LIFE Lynx

Preventing the extinction of the Dinaric-SE Alpine lynx population through reinforcement and long-term conservation

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Action A6: Habitat suitability and connectivity models for lynx between and within the Southeastern Alps and Dinaric Mountains area

Final report

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Introduction

Following the extirpation from Central and Southeastern Europe by the end of the 19th century, Eurasian lynx (*Lynx lynx*) was reintroduced in the Alps and Dinarics. The recovering population sizes fluctuated over the years; however, they remained relatively small and isolated since their distribution after the establishment has not significantly expanded by natural colonisation. One of the most radical changes to the landscape of Europe over the past centuries has been the creation of vast urban and agricultural areas and subsequent extension of infrastructure, causing increasingly fragmented landscapes, especially for weak dispersers like lynx. There is a pressing need to establish greater connectivity between the genetically isolated populations, particularly throughout the Alps and Dinarics, to achieve a viable metapopulation structure.

Modern computational approaches involving machine learning methods are widely used in ecological research. A clear example is the habitat suitability modelling, an exceptional analytical tool that allows researchers and conservationists to estimate the potential distribution of a species in a particular geographic area based on various environmental variables. It provides insights in areas that are suitable for specific species, can guide conservation efforts, and can help inform land use planning and management decisions, providing a valuable means of balancing human activities with the preservation of natural ecosystems. The maximum entropy method (MaxEnt), which has proven to be extremely robust in previous studies, is a popular approach for building such models as it allows the construction of a model using species occurrence and environmental data.

Another important concept in conservation biology is landscape permeability that describes the degree to which a landscape allows for the movement of animals through it. It is a measure of how easy or difficult it is for them to move between habitats or across a landscape, and is influenced by a range of factors, such as the type of land cover, the presence of barriers, and the scale of the landscape. Understanding landscape permeability is essential for conserving biodiversity because it enables us to identify areas that are likely to act as barriers to the movement of species and to prioritise conservation actions accordingly. For example, if a species requires large areas of habitat and needs to move between different habitats, identifying the most permeable corridors between these habitats can help to ensure the species' survival. Landscape permeability can also be used to assess the potential impacts of landscape changes, such as urbanisation or land-use changes, on the movement of species. By modelling changes in landscape permeability, we can predict the potential impacts of these changes on biodiversity and develop strategies to mitigate negative effects.

Habitat suitability models thus offer an insight into areas that would, in our case, be suitable for territories of resident lynx, whereas landscape permeability prediction outlines the probable routes of dispersing animals. Here we present a habitat suitability model and landscape permeability analysis for the Eurasian lynx in the SE Alps and the northern Dinarides, an area that represents a stepping stone between the Dinaric and Alpine lynx populations. We used GPS telemetry monitoring data of 31 lynx and the location of collected non-invasive genetic samples, while the environmental layers included data on forest cover, human impact, terrain slope and elevation. This was to capture all the key factors influencing the presence or absence of lynx. It would certainly have been useful to include data on biotic interactions (e.g. wolf and lynx are in indirect competition for prey, bears are an important kleptoparasite), but unfortunately these data are not available for the whole study area.

Methods

Data preparation

Occurrence data

Our occurrence dataset consisted of GPS telemetry data from 45 animals, non-invasive genetic sample collection sites, and C1 and C2 occurrence records (SCALP). GPS telemetry data from the project area was complemented by the data of 6 lynx from the Kalkalpen National Park in order to ensure as representative a dataset as possible.

During the data cleaning process we removed records with missing coordinates, duplicated records and applied spatial thinning to the occurrence dataset provided by spThin R package (Aiello-Lammens et al. 2015) with thinning parameter set to 1 km. The final occurrence dataset consisted of 3503 datapoints (Fig. 1).

