Individual-based models allow accurate prediction of introduced large herbivore populations in rewilded landscapes

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Running title

Recolonisation of Corsica by red deer

Abstract

1. Trophic rewilding via the (re)introduction of keystone species, such as large herbivores, is increasingly being considered in Europe to support nature recovery and improve the resilience of ecosystems in the face of rapidly changing environmental conditions. Large herbivore presence can both benefit and disbenefit local communities, making it important to predict likely expansion patterns and identify, among other things, possible zones of human-wildlife conflicts.
2. We built a predictive, spatially-explicit, individual-based model (IBM) to examine reintroduced Corsican red deer (*Cervus elaphus corsicanus*) population expansion in Corsica using the recently developed integrated Step Selection Function (iSSF) approach. We used GPS data collected during a 5-year intensive field study of reintroduced red deer to develop an SSF describing habitat selection. We then combined the outputs of this SSF with information on deer life histories in an IBM to predict deer expansion on the island in the coming years.
3. Our model accurately recreates the observed recolonization patterns to date in the three monitored reintroduction sites, adequately predicting home ranges, mother-offspring home range centroid distances, and habitat use. We therefore used this model to predict deer distribution expansion in the next five years, using information from all known reintroduced populations on the island. Under this model, we predict deer range expansion rate to vary between ca. 130 km^2 and 166 km^2 per annum. Furthermore, we identify potential zones of future human-deer conflict, with the greatest potential conflict identified for the southern populations.
4. *Synthesis and applications*. As the number of trophic rewilding projects increases in Europe, there is a real need to anticipate the ecological and societal consequences of species (re)introductions to ensure their long-term success. Predictive approaches that

integrate locally-calibrated information on movement and life histories provide a unique opportunity to increase the cost-effectiveness of such projects, enabling the identification of potential human-wildlife conflict zones before conflict occurs. This is especially important for island fauna such as the Corsican red deer, which are known to be more vulnerable to extinction and for which reintroduction outcomes tend to be less studied.

Keywords

Adaptive management, recolonisation, red deer, spatially explicit individual-based model, trophic rewilding, Corsica, step selection function

Introduction

In the face of rapidly changing environmental conditions and dramatic declines of biodiversity, nature recovery has become a priority. The United Nations has declared this the Decade on Ecosystem Restoration to spur global actions to prevent, halt and reverse the degradation of ecosystems. In this context, trophic rewilding, an environmental management approach that aims to diversify and complexify ecological interactions through the (re)introduction of keystone species, has gained significant traction in Europe (Pettorelli et al., 2018; Jepson et al., 2018).

Trophic rewilding discussions and initiatives have primarily focused on large herbivore (re)introductions, given their significant impacts on ecosystems (Svenning et al., 2024). Large herbivores, through their presence and activities (e.g., feeding, trampling, urination and defecation), directly and indirectly influence ecosystem structure and processes, ultimately leading to changes in ecosystem composition, functioning and services delivery (Pringle et al., 2023). They tend to be more socially acceptable than carnivores, particularly for the local communities most likely to be impacted by (re)introduction projects (Dunn-Capper et al., 2024). (Re)introductions of large herbivores are however not without risks and can lead to conflicts with human populations as large species interact with human activities such as agriculture, logging, hunting, and development. In the United States, for example, the reintroduction of wapiti (*Cervus canadensis)* was associated with increased costs to local communities due to damage to fences and crops, and livestock disease (McCann et al., 2021).

One way to prevent increases in human-wildlife conflicts following species (re)introductions is to identify areas likely to be colonized by introduced individuals, so that targeted early actions can be taken to mitigate the risks associated with population expansion. This step is generally done by mapping habitat suitability at landscape scales using approaches such as species distribution modelling, and rarely, individual based modelling (see e.g., Marucco &

McIntire, 2010). By spatially simulating individual animals and their interactions with one another and the environment (Accolla et al., 2021; McLane et al., 2011), mechanistic Individual-Based Models (IBMs) can make readily interpretable predictions of emergent population expansion (e.g. Fernández et al, 2006; Philips 2020). However, their reliability strongly depends on how accurately the simulated movement of individual animals reflects their true movement. Developing movement rules heuristically, or based on separately defined habitat suitability maps, has previously generated interesting insights into translocation success and the dispersal abilities of (re)introduced populations (e.g. Mims et al., 2019; Philips, 2020). However, how movement rules derived in such a manner fit local behavioral patterns, and the extent to which these ultimately enable accurate predictions, remains highly uncertain. An alternative methodology is to derive information on movement behaviour directly from local empirical movement data collected by GPS collars. Prior work has exploited GPS data by restricting movement decisions to realistic step lengths and turning angles (e.g., Crevier et al. 2021) and validating IBMs against this observed animal movement data (e.g., D'Elia et al., 2022).

In this work, we aim to build on these studies and demonstrate the value of the recently developed integrated Step Selection Function (iSSF) approaches (Potts et al., 2022; Signer et al., 2024) to inform the management of reintroduced Corsican red deer (*Cervus elaphus corsicanus*) in Corsica. The case of the Corsican red deer is particularly interesting here; island fauna, in general, have been known to undergo a much higher extinction rate than continental fauna (Wood et al., 2017). Despite this, research on the consequences of species (re)introductions within islands remains poorly studied. We considered the iSSF approach as we believe this integrated SSF-IBM method provides a number of advantages over previously used methodologies, as it (i) allows for individual-, landscape-, and global-level factors and associated interactions to influence deer movement, and (ii) can incorporate both locational and directional autocorrelation of moving animals (Potts et al., 2022). Although previously abundant, the Corsican deer completely disappeared from this highly topographically heterogeneous island in 1970 due to illegal hunting and habitat fragmentation (driven, among other things, by the expansion of vineyards). Following its extinction in the wild, a conservation program started in the 1980s (Riga et al., 2022), with deer translocated from Sardinia and raised in a semi-controlled breeding enclosure in Corsica for several years before being released into the wild in 1998.

Red deer are highly adaptable, occupying a range of habitats including forests, grasslands, and alpine meadows (Alves et al., 2014). Their habitat preference can vary with season and geographic location and is primarily influenced by the presence of both food and cover (Carvalho et al., 2018). In general, they are known to seek cover in forested areas, and forage in open clearings. In topographically variable environments, red deer tend to move to higher elevations during the summer for better forage while occupying lower elevations during winter to avoid deep snow and harsh conditions (Dagtekin et al., 2023). In Sardinia, the Corsican red deer has been shown to select areas with natural forests and/or Mediterranean maquis close to water sources; their tolerance of humans and roads has been previously described as low (Puddu et al. 2009). Considering these species-environment relationships, we expected landcover type, topography, season and anthropogenic activity to strongly influence deer movement, and therefore the connectivity of the landscape. We first calibrated and validated our model using data on 26 individuals from three reintroduction sites; we then used this model to predict future patterns in red deer recolonization for the whole island.

