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Abstract

Assessing landscape connectivity allows defining the degree to which the landscape facilitates or impedes the movement of a species between resource patches. In this phase of climate change and biodiversity crisis, maintaining landscape connectivity by restoring and protecting connecting areas and corridors is a key strategy to ensure the survival of many species. The Eurasian otter (*Lutra lutra*) is a freshwater top predator that is slowly recovering after a dramatic decline occurred in central and southern Europe in the last century. To assess the chances of otter recolonization of the western Alps, we analyzed environmental connectivity by applying electrical circuit theory to an expert-based resistance surface using the *Circuitscape* software. The study area included South-eastern France, North-western Italy, and Switzerland. We produced a cumulative current flow map and a gap analysis was also conducted to highlight the "conservation gaps" for optimal corridors. The results revealed that the orography of the landscape was the main factor influencing the quantity and quality of the pathways in the western Alpine landscapes. As main corridors were concentrated on valley bottoms, human pressure could severely diminish animal movement. Despite this, some heavily populated areas showed high connectivity values. Some important pathways did not fall within protected areas, potentially hindering otter dispersal and highlighting the need to expand the system of protected areas in the Alpine arc. Recolonization of Alpine territories by otters can therefore only occur if connectivity and environmental suitability combine to ensure the animals' survival over time.

Keywords (separated by '-')

Circuit theory - Connectivity - Dispersal - Protected areas - GIS - Habitat fragmentation - *Lutra lutra* - Mammal conservation

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ORIGINAL RESEARCH

Come back to stay: landscape connectivity analysis for the Eurasian otter (*Lutra lutra*) in the western Alps

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Abstract

Assessing landscape connectivity allows defining the degree to which the landscape facilitates or impedes the movement of a species between resource patches. In this phase of climate change and biodiversity crisis, maintaining landscape connectivity by restoring and protecting connecting areas and corridors is a key strategy to ensure the survival of many species. The Eurasian otter (*Lutra lutra*) is a freshwater top predator that is slowly recovering after a dramatic decline occurred in central and southern Europe in the last century. To assess the chances of otter recolonization of the western Alps, we analyzed environmental connectivity by applying electrical circuit theory to an expert-based resistance surface using the *Circuitscape* software. The study area included South-eastern France, North-western Italy, and Switzerland. We produced a cumulative current flow map and a gap analysis was also conducted to highlight the "conservation gaps" for optimal corridors. The results revealed that the orography of the landscape was the main factor influencing the quantity and quality of the pathways in the western Alpine landscapes. As main corridors were concentrated on valley bottoms, human pressure could severely diminish animal movement. Despite this, some heavily populated areas showed high connectivity values. Some important pathways did not fall within protected areas, potentially hindering otter dispersal and highlighting the need to expand the system of protected areas in the Alpine arc. Recolonization of Alpine territories by otters can therefore only occur if connectivity and environmental suitability combine to ensure the animals' survival over time.

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Introduction

Movements of wildlife among habitat patches promote genetic exchange, reduce fluctuations in abundance, and thus promote the persistence of populations over time (Tischendorf and Fahrig 2000). Assessing landscape connectivity allows defining the degree to which the landscape facilitates or impedes the movement of a species between resource patches (Taylor et al. 1993). In this phase of climate change and biodiversity crisis, maintaining landscape connectivity by restoring and protecting core habitat areas and corridors is a key strategy to ensure the survival of many species (Beier and Noss 1998; Tewksbury et al. 2002; Hoegh-Guldberg et al. 2008; Corlatti et al. 2013).

Habitat connectivity is related to both functional and structural connectivity. Functional connectivity is species-specific and is related to the species' behavior (Doak et al. 1992; Gustafson and Gardner 1996) and the investigated spatio-temporal scale (Wade et al. 2015). Functional connectivity analyses are usually based on measures of movement probability between habitat patches, time spent searching for new patches, immigration rates, and landscape permeability (Kindlmann and Burel 2008). On the other hand, structural connectivity is only related to the landscape structure (Green 1994; With et al. 1997) and is based on the assumption that naturalness and biodiversity increase in areas with low anthropogenic pressure or with uniform abiotic features (Beier and Brost 2010; Theobald et al. 2012). Structural connectivity analysis generally uses approaches based on the configuration of ecological corridors, spacing between elements, and the amount of suitable habitat in the landscape. Connectivity models are especially useful for the study of large mammals (particularly carnivores), birds, reptiles, and amphibians (Correa Ayram et al. 2016; Wood et al. 2022). Also, they can be useful to explore the connectivity in habitats that are particularly vulnerable to anthropic pressures, such as riparian ones (Capon et al. 2013).

