, Grilo et al. 2019, Nakamura et al. 2023).
2. Prey availability covariates consisted of a wild ungulate richness index (ung), and the number of livestock pastures per municipality (livestock). The wild ungulate index was based on the presence of six ungulate species, red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, chamois *Rupicapra rupicapra*, wild boar *Sus scrofa*, fallow deer *Dama dama* and mouflon *Ovis ammon*, from Linnell et al. (2020) as in Gervasi et al. (2024). The number of livestock pastures per municipality was obtained from the Banca Dati Nazionale dell'Anagrafe Zootecnica of Italy, as a proxy for the availability of domestic prey. We expected the proxy for ungulate presence to be positively associated with wolf presence, as well as the number of livestock pastures, since livestock can compensate for the depletion of wild ungulate populations and is also associated with farm waste that can be attractive for wolves, e.g. carrion (Meriggi and Lovari 1996, Torres et al. 2015, Grilo et al. 2019).
3. To represent human disturbances, we used the logarithm of human population density (pop) obtained from WorldPop (https://hub.worldpop.org/), and an index of light pollution (lightpoll). We used the logarithm of human density to allow areas with moderate human presence to be highlighted in comparison to large cities. Lightpoll was obtained from the annual Visible and Infrared Imaging Suite of the Earth Observation Group https://eogdata.mines.edu/products/vnl/). We expected human population density to have a negative effect on wolf occurrence and dynamics (Glenz et al. 2001, Cimatti et al. 2021, Marucco et al. 2023a). We also expected a negative effect of light pollution, which has been used as a proxy that is less related to the direct presence of humans, and more to human infrastructure (Stevens et al. 2023).

In addition, we used the 2012 IUCN wolf presence layer (Kaczensky et al. 2021) as a covariate (wolfpres) on initial occupancy probability (below) to better capture the state of the population at the beginning of our study period.

Although annual data were available for some covariates (light pollution, livestock pastures, human population density), temporal variation in these variables during our study period (2014–2020) was negligible at the resolution at which we modelled occupancy (5 × 5 km); we therefore used temporally averaged values for all covariates. In addition, we considered using elevation as another potentially important environmental covariate in this type of landscape with strong elevational gradient but did not include it as it was highly correlated with multiple covariates (Supporting information). See the Supporting information for more information on the choice and distributions of covariates.

Ecological process

In the dynamic occupancy model, $z_{i,1}$, the wolf occurrence at site *i* in the first year of monitoring (2014) follows a Bernoulli distribution:

$$z_{i,1} \sim \text{Bernoulli}(\psi_i) \quad (1)$$

where ψ_i represents the occupancy probability in cell i during the first monitoring season. To account for spatial variation in wolf occurrence, we modelled ψ_i as:

$$\begin{aligned}\text{logit}(\psi_i) = \text{logit}(\psi_0) &+ \beta^{\psi}_{\text{forest}} \times \text{forest}_i \\ &+ \beta^{\psi}_{\text{shortveg}} \times \text{shortveg}_i + \beta^{\psi}_{\text{ung}} \times \text{ung}_i \\ &+ \beta^{\psi}_{\text{livestock}} \times \text{livestock}_i \\ &+ \beta^{\psi}_{\text{pop}} \times \text{pop}_i + \beta^{\psi}_{\text{wolfpres}} \times \text{wolfpres}_i \end{aligned} \quad (2)$$

where ψ_0 is the baseline initial occupancy probability and is β^{ψ}_X the regression coefficient for covariate X.

For subsequent primary occasions, we modelled changes in occupancy between years as a first-order Markov process. This means that the probability that a site is occupied in a given year depends on the occupancy status in the previous year (MacKenzie 2017). For subsequent years ($t > 1$), wolf occurrence was then modelled as:

$$z_{i,t} \sim \text{Bernoulli}\left(z_{i,t-1} \times \Phi_{i,t-1} + (1 - z_{i,t-1}) \times \rho_{i,t-1}\right) \quad (3)$$

where $\Phi_{i,t-1}$ is the probability of persistence, i.e. the probability that a site i occupied in year t − 1 remains occupied in year t; and $\rho_{i,t-1}$ is the colonisation probability, i.e. the probability that an unoccupied site i in year t − 1 becomes occupied in year t. Note that the wolf occupancy status $z_{i,t}$ is modelled for all years $t = (1, \ldots, 7)$ even though data were collected in four out of the seven years only.

Annual colonisation and persistence probabilities were then modelled as:

$$\textit{logit}(\rho_{i,t}) = \rho_0 + \beta^{\rho}_t \times t + \beta^{\rho}_X \times X_i + \beta^{\rho}_{X,t} \times X_i \times t \quad (4)$$

and

$$\text{logit}(\Phi_{i,t}) = \Phi_0 + \beta^{\Phi}_t \times t + \beta^{\Phi}_X \times X_i + \beta^{\Phi}_{X,t} \times X_i \times t \quad (5)$$

where ρ_0 and Φ_0 are the baseline probabilities on the logit scale, β^{ρ}_X and β^{Φ}_X are the regression coefficients associated with a set of covariates X, β^{ρ}_t and β^{Φ}_t are the regression coefficients associated with time considered as a continuous variable (t denoting the number of years since the start of the study, i.e. t = 1 in 2014), and $\beta^{\rho}_{X,t}$ and $\beta^{\Phi}_{X,t}$ are the regression coefficients associated with the interaction of covariates X and time for the colonisation and persistence probabilities, respectively. For both colonisation and persistence probabilities, the set of covariates X was composed of forest cover (forest), cover of short vegetation (shortveg), wild ungulate richness (ung), the number of livestock pastures per municipality (livestock), the logarithm of human population density (pop) and the index of light pollution (lightpoll). This formulation allowed us to quantify potential temporal changes in the effect of the different covariates throughout the study period.