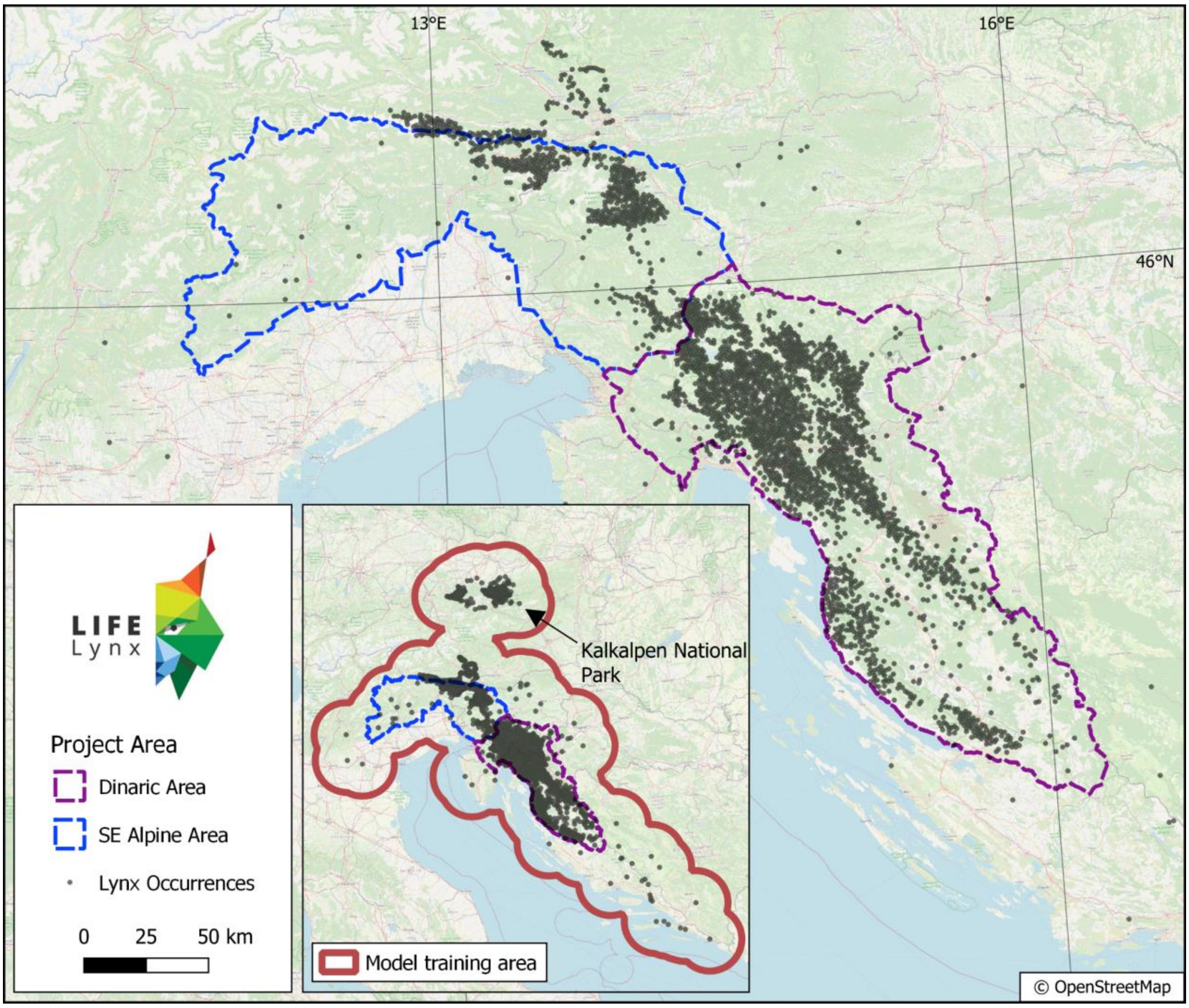

Figure 1: Outline of the project area, study areas, and thinned occurrence dataset.

Environmental variables

We prepared Digital Elevation Model (DEM), DEM-derived variables (aspect, roughness, TPI, TRI, slope), Tree Cover Density layer (obtained from Copernicus project) and Human Footprint Index obtained from the Wildlife Conservation Society website.

TRI (Terrain Ruggedness Index) is the mean of the absolute differences between the value of a cell and the value of its 8 surrounding cells. TPI (Topographic Position Index) is the difference between the value of a cell and the mean value of its 8 surrounding cells. Roughness is the difference between the maximum and the minimum value of a cell and its 8 surrounding cells.

Tree Cover Density provides information on the proportional crown coverage per pixel at 10m spatial resolution and ranges from 0% (all non-tree covered areas) to 100% and is

defined as the „vertical projection of tree crowns to a horizontal earth's surface".
The Human Footprint Index is created as a weighted sum of maps of population density, infrastructure (including roads, railways, factories, and other kinds of infrastructure), accessibility, use of electrical energy, a proxy for access to industrial energy supplies, as measured by the night-time lights. Scripts for calculating HII are available at GitHub repository.

Environmental layers (covariates) were cropped to the extent of the occurrence dataset and tested for multicollinearity by Variance Inflation Factor (VIF) and those with VIF > 5 (Guissan et al. 2017) were omitted. Final selection of covariates (Table 1) consisted of: Human Footprint Index, Tree Cover Density, Topographic Position Index, Roughness and DEM (Fig. 2).

Table 1: VIF analysis results of the final selection of environmental variables.

variable	VIF
DEM	2.544629
HumanFootprintIndex	1.761245
TreeCoverDensity	1.467348
Roughness	2.513238
TPI	1.015904

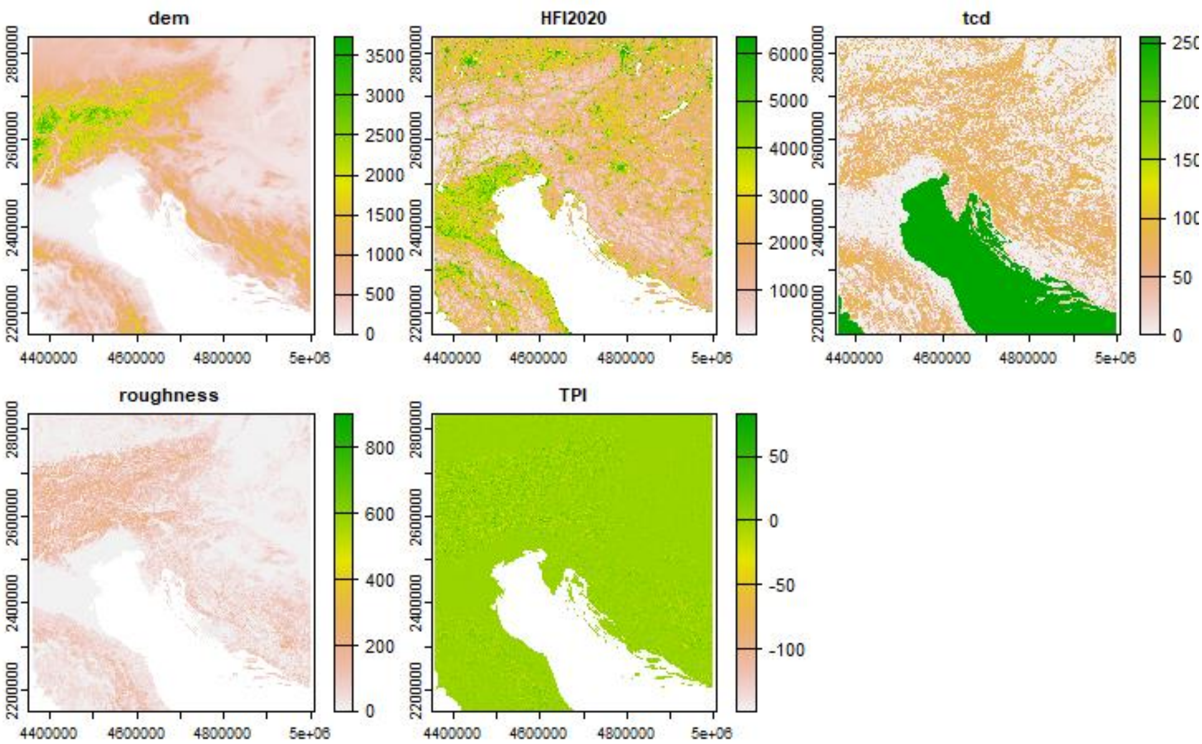

Figure 2: Environmental variables used in the final model.

Habitat suitability modelling

The model training was done using the aforementioned occurrence dataset and 10000 background points sampled in a buffered area (r = 50 km) around occurrences (see figure 3) and then extrapolated to the entire extent of the occurrence dataset.

