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Landscape permeability for ecological connectivity at the macro-regional level: The Continuum Suitability Index and its practical implications

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A R T I C L E I N F O

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A B S T R A C T

Over the past decade, ecological connectivity has entered the political agenda, especially within the European transnational context. This evolution has driven the development of structural ecological connectivity and landscape permeability methodologies, such as the Continuum Suitability Index (CSI) presented here, which considers a range of anthropogenic factors that impact ecosystems. Numerous international and national projects have adopted the CSI to assess terrestrial landscape permeability on the macro-regional scale and prioritize areas for the implementation of ecological conservation and restoration measures. Although the CSI methodology has been applied several times, its sensitivity to individual factors, plausibility and ability to maintain consistency and robustness across different data sources and levels of spatial data precision have remained largely unexplored. Here, we presented the conceptual aspects of the CSI methodology, incorporating the outcomes from a literature review and expert workshops, and examined the CSI results for three projects spanning the Alps and Dinaric Mountains. Five key factors—namely, land use, population pressure, landscape fragmentation, environmental protection and topography—were identified as pivotal for analyzing landscape permeability and thus ecological connectivity. Notably, among these factors, population pressure exhibited the highest sensitivity, while fragmentation exerted the least influence on CSI outcomes. When comparing the CSI factors with data on the presence of red-listed species, the environmental protection indicator emerged as the most influential factor. Furthermore, our investigation comparing the different projects indicated that the chosen level of detail and data sources had minimal impact on the CSI results. Collectively, these analyses highlight CSI's adaptability and considerable potential as a versatile and straightforward applicable tool for an initial assessment of ecological connectivity at the macro-regional scale.

1. Introduction

Given the ongoing loss of biodiversity (Barnosky et al., 2011; Dirzo et al., 2014; Pimm et al., 2014), conservation efforts to prevent further extinctions are urgently needed. While large, functional, and well-managed protected areas play a vital role in addressing these needs, it is essential to recognize that vast amounts of biodiversity and ecosystems exist beyond such areas (De Alban et al., 2021). Therefore, conservation planning and actions must expand into complex and multi-use landscapes while prioritizing connectivity among protected areas (e.g., Boscolo and Paul Metzger, 2011; Shanahan et al., 2011). By fostering ecologically connected landscapes, conservation efforts can enhance population resilience, genetic diversity, and ecosystem health, contributing to species survival in changing environments and mitigating biodiversity loss (e.g., Heller and Zavaleta, 2009; Klausmeyer and Shaw, 2009; Mawdsley et al., 2009; Stein et al., 2013; Steinbauer et al., 2018; Wessely et al., 2017).

At the European level, scientific concerns about landscape connectivity have entered the political agenda since the 1990s (Ferretti and Pomarico, 2013). The EU Biodiversity Strategy 2030 outlines crucial

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objectives, primarily establishing a coherent network of protected areas covering at least 30 % of the EU's land area and "integrating ecological corridors, as part of a true Trans-European Nature Network" (European Commission, 2022).

Due to the ecological significance and importance placed by policymakers, various connectivity concepts and approaches have been proposed. Along a continuum of approaches, two extremes can be distinguished: the species-specific habitat connectivity and the connectivity of human-defined patterns of landcover. The two approaches differ in their respective focus: the first centres on patterns of habitat suitable for a particular species or the needs of a set of species (Cushman and Landgüth, 2012), while the second concentrates on the arrangement of land-cover/land-use patterns within a landscape (Lindenmayer and Fischer, 2007). Species-specific approaches have been used in several transnational European projects (Kohler, et al., 2009; Walzer et al., 2011; Favilli et al., 2015) and were applied in support of biodiversity conservation and landscape and urban planning (Modica et al., 2021; Tarabon et al., 2020). Over time such approaches have been constantly improved by the deployment of connectivity models such as least-cost path (Etherington, 2016), resistant kernels (Compton et al., 2007), circuit theory (McRae et al., 2008) and randomized shortest paths (Long, 2019). However, the use of species-oriented approaches for estimating connectivity at the macro-regional is often challenged by the absence of transnational, evenly distributed and comparable data on species occurrence, introducing spatial and temporal biases (Boakes et al., 2010). These biases can potentially distort the assessment of habitat requirements, movement patterns and population dynamics necessary for accurately quantifying species-specific connectivity.