Material and methods

Study location and animal data

320 Corsican red deer were released into the wild in five locations across Corsica between 1998 and 2017 (Figure 1). Three of these locations, Caccia-Ghjunsani (North), Central Corsica – Venacais (Central), L'Alta Rocca – Altu Taravu (South), included GPS-tracked deer, whilst two locations, Fium'Orbu and Deux Sorru, did not.

Caccia-Ghjunsani is broadly characterized by shallow and arid soils on gneiss and granite bedrocks; the landscape combines open and wooded countryside, with grasslands and maquis covering the gentler slopes and forests growing on the steeper slopes. Central Corsica - Venacais, in the Massif du Rotondo, is part of the geological series known as the "Medium-grained granite of central Corsica"; the area is characterized by mountain valleys covered by oaks, beeches, bushes, and scrubs. L'Alta Rocca - Altu Taravu in the plateau du Cuscione, is a mid-mountainous site characterized by its Euro-Siberian physiognomy and features beech, fir, larch, and alder trees. The hilly and rugged landscape hosts numerous springs, streams, and marshes.

Twenty-six individuals (20 females and 6 males; Table S1) were GPS collared to gather information on the animals' survival, dispersion, and habitat use in the three previously described localities (Caccia-Ghjunsani: 2F and 2M; Central Corsica - Venacais: 11F and 3M; L'Alta Rocca - Altu Taravu: 7F, 1M). The devices collected data for 5 years, between December 17th of 2015 until January 9th of 2020. Animals' locations were recorded twice a day – at 10 a.m. and 10 p.m. for a median of 25 months. Appropriate licences and permits to carry out the work were granted by the Préfet de la Haute-Corse (Arrêté DDTM2B/SEBF/FORET/N°436-2015).

Overall approach

We followed Potts and colleagues (2022) in developing an initial SSF, using this SSF to parameterise an IBM, identifying discrepancies between the IBMs predictions and empirical patterns, and then refining the SSF. We iterate through this process until we arrive at a satisfactory IBM. IBM evaluation was based on the model's ability to replicate patterns observed in GPS-tracked red deer; namely home range size, the distance between the mother and its offspring home ranges, and the spatial distribution of deer activity. We built the IBM in NetLogo (Wilensky, 1999), while data preparation, analysis, and visualisation was undertaken in R using package amt (v0.2.2.0; Signer et al., 2019).

Movement data analysis

We fit an SSF using a conditional logistic regression model, contrasting each observed step with 15 randomly generated null steps. To generate these null steps, the length and angle of a random selection of steps from the distribution of observed steps were sampled using the random_step function in the amt package. The choice of 15 random steps (50% higher than the amt default value of 10) was made to reduce estimation error, while keeping computation times low (Signer et al., 2019). Based on data availability and known factors shaping deer movement, we modelled step selection as a function of sex, season, landcover, slope and distance to roads: slope and distance to roads were treated as continuous variables, and sex, landcover and season as categorical variables. To align with movement variation observed in red deer elsewhere (Dagtekin et al., 2023), only two seasons are considered: summer (which begins on 15th April) and winter (begins on 15th October). Elevation and landcover values were extracted from the Shuttle Radar Topography Mission (Jarvis et al. 2008) and the 2018 CORINE Land Cover inventory (https://doi.org/10.2909/960998c1-1870-4e82-8051-6485205ebbac), respectively. We reclassified CORINE landcovers as artificial, agricultural, forest, scrub, bare and wetland, noting that agricultural lands, as described by the CORINE product, mostly correspond in those areas to mountain and summer pasture areas, that is, areas not currently exploited for crop production. We used broad landcover classifications as red deer can utilise a wide variety of landcover and habitat types (e.g., Pérez-Barbería et al., 2013). Distance to roads was calculated from the Global Roads Inventory Project (Figure S1; Meijer et al., 2018).

We used variance inflation factors (VIF) and pairwise correlations to test for multicollinearity of variables with thresholds of 10 and ±0.70, respectively. We then developed a theoretically derived saturated model that included all factors and interactions likely to influence deer movement; this provided the structure of our initial SSF. This model included all previously mentioned variables as well as step specific variables, namely the log length of a step and the cosine of the turning angle of a step relative to a previous step. We additionally logged distance to road, but no further data transformations were required. We treated each individual as a separate fixed-stratum to account for individual variation among deer. Starting with this saturated model we performed stepwise model selection using Akaike Information Criterion (AIC) to compare hypothesis-based candidate models and identify the best model (Table S2).

Individual-Based Model

To model red deer expansion, Corsica was divided into non-overlapping 1 ha patches (i.e., spatial square units) associated with the following state variables: landcover class; average slope; average distance to the road. Several global variables were defined, including the simulated date-time and the season. In this modelled world, a time step is a 12-hour period – equivalent to the gap between GPS recordings, meaning the GPS data, SSF, and IBM time steps all aligned.

Simulated deer were added to the IBM as individuals. All deer were characterised based on their sex (male/female), their maturity (mature if ≥ 1 year old/immature if < 1 year old), their reproductive status for mature females (with offspring/without offspring), their mother's identity (for immature deer), and the coordinates of the centre of their home range. For reintroduced deer, these coordinates correspond to their release site; for other individuals this corresponds to the furthest distance from the centre of their mother's home range which they had visited as an immature offspring. This choice is based on local observations (SM, *unpublished*) that suggest that (i) the originally released deer did not disperse far from their release sites, and (ii) young deer tend to establish territories on the edge of their mother's home range.