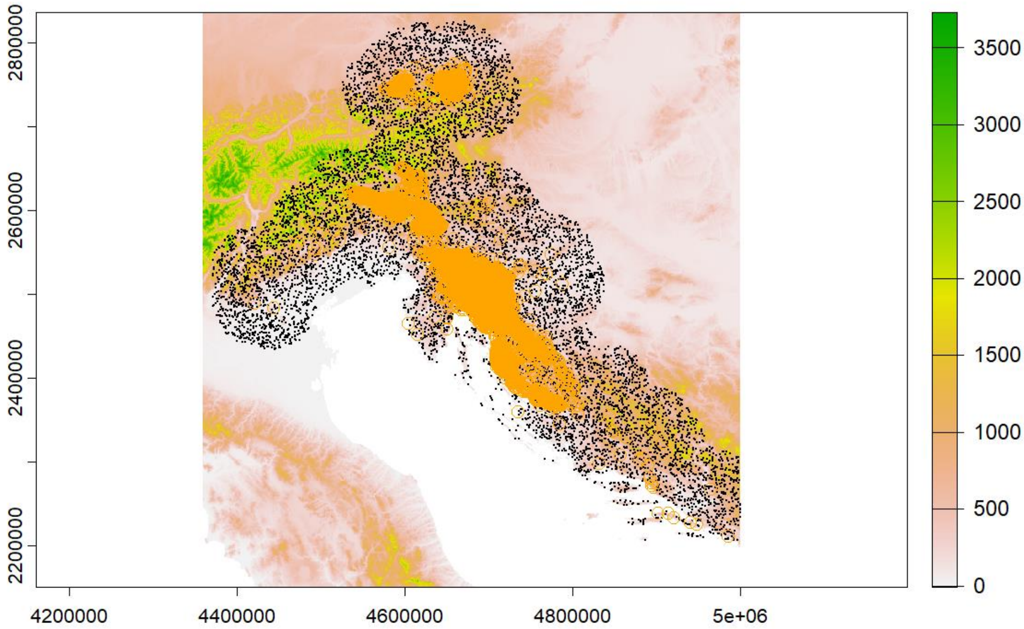

Figure 3: DEM layer (representing study extent) overlaid by the background points (black dots) and occurrence data (orange dots) used during model training.

We have used the MaxEnt algorithm implemented in the ENMeval R package (Kass et al. 2021). Maximum entropy (MaxEnt) algorithm is a machine learning method used in species distribution modelling to predict the potential distribution of a species based on its occurrence data and environmental variables. The MaxEnt model maximises the entropy of a probability distribution, subject to constraints imposed by the available data. It estimates the probability distribution of environmental conditions at the locations where the species is known to occur and then extrapolates this distribution to other areas of the study region. MaxEnt has been shown to be effective in predicting the distribution of species, even when there are few occurrence records, and has been widely used in conservation biology and ecology.
Using the ENMeval R package (Kass et al. 2021) we built multiple models with a range of settings (Regularization multiplier ranging from 2 to 5 in 0.5 steps and Linear, Quadratic, and Hinge feature classes). The regularization multiplier (RM) determines the penalty associated with including variables or their transformations in the model. Higher RM values impose a stronger penalty on model complexity and thus result in simpler (flatter) model predictions. The feature classes determine the potential shape of the marginal response curves. A model

that is only allowed to include linear feature classes will most likely be simpler than a model that is allowed to include all possible feature classes.The partitioning method was set to "checkerboard2", we used the "maxent.jar" method and 10000 background points. Model selection was performed using four different approaches, one based on dAICc values, the second based on sequential method (where we first used the cross-validation results by selecting models with the lowest average test omission rate, and to break ties, with the highest average validation AUC (Radosavljevic & Anderson 2014, Kass et al. 2020). The third selection criteria was based on the Continuous Boyce index (CBI) values and the last approach combined all these by ranking models by each of them and then taking the combined rank in the account. Out of the four best performing models, we have opted for the simplest one (least number of coefficients) and used it in further analyses. We have used the cloglog output, which is the simplest to understand: it gives a probability of occurrence estimate between 0 and 1.

Transitional habitat patches (see Fig. 5) were calculated from the cloglog model prediction with the cutoff value of 0.3 (30% probability of presence), suitable habitat patches with the cutoff value of 0.5 (50% probability of presence). Optimal habitat patches were obtained from the same model prediction but with the cutoff value of 0.77 (the 50th percentile of the model prediction values at occurrence points). In all cases, patches smaller than 10 km^2 were filtered out.

Landscape permeability

Landscape permeability was analysed using Omniscape software running in Julia programming language (Bezanson et al. 2017). The Omniscape algorithm works by applying Circuitscape (Anantharaman et al. 2020) iteratively through the landscape in a moving window with a user-specified radius. The radius used in this study was set to 150 pixels, which means the radius measured 75 km (as pixel size was 500 x 500 m), which corresponds to the lynx dispersal distances summarised by Potočnik et al. (2020). Omniscape requires two basic inputs: a resistance raster, and a source strength raster. The resistance raster defines the traversal cost for every pixel in the landscape, in our case the cost was ranging from 1 to 100. Resistance raster consisted of DEM, treeCoverDensity, HumanFootprintIndex and Terrain Ruggedness Index. We modelled elevation resistance coefficients as an inverse Gaussian function of elevation with an optimal elevation of 886 m (median value of lynx occurrence points) and a SD of 590 m to account for increased costs of moving at low altitude due to human presence and of moving at high altitude due to unfavourable conditions. Forest resistance was modelled as a linear function of a TCD (Tree Cover Density) as a result of the lynx habitat preference for forest cover. Values of the Human Footprint Index were squared and rescaled to 0-100 to account for increased cost of moving through densely populated areas. TRI (Terrain Ruggedness Index) was scaled to 0-100, with higher values indicating more rugged terrain with increased cost of moving through.