In response to this challenge, models based on the connectivity of human-defined patterns of landcover, i.e., structural connectivity, assessing the connectivity of intact natural ecosystems irrespective of any species (Lumia et al., 2023), have been increasingly used (Theobald, 2013; Dickson et al., 2017; Staccione et al., 2022). Among these approaches, the Continuum Suitability Index (CSI) was developed for European mountainous areas (Affolter et al., 2011; Favilli et al., 2023), considering terrestrial ecosystems, including forests, wetlands and open land, rather than solely focusing on core areas and corridors. In particular, the CSI accounts for factors that alter ecosystems and considers the landscape as an ecological continuum – analogue to connectivity analysis based on a cost raster (Adriaensen et al., 2003). The main assumption of CSI is that areas with a low degree of human disturbance and modification tend to exhibit greater ecological connectivity (Hilty et al., 2020). In this regard, the CSI represents the permeability and suitability of the landscape in terms of ecological connectivity rather than focusing on the actual connectivity between areas via corridors and linkage zones. Thus, the CSI serves as an area-wide initial assessment of patches that either enhance or hinder ecological connectivity, marking the initial stage in the process of modelling connectivity.

The CSI was initially calculated for different pilot regions in the framework of the ECONNECT project (Affolter et al., 2011). In the Life Belt Alps Project, a European follow-up project of ECONNECT, the methodology was expanded to the macro-regional scale and the first comprehensive assessment of ecological connectivity in the transnational Alpine Convention area was conducted (Haller, 2016). A significant milestone in the application of the CSI was its implementation in the Interreg Alpine Space project, ALPBIONET2030. The project utilized the CSI, relying on five spatially explicit factors, to identify priority areas for the ecological continuum in the EUSALP (European Strategy for the Alpine Region) area (Plassmann et al., 2019). The methodology was further transferred to the Alpine-Dinaric Alps area within the Interreg ADRION project, DINALPCONNECT (Laner and Favilli, 2022a; Laner and Favilli, 2022b; Favilli et al., 2023), and used in combination with high spatial resolution data for Switzerland, i.e., "*Aktionsplan Biodiversität Schweiz*" (ABCH; Rossi et al., 2020a).

Despite the widespread application of the CSI approach across various projects, ranging from pilot regions to the macro-regional level, a thorough validation of this approach has not yet been carried out, and the selection of CSI factors partially lacks clarity and transparency. In this study, we therefore present in detail the development of CSI and its validation to ensure its accuracy and effectiveness in modelling ecological connectivity. Specifically, our objectives were: (1) to comprehensively describe the CSI methodology and the selection of its five main factors emerging from a literature review and expert workshops; (2) to assess the sensitivity and plausibility of the CSI approach by comparing CSI factors with threatened species presence in Switzerland, and; (3) to investigate the impact of different data sources and levels of spatial data precision on CSI results by comparing three different projects that share certain geographical areas. By enhancing our understanding of the straightforward CSI approach that can be applied to large-scale areas and multiple countries, our study facilitates the integration of ecological connectivity into spatial planning policies and decision-making processes (Perrin and Bertrand, 2019; Job et al., 2022).