Mammals are among the taxonomic groups most affected by habitat fragmentation (Andren 1994; Cardillo et al. 2005; Rivera-Ortíz et al. 2015). The magnitude of this negative effect is related to body size, vagility, degree of specialization, and generation time. In particular, medium- and large-sized or specialized species are more strongly affected by fragmentation (Crooks 2002). Similarly, species with little vagility and short generation times, if isolated, are at greater risk of suffering genetic erosion and becoming extinct (Rivera-Ortíz et al. 2015). Among mammals, carnivores play a key role in regulating ecological communities and ecosystems, even at low densities (Ripple et al. 2014). Predation can certainly limit the presence of herbivores, but it can also affect other carnivores. Carnivores are especially threatened, since they usually have high energy requirements, disperse over large areas in search of prey, and live at low population densities (Ripple et al. 2014). In Europe, for example, the brown bear (*Ursus arctos*) and Eurasian lynx (*Lynx lynx*) have been strongly affected by habitat fragmentation (Schmidt et al. 2011; Newbold et al. 2015; Waller and Servheen 2016). The Eurasian lynx, in particular, has suffered a severe contraction of its distribution range over the centuries, and currently, most populations are small and isolated (Von Arx et al. 2004). This has led to the loss of genetic variability, which is one of the major causes of extinction for wild species with a fragmented distribution range (Frankham 2005).

The Eurasian otter (*Lutra lutra*) is a carnivore mustelid whose ecology is strictly linked to the riparian ecosystem. Despite otters resting and reproducing on the ground, they use waterbodies (lakes, artificial basins, rivers, swamps, and coastal areas) for moving and hunting (Roos et al. 2015). It is considered a flagship species, and its protection helps to drive conservation issues for freshwater habitats and associated species (Dudgeon et al. 2006; Cianfrani et al. 2011; Fuller et al. 2015). The Eurasian otter is one of the species that suffered a strong decline in Europe during the second half of the twentieth century (Mason and Macdonald 1986; Hung and Law 2016). Together with other major threats such as water pollution and human persecution, the destruction, and fragmentation of freshwater habitats (dams construction and clearing of riparian vegetation) led the otter to go extinct in most of Europe (Mason and Macdonald 1986; Kruuk 2006; Ruiz-Olmo et al. 2008; Duplaix and Savage 2018). Nowadays, thanks to conservation policies, its inclusion in Annex I of CITES and Annexes II and IV of the Habitats Directive (Council Directive 92/43/EEC), and the banning of harmful pollutants, the otter is slowly re-colonizing its previous distribution range, and European populations are progressively increasing (Roos et al. 2015; Loy and Duplaix 2020).

Notwithstanding an increase in their distribution range and population numbers throughout Europe, otters' re-colonization patterns are slow in the mountainous areas of the Alpine range (Loy and Duplaix 2020). Specifically, Austria and Slovenia are the only countries where the underway recolonization is including the Alpine range. In Switzerland, the presence of otters is limited to a few scattered sites, whereas the French Alps still lack a stable population (Loy and Duplaix 2020). In Italy, the only viable otter populations occur in south-central regions (Balestreri et al. 2016; Giovacchini et al. 2018), whereas only a few scattered records are available for the Alps in the North-East (Alto Adige and Friuli-Venezia-Giulia regions), likely following dispersion from Austria and Slovenia (Angst and Weinberger 2020; Arthur and Barthélemy 2020; Kranz and Poledník 2020; Lapini et al. 2020; Tremolada et al. 2020).

Otter recovery in the Alps is crucial for the survival of European populations, also considering that almost all populations proved to be genetically isolated from each other (Randi et al. 2003; Buglione et al. 2021). Therefore, this work aims to identify pathways for the dispersal of Eurasian otters in the Western Alps through a large-scale connectivity analysis that may i) offer an accurate framework for the number and quality of corridors; and ii) identify gaps in the network of protected areas where to concentrate efforts to promote gene flow and otter dispersal. For this purpose, we applied circuit theory to predict connectivity corridors highlighting connections from peri-Alpine territories, where permanent populations of otters are currently present, to the core of the Western Alps. The results obtained will therefore serve as an indication for future environmental protection and restoration measures.

Materials and methods

Study area

The connectivity analysis was implemented in an area of c. 240,000 km^2 including South-eastern France, North-western Italy, and part of Switzerland (Fig. 1). The area is dominated by central European mountain chains: the Alps, French Central Massif, and Jura Massif. Altitude ranges from the sea level to 4810 m above sea level (a.s.l.) of Mont Blanc.