Observation process

The observation data for site i, monthly secondary occasion j and monitoring season k ($y_{i,j,k}$) were then modelled as a Bernoulli process:

$$y_{i,j,k} \sim \text{Bernoulli}\left(z_{i,\text{year}(k)} \times p_{i,j,k}\right) \quad (6)$$

Note that because wolf monitoring occurred during four out of seven years only, detection probability was modelled for the four monitoring seasons only, hence the monitoring season index $k = (1, \ldots, 4)$ is different from the year index $t = (1, \ldots, 7)$. The indexing function year(k) was used to ensure that the occupancy status to the kth monitoring season was used (model code in the Supporting information). $p_{i,j,k}$ the detection probability in site i, month j and monitoring season k (conditional on occurrence $z_{i,\text{year}(k)} = 1$) was modelled as:

$$\begin{aligned} p_{i,j,k} = \text{logit}^{-1}\begin{bmatrix} p_0 + \beta_{\text{searcheffort},k} \times \text{searcheffort}_{i,j,k} \\ + \beta_{\text{snowfall},k} \times \text{snowfall}_{i,j,k} \end{bmatrix} \\ \times \text{isMonitored}_{i,k} \end{aligned} \quad (7)$$

where p_0 is the baseline detection probability, $\text{search effort}_{i,j,k}$ is the number of kilometres searched at site i, occasion j (month) and monitoring season k, and $\text{snowfall}_{i,j,k}$ is the mean accumulated surface snow (in metres of equivalent water) at site i, occasion j and monitoring season k. We used the number of kilometres walked looking for wolf signs per month and site as a measure of search effort (Marucco 2009, Louvrier et al. 2018). Sites with no transects had a $\text{search effort}_{i,j,k} = 0$ and were thus considered as monitored opportunistically only. We used snowfall, assuming higher probability of detecting wolf presence when snow is on the ground (Marucco 2009). Snowfall data were obtained from the ECMWF (European Center for Medium-Range Weather forecasts) ERA-5 reanalysis (https://cds.climate.copernicus.eu/) Table 1.

Additionally, we used a binary indicator ($\text{isMonitored}_{i,k}$) to turn off grid cells that were not monitored with certainty, or where data were unavailable (data not communicated) in a given monitoring season, and where detection probability was effectively 0 (dark grey cells in Fig. 1 and the Supporting information).

Derived parameters

We calculated annual population expansion rates as $\breve{N}_t / \breve{N}_{t-1}$, where $\breve{N}_t$ is the number of occupied sites in year t and $\breve{N}_{t-1}$ is the number of sites occupied the previous year. The number of occupied sites in a given year was obtained by summing the number of sites with an occupancy status $z_{i,t} = 1$:

$$\breve{N}_t = \sum_{i=1}^{M} z_{i,t}$$

Table 1. Covariates used in the dynamic occupancy analysis of the wolf in the Italian Alps and their expected effects. Where ψ is occupancy probability, ρ is colonisation probability, φ is persistence probability and p is detection probability.

Covariate	Abbreviation	Hypothesis				Description	Reference
		ψ	ρ	φ	p		
Wolf previous presence	wolfpres	+				Wolf known presence in 2012 from IUCN layer	Kaczensky et al. 2021
Forest cover	forest	+	+	+		Percentage of mixed, coniferous or broad-leaved forest cover	Oakleaf et al. 2006, Falcucci et al. 2013, Nowak et al. 2017, Louvrier et al. 2018, Nakamura et al. 2023, Marucco et al. 2023b, Gervasi et al. 2024
Cover of short vegetation	shortveg	+	+	+		Percentage of natural grassland, transitional woodland–shrub, moors and heathlands	Falcucci et al. 2013, Nakamura et al. 2023, Marucco et al. 2023b
Wild ungulate richness	ung	+	+	+		Number of ungulate species available per grid cells (see Linnel et al., 2020 for more details about data used to produce it)	Glenz et al. 2001, Falcucci et al. 2013, Grilo et al. 2019, Gervasi et al. 2024
Livestock pastures	livestock	=	+	–		Numbers of livestock pastures	Nakamura et al. 2023
Human population density	pop	–	–	–		Logarithm of human inhabitants per 1 km grid cell	Glenz et al. 2001, Falcucci et al. 2013, Nowak et al. 2017, Cimatti et al. 2021, Nakamura et al. 2023, Marucco et al. 2023b, Gervasi et al. 2024
Light pollution	lightpoll	–	–	–		Mean nighttime from satellite imagery map (VIIRS)	
Snowfall	snowfall				+	Amount of snow fallen on the ground per month per year (ERA-5 reanalysis)	Marucco et al. 2023b, Gervasi et al. 2024
Search effort	searcheffort				+	Number of kilometres walked per 5 km grid cell per month per year	Louvier et al. 2018, Nakamura et al. 2023

where M = 3917 is the total number of sites in the study area. This process was done for all MCMC iterations, thus leading to the posterior distributions for the annual numbers of occupied sites and annual expansion rates, from which the posterior mean and confidence intervals could be derived.

Model fitting

We used 'nimble' ver. 1.3.0 (de Valpine et al. 2017) in R ver. 4.1.3 (www.r-project.org) to fit the model in a Bayesian framework using Markov chain Monte Carlo (MCMC) simulation. We ran eight chains of 400 000 iterations each and discarded the first 200 000 as burn-in. To facilitate post-processing, we used a thinning rate of 10. All diagnostics and further output processing were thus based on 160 000 posterior samples (20 000 per chain). We assessed model convergence by checking the traceplots and calculated the $\hat{R}$ parameter, considering that model convergence was reached when $\hat{R} < 1.1$ (Gelman et al. 2013).