Demographic structure and rates were based on known red deer life history and local information. In terms of reproduction, site data indicated an average of 6 – 7 fawns per 10 female deer (SM, *unpublished*), leading us to apply an annual reproduction rate of 65% to all females regardless of whether they had a fawn or not, but only allowing females without an offspring from the previous year to subsequently give birth. At any point in time, females could only have a maximum of one single offspring which matured at one year of age, giving a minimum inter-birth interval of one year. Under our model, the maximum lifespan was assumed to be 14 years (although data from the field suggest a potentially higher limit; SM, *pers. comm.*), whilst the annual survival rate was assumed to be 97% (Pérez-Barbería et al., 2015). Immature deer <1 year old were also set to die if their mother dies, thus their annual survival rate became c.94%. In our model, deer do not interact beyond immature deer following their mother's movements and sharing their location until they mature, whilst no regulatory demographic parameters were included. This is because (i) we did not have data available on the intra-specific interactions within this population, (ii) reintroduced populations often initially show little or weak density-dependence (see Manning et al., 2019; Sæther et al., 2007) and (iii) observations on the ground suggest that no hunting or other conflict related demographic regulation processes are occurring yet (SM, *unpublished*).

During each 12-hour step of the model, each mature deer makes one move towards a new patch. The relative probability the deer moves from their current patch y to their new patch z is given by:

$$p(z \vee y) = \frac{e^{\left[\beta_1 x_{1,z} + \cdots \ldots + \beta_i x_{i,z}\right]}}{\sum_1^n e^{\left[\beta_1 x_{1,z} + \cdots \ldots + \beta_i x_{i,z}\right]}} \text{ where } |z - y| \leq \text{max step length}$$

$|z – y|$ represents the Euclidean distance between patches y and z, meaning only patches within a max step length are considered. These patches are termed ‘target-patches’ and are the patches each deer could reach in one model step from its current patch. This max step length was set as the 99th percentile of the observed deer step lengths as identified from the GPS data. $x_{i,z}$ represents the deer- and patch-level main and interactive variables associated with patch z that influence deer movement. β_i represents the effect size for each variable, as identified in the SSF. β_i is determined by sampling from a normal distribution with a mean equal to the effect size and standard deviation equal to the standard error of our best SSF model. Patch-level main and interactive β_i coefficients, where possible, were calculated once at the start of the simulation, and then combined with deer-level variables to predict the movement of each deer. In addition, to account for home range behaviour we added a distance to home range centre parameter to our IBM; the value of this parameter (-0.5) was set so as to generate realistic home range sizes. These input variables and coefficients dictating deer movement are the same as those found in our best SSF model, and are all presented in Table 1. Finally, the denominator term sums the probabilities of all target-patches and is used to calculate a relative probability for each target-patch that the deer will move towards it (the *movement-prob*). Once the *movement-prob* has been calculated for each target-patch, a target-patch is then randomly selected for the deer to move to, weighted by the movement-prob of each target-patch. For a full Overview, Design Concepts, and Details (ODD) description of the model, please see supplementary information 1.

Individual-based model evaluation and validation

To evaluate whether our IBM adequately simulates red deer movement in Corsica, we simulated reintroduced deer from the date of the first release (10:00 16/12/2015) to the date of the final GPS transmission (10:00 09/01/2020). Individual deer were initialised into the model with state variables, locations, and at a time matching their real-world counterparts (Table S1). We repeated these simulations 100 times.

As a first step, we assessed how ecologically realistic our simulated deer home range sizes and average mother-offspring home range centroid distances were. We estimated home range sizes of simulated deer by counting the number of unique patches each deer individual visited (i.e., if a deer visited 100 unique patches, its estimated home range size would be 100 ha). Average mother-offspring home range centroid distances were calculated as the distances between a mother and their offsprings home range centroids. We then compared these values to observed home range sizes and mother-offspring home range distances (Figure S2), noting that our simulated values were likely to be upper estimates. For mother-offspring home range centroid distances, no offspring were radio-collared and thus there are no data enabling us to calculate the average mother-offspring home range centroid distances among observed deer. However, existing estimates from the Isle of Rum point toward an average distance of 312m (Conradt et al., 1999). This comparison process provided further reassurance that our distance to home range centre parameter was functioning as intended.

As a second step, we compared parameters from habitat suitability models trained on the observed deer data and the simulated deer data. To do so, we modelled cumulative visit rate (defined as a standardised value reflecting the number of observed deer visits for each 1 ha pixel) using random forest models for both the observed and simulated data, with the previously considered landscape variables (elevation, slope, distance to roads and landcover type) as predictors. Random forest models were implemented in the R package ranger with hyperparameters ntree = 500, and mtry = 2. As our aim was not prediction but parameter comparison, we did not implement a train-test split in our data but confirmed model R^2 were reasonable before proceeding (observed data, $R^2 = 0.23$; simulated data $R^2 = 0.56$).

Predicting population dynamics and range expansion

We simulated deer reintroductions, population growth, and spatial expansion on Corsica using our individual-based model. Simulations began on 10:00 1st January 2025 and ran for five years until 10:00 1st January 2030.

Deer were initialised into the model at areas and population densities estimated by field surveys in Corsica (SM, *unpublished data*). In total, five populations were identified in Corsica, with each of these populations having an estimated location and a minimum and maximum population size, ranging from 400 – 3000 (Table S3). Deer starting locations were initialised by first spacing them equally across the area the population occupied. These deer locations were then randomly moved in the x and y directions by up to half the distance between deer, to randomise the starting locations whilst ensuring an even spread across the area. This process was repeated 50 times for minimum and 50 times for maximum population sizes, yielding 100 semi-randomised starting distributions (Figure S3). Deer were initialised at these locations as mature individuals with no young, 50:50 sex ratio, and an age drawn randomly from a uniform distribution between 1 and 14 years old (as we had no information concerning the true distribution in Corsica).

As each simulation ran for five years, the population size, number of mature and immature deer, and the number of visited patches was exported from the model on 10:00 1st January in years 2026, 2027, 2028, 2029, 2030. Output maps of patch visit frequencies were also exported to visualise the spatial dynamics of the deer populations. To assess likely population and range expansion rates, for minimum and maximum scenarios we calculated mean population sizes, the number of visited patches, and cumulative visit maps across simulations.

Results

Red deer movement

Our dataset (n = 26 individuals) included 25,584 steps, with a median of 1147 steps per deer [range: 29–1497]; median step-length was 240m and the 99th percentile max step distance was 2.60 km. The best model explaining red deer movement included landcover, slope, distance to roads, sex, season, step length and turning angle. Red deer under this best model avoided roads and selected for areas of agricultural (as defined by the CORINE land cover product), bare and scrub cover, relative to artificial surfaces (Table 1). They preferred, on average, shorter step lengths and moving towards steeper slopes, favouring sharper turning angles. Step length (i.e., the distance between two locations over a 12-hour window) increased when deer moved towards agricultural, forest, scrub, and bare landcovers. Deer were also (i) more likely to take sharp turns to reach agricultural cover, and less likely to take sharp turns to reach bare ground; (ii) more likely to head in a straight line to reach a site further away from roads and more likely to go closer to road when agriculture and bare ground landcovers are present. Season was an important factor shaping deer movement, with deer avoiding steeper slopes and preferring sites further away from roads in summer.