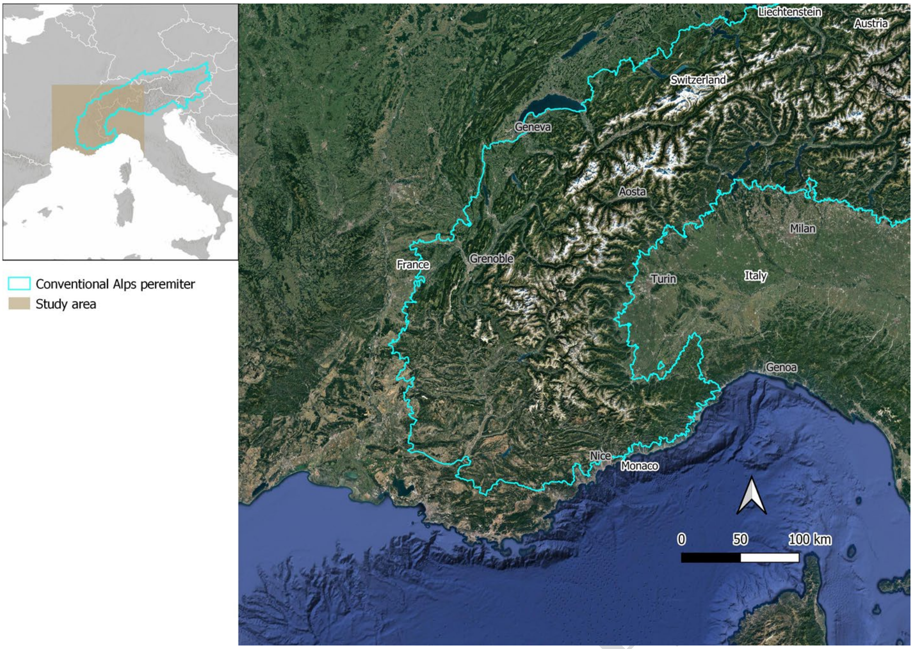

Fig. 1 Map of the study area. The area is dominated by central European mountain chains: the Alps, French Central Massif, and Jura Massif

Resistance surface

To describe the relationship between landscape structure and animal movement, we generated a resistance surface as a raster layer where each pixel is assigned a value describing its resistance to the movement of the target species (Adriaensen et al. 2003). To calculate the resistance surface, we selected the following six environmental variables relevant to otter movements and available for the entire study area: the Hydrographic network derived from the HydroSHED dataset (https://www.hydrosheds.org/products/gloric); Digital Elevation Model with a 25 m resolution of the Copernicus program (European Digital Elevation Model, EU-DEM, version 1.1); slope, extracted from the EU-DEM; CORINE Land Cover (scale 1:100.000) with a 100 m resolution; road network (Global Roads Inventory Database, GRIP); dams location (Global Dam Watch dataset, GDW, http://globaldamwatch.org). We decided to exclude datasets describing the width and depth of watercourses of our study area, or distance maps from watercourses o road networks, since the effect of these environmental characteristics on otter dispersal is still unknown, although probably very important for a mammal strongly dependent on water bodies, *e.g.*, for food. Variables were rasterized at 100 m spatial resolution because of the need to have uniform data over the entire study area, but also because the use of high-resolution data for such a large study area would have required an excessively high computational effort, which was not necessary for the result we wanted to achieve, i.e., an overview for the Western Alps. For each variable, we used an expert-based approach to assign a resistance value to each pixel, ranging from 1 (minimum resistance) to 100 (total barrier) (Fig. 2) (Three experts: AL, MdF, CF). We

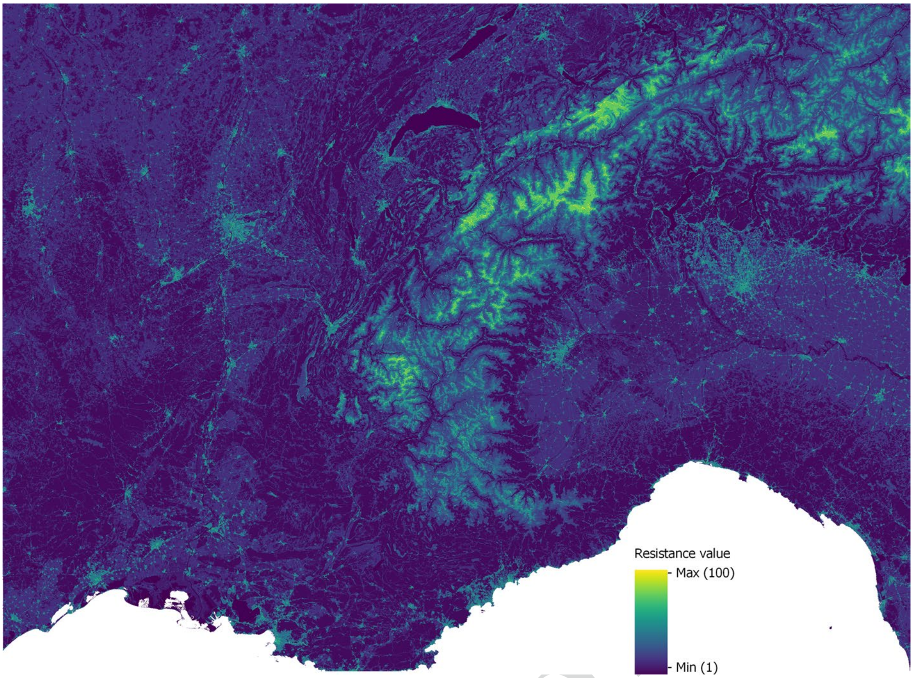

Fig. 2 Resistance surface where each pixel is assigned a value describing its resistance to the movement of the target species