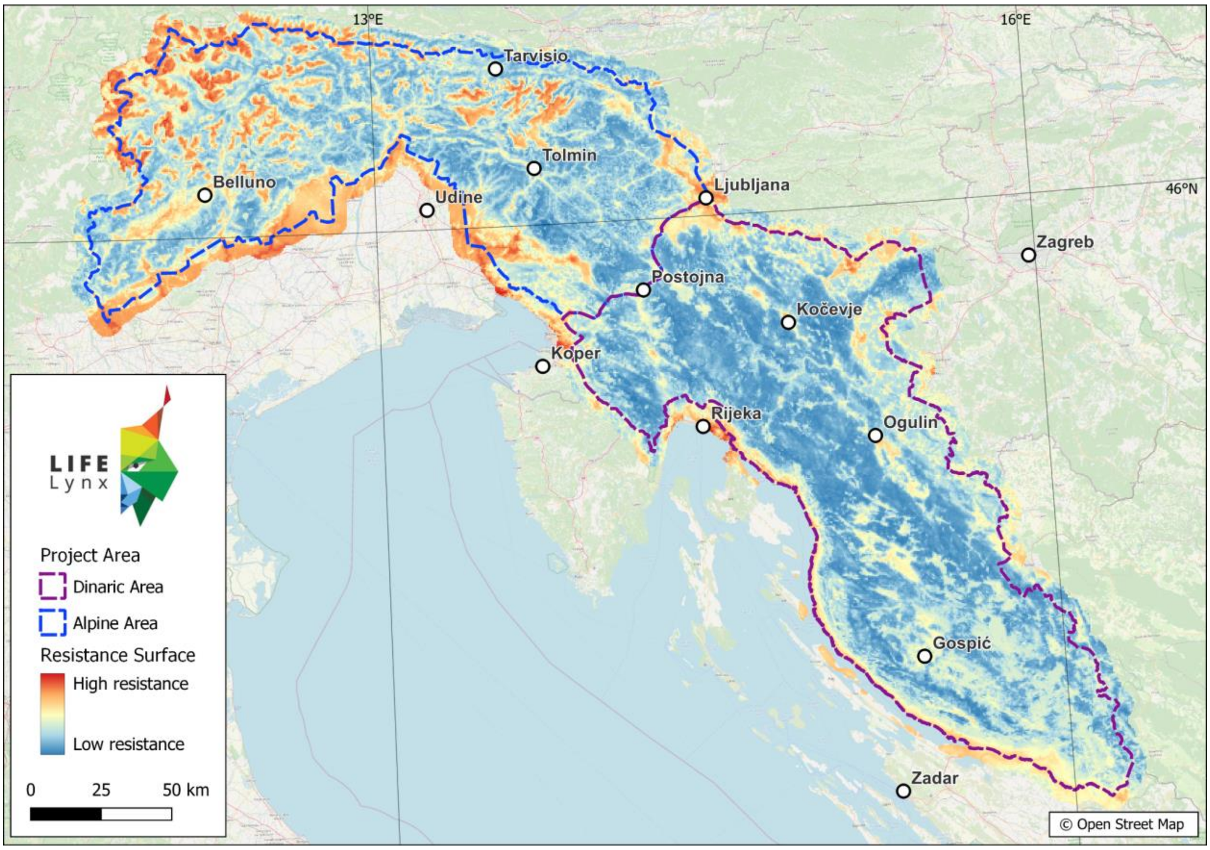

Figure 3: Resistance surface used for the landscape permeability analysis. Blue shades indicate low traversal cost, while red shades indicate high traversal cost.

The source strength raster defines for every pixel the relative amount of current to be injected into that pixel. In this study, the source strength raster originated from a resistance layer using the *source_from_resistance argument* set to true.
The window centers on a pixel in the source strength surface that has a source strength greater than 0 - this is referred to as the target pixel. The source strength and resistance rasters are clipped to the circular window of the aforementioned radius. Every source pixel within the search radius that also has a source strength greater than 0 is identified. These are referred to as the source pixels. Circuitscape is run using the clipped resistance raster in "advanced" mode, where the target pixel is set to ground, and the source pixels are set as current sources. The total amount of current injected is equal to the source strength of the target pixel and is divided up among the source pixels in proportion to their source strengths. These four steps are repeated for every potential target pixel. The resulting current maps are summed to get a map of cumulative current flow. The Omniscape algorithm evaluates connectivity between every possible pair of pixels in the landscape that are valid sources (i.e. have a source strength greater than 0) and no further apart than the moving window radius. For visualisation purposes, we used the normalised cumulative current. Normalised current helps identify areas where current is impeded or channelized (e.g. more or less current than expected under null resistance conditions). High values mean current flow is channelized (above 1), low values mean current is impeded (below 1) and values around 1 represent diffused flow.

Genetic samples and gene flow

Noninvasive genetic samples (faeces, urine, hair, saliva on an object, direct saliva) were collected opportunistically before the LIFE Lynx project and with the start of the project the samples are being systematically collected. Blood samples are taken from the animals captured for telemetry and tissue samples from dead lynx. Genetic samples were collected and genotyped in scope of actions A3 (Skrbinšek et al. 2019) and C5 (Krofel et al. 2021, Fležar et al. 2022, Fležar et al. 2023). Samples, where we were able to reliably recognize individual animals that also had locations and collection dates were placed on a map to present the movement of the animals. Because of high relatedness and inbreeding of the Dinaric population, the number of genetic markers doesn't allow a detailed reconstruction of the pedigree, where family ties would enable to assess the direct gene flow between different areas. We thus tried to assess the potential gene flow based on the non-invasive genetic samples and GPS telemetry data by inspecting the potential movements of the animals between Dinaric and SE Alpine populations.

Results and discussion

Potočnik et al. (2020) extrapolated the habitat suitability model made by Skrbinšek (2004) to the entire range of Slovenia, Croatia, Bosnia and Herzegovina, NE Italy and the border area with Austria (Fig. 4 shows the model prediction for the Life Lynx project area). The model renders large parts of the Dinarics and Alps as (highly) suitable habitat. Even though its prediction is more general it corresponds to the prediction of the MaxEnt model, presented hereinafter.