Compared to females, males in summer took longer steps to access agricultural, forest, and scrub landcovers. Meanwhile, in winter, females took longer steps to reach artificial cover and shorter steps to reach bare ground.

Model evaluation and validation

Average observed home range size for all deer was 1166 (mean) or 593 (median) [range: 172 - 6819] ha; this compared to an average simulated home range size of 674.8 (mean) or 673.8 (median) [range: 640.0 - 706.9] ha. The average mother-offspring home range distance of 312m obtained from the Isle of Rum is smaller than an average simulated distance of 1925m (mean), or 1922 (median) [range: 1807 – 2032] between mother-offspring home range centroids.

Observed and simulated visit rates were comparable (Figure 1), with the distribution of distances to roads, slope and elevation visited by simulated and observed deer being qualitatively similar. In addition, habitat suitability maps derived from observed and simulated visitation rates were broadly aligned in central highland regions for which we had data; coastal regions - where no deer are currently observed - showed greater disagreements (Figure S4; Table S4).

Deer expansion

The mean annual growth rate (ʎ) of simulations for all scenarios was 1.12 [range: 1.12 – 1.13]. By 2030, the minimum population model estimated a mean population size of 6,738 [range: 6,556 – 6,890] deer, of which 5,480 [range: 5,367 – 5,624] will be mature adults and 1,257 [range: 1,186 – 1,331] will be immature young (Table 2). By 2030, the maximum population simulations estimated a mean population size of 18,797 [range: 18,444 – 19,166] deer, of which 15,241 [range: 14,997 – 15,499] will be mature adults and 3,556 [range: 3,440 – 3,694] will be immature young.

The mean annual expansion rates (km^2 per year) for minimum and maximum scenarios were 129.5 [range: 116.6 – 139.1] and 165.7 [range: 154.9 – 180.0], respectively (Figure 2). Expansion rates differed across the populations considered: for the northern population, minimum and maximum range expansions (km^2 per year) were 25.5 [20.9 – 30.3] and 32.6 [26.7 – 38.3], respectively. For the central two populations, minimum and maximum range expansions (km^2 per year) were higher, at 54.1 [45.0 – 60.8] and 69.3 [64.7 – 73.9], respectively. Expansion rates for the southern population were comparable to the central populations, with minimum and maximum range expansions (km^2 per year) at 49.7 [44.9 – 55.7] and 63.8 [56.1 – 72.4], respectively.

Zones of potential human-wildlife conflict

Simulated populations showed very different patterns in the distribution of potential areas of conflict across the major reintroduction sites, as examined by the overlap of the simulated population cores (where between 1000 and 100,000 cumulative simulated deer visits were observed) and landcover and roads. The highest risk of conflict was observed in South Corsica, where the simulated population core overlapped with 3.5 km^2 of built-up areas and 2.6 km^2 of croplands (bearing in mind that this category primarily includes, in the zones considered, mountain and summer pasture areas). There is also overlap with the major RT10 road on the edge of the simulated population core. In Central Corsica the risk of conflict was estimated to be moderate in the coming years, with 1.3 km^2 overlap between the simulated population core and built-up areas though almost none with croplands. The major T20 road also passes through the simulated population core, while the T50 passes along its edge. In North Corsica the conflict risk was estimated to be low, with the simulated population core overlapping with only 0.88 km^2 of built-up areas and 0.16 km^2 of croplands. The most important road in the vicinity is the minor RT301, which passes along the far edge of the total simulated population range (Figure 3; Table 3).

Discussion

Trophic rewilding is a growing conservation and nature recovery technique which, through species (re)introductions, is expected to benefit biodiversity, enhance ecosystem functioning, and create more resilient ecosystems (Bakker & Svenning, 2018; Schmitz et al., 2023; Svenning et al., 2024). This approach is especially relevant to islands, which fauna is known to be particularly vulnerable to extinction (Wood et al. 2017). However, reintroduction research is often focussed on population establishment rather than potential future population dynamics and associated impacts (Sakurai et al., 2024; Taylor et al., 2017). Here, we showed how simulating reintroduced Corsican red deer space use from fitted integrated step-selection functions provides realistic, spatially-explicit, short-term predictions regarding changes in distribution, ultimately enabling wildlife managers to identify areas where potential human-wildlife conflicts may occur. By using a GPS dataset to parameterise the simulation, we improved on prior, often heuristic individual-based simulations of species reintroductions (i.e., Mims *et al.*, 2019; Philips, 2020), considering the influence of interactions between individual-level factors (i.e., deer sex, deer heading, step lengths), landscape-level factors (i.e., landcover, slope, distances to roads), and global-level factors (i.e., season) on species movements. Our model, underpinned by locally relevant population dynamic parameters, thus represents a significant advance in our understanding of reintroduced red deer populations on Corsica, demonstrating the value of such approaches to guide management.

Our evaluation process suggested that our mean simulated home range sizes, although lower than the mean recorded home range size from GPS-tagged deer, was within the range of recorded home range sizes (Figure S2). Simulated mother-offspring home range centroid distances were larger than estimates from red deer elsewhere – although this was expected given how we measured this parameter (using centroid distances, which would inflate the measured distance), and given the tendency for Corsican offspring to establish territories on the edge of their mother's home range (SM, *unpublished*). Home range sizes and mother-offspring home range centroid distances likely positively correlate with expansion rate, and thus ensuring these values are realistic is important. Future work should try to obtain such information from the field and assess the impacts these variables have on range expansion (e.g., via sensitivity testing). Should more data or knowledge become available, the IBM could be easily re-parameterised.