decided to use an expert-based approach because inferential data on otter dispersal are extremely scarce and expensive to obtain and because using inferential data applied to peripheral areas of an expanding species' range may fail to discriminate between suitable and unsuitable areas since suitable areas not yet be utilized as pathways (Clevenger et al. 2002). The criteria used to determine the resistance values were selected using the Delphi methodology, based on group comparisons between experts (McMillan and Marshall 2006). Specifically, since otters move preferentially along rivers and other water bodies (Tarasoff et al. 1972; Roos et al. 2015), the hydrographic network was expected to provide the least resistance (highest permeability) to otter movements. However, we did not include in our analyses watercourses of Strahler order equal to 1, i.e., those watercourses with a torrential character that have lower flow and are more likely to run dry during certain months of the year (Horton 1945). Also, we considered that otters in Europe are rarely observed above 2000 m a.s.l. (Ruiz-Olmo 1998; Kruuk 2006), have no good climbing skills (Loy et al. 2009; Cianfrani et al. 2013), and tend to avoid intensively cultivated and urbanized areas (Kruuk 2006; Loy et al. 2009). In addition, roads and dams could limit otter movements under specific circumstances, such as the presence of two-lane paved roads (Shepard et al. 2008), or dams located on steep slopes. Details about the permeability scores assigned to each variable are reported in Table S2. Finally, with a swing weights procedure (Malczewski 2000), three experts in agreement ranked the variables in descending order, starting with a score of 100, according to their importance to the otter ecology. Then, the weight of each variable was obtained by dividing the ranking value itself by the sum of all ranking values, results ranged from

0.25 for the hydrographic network to 0.10 for the road network (Table 1), and used as a multiplier when combining the six layers in the final resistance map (Figs. 2, S1).

Due to the lack of precise documentation available regarding landscape development plans, land use transformation, or effects of drought on watercourses it was not possible to construct several resistance maps to analyze possible future scenarios.

Quantifying landscape connectivity

To estimate the connectivity in the study area, we used the *Circuitscape* software version 4.0 (https://circuitscape.org), which adapts concepts from circuit theory to animal movement. The metric used to estimate connectivity is the *''resistance distance''*, defined as the effective resistance between a pair of nodes, also considering multiple paths separating them (McRae et al. 2008), in contrast to minimum cost analysis, which instead only identifies the path with the lowest cost and therefore shortest distance (Adriaensen et al. 2003). Even if *Circuitscape* is mostly used for modeling the dispersal of terrestrial species, it was recently used also for works focusing on species that disperse along linear routes and are strongly related to fluvial habitats, such as the manatee (Haase et al. 2017) and the water vole (Foltête et al. 2016) and also many other aquatic vertebrate and invertebrate species (Dickson et al. 2018). The software reads the resistance surface map as an electric circuit, where habitat patches and dispersal connections are replaced by nodes and resistors (McRae et al. 2008). The current flows from one patch to another and the current values at each pixel are interpreted in terms of the probability that a random "walker" (*i.e.,* an otter in this case) passes through the cell (McRae et al. 2008). A high current flow value of a pixel represents a high probability of passage, and the degree of connectivity between patches increases with the number of connections between pixels. This approach, therefore, highlights the best connection corridors in the study area (McRae et al. 2008). As focal nodes (animal dispersion sources), we used the centroids of peri-Alpine basins in which the otter presence is known (Loy and Duplaix 2020) (Table S3). We produced a cumulative current flow map, showing the sum of all current flows between all possible patches, useful for highlighting essential areas for the maintenance of connectivity in the entire study area.

Gap analysis

To represent only the pathways with a high probability of being undertaken by a random walker, from the cumulative current flow map we extracted a layer containing all pixels with a current flow value ≥ the mean value + 1(SD) of all current flow values (Elliot et al. 2014). The map of protected areas (https://opendata.swiss, combined with https://www.

Table 1 Experts' priority values and weights used for the creation of the resistance map

Variable	Priority value	Weight
Hydrographic network	100	0.25
Land cover	80	0.20
Dams	70	0.17
Slope	60	0.15
Elevation	50	0.12
Road network	40	0.10

eea.europa.eu) was overlapped with the resulting map to identify high-probability pathways needing protection (Ducci et al. 2019). In addition, for protected areas crossed by optimal corridors, we calculated the area-weighted centrality score, defined as the sum of current flow values passing through all pixels in each protected area divided by the surface of the protected area. This score shows the relative importance of each protected area in providing connectivity to the network (Dickson et al. 2013).