Lastly, we implemented a reversible-jump Monte Carlo Markov chain (RJMCMC) approach to select among covariates in the model (Green 1995, O'Hara and Sillanpää 2009). Following this procedure, all regression coefficients (β)in the linear regressions targeting initial occupancy, colonisation and persistence probability (Eq. 2, 4 and 5) were associated with a binary indicator parameter that determined the probability of inclusion of each covariate as a measure of its importance. To identify the most important covariates, we calculated posterior inclusion probabilities (PIPs) as the proportion of the MCMC iterations when the parameter of interest was included and checked whether the 95% Bayesian credible interval of each coefficient, when included in the model, did not overlap 0, as an indicator of its significance. In the remainder of the article, we report summary statistics (means and 95% Bayesian credible intervals) for all regression coefficients conditional on their inclusion in the model, while we report summary statistics based on all MCMC iterations for all derived quantities (average colonisation and persistence probabilities, population expansion rate, site-specific occupancy, etc.).

All models were run on the HPC cluster system OCCAM (Aldinucci et al. 2017).

Results

Occupancy patterns

In 2014, average wolf occupancy probability in the Italian alpine region was 0.07 [0.00; 0.60] (mean [95% Bayesian credible interval]). The highest occurrence probabilities were concentrated on the western alpine arc (Fig. 2). Overall, our

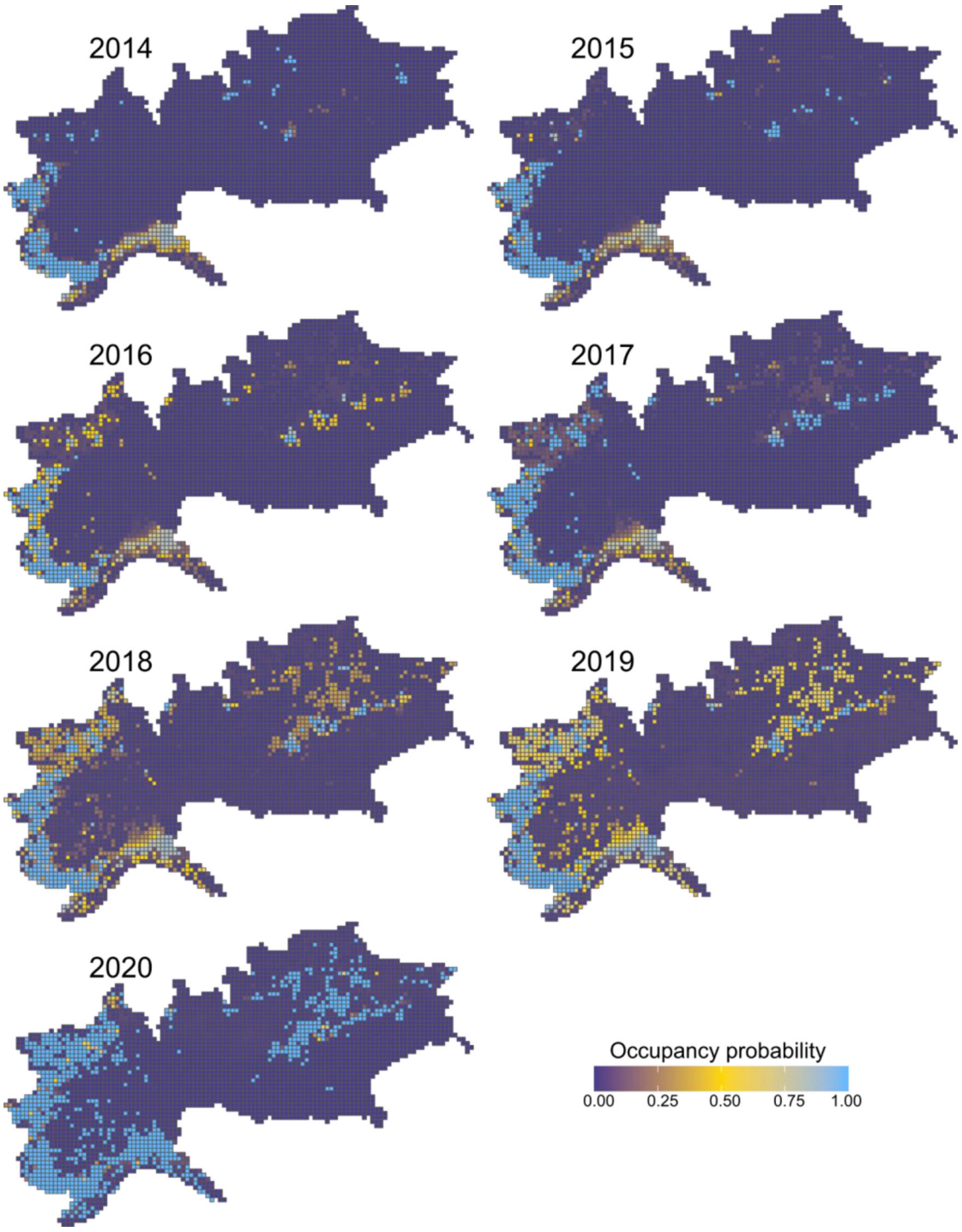

Figure 2. Annual wolf occupancy probabilities in the Italian alpine region between 2014 and 2020 based on a dynamic occupancy model based on four surveys.

results indicate a major expansion of the population towards the north and east of the region between 2014 and 2020. The average annual population expansion rate during the study period was 1.21 [1.15; 1.27]. This corresponded to an increase from 287 [270; 305] occupied sites in 2014, to 901 [886; 917] in 2020. Population expansion varied also over time, and we observed an acceleration, from an expansion rate of 1.05 [1.00; 1.10] between 2014 and 2015 up to 1.28[1.22;1.43] between 2018 and 2019. The expansion rate seemed to stabilize in the last years of the study, with a rate of 1.27 [1.22; 1.33] between 2019 and 2020 (Supporting information).