The simulated range expansion rate of 130 to 166 km^2 per year is higher than red deer range expansions reported elsewhere (see Ward, 2005; Carden et al., 2011). However, when compared to observed increases in cumulative occupied area (a measure which more closely matches our estimate of annual increase in the number of visited patches) our range expansion rate is lower than observed rates (Carvalho et al., 2018). A high expansion rate may result from deer populations recolonising new suitable, previously unoccupied areas; an effect observed in real-world and modelled recolonising ungulates (Carvalho et al., 2018; Saito et al., 2012). Using birth and death rates obtained from local experts, we moreover estimated a growth rate of 1.12, comparable to red deer growth rates estimated *in situ* and observed elsewhere (1.02 to 1.17; Benton et al., 1995; Beskardes, 2012; Langvatn & Loison, 1999; SM, *unpublished*). These simulated growth rates were consistent across all simulations as they do not include any dependence on the spatial aspects of the model (e.g., density-dependence or landcover influence on fertility or mortality). They depend only on (i) the constant birth and death probabilities; (ii) the ages at which deer become fertile and independent of the mother; and (iii) the age at which they die with 100% probability (14 years – their maximum age). This simplification is likely acceptable for a recolonisation scenario as red deer have the potential to achieve densities as high as 67 individuals per km^2 in favourable habitat, and recolonisation implies the presence of large quantities of uninhabited favourable habitat (Acevedo et al., 2008). However, consistent underlying growth rates coupled with a uniformed distribution of mature individuals across age classes in simulated starting populations means that the simulated population sizes at year 2030 is highly sensitive to initial starting population sizes. As the exact current red deer population size on Corsica is unknown, we used minimum and maximum population estimates to predict the full range of possible scenarios, varying nearly three-fold from 6,738 to 18,797 after increasing by approximately 90% from 2025 estimates. This high sensitivity highlights the requirement for accurate starting population estimates (and spatial population dependence) if the goal is to more accurately predict future population sizes. Nonetheless, the potential for rapid range expansion means wildlife managers should be prepared for increased human-wildlife conflict in new parts of the island and targeted mitigation efforts should be considered in places where a high visit frequency of deer overlaps with human settlements, main roads, food production and forestry (e.g. Falaschi et al., 2024), such as parts of the areas encompassing the southern populations. Ongoing *in-situ* work will aid in refining predictions of impacts: current work assessing Corsican red deer diets will for example be helpful when assessing the likely positive and negative environmental and economic impacts, helping test the current expectations that likely agricultural impacts should be low as much of the agricultural lands include abandoned mountain and summer pasture areas. To evaluate potential mitigation strategies, our individual-based model could be moreover expanded to include the potential negative impacts of deer on human populations, such as those originating from road collisions or disease transmission to livestock, as well the impact of various deer management approaches, such as culling (Husheer & Tanentzap, 2024; Riga et al., 2022). When doing so, considering metapopulation connectivity will be important, as the northern population appears likely to remain genetically isolated (Stanbridge et al., 2023).

Although informative, our approach is associated with several limitations. First, little information was available on habitat selection by immature deer as they leave their mothers, which is a key parameter for predicting how far offspring deer may venture from the maternal home range. Our estimate of average mother-offspring home range centroid distance was conservatively based on a simple “edge of range” assumption, meaning that mean annual expansion rates may be higher than reported. Indeed, sub-adult red deer, particularly males, can disperse further than our average mother-offspring home range centroid distance (Loe et al., 2009; Prévot & Licoppe, 2013). Secondly, when parameterising population dynamics, we only had access to relatively basic annual reproduction and survival probability estimates (65% and 97%, respectively). However, reproduction and survival rates are influenced by complex interactions between age, habitat quality, and density-dependence (e.g., Albon et al., 2000; Nussey et al., 2006), parameters for which we do not have information on. As such, the projected growth rates should be interpreted as optimistic. Thirdly, ecological interactions are primarily and intentionally excluded from our model. This is because (i) we expect trophic interactions to be well captured by the SSF (Esmaeili et al., 2021); and (ii) in a sparsely populated landscape into which the deer are expanding, we expect intra-specific interactions (including those underlying density-dependence) to be weak and limited (Manning et al., 2019; Sæther et al., 2007). These assumptions would however be violated once demographic regulation processes become dominant, limiting the long-term suitability of our modelling approach for deer management on the island. Fourthly, radio collared deer primarily roamed the centre and south of the island, with only three individuals monitored in the north. The northern part of the island is yet more arid and less hilly than other parts of Corsica; this lack of representation may have led to a suboptimal understanding of red deer habitat selection across the range of available habitats on the island. Finally, a limitation of the integrated SSF-IBM approach is that it failed to adequately replicate home ranging behaviour of deer, requiring the consideration of an additional parameter (the ‘distance from home range centre’ parameter). The model itself here represents a tool to improve on all these limitations by providing a framework for deepening our understanding of red deer ecology on the island, by, for example, generating null distributions to test for evidence of site fidelity and/or memory (Signer et al. 2024).

Conclusion

Trophic rewilding presents an opportunity to restore ecosystems using large herbivore (re)introductions (Pettorelli et al., 2018; Jepson et al., 2018). While there is much benefit to be derived from trophic rewilding, large herbivores can be associated with significant negative ecological, economic, and societal impacts, which can undermine rewilding efforts (Butler et al., 2021; Manning et al., 2024). Our results highlight how an integrated SSF-IBM approach can be used to predict medium to long-term (re)introduction outcomes, generating important information for practitioners to anticipate potential social-economic-ecological issues. Further developing these predictive models into an iterative adaptive management framework, whereby the modelled outcomes of species (re)introductions can be evaluated, interventions tested, and results fed back to key stakeholders, could be a powerful way to ensure trophic rewilding sustainably benefits ecosystems (Butler et al., 2021; Gomez et al., 2025).

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Conflict of interest

The authors declare no conflicts of interest which could impact on the findings of this work.

Authors contributions

Study conceived and planned by NP. Field data collected by SM. JW constructed the SSFs, CL built and ran the IBM, and both JW and CL conducted relevant analyses. NP led manuscript writing, with JW, CL, and SM contributing substantively. All authors reviewed drafts and approved manuscript for submission.

Statement on inclusion

Our work includes authors based in both the UK and Corsica; the area where the study was carried out.

Data availability statement

Data and reproducible code are available on Zenodo (Lovell et al., 2025a; Lovell et al 2025b).