Results

Cumulative current flow map

Values in the final resistance map ranged from 1 to 100 (mean = 15.65, SD = 14.10) (Fig. 2). On the French territory, the basin of River Rhone showed high connectivity downstream to its mouth in the Camargue region. In particular, in the southeastern area (nodes 6, 9, 10) the River Durance, a direct tributary of the Rhone, and its tributaries showed good connectivity values up to their springs, located close to the Italian border (Fig. 3). Further North, in the Savoy region, the River Isère and its tributaries are excellent corridors through the core area of the Western Alps (Fig. 3). Compared to the French-Italian border, the northern part of the study area showed lower current intensities and over smaller

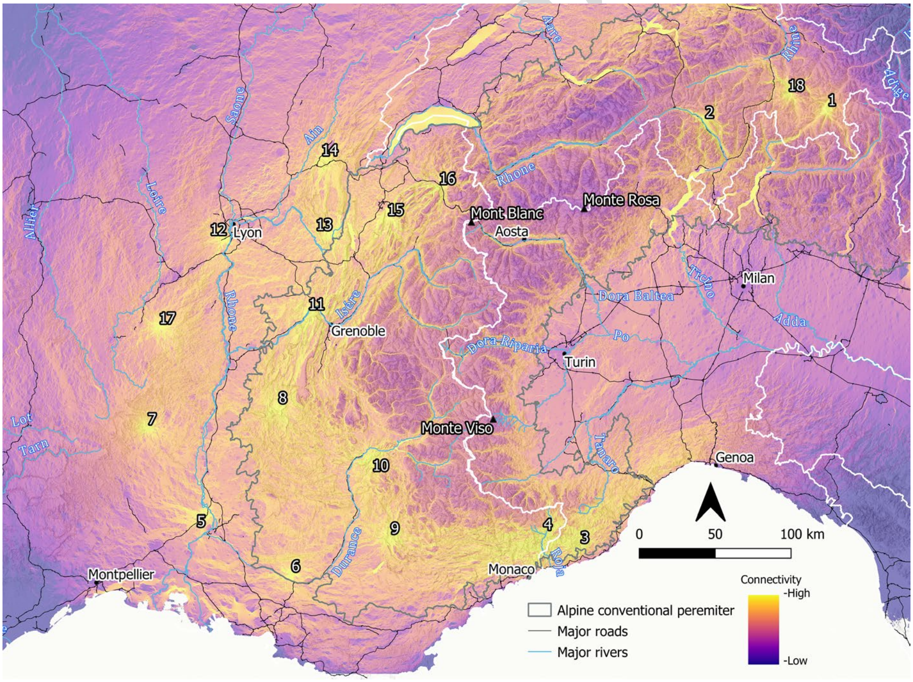

Fig. 3 Cumulative current flow map displayed using histogram equalization to increase contrast; numbers refer to focal nodes. The cumulative current flow map represents the sum of the intensity of the currents when all pairs of nodes are connected simultaneously. The map highlights which areas are most important for the connectivity of the whole study area

portions of territory, generally corresponding to the valley bottom of major watercourses. The lowest connectivity values were detected along the border between Italy and Switzerland, the central area of the Pennine Alps (Fig. 3). In the North of the Rhone, in the Swiss Pre-Alps, connectivity increased due to the presence of several water bodies, such as the Lake of Geneva. In Italy, the Po Valley showed overall low connectivity values due to the absence of nearby focal nodes, although the network including the rivers Adda, Ticino, Dora Baltea, Dora Riparia, Po, and Tanaro offered several low-resistance connections. Their tributaries originate in the Alpine territories of Liguria, Piedmont, Valle d'Aosta, and Lombardy regions forming along the eastern perimeter of the Alpine chain a low resistance belt, which starts from the Maritime Alps and reaches the Swiss border (Fig. 3).

Gap analysis and protected area's centrality

The area occupied by high probability pathways (optimal surface for dispersal) covered 21,575 km^2, of which 77% fell in France (16,580 km^2), 12% in Italy (2556 km^2), and 11% in Switzerland (2414 km^2). About 42% (9095 km^2) of high probability pathways were included in protected areas and their buffer zones, while the remaining 52% (12,480 km^2) do not (Fig. 4; Table 2). France hosts 48% (7903 km^2) of the best-protected corridors and 69% (8677 km^2) of the unprotected ones, Italy hosts 29% (742 km^2) of the best-protected corridors and 14% (1814 km^2) of the unprotected ones, and Switzerland hosts 19% (450 km^2) of the protected and 16% (1964 km^2) of the unprotected ones. French corridors were concentrated in the Provence-Alps-Côte Azur and Auvergne Rhone Alpes regions (Fig. 4). Several regional nature parks and their buffer zones are crossed by them and may guarantee protection to otters, such as the Préalpes D'Azur Regional Natural Park, Geological Nature Reserve of Digne les Bains (buffer zone included), Provençal Baronies Regional Natural Park, the Vercors Regional Nature Park, Chartreuse and Les Bauges Regional Nature Parks (Fig. 4; Table 3, S4). In Switzerland, the best corridors fell in Bern, Luzern, Uri, Ticino, and Graubünden's cantons (Fig. 4; Table 3, S4). Protected areas showing high values of centrality were Les Grangettes Nature Reserve, the Rive Sud du lac de Neuchatel, and the Fanel et Chablais de Cudrefin RAMSAR sites and, Piano di Magadino Park, (Fig. 4; Table 3, S4). In Italy, optimal corridors were mainly located in western Liguria and Piedmont, where large lakes Como and Maggiore are found (Fig. 4). A large part of the protected corridors of the Liguria region fell in Natura 2000 protected sites, e.g., Lecceta di Langan, Monte Galero and Lago di Osiglia Sites of Community Importance (SCI) (Fig. 4, Table 3, S4). In the Piedmont region, the Gran Bosco di Salbertrand Natural Special Protection Area (SPA) in the western part of Torino municipality, along the River Dora Riparia, showed higher centrality values than other protected areas bordering French regions. In the Po Valley, the most important protected areas were the Valle del Ticino Park and the System of Protected Areas of the Po River Banks (Fig. 4; Table 3, S4).