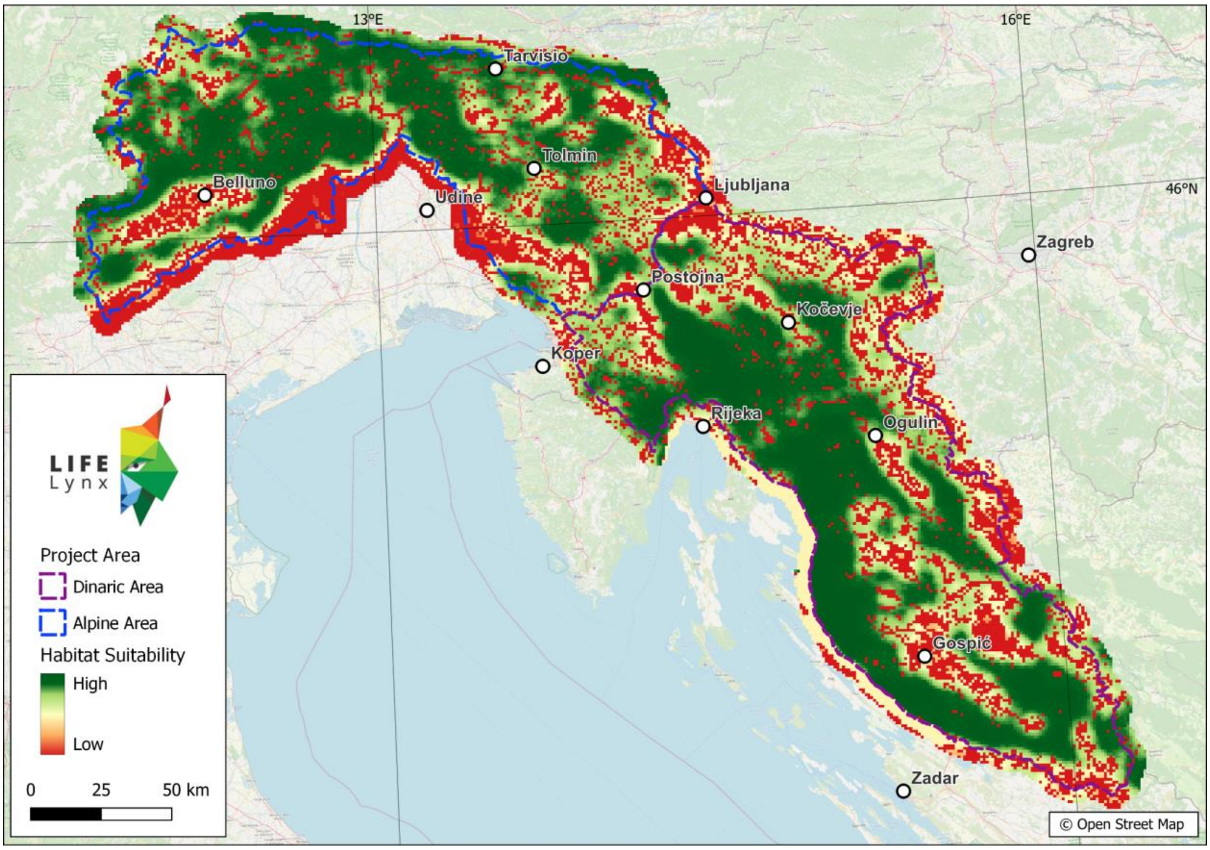

Figure 4: GLM based Lynx Habitat Suitability Map (Potočnik et al. 2020). Green shades indicate suitable habitat while red shades indicate less favourable and unsuitable habitat. While the prediction renders large parts of the Dinarics and Alps as (highly) suitable habitat and is usable on a larger scale, it does not discern habitat suitability on a smaller scale.

Habitat Suitability Model

We built 35 different MaxEnt models with a range of settings (with different Regularization Multiplier values and Feature Classes). The selected model (Fig. 5), based on combined rank selection criteria, had Linear feature class (L) and regularization multiplier of 3.5 to avoid overfitting. Validation AUC values were quite high at 0.833.

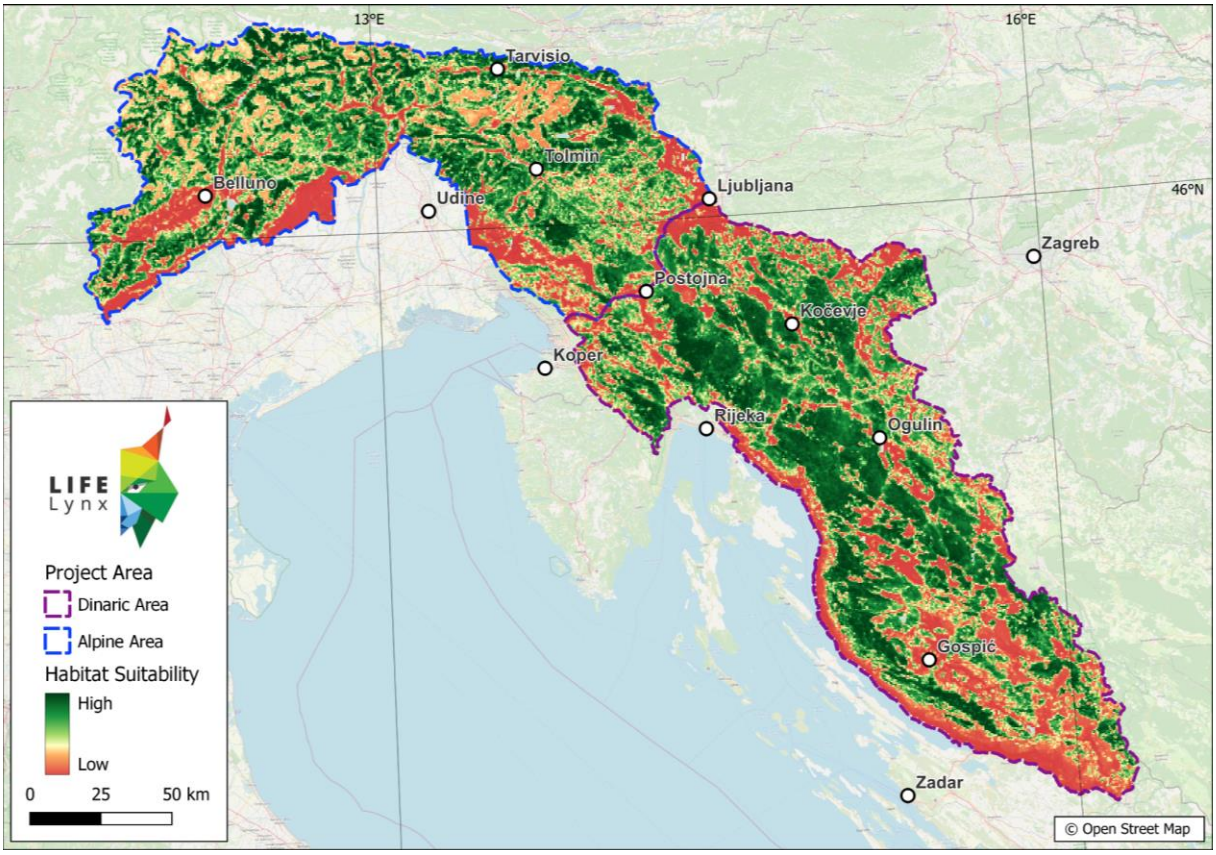

Figure 5: Maxent based Habitat Suitability Map. Green shades indicate suitable habitat while red shades indicate less favourable and unsuitable habitat. Model prediction renders large and mostly well connected forest complexes of the Dinarics as highly suitable habitat for lynx, while suitable habitat in the Alps is highly fragmented.