Covariate effects

Wolf occupancy during the first year of monitoring (2014)

Our results highlight that wolf initial occupancy probability ψ was strongly and positively associated with known wolf presence in previous years ($\beta_{wolfpres} = 1.06$ [0.96; 1.17], PIP = 1.00, Fig. 3A), forest cover ($\beta_{forest} = 0.76$ [0.56 0.97], PIP = 1.00) and cover of short vegetation ($\beta_{shortveg} = 0.56$ [0.37; 0.75], PIP = 1.00). Initial occupancy probability was also positively associated with the presence of livestock ($\beta_{livestock} = 0.20$ [0.02; 0.39], PIP = 0.90) and to a lesser extent with the presence of wild ungulates ($\beta_{ung} = 0.16$ [−0.11; 0.45], PIP = 0.72), while human-related covariates were not significantly associated with wolf occupancy in 2014. Both human population density ($\beta_{pop} = -0.07$ [−0.28; 0.14], PIP = 0.57) and light pollution ($\beta_{lightpoll} = -0.10$ [−0.44; 0.21], PIP = 0.65) had slight negative effects on wolf occupancy probability, but both effects overlapped zero. Summary statistics for all initial occupancy parameters are provided in the Supporting information, included PIP, $\hat{R}$ and effective sample sizes.

Colonisation probability

Overall, the average colonisation probability increased with time in the Italian alpine region, going from $\bar{\rho}_{2014} = 0.01$ [0.01; 0.02] to $\bar{\rho}_{2020} = 0.08$ [0.07; 0.09] (Supporting information). This increase was also evidenced by a clear positive effect of time on colonization probability ($\beta_t = 0.38$ [0.31; 0.46], PIP = 1.00, Fig. 4A), but mostly visible in the eastern part of the region (Fig. 4D).

Ecological process

Parameter estimates associated with the effects of spatial covariates indicated that wolves used to have greater probabilities of colonising sites with – in decreasing order of magnitude – higher numbers of livestock pastures ($\beta_{pas} = 0.38$ [0.08; 0.63], PIP = 0.97), higher numbers of ungulate species present ($\beta_{ung} = 0.37$ [0.12; 0.71], PIP = 0.99), higher percentages of short vegetation cover ($\beta_{shortveg} = 0.31$ [0.16; 0.57], PIP = 1.00) and forest cover ($\beta_{forest} = 0.18$ [−0.01; 0.36], PIP = 0.91). On the other hand, colonization probability seemed to not be affected by human density ($\beta_{pop} = 0.07$ [−0.16; 0.22], PIP = 0.62), while light pollution tended to have a negative effect ($\beta_{lightpoll} = -0.19$ [−0.48; 0.17], PIP = 0.78).

Most interaction term estimates were negative but relatively weak (Fig. 4B). Over time, this led to a slight decrease in the magnitude of the effect of most spatial covariates (Fig. 4C), sometimes leading them to fade away, as in the case of the wild ungulate index, with annual coefficients going from $\beta_{ung,2014} = 0.34$ [−0.09; 0.66] to $\beta_{ung,2020} = 0.19$ [−1.66; 2.18], or even reversing, as in the case of livestock pastures ($\beta_{pas,2014} = 0.30$ [−0.09; 0.51] to $\beta_{pas,2020} = -0.06$ [−0.77; 0.77]). On the other hand, interaction terms for forest cover ($\beta_{forest,t} = 0.01$ [−0.06; 0.07], PIP = 0.31), short vegetation cover ($\beta_{shortveg,t} = -0.03$ [−0.09; 0.04], PIP = 0.34), and population density were not significant ($\beta_{pop,t} = 0.02$ [−0.03; 0.0.07], PIP = 0.32), leading to no noticeable change in the annual effects (Supporting information). Only the negative effect of light pollution tended to strengthen with time ($\beta_{lightpoll,t} = -0.07$ [−0.15; 0.01], PIP = 0.62). Summary statistics for all colonisation probability parameters are provided in the Supporting information, including PIP, $\hat{R}$ and effective sample sizes, and all annual regression coefficients are also provided in the Supporting information.

Probability of persistence

Despite a positive effect of time on the intercept of the persistence probability regression (Fig. 5A), the average probability of persistence in the study area showed no significant temporal trend, going from $\bar{\varphi}_{2014} = 0.74$ [0.57; 0.90] to $\bar{\varphi}_{2020} = 0.72$ [0.21; 0.99] (Supporting information). However, the persistence probability maps highlight that the spatial variation of the persistence probabilities increased during the study period. Persistence probabilities decreased, particularly in low elevation regions (Fig. 5D). Covariates' effects on wolf persistence were less marked than for colonisation (Fig. 5; Supporting information), but contrary to the latter, the strength of the effects tended to increase with time (Fig. 5C–D). The spatial covariate with the highest initial effect on persistence probability was short vegetation cover ($\beta_{shortveg} = 0.31$ [−0.03; 0.61], PIP = 0.9), followed by wild ungulate richness ($\beta_{ung} = 0.08$ [−0.29; 0.43], PIP = 0.67), livestock pastures ($\beta_{livestock} = 0.07$ [−0.26; 0.41], PIP = 0.64), light pollution ($\beta_{lightpollution} = 0.06$ [−0.33; 0.44], PIP = 0.66), forest cover ($\beta_{forest} = 0.03$ [−0.31; 0.38], PIP = 0.63) and human population density ($\beta_{pop} = 0.03$ [−0.32; 0.39], PIP = 0.64). Notably, all 95% credible intervals overlapped 0.