The conservation gap affected most of the corridors located close to French, Italian, and Switzerland borders (Fig. 4). Among the tributaries of the French Rhone, the rivers Isere, Arc, Doron de Bozel, and Durance were highlighted as threatened. In Switzerland, only a small portion of the corridors along the rivers Rhone, Ticino, Adda, and Anterior Rhine are protected. In Italy, the watercourses flowing from the Alps and pre-Alps towards the Po Valley, such as the rivers Tanaro, Doria Riparia, and Dora Baltea, and their tributaries (i.e., Stura di Demonte, Maira, Variata) are far from the available network of protected areas (Fig. 4).

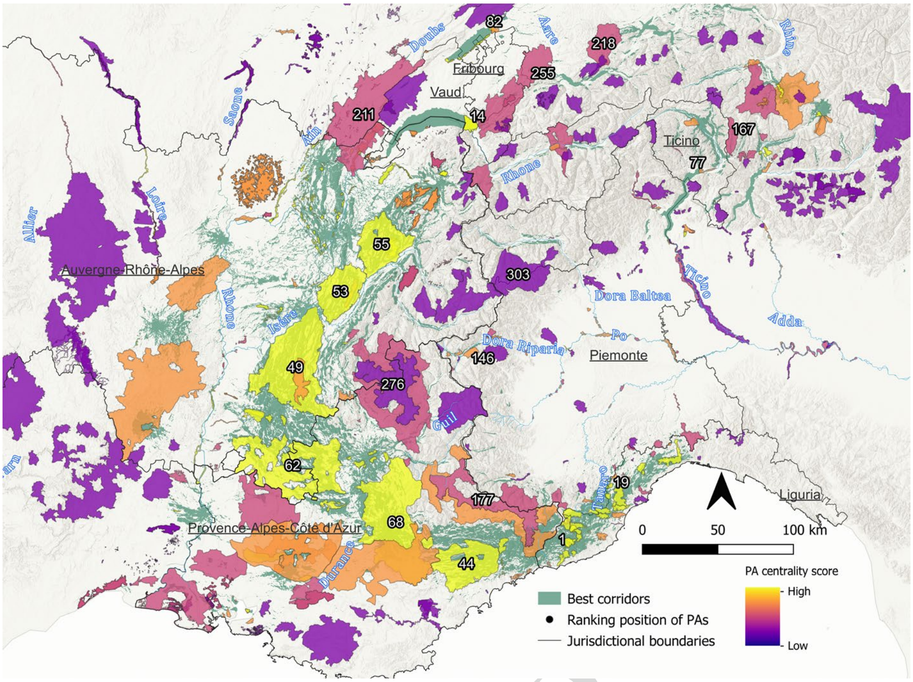

Fig. 4 Gap analysis and centrality of protected areas results. The protected areas are colored by a gradient following their area-weighted centrality score. The centrality score was obtained as the sum of all current values into each protected area's perimeter divided by its area. The numbers refer to the ranking position of PAs by centrality score (see also Table 3): SCI Lecceta di Langan (1); The Grangettes Nature Reserve (14); SCI Lago di Osiglia (19); The Préalpes d'Azur Regional Natural Park (44); The Vercors Regional Nature Park (49); Chartreuse Natural Regional Parks (53); The Natural Regional Park Massif des Bauges (55); Provençal Baronies Regional Natural Park (62); Protection perimeter of the Geological Nature Reserve of Digne les Bains (68); Fanel et Chablais de Cudrefin Ramsar site (82); Gran Bosco di Salbertrand SPA (146); Val Calanca Park (167); Mercantour National Parc (177); Haut-Jura Natural Regional Park (211); UNESCO Biosphere Entlebuch (218); Gantrisch Natural Park (255); Ecrins National Park (276); Gran Paradiso National Park (303)

Table 2 Gap analysis results, indicating total area and protected area of optimal corridors for each country

Country	Corridors (km^2)	Protected corridors (km^2)	% of protected surface
France	16,580	7903	48
Italy	2556	742	29
Swiss	2414	450	19
Total	21,575	9095	40