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TABLES

Table 1: Coefficient and standard error associated with the best step selection model for red deer in Corsica. In this table, "turning angle" corresponds to the cosines of the turning angle while "distance to roads" and "step length" correspond to the log of these parameters. Agricultural lands, as described by the CORINE product, mostly correspond in the regions considered to mountain and summer pasture areas, that is, areas not currently exploited for crop production

* indicates significance ($P<0.05$)

Parameter	**Coefficient**	**Standard error**
Agricultural land	1.31*	0.23
Forest	0.00	0.20
Scrub	0.61*	0.22
Bare ground	1.55*	0.25
Slope	0.03*	0.00
Distance to roads	0.01	0.04
Step length	-0.28*	0.11
Turning angle	-2.79*	0.11
Agricultural land:step length	0.57*	0.11
Forest:step length	0.54*	0.11
Scrub:step length	0.43*	0.11
Bare ground:step length	0.51*	0.11
Distance to roads:Turning angle	0.15*	0.01

Agricultural land:Turning angle	-0.42*	0.11
Forest:Turning angle	-0.03	0.10
Scrub:Turning angle	0.03	0.10
Bare ground:Turning angle	0.54*	0.10
Slope:Step length	-0.01*	0.00
Agricultural land:Distance to Road	-0.19*	0.04
Forest:Distance to roads	0.03	0.04
Scrub:Distance to roads	-0.04	0.04
Bare ground:Distance to roads	-0.19*	0.04
Slope:Summer	-0.01*	0.00
Distance to roads:Summer	0.09*	0.03
Slope:Turning angle	0.01*	0.00
Artificial landcover:Step length:Winter:Male	-0.11	0.16
Agricultural land:Step length:Winter:Male	0.05	0.08
Forest:Step length:Winter:Male	0.02	0.04
Scrub:Step length:Winter:Male	0.03	0.03
Bare ground:Step length:Winter:Male	-0.05	0.04
Artificial landcover:Step length:Summer:Male	0.23	0.33
Agricultural land:Step length:Summer:Male	0.26*	0.06
Forest:Step length:Summer:Male	0.12*	0.04
Scrub:Step length:Summer:Male	0.12*	0.03
Bare ground:Step length:Summer:Male	-0.03	0.04
Artificial landcover:Step length:Winter:Female	0.25*	0.12
Agricultural land:Step length:Winter:Female	0.00	0.05

Forest:Step length:Winter:Female	0.01	0.02
Scrub:Step length:Winter:Female	0.03	0.02
Bare ground:Step length:Winter:Female	-0.09*	0.04

Table 2 Mean deer population (MDP), mean mature deer population (MMDP), mean immature deer population (MIDP), mean immature to mature deer ration (MIMDR) and mean number of visited patches (MNVP) at each time point across the 100 simulations from 2026 – 2030, split between the 50 maximum and 50 minimum population scenarios. Standard deviations are provided in brackets.

Year	Scenario	MDP	MMDP	MIDP	MIMDR	MNVP
2026	Min	4,248 (20.88)	3,231 (9.46)	1,017 (17.07)	0.31 (0.005)	127,638 (291.8)
	Max	11,715 (38.16)	8,863 (17.34)	2,852 (31.38)	0.32 (0.004)	133,765 (219.9)
2027	Min	4,721 (33.65)	3,817 (22.55)	903 (20.58)	0.24 (0.005)	144,327 (1,004)
	Max	13,056 (64.39)	10,524 (43.67)	2,532 (39.85)	0.24 (0.004)	157,793 (1,177)
2028	Min	5,271 (51.64)	4,293 (33.57)	978 (27.09)	0.23 (0.006)	156,877 (1,345)
	Max	14,631 (92.30)	11,876 (64.51)	2,755 (47.31)	0.23 (0.004)	173,223 (1,372)
2029	Min	5,932 (64.52)	4,827 (48.11)	1,105 (30.51)	0.23 (0.006)	168,331 (1,626)
	Max	16,532 (132)	13,401 (91.71)	3,131 (58.99)	0.23 (0.004)	187,062 (1,531)
2030	Min	6,738 (89.32)	5,480 (63.91)	1,257 (36.79)	0.23 (0.006)	179,452 (2,039)

	Max	18,797 (174.6)	15,241 (127.7)	3,556 (62.58)	0.23 (0.003)	200,039 (1,805)

Table 3 Km^2 of landcover types falling within zones of potential deer-human conflict. These tables have been generated by coupling the mean cumulative visit maps for red deer in Corsica up to 2030 (n = 100 simulations; 50 maximum scenarios, 50 minimum scenarios) with the European Space Agency (ESA)'s WorldCover 10m resolution map for 2020 (see also Figure 3). In several parts of Corsica, agricultural lands (as defined by WorldCover) correspond to mountain and summer pasture areas, that is, areas not currently exploited for crop production.

North Corsica

Visits	Tree cover	Shrubland	Grassland	Cropland	Built-up	Bare / sparse vegetation	Permanent water bodies	Herbaceous wetland
0-10	88	61	67	0.84	0.82	7.8	0.035	0
10-1000	92	62	51	0.17	1.5	6.6	0.068	1.00E-04
1000-100000	82	110	85	0.16	0.88	2.5	0.0034	0

Central Corsica

Visits	Tree cover	Shrubland	Grassland	Cropland	Built-up	Bare / sparse vegetation	Permanent water bodies	Herbaceous wetland
0-10	240	52	84	0.15	0.79	5.3	0.055	0.017
10-1000	260	45	94	0.35	2.9	8.5	0.43	0.024
1000-100000	250	35	79	0.023	1.3	6	0.012	6.00E-04

South Corsica

FIGURES

Visits	Tree cover	Shrubland	Grassland	Cropland	Built-up	Bare / sparse vegetation	Permanent water bodies	Herbaceous wetland
0-10	230	28	35	4.7	1.6	3.8	1	1.5
10-1000	260	20	46	4.8	3.8	4.8	0.6	1.2
1000-100000	420	34	140	2.6	3.5	7.3	0.089	0.0076

Figure 1 Visitation maps for observed (A) and simulated (B) red deer. In both cases, visitations cover the period 16th December 2015 to January 9th of 2020. The three visited areas correspond to the areas where red deer have been released (Moltifau (North), San Petru di venacu (Centre) and Zicavu (South)). In panel C, the predicted visit rates (from habitat suitability modelling) of observed (top row) and simulated deer (bottom row) across the existing elevation, slope and distance to roads gradients are compared.

Figure 2 Mean cumulative visit maps for red deer on Corsica in one-year gaps from 2026 to 2030 (n=100 simulations; 50 maximum scenario, 50 minimum scenario), with patches coloured according to their quartile. Note: the south most collection of deer consists of two partially overlapping populations with separate estimated starting population sizes.