Regarding temporal interactions, we observed two groups of covariates. The first consisted of forest cover ($\beta_{forest,t} = 0.23$ [0.11; 0.36], PIP = 1.00), ungulate richness ($\beta_{ung,t} = 0.13$ [−0.01; 0.28], PIP = 0.77) and short vegetation ($\beta_{shortveg,t} = 0.11$ [−0.05; 0.27], PIP = 0.64), which displayed increasingly positive effects with time, albeit with different intensities (Fig. 5B–C). The second consisted of livestock pastures ($\beta_{livestock,t} = -0.13$ [−0.30; 0.02], PIP = 0.74) and human population density ($\beta_{pop,t} = -0.19$ [−0.38; 0.02], PIP = 0.9), which tended to show increasingly negative effects with time (Fig. 5B–C). Finally, the effect of light pollution showed no significant temporal trend ($\beta_{lightpoll,t} = 0.03$ [−0.23; 0.27], PIP = 0.55). Summary statistics for all persistence probability parameters are provided in the Supporting information, including PIP, $\hat{R}$ and effective sample sizes, and all annual regression coefficients are also provided in the Supporting information.

Detection probability

Detection probability strongly increased with search effort in all monitoring seasons ($\beta_{searcheffort,2014} = 0.83$ [0.63; 1.02]; $\beta_{searcheffort,2015} = 0.53$ [0.38; 0.68]; $\beta_{searcheffort,2017} = 0.77$ [0.64; 0.92]; $\beta_{searcheffort,2020} = 0.82$ [0.72; 0.92]; Supporting information), while snow cover had smaller and variable effects ($\beta_{snowfall,2014} = 0.1$ [−0.00; 0.21]; $\beta_{snowfall,2015} = -0.19$ [−0.32;

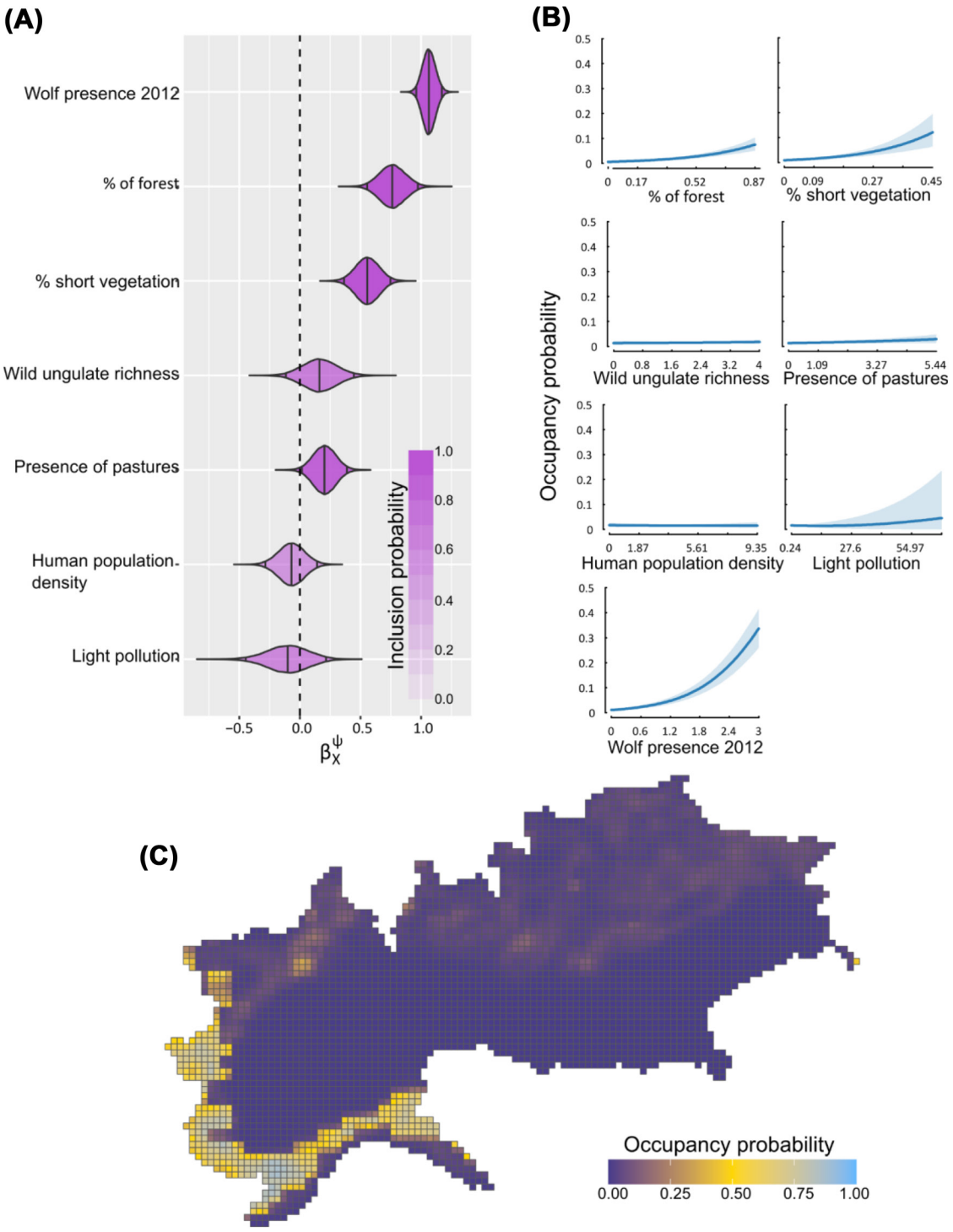

Figure 3. Wolf occupancy probability and covariate effects in the Italian alpine region in 2014 estimated by a dynamic occupancy model based on four years of surveys. (A) Posterior distributions, conditional on inclusion in the model, of the effects of spatial covariates on wolf initial occupancy (β_X^{ψ}). Inclusion probabilities, obtained from a reversible jump MCMC implementation of the model, and indicative of the importance of the parameter considered, are represented by the transparency level. (B) Marginal effect plots of the same covariates. Coloured lines indicate mean estimated effects, and coloured polygons indicate 95% Bayesian credible intervals. (C) Map of wolf occupancy probability in the Italian alpine region in 2014. Light blue, yellow and dark violet colours highlight high, medium and low wolf occupancy probabilities, respectively.