Model prediction corresponds to previous habitat suitability models for large carnivores (eg. Rodríguez-Recio et al. 2018, Kuralt et al. 2021, Potočnik et al. 2020), where the most suitable areas are large forest complexes that are present especially in the Dinaric part of the project area. The prediction outlines a few patches of highly suitable habitat in the Alpine area (mostly 1000-1500 m. asl. plateaus such as Jelovica and Pokljuka) where lynx is already present, whereas patches in the western part of the Alpine area tend to be smaller and farther apart (Fig. 5, 6), stressing the importance of the connectivity amongst these patches. While large parts of the Dinaric area form more or less a homogeneous area of suitable habitat, the situation north of the LJ-KP highway is drastically different. Nanos, Hrušica and Trnovski gozd plateaus still have moderately large forest complexes, whereas forests in Polhograjsko and Škofjeloško hribovje are highly fragmented. The fragmentation of suitable and especially optimal habitat is even more apparent in the Italian part of SE Alps, where deep valleys interrupt otherwise suitable habitats. Areas above the treeline are also rendered as less suitable, which could also be an modelling artefact due to the fact that Tree Cover Density environmental layer played an important part in the model training, resulting in areas above the treeline being less suitable. GPS-telemetry data from the SE Alps shows that lynx move at higher altitudes where tree cover is scarce as well. However, it is uncertain whether lynx would establish territories there. While prey is definitely present (eg. chamois, ibex, European mouflon), tree / vegetation cover that lynx uses during hunting prey could be the limiting factor. This is, however, a strong assumption, as lynx inhabits rocky-steppe habitats with very little tree cover in the Eastern parts of its areal.

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Optimal and suitable habitat patches

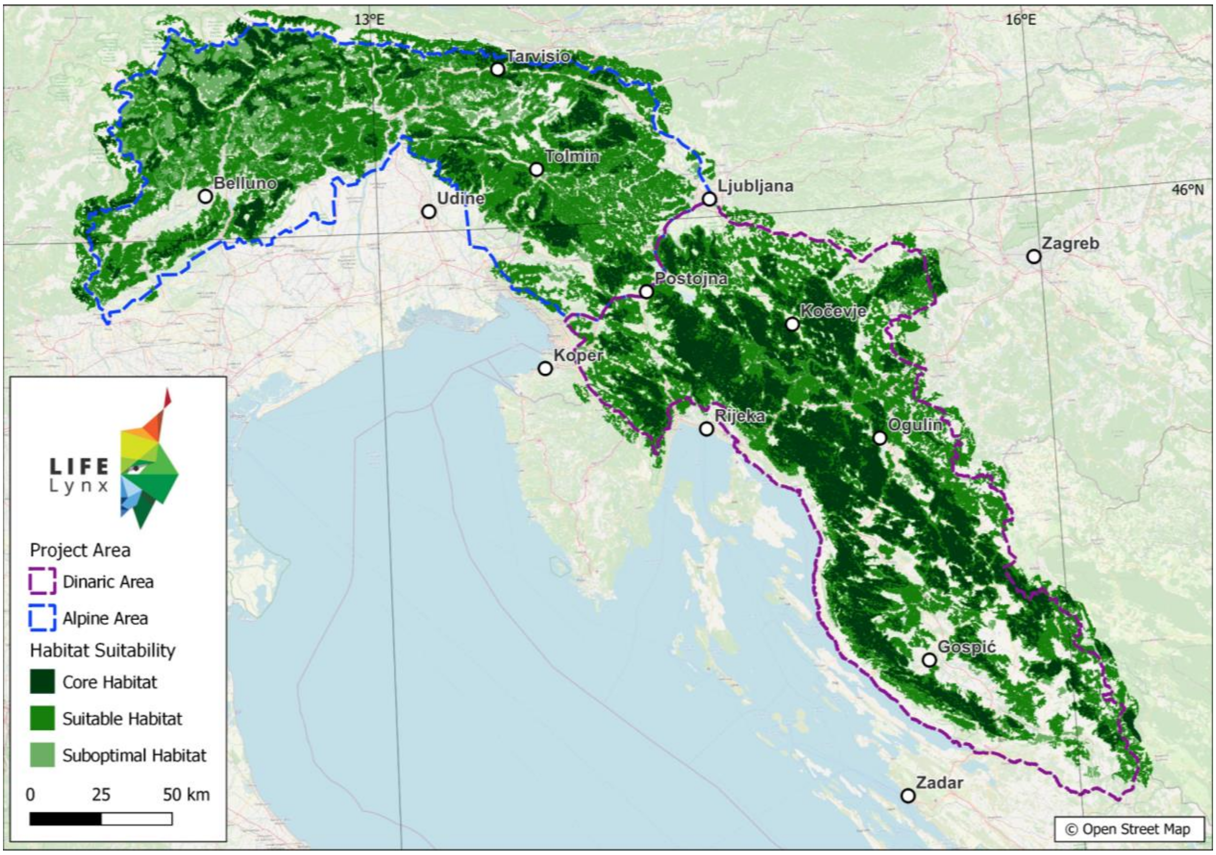

Figure 6: Suitable habitat and optimal habitat patches. Large amount of the Dinaric area falls under suitable and even core habitat classification. These patches also seem to be well connected and in practice probably function as a single habitat patch. Situation in the Alps is completely different, as optimal habitat patches are smaller and farther apart, with suitable habitat patches creating "stepping stones" for dispersing lynx.

Based on the model prediction we estimate that there is 2878 km^2 of optimal habitat and 6977 km^2 of suitable habitat in the Alps, while the Dinarides host 4634 km^2 of optimal habitat and 8656 km^2 of suitable habitat (Fig. 5). Potočnik et al. (2020) provides home range (HR) sizes for female and male lynx for Slovenian Dinarics. Average female HR size measured 178 km^2, while male HR sizes are slightly larger at 222 km^2. Female HR sizes in the Jura mountains measured from 150 to 168 km^2 and male lynx HR sizes from 258 to 264 km^2 (Stahl et al. 2002). In the Northwestern Alps (Switzerland) these numbers were 106 km^2 for females and 159 km^2 for males (Breitenmoser-Wursten et al. 2001). Lynx HR sizes in the Vosges Mountains (France) measured 516 km^2 for a female and 235 km^2 for male lynx (Schmidt et al.

1997). Using our GPS telemetry data of lynx from the Alpine area obtained during the Life Lynx project and GPS telemetry data of 5 lynx from Italian SE Alps, we calculated the HR sizes (as the area of the minimum convex polygons) of the “SE Alpine lynx”. These averaged 195 km^2 for female and 318 km^2 for male lynx. It is apparent that home range sizes vary significantly across different regions and are mostly dependent on prey availability and animal sex (Herfindal et al. 2005).

Based on the data of the average home range sizes and available optimal / suitable habitat we estimated the number of territorial animals that could reside in each of the areas (see table 2). Altogether the entire study area could therefore support somewhere between 71 and 146 resident animals.

Table 2: Estimated numbers of resident lynx in each study area.