Figure 3 Zones of potential deer-human conflict. This figure has been generated by coupling the mean cumulative visit maps for red deer in Corsica up to 2030 (n = 100 simulations; 50 maximum scenarios, 50 minimum scenarios) with the European Space Agency (ESA)'s WorldCover 10m resolution map for 2020. In several parts of Corsica, agricultural lands (as defined by WorldCover) correspond to mountain and summer pasture areas, that is, areas not currently exploited for crop production.

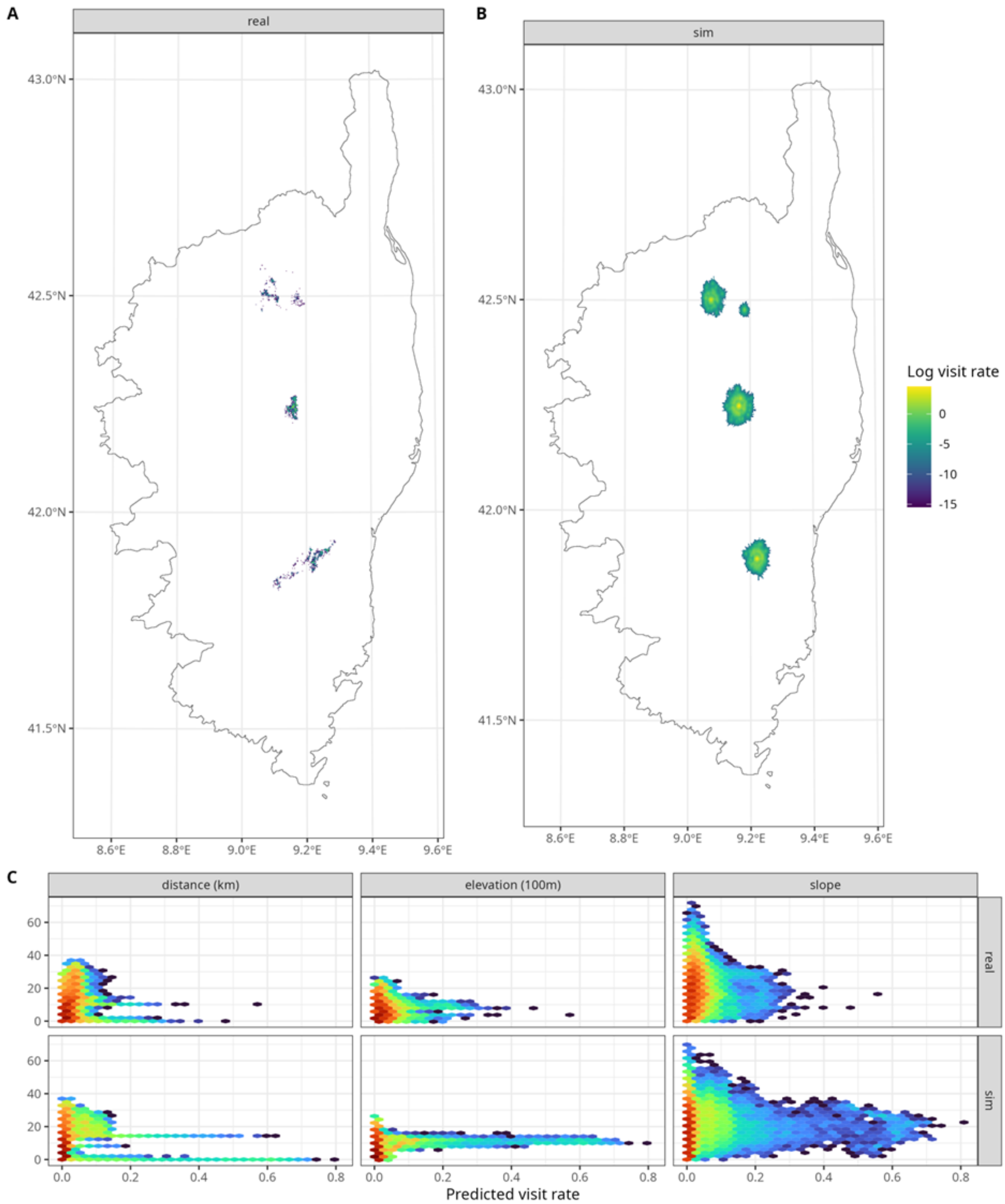
A
real
43.0°N
42.5°N
42.0°N
41.5°N
8.6°E
8.8°E
9.0°E
9.2°E
9.4°E
9.6°E
B
sim
Log visit rate
0
-5
-10
-15
C
distance (km)
elevation (100m)
slope
real
sim
0
20
40
60
0.0
0.2
0.4
0.6
0.8
Predicted visit rate