2. Materials and methods

2.1. Study areas

To present the CSI approach and to test its sensitivity, plausibility and consistency, we used the results from three projects applying the CSI on mountain ranges in Europe, i.e., Alps and Dinaric Mountains (Fig. A1 and Table A2 in Appendix). In particular, the CSI approach presented in the next section was developed for the macro-region EUSALP (Fig. 1), which comprises the perimeter of the Alpine Convention and the surrounding areas, including the entire administrative regions that are part of the Alpine Convention (NUTS 2 regions in Italy and France, and Austria; NUTS 1 regions in Germany). In total, the EUSALP macro-region consists of 48 regions in 7 countries with about 80 million people and an area of 450,000 km^2. Population density considerably varies between urban areas surrounding the Alps and agglomerations in the inner-Alpine valleys or close to transport corridors compared to sparsely populated rural or high-altitude areas (>1,500 m a.s.l.). The second CSI application on the Dinaric Mountains was considering of the entire countries of Albania, Bosnia and Herzegovina, Croatia, Montenegro, and Slovenia, as well as three regions from north-east Italy, Carinthia (AT), and the central and western mainland of Greece. It consists of 274,981 km^2 with more than 23 million inhabitants. The third study where the CSI was used, considered the entire state territory of Switzerland.

2.2. Presentation of the Continuum Suitability Index (CSI)

The CSI was defined as a spatially explicit set of factors that determine the level of ecological connectivity of a predefined patch, considering both natural and anthropogenic characteristics of the landscape. In particular, the CSI was based on a multi-criteria weighted-overlay analysis (Malczewski, 2006), in which distinct factors were combined using a weighted linear combination. To define the relevant factors and their weights, a combination of literature review and expert workshops were employed. Following a systematic review and meta-analysis scheme, the scientific literature was reviewed using the search terms "("ecological connectivity") AND (influenc* OR impact OR factor OR effect)" and "("mean species abundance") AND (influenc* OR impact OR factor OR effect)" in the ISI Web of Knowledge. The search process was restricted to articles published online in the proximity of the last expert workshop (i.e., 2018), resulting in 210 articles. Subsequently, the articles were screened to guarantee that all articles met the research criteria. As a result, 44 articles were chosen (A1 in Appendix).

In addition to the literature review, three expert workshops, with approximately 60 participants in total, were held between 2011 and 2017. Experts from science, nature conservation, landscape planning, protected areas administration and public administration participated. Two of the expert workshops were held before the literature review, within the framework of the Interreg project ECONNECT (2008-11) and

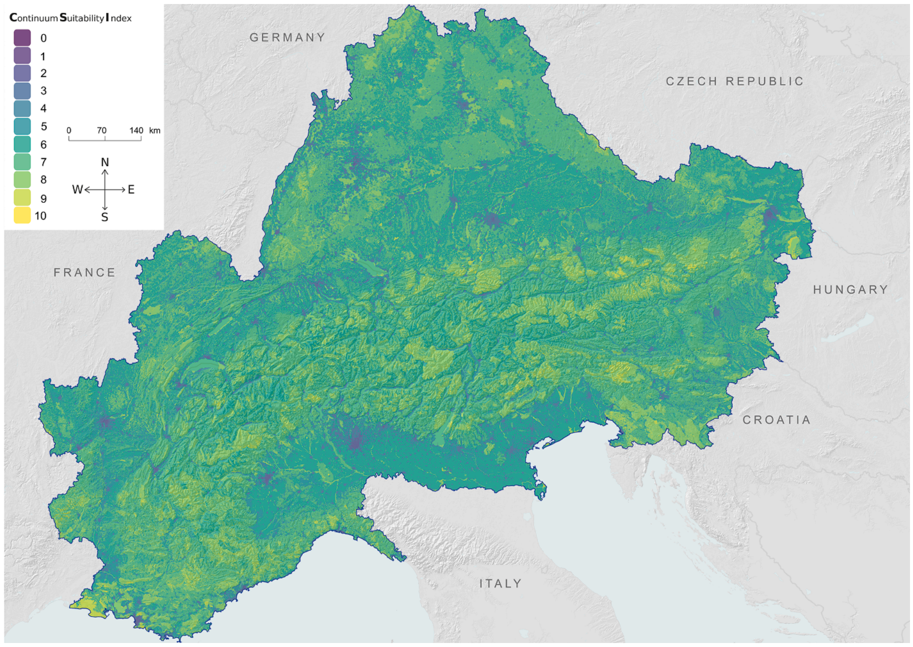

Fig. 1. Application of the Continuum Suitability Index (CSI) in the European Strategy for the Alpine Region area in the framework of the ALPBIONET2023 project. The CSI ranges from zero to ten (lowest to highest permeability). Data Source JAXA, SNP.