Study area	Optimal habitat (km^2)	Suitable habitat (km^2)	No. females	No. males
SE Alpine	2878	6977	15 - 36	9 - 22
Dinaric	4634	8656	26 - 49	21 - 39

These estimates should be interpreted carefully as we did not account for individual habitat patch sizes, but did our calculations based on cumulative area of optimal and suitable habitat patches per study area. While optimal habitat patches in the Dinaric area are fairly large and could support multiple animals, patches in the SE Alps are smaller and only few of them reach an average HR size of a female or male lynx.

Landscape permeability

Results of the permeability analysis reveal that large and continuous forest complexes form transport networks for lynx movement. While the landscape in the Dinarics seems to be well connected, the map (Fig. 7) outlines the critical area that serves as a bridge between Dinaric and SE Alpine lynx populations. The area between Vrhnika and Razdrto incorporates vast forested areas that are sporadically interrupted by settlements but crucially, the flow in that area is substantially obstructed by the Ljubljana-Koper fenced highway that is definitely one of the most influential barriers between the two populations. From 36 GPS tracked lynx, only one (male lynx named Maks) has learned to cross the highway and then crossed it on multiple occasions (see Fig. 9). Three potential corridors are delineated on that 40 km section of highway (inset map of Fig. 7). The first corridor crosses the highway between Vrhnika and Unec, the second one between Unec and Postojna and the third one between Razdrto and Divača.

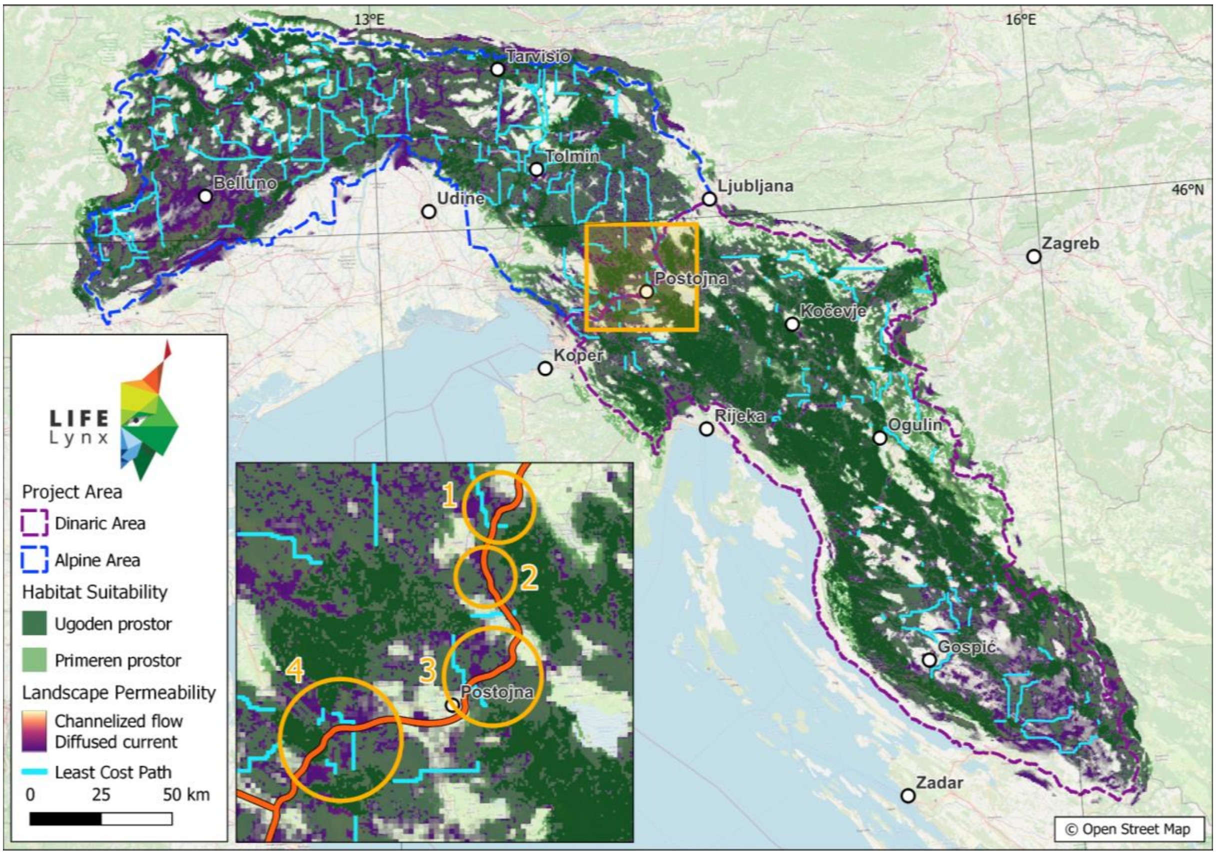

Figure 7: Map shows landscape permeability overlaid with optimal habitat patches and least cost paths amongst the patches. The purple colour indicates diffuse permeability, which in practice means that an animal can move through space unhindered. In some areas, however, the passage is highly channelized (pink and yellow shades), which means that the lynx has little opportunity to take an alternative route. Cases where such bottlenecks are crossed by linear barriers (e.g. motorway, railway) are particularly problematic, as such barriers can be virtually impassable for the lynx. The inset map shows that Ljubljana-Koper highway (orange line in the crosses four potential corridors, first being the Vrhnika-Logatec section, second Logatec-Unec, third Unec-Postojna and fourth Postojna-Divača section. Areas with impeded permeability were made transparent for clarity.

Landscape permeability in the Alpine area is highly impeded in the valleys with high levels of human footprint. Areas with high permeability are therefore mostly mountain ranges up to the treeline, but not much above. That is partly due to the combined effect of data layers - Tree Cover Density, Terrain Ruggedness Index and DEM - included in the resistance surface. TCD values are low in such areas, TRI tends to be high, and elevation resistance was modelled as an inverse Gaussian function of elevation with an optimal elevation of 886 m and a SD of 295 m to account for increased costs of moving at low altitude due to human presence and of moving at high altitude due to unfavourable conditions.

The importance of wildlife overpasses and tunnels

The habitat suitability model thus predicts the suitability of the area for the establishment of resident lynx territories. However, other factors besides habitat suitability also influence the landscape permeability, as dispersing individuals are likely to move in less favourable habitat. The results of the Landscape permeability analysis (Figure 6) could therefore be interpreted as a "transport" network for young dispersing lynx in search of their own territory. In some places the permeability is diffuse (purple shades), which in practice means that the animal can move unhindered through the space. In some areas, however, the passage is highly channelized (pink and yellow shades), which means that the lynx has little opportunity to find an alternative route. Cases where such bottlenecks are crossed by linear barriers (e.g. motorway, railway) are particularly problematic, as such barriers may be virtually impassable for the lynx.