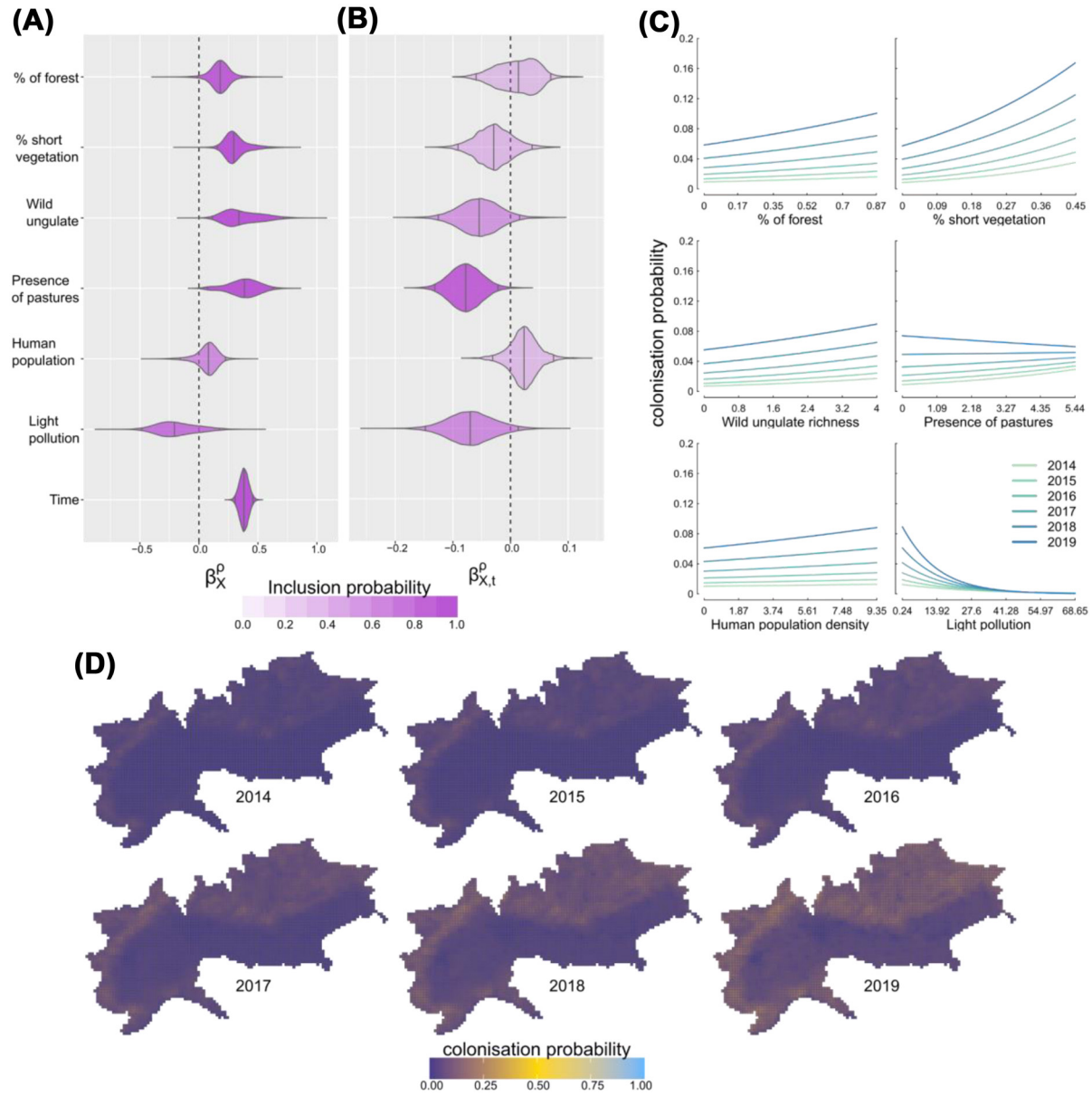

Figure 4. Wolf colonisation probability in the Italian alpine region between 2014 and 2019 estimated by a dynamic occupancy model based on four years of surveys. (A) Posterior distributions, conditional on inclusion in the model, of the effects of spatio-temporal covariates on colonisation probability (β^{ρ}_{X}), and (B) two-way interactions between the spatial covariate and time ($\beta^{\rho}_{X,t}$). In (A) and (B) inclusion probabilities, obtained from a reversible jump MCMC implementation of the model, and indicative of the importance of the parameter considered, are represented by the transparency level. (C) Annual marginal effect plots of the spatial covariates between 2014 (green) and 2019 (blue). (D) Maps of estimated annual wolf colonisation probabilities throughout the Italian alpine region. Light blue, yellow and dark violet colours highlight high, medium and low wolf colonisation probabilities, respectively.

-0.05]; $\beta_{\text{snowfall},2017} = -0.27$ [-0.38; -0.17]; $\beta_{\text{snowfall},2020} = 0.03$ [-0.02; 0.09]; Supporting information).