Discussion

In this work, we showed that landscape characteristics affect both the quantity and quality of connectivity corridors for Eurasian otters across the Western Alps. Multiple potential corridors were identified by the connectivity analysis, especially in the French peri-Alpine

Table 3 Information on the top 20 PAs based on their centrality score, including country (IT = Italy, FR = France, CH = Switzerland), region or canton, department or municipality or province, the sum of current, and area in km^2

Rank	PAs name	Country	Region/Canton	Department/ municipality/ province	Sum current	Area (km^2)	Centrality score
1	Lecceta di Langan (SAC)	IT	Liguria	Imperia	228.03	2	114.01
2	Campasso—Grotta Sgarbu Du Ventu (SAC)	IT	Liguria	Imperia	113.02	1	113.02
3	Monte Spinarda—Rio Nero (SAC)	IT	Liguria	Savona	1015.91	9	112.88
4	Monte Galero (SAC)	IT	Liguria	Savona	3539.32	32	110.60
5	Pelouses, forts et grottes du massif de Sao (SPA)	FR	Auvergne-Rhône-Alpes	Drôme	2581.94	24	107.58
6	Étangs, landes, vallons tourbeux humides et ruisseaux crevisses de Chambaran (SAC)	FR	Auvergne-Rhône-Alpes	Isère	2664.82	25	106.59
7	Monte Carmo—Monte Settepani (SAC)	IT	Liguria	Savona	7917.73	76	104.18
8	Castell'Ermo—Peso Grande (SAC)	IT	Liguria	Savona	2077.19	20	103.86
9	Grotte chauves-souris des Sadoux (SAC)	FR	Auvergne-Rhône-Alpes	Drôme	1318.61	13	101.43
10	Pelouses, landes, falaises et forts de la montagne d'Aucelon (SAC)	FR	Auvergne-Rhône-Alpes	Drôme	1508.41	15	100.56
11	Foresta Cadibona (SAC)	IT	Liguria	Savona	496.79	5	99.36
12	Bosco di Bagnasco (SAC)	IT	Piemonte	Cuneo	396.68	4	99.17
13	Les Grangettes (NR)	CH	Vaud	Losanne	5720.06	60	95.33
14	Brec d'Utelle (SCI)	FR	Provence-Alpes-Côte d'Azur	Alpes-Maritimes	3675.96	39	94.26
15	Massif de Sao et crêtes de La Tour (SPA)	FR	Auvergne-Rhône-Alpes	Drôme	6285.11	67	93.81
16	Réserve naturelle nationale du Haut-Rhône français (NR)	FR	Auvergne-Rhône-Alpes	Ain	1581.52	17	93.03
17	Monte Ciazze Secche (SAC)	IT	Liguria	Savona	278.39	3	92.80
18	Lago di Osiglia (SAC)	IT	Liguria	Savona	364.31	4	91.08
19	Bassa Valle Armea (SAC)	IT	Liguria	Imperia	725.99	8	90.75
20	Marais de Lavours (SPA)	FR	Auvergne-Rhône-Alpes	Ain	357,10	4	89.27

The ranking number is reported in Fig. 4 for better visualization of PAs location

SPA special protection areas, *SCI* sites of community importance, *SAC* special areas of conservation, *NR* nature reserve territories at the Alpine foothills, where existing populations are well connected and could act as a source of dispersers in the next future.

Valley bottoms were identified as the areas most conducive to otter dispersal, despite a high rate of human pressure. In these areas, the increasing urban development along river banks may negatively affect the likelihood of otter dispersal. In Europe, the main cause of death of Eurasian otters is roadkill, which occurs mainly within a 100 m radius buffer from watercourses and on roads with relatively low traffic density (Philcox et al. 1999; Poledník et al. 2011; Červinka et al. 2015). Therefore, urbanized areas may act as barriers, but they are not the only element that negatively affects dispersal movements. This is evident, for example, from the high connectivity values obtained along the entire basin of the River Rhone, where human-made development is strong to its mouth in the Camargue region. Moreover, otters seem to be more able of colonizing sub-optimal environments than previously believed (Baltrulnaite et al. 2009; Pita et al. 2009; Romanowski et al. 2013; Weinberger et al. 2016). In Portugal, for example, a positive correlation between otter abundance and irrigation canals in a cultivated landscape has been demonstrated (Pita et al. 2009). This is encouraging, as a large part of northern Italian regions are characterized by similar agricultural landscapes that could therefore guarantee otters' dispersal and stabilization.

Dams did not seem to have a significant effect on dispersal paths. In the Alpine regions, most dams are located near the springs of watercourses, where the environmental conditions are already unfavorable for the passage of otters (i.e., high elevation and steep slope). At lower elevations, the presence of multiple passages, both in water and on land, seems to compensate for the interruptions of the current flow. However, weirs along watercourses should be analyzed at a more detailed scale to more accurately interpret how otters perceive them.