Figure 1

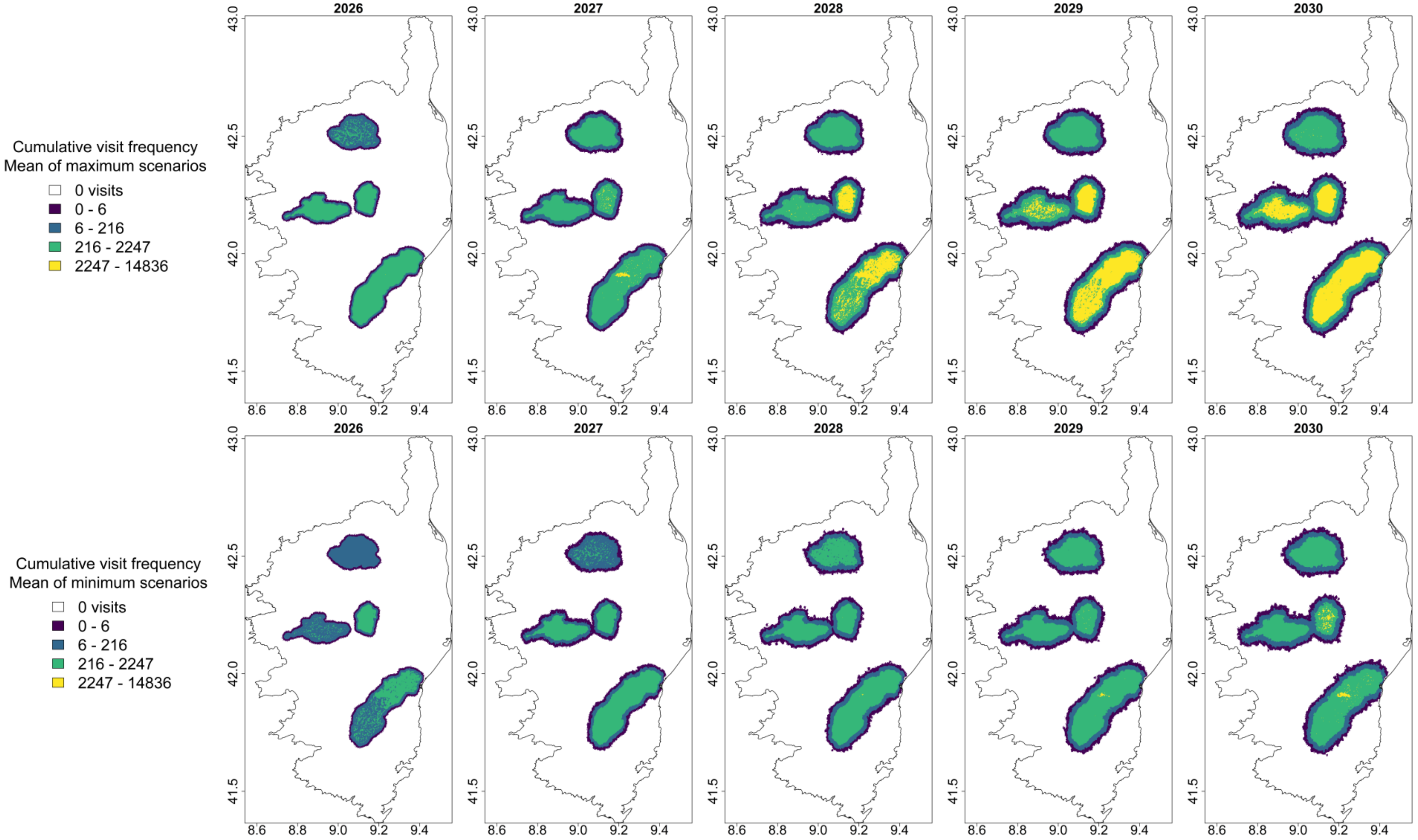
Cumulative visit frequency
Mean of maximum scenarios
0 visits
0 - 6
6 - 216
216 - 2247
2247 - 14836
Cumulative visit frequency
Mean of minimum scenarios
0 visits
0 - 6
6 - 216
216 - 2247
2247 - 14836
2026
2027
2028
2029
2030
43.0
42.5
42.0
41.5
8.6
8.8
9.0
9.2
9.4

Figure 2

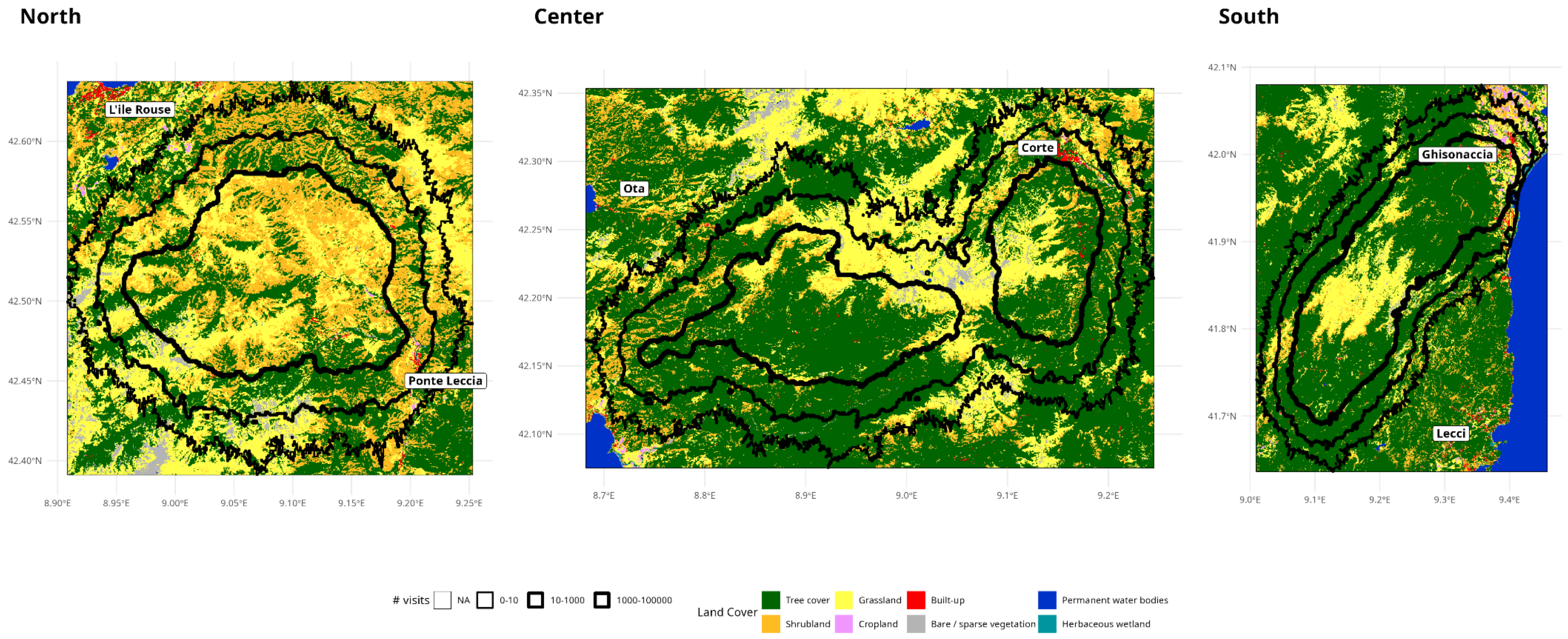
North
Center
South
L'île Rouse
Ponte Leccia
Ota
Corte
Ghisonaccia
Lecci
42.60°N
42.55°N
42.50°N
42.45°N
42.40°N
8.90°E
8.95°E
9.00°E
9.05°E
9.10°E
9.15°E
9.20°E
9.25°E
42.35°N
42.30°N
42.25°N
42.20°N
42.15°N
42.10°N
8.7°E
8.8°E
8.9°E
9.0°E
9.1°E
9.2°E
42.1°N
42.0°N
41.9°N
41.8°N
41.7°N
9.0°E
9.1°E
9.2°E
9.3°E
9.4°E
visits
NA
0-10
10-1000
1000-100000
Land Cover
Tree cover
Grassland
Built-up
Permanent water bodies
Shrubland
Cropland
Bare / sparse vegetation
Herbaceous wetland

Figure 3