Discussion

Our analysis of wolf occupancy dynamics in the densely human-populated Italian alpine region during 2014–2020 provides new insights into the species' recolonisation process. We demonstrated that wolf expansion was an ongoing and dynamic process up to 2020, characterised by increasing colonisation probabilities and relatively constant but spatially variable persistence, leading to expansion rates that appear to be plateauing in recent years. Importantly, this population expansion has been accompanied by temporal shifts in the relationships between landscape characteristics and both

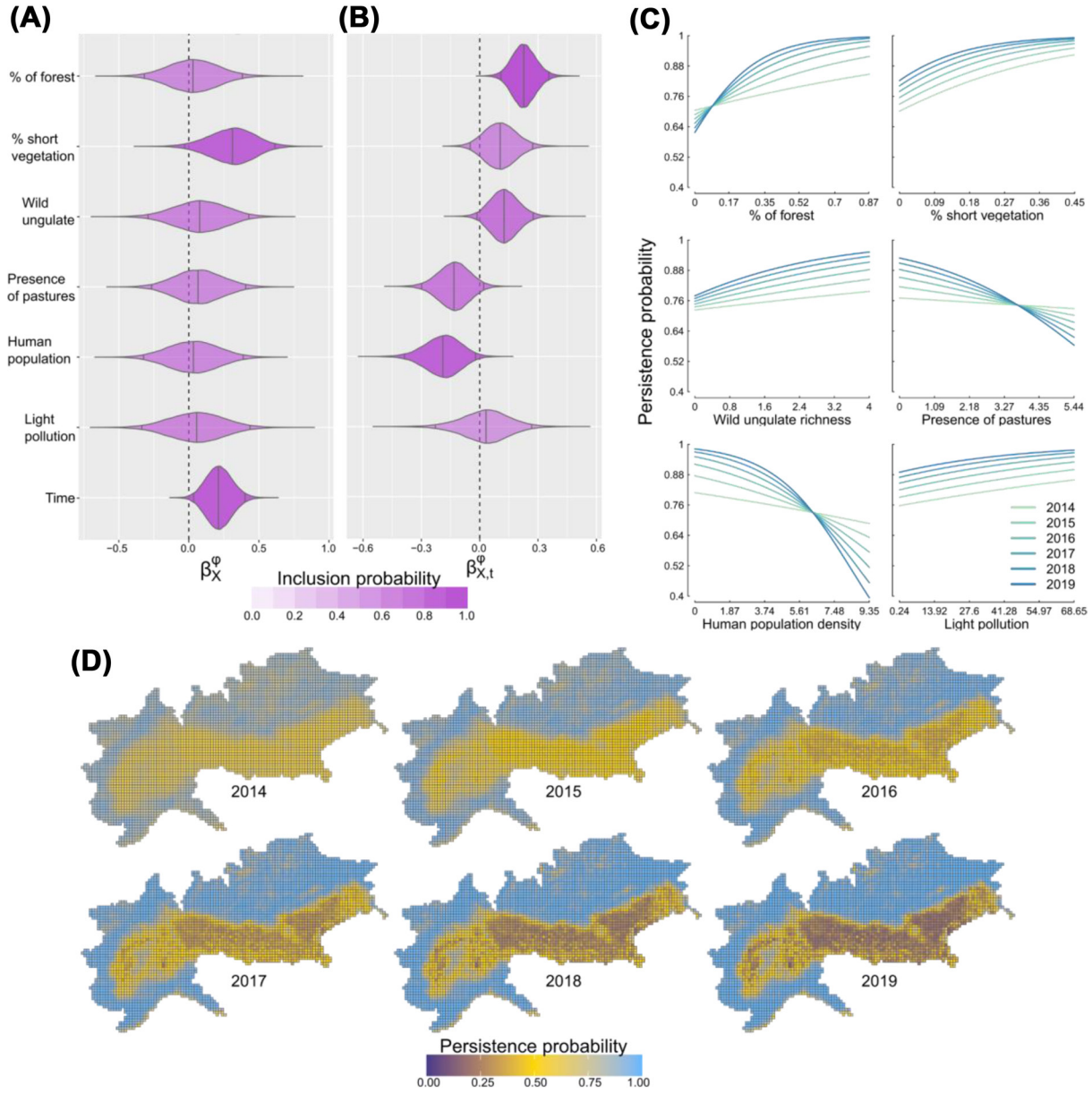

Figure 5.Wolf persistence probability in the Italian alpine region between 2014 and 2020 estimated by a dynamic occupancy model based on four years of surveys. (A) Posterior distributions, conditional on inclusion in the model, of the effects of spatio-temporal covariates on persistence probability (β_X^{Φ}) and (B) two-way interactions between the spatial covariate and time ($\beta_{X,t}^{\Phi}$). In (A) and (B) inclusion probabilities, obtained from a reversible jump MCMC implementation of the model, and indicative of the importance of the parameter considered, are represented by the transparency level. (C) Annual marginal effect plots of the spatial covariates between 2014 (green) and 2019 (blue). (D) Maps of estimated annual wolf colonisation probabilities throughout the Italian alpine region. Light blue, yellow and dark violet colours highlight high, medium and low wolf colonisation probabilities, respectively.

colonisation and persistence probabilities, reflecting the species' ability to adapt to human disturbance while maintaining selectiveness for natural habitats.

The first-year occupancy pattern we observed aligned with historical habitat selection documented for wolves in Europe. In 2014, wolves were occupying sites characterised by high percentages of vegetation cover (both short natural vegetation and forest), higher richness of wild ungulate species, and livestock pastures, while avoiding densely human-populated areas (Marucco 2009, Milanesi et al. 2017, 2022, Roder et al. 2020, Cimatti et al. 2021, Planillo et al. 2024). The fact that previous wolf presence emerged as the most significant predictor for occupancy probability at the beginning of the study period stresses the importance of considering the history of the population when studying its dynamics. In our case, this helped the model identify areas with higher occupancy probabilities in the southwestern Alps, where wolves first re-established in 1995, and which later served as the starting