for a regional study in Grisons (2015), Switzerland. The third workshop, grounded on the literature review and documentation of the former workshops, took place in October 2017 in Trenta, Slovenia, with a total of 24 participants. In the workshops, the experts were asked to identify, check the feasibility and availability of, and weigh the relevant factors that determine ecological connectivity on a macro-regional level. The individual factors should complement each other by not including specific datasets more than once. The feasibility questions asked whether the defined problem could be presented sufficiently with the available data and whether the factor(s) could be represented in an adaptable way with varying datasets.

Five key CSI factors relevant at the macro-regional level were identified by collating the literature review and expert workshops: (1) Land use (LAN), (2) Environmental protection (ENV), (3) Population pressure (POP), (4) Fragmentation (FRA), and (5) Altitude and topography (TOP). Each category within all five factors was assigned a value between zero (lowest permeability) and ten (highest permeability) based on the literature review and results of expert workshops. In the following sections, the five factors will be briefly explained, together with suggested datasets for the EUSALP macro-regional level analysis and the factor value allocation scheme. In addition, we provide an example showcasing how the CSI was used to identify priority areas for ecological connectivity.

2.2.1. *Land use factor (LAN)*

The LAN factor represents the current land uses and their effect on ecological connectivity. Altering natural landscapes for human needs influences biodiversity and the functioning of ecosystems and, consequently, ecological connectivity (Foley et al., 2005; Metzger et al., 2006; de Baan et al., 2013; Teixeira et al., 2016). Urbanization as well as intensive agriculture are major threats to biodiversity and ecosystems (McKinney, 2002; Tsiafouli et al., 2015; Tuck et al., 2014), while unproductive or extensive agriculture may have the opposite effect (Evans et al., 2017; Kleijn et al., 2006; Wolff et al., 2001).

The European Corine Land Cover dataset (EEA, 2016), with a 100-metre spatial resolution, offers a macro-regional baseline for the LAN factor. The mean species abundance index values (Brink et al., 2007) were used as a basis to assign the Corine Land Cover 2012 Level 3 classes (EEA, 2016) values from zero to ten (Table 1). Brink et al. (2007) assigned fourteen land-cover/land-use classes categorized into seven group classes with a mean species abundance value from 0.05 (lowest for built- up areas or irrigated or drained land) to 1 (highest for undisturbed primary vegetation), based on the global biodiversity assessment model GLOBIO3. The resulting values were adapted to the regional circumstances based on the literature reviews and expert knowledge.

The LAN value assigned to coniferous forests forest was lower than for broad-leaved and mixed forests, as in many alpine countries the naturalness in coniferous forests is reduced due to spruce monocultures and plantations of fast-growing conifers. Nevertheless, for coniferous forests, it was assumed that those occurring inside areas where coniferous forests occur naturally have a higher likelihood of being in a more pristine coniferous forest state and were therefore valued with 7 instead of 6. The distinction has been made with the help of the Map of the Natural Vegetation of Europe (Bohn et al., 2003). Furthermore, the assumption was made that less accessible forests are used to a more limited extent and are therefore more natural. Poorly accessible forests were defined as forest pixels which exceed the 70th percentile of the altitudes of the surrounding 10 square kilometres of forested area from a digital elevation model (NASA et al., 2011). Less accessible forests were valued with 8.