Although the presence of steep terrain can compromise otter dispersal (Janssens et al. 2008), altitude is certainly a more limiting factor (Kruuk 2006). In this regard, noteworthy is the high connectivity values obtained along the southern limits of the Alpine range, where the availability of low-altitude passes is higher. In Maritimes and Ligurian Alps watercourses are fed almost exclusively by rainfall and are therefore subject to periods of low water in summer. These catchments of water are usually not able to sustain breeding populations, although otters have been shown to visit small watercourses to hunt or to use them as migration routes (Sulkava et al. 2007; O'Néill et al. 2009; Romanowski et al. 2013). In this study, we did not incorporate data on the availability of trophic resources and the seasonality of watercourses, since they were not available for the entire study area. However, previous observations in France (Malthieux 2020) and southern Italy (Giovacchini et al. 2018) suggest that otter populations persist and may even expand where water availability is limited, thus supporting our speculation on the Maritimes and Ligurian Alps.

Some relevant conservation gaps for important corridors were revealed in the study area, especially in the regions Auvergne-Rhône-Alpes, in the territories between the Haute Jura Natural Regional Park and the Massif des Bauge and Chartreuse Natural Regional Parks, and further south, in the territories between the Vercors, Baronnies Provençales and Ecrins National Parks. Then between the Alpes-Cote d'Azur province and the Liguria region, the coastal territories especially those south of the Mercantour National Park. In Aosta Valley, north of the Gran Paradiso National Park along the Dora Baltea river, and in the cantons Valais (along the Rhone river), Bern (in the territories between the Gantrisch Natural Park, Diemtigtal Natural Park, and the UNESCO Biosphere Entlebuch), and Ticino (along Ticino river, in the proximity of Val Calanca Park). Protected areas are the main tool used to cope with the loss of biodiversity (Spalding et al. 2008; Pacifici et al. 2020; Chen et al. 2022). Although many species of mammals, amphibians, and birds have become extinct in recent decades, the rate of extinction could have been 20% higher in the absence of protected areas (Hoffmann et al. 2010). Moreover, today, compared to the past, the distribution range of many wild species falls mainly in protected areas, this is due in minor part to the increase in the global protected area, but, mainly, to the disappearance of these species from unprotected territories (Pacifici et al. 2020). The success of dispersal movement depends on the dispersal capabilities of the species and the permeability of the matrix between protected areas, which is why a high number of protected areas favors the dispersal of wild species (Santini et al. 2016). Due to an inadequate state of protection and therefore a significant human presence, the connectivity in cross-border territories between nations is usually lower than within a national protection network (Santini et al. 2016). For these reasons the absence of protected areas comprising the corridors along the Isére, Dora Baltea, Dora Riparia, Tanaro, and Anterior Rhine rivers could significantly slow the dispersal and recolonization processes for otters. To account for these problems, many conservation projects have been implemented. Among these, the Target 11 of the Strategic Plan for Biodiversity 2011–2020 of the Convention on Biological Diversity, aims to expand the current protected area network to cover 17% of the terrestrial environment while maintaining and improving network connectivity. In the Alps, the Continuum Project (Kohler et al. 2008) is another example of a conservation initiative designed to enhance transboundary connectivity. An effective action for creating connections would be to increase structures that mitigate wildlife mortality and interactions with humans (green infrastructures), which would greatly benefit several animal species, including the Eurasian otter (Villalva et al. 2013; Niemi et al. 2014). In our study, areas with a high area-weighted centrality score represent in a straightforward manner the territories that could be a good conservation investment given their role in the stability of the entire network. This result also shows that even the smaller protected areas, which are generally also the most vulnerable, can play a key role in maintaining connectivity and thus in the survival of wild animals. Ensuring connections even between small areas could be equally important.

Conclusion

For wild animal species, the ability to move freely is a necessary condition for dispersal, reproduction, and persistence (Turner et al. 2001; Nathan et al. 2008). However, today animal movements are often hindered by the destruction and fragmentation of their habitats (Lindenmayer and Fischer 2006). Despite the agricultural land abandonment in mountain areas over the past years due to socio-economics changes (Dax et al. 2021), the Alpine environment has suffered important transformations by humans in the last century, such as the mechanization and intensification of agriculture (Britschgi et al. 2006; Scolozzi and Geneletti 2011), urbanization for tourism, and the increase of road networks (Caprio et al. 2011). Nevertheless Alps is still a region rich in protected areas that can help maintain and increase wildlife populations (Geldmann et al. 2013; Walston et al. 2016). Otters are also capable of adapting their ecological requirements to available conditions during recolonization processes (Baltrulnaite et al. 2009; Clavero et al. 2010; Romanowski et al. 2013; Weinberger et al. 2016). Therefore, our results stand as a necessary reference for environmental restoration actions aiming to promote the recolonization of the Western Alps by otters that can therefore only occur if connectivity and environmental suitability combine to ensure the animals' survival over time and reduce the mortality of dispersing animals.

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