An illustrative example of such a barrier is the Ljubljana-Koper fenced motorway, which was first built (the section from Vrhnika to Postojna) in 1972, at a time when the animal habitat connectivity was not yet considered. The motorway thus crosses the forested ridges of the northern Dinarides and, with only a few road underpasses and overpasses, creates a barrier that cuts the central habitat of large carnivores in Slovenia in two. This is confirmed by telemetry data of lynx (and other large carnivores), which show that the permeability of the highway is severely limited in some sections. For example, no (successful) crossing has yet been recorded on the Unec - Postojna section. Plans for wildlife overpass on this section are therefore certainly justified.

The importance of wildlife overpasses is evident at the nearby 68.5 km long Zagreb-Rijeka highway section, which runs through the heart of the Gorski Kotar, part of a wider complex of core lynx habitat. Due to the relatively rough terrain, there are 43 viaducts and tunnels on this section of the motorway, and one specially designed 100 m wide wildlife overpass to allow animals to cross. These structures represent 25% of the length of the Zagreb-Rijeka motorway. Kusak et al. (2009) report that in total, 12519 large mammal crossings were recorded over 793 days using motion sensors and photo-monitoring. The results of the survey showed that in such a case of motorway construction, when 25 % of the motorway length is open to large mammal passage, habitat connectivity is sufficiently maintained. Interestingly, 13.3 % more animals crossed the 100 m long green bridge than crossed under all narrow (5-15 m) underpasses on this section of the motorway, stressing the importance of implementing such structures in the transport network.

Potential gene flow

From collected genetic data we filtered out 307 genetic samples with known location and collection date data from which we could reliably identify individual animals (N=113). Among them 73 were identified as male and 40 as female. We also added the locations of release sites of reintroduced lynx, as a few were later identified also genetically and we could track their movement with genetic sampling. None of the genetically recognized offspring of reintroduced lynx in the Dinaric area were detected in moving to the direction of the SE-Alps. However the dispersion of offspring of the lynx reintroduced to the Alpine area is being closely monitored and in the ongoing monitoring season we confirmed the dispersion in the SE direction from the Alps.

Genetic data additionally indicate the LJ-KP highway as a major barrier for animal dispersal and thus potential gene flow. Out of 307 genetic samples, only 28 samples, all from male lynx, were collected north of the highway. We were able to detect two highway crossings (Figure 8) from the genetic data, implicating a potential gene flow between the populations. Additionally, one GPS collared lynx named Maks has learned to cross the highway (Vrhnika-Logatec section) and then crossed it on multiple occasions (Fig. 8). Maks later made an excursion up to the Julian Alps, a journey that shows that once the lynx learn to move across the barrier, they can quickly cover long distances in search of a suitable environment to establish a territory.

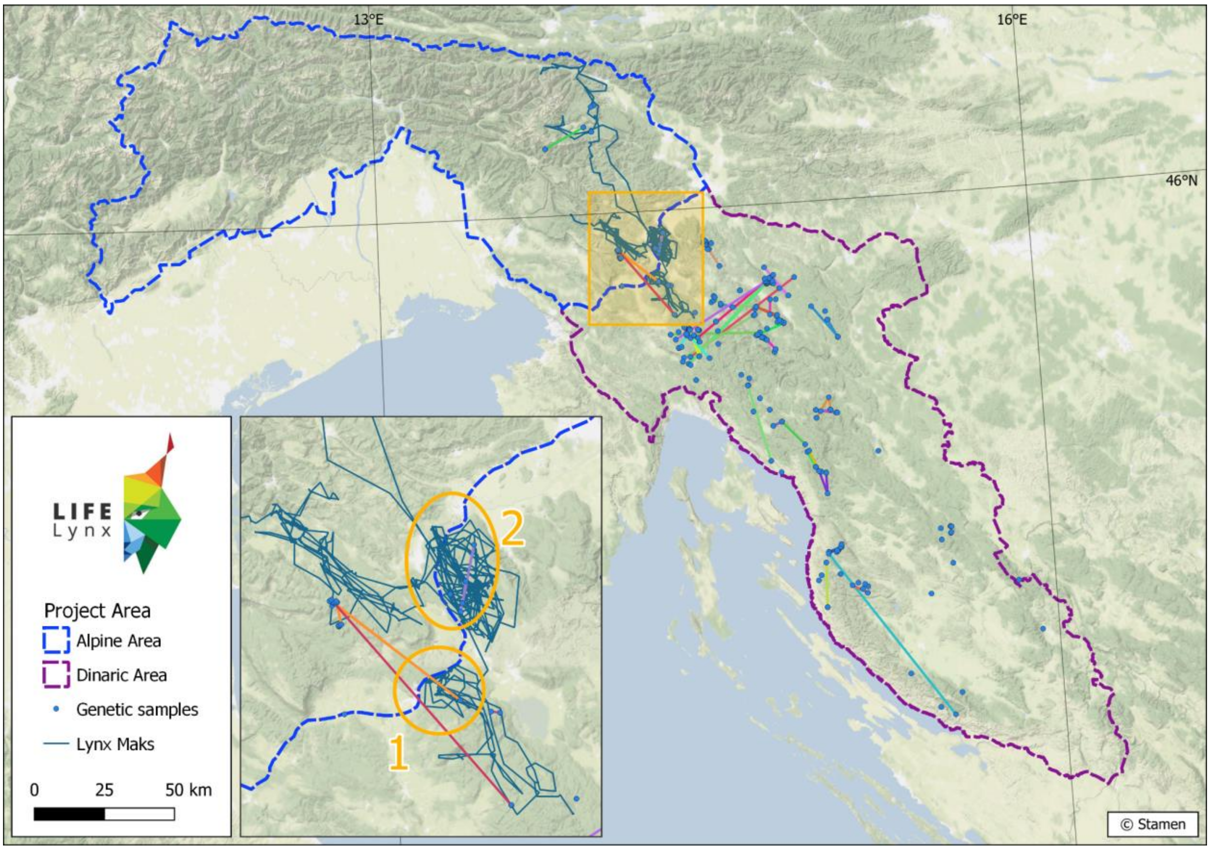

Figure 8: Collected genetic samples. Samples from the same animal are connected with a coloured line. Red and orange lines indicate two male lynx (M2CY5_3 and M2EPK) that probably crossed the highway. Maks' excursion to the Julian Alps can also be seen. The inset map shows a critical section of LJ-KP highway from Vrhnika to Postojna. Maks initially attempted to cross the highway at the Unec-Postojna section (1) and later moved north to Menišija region, where several successful crossings were detected (2).

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