2.2.2. *Environmental protection factor (ENV)*

The ENV factor reflects the legal protection status of the different protected areas (PAs), as a critical strategic element for conservation in all ecoregions worldwide (e.g., Ostermann, 1998; Saunders et al., 2002). Since the effectiveness of a PA is determined by its management (Jones et al., 2018), the experts assumed that stricter regulations (up to no use of the area allowed) would favour a more effective management and could therefore be used as a proxy for the effectiveness of protected areas (Table 2).

The World Database on Protected Areas (WDPA) (UNEP-WPMC, 2017) containing all protected areas listed by the European Environment Agency, the Natura 2000 sites and the nationally designated areas (CDDA) was used as the baseline for the ENV factor. However, since the WDPA varies among countries regarding correctness and completeness, complementary national and regional datasets were also consulted. A differentiation between varying levels of protection within national parks was not feasible due to the absence of a comprehensive spatial

Table 1
The assigned LAN factor values for Corine Land Cover version 18.5.1 dataset Level 3 classes (EEA, 2016).

Land cover class	Factor value (0–10)	Land cover class	Factor value (0–10)
1.1.1. Continuous urban fabric	0	3.1.1. Broad-leaved forest	7
1.1.2. Discontinuous urban fabric	0	3.1.2. Coniferous forest	6
1.2.1. Industrial or commercial units	0	3.1.3. Mixed forest	7
1.2.2. Road and rail networks and associated land	1	3.2.1. Natural grasslands	8
1.2.3. Port areas	1	3.2.2. Moors and heathland	10
1.2.4. Airports	0	3.2.3. Sclerophyllous vegetation	8
1.3.1. Mineral extraction sites	2	3.2.4. Transitional woodland-shrub	9
1.3.2. Dump sites	0	3.3.1. Beaches, dunes, sands	7
1.3.3. Construction sites	0	3.3.2. Bare rocks	7
1.4.1. Green urban areas	2	3.3.3. Sparsely vegetated areas	8
1.4.2. Sport and leisure facilities	2	3.3.4. Burnt areas	8
2.1.1. Non-irrigated arable land	4	3.3.5. Glaciers and perpetual snow	7
2.1.2. Permanently irrigated land	2	4.1.1. Inland marshes	10
2.1.3. Rice fields	4	4.1.2. Peat bogs	10
2.2.1. Vineyards	4	4.2.1. Salt marshes	10
2.2.2. Fruit trees and berry plantations	2	4.2.2. Salines	10
2.2.3. Olive groves	4	4.2.3. Intertidal flats	10
2.3.1. Pastures	5	5.1.1. Water courses	8
2.4.1. Annual crops associated with permanent crops	4	5.1.2. Water bodies	7
2.4.2. Complex cultivation patterns	2	5.2.1. Coastal lagoons	10
2.4.3. Land principally occupied by agriculture, with significant areas of natural vegetation	6	5.2.2. Estuaries	10
2.4.4. Agro-forestry areas	5	5.2.3. Sea and ocean	10

dataset across countries.

2.2.3. Population pressure factor (POP)

With the POP factor, human pressure on ecological connectivity is represented as a direct consequence of population density. Humans are seen as the main drivers of change in the state of ecological systems by the Millennium Ecosystem Assessment (2005), and the threat to biodiversity increases as human population density increases (Luck, 2007). Human population density impacts species richness, especially threatened and geographically restricted species. For the European Union, a population density grid disaggregated with CORINE landcover is available (Gallego, 2010). For the population density in Switzerland, the Swiss Geostat data 2015 (BfS, 2016) was used. Both datasets have a spatial resolution of 100 m.

Furthermore, the effect of human population density is not limited to settlements. Therefore, a kernel density estimation with a radius of 1500 m to the population density grid was applied. The new grid consisting of the maxima of both grids (human population density and kernel estimation) was then reclassified according to the developed classification scheme in Table 3.

2.2.4. Fragmentation factor (FRA)

Landscape fragmentation results