point for the population expansion towards the north and east (Marucco et al. 2023b). Between 2014 and 2015, colonisation probabilities were low overall but higher in areas with high percentages of forest and short vegetation cover, high wild ungulate richness and abundant livestock pastures (Fig. 4), reflecting an initial preference for natural habitats with good prey availability (Supporting information). Over time, colonisation probabilities increased throughout the study area, probably reflecting the overall increase in the wolf's population size, following the wolf recovery in the region (Marucco et al. 2023a). At the same time, the positive association between colonisation probability and the different covariates representing natural habitats seemed to weaken, leading to slightly lower relative preferences of wolves for colonizing these types of habitats. This could be indicative of an expansion of the wolf population towards lower elevations also observed in other places (Louvrier et al. 2018, Cimatti et al. 2021, Vorel et al. 2024). The declining effect of ungulate richness, and the reversal of the effect of livestock pastures, from positive to negative, are also in accordance with the wolf population expanding into the lowlands, where wild ungulates and livestock pastures are less present (Canova and Meriggi 2025). This is also in line with recent evidence suggesting that wolves in the region have broadened their diet to not include ungulates only, increasingly relying on a wider array of prey species (Lazzeri et al. 2024, Travain et al. 2025). In addition, the slight positive trend of the logarithm of human population density together with the negative trend observed for light pollution, suggest that areas with low to moderate human presence are not excluded from wolf expansion, while highly urbanised areas are still avoided. Indeed, light pollution primarily identifies urban centres while the log-transformed human density better captures effects at low to mid-densities (Supporting information). This pattern aligns with evidence from other recolonising populations that wolves increasingly probed more anthropogenic landscapes as natural habitats approach saturation in recent years (Zanni et al. 2023, Kuijper et al. 2024). While wolves seem to gradually colonise more diversified areas, wolf persistence seems to be increasingly grounded in natural habitats and human avoidance. Parameter estimates indicate that wolf persistence probabilities at the beginning of the study period (2014) were relatively homogeneous throughout the study region and only moderately associated with spatial covariates, positively with short vegetation and forest cover, wild ungulate species richness, and light pollution, and negatively with human density and presence of pastures. Over time, both positive and negative effects increased in intensity, leading to an increasingly contrasted spatial pattern in persistence probability (Fig. 5D). These findings are in accordance with previous studies showing that natural areas play a fundamental role in sustaining established packs in human-dominated landscapes (Llaneza et al. 2016, Torretta et al. 2024). The fact that forest cover is the covariate whose effect strengthened the most over time is also in accordance with previous studies showing the importance of refuge areas, usually defined as forested areas, for wolves' survival even in anthropised environments (Grilo et al. 2019, Hipólito et al. 2026). On the other hand, both human density and, to a lesser extent, the presence of livestock pastures showed increasingly negative effects on persistence, potentially indicating zones of intensifying human–wildlife conflict. Livestock depredation often triggers retaliatory attitudes and illegal persecution (Linnell et al. 2001, Marino et al. 2016), which can severely compromise wolf persistence even in otherwise suitable habitats. The increased negative effect of human density may also reflect the challenges wolves face in anthropogenic landscapes, like increased accidental mortality from vehicle collisions (Lovari et al. 2007, Musto et al. 2021) or heightened human–wildlife conflicts (Torretta et al. 2022) caused by negative interactions, such as predation on domestic dogs and other pets (Iliopoulos et al. 2021, Kojola et al. 2023).

Our analysis further reveals distinct regional patterns, reflecting the progressive saturation of optimal wolf habitat in the region (Fig. 2). Wolves first successfully established in the high elevation areas of the western and central Alps, as evidenced by the high initial occupancy and persistence probabilities which remained consistently high in these regions. In contrast, colonisation in recent years mostly occurred eastward and towards lower elevations (Avanzinelli et al. 2024). Even though our model predicts that colonisation is more likely in high elevation areas, characterised by higher proportions of short vegetation and forest (Fig. 4D), most of these areas were already occupied by 2020, and newly colonised areas tended to be at lower elevation and more anthropised (Fig. 2). This spatial progression of colonisation may indicate that the wolf population has reached saturation in high-elevation natural habitats, like in the western Alps, and is now expanding into more anthropogenic landscapes. This shift appears to be driven by habitat saturation rather than active selection for human-dominated areas, as indicated by the continued relative preference for natural habitats and the absence of strong positive effects of anthropogenic variables. Accordingly, other studies have shown that, at the European scale, environmental variables, rather than human impact metrics, are still the strongest predictors of large carnivore distribution (Cretois et al. 2021), and that wolves have successfully recolonised moderately anthropised landscapes such as forest–farmland mosaics (Blanco and Cortéz 2007, Chapron et al. 2014) and agroecosystems (Ahmadi et al. 2014), but do not permanently establish in areas of high human density (Chapron et al. 2014). This is also in agreement with our findings, which showed that wolves struggle to persist in these lowland, human-modified landscapes, likely driven by elevated mortality risk and human–wildlife conflict. These transitional zones, where colonisation attempts occur but persistence remains low, will likely represent the critical frontiers for wolf conservation, requiring targeted management efforts and research to reconcile wolf expansion with human activities.

In that regard, future analyses explicitly incorporating spatial autocorrelation, movement dynamics during colonisation (Chandler et al. 2015) or connectivity between neighbouring cells (Solà et al. 2024) could help better predict these

population dynamics and further refine our understanding of the processes behind it.

Acknowledgements – The authors would like to thank all the park rangers, park staff, police and forestry services, technicians, researchers and volunteers who participated and enabled wolf monitoring in the Italian alpine regions during these years. Open access publishing facilitated by Universita degli Studi di Torino, as part of the Wiley - CRUI-CARE agreement.
Funding – All authors received funding from the LIFE WolfAlps project (LIFE12 NAT/IT/000807, 2014–2018), LIFE WolfAlps EU (LIFE18 NAT/IT/000972, 2020–2024). FM and MVB were also supported by the LIFE Wild Wolf (LIFE21 NAT/IT/101074417, 2023–2027). MVB was also supported by the Sustainable Futures PhD scholarship. PD and RB received funding from the Research Council of Norway under grant (NFR 286886) Wild Map and project PopFlow (NFR 345279).
Conflict of interest – The authors declare no conflict of inte rest.

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Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/ecog.8044.

Data availability statement

Data are available from the Zenodo: https://doi.org/10.5281/zenodo.19556978 (Boiani et al. 2026).
Supporting information The Supporting information associated with this article is available with the online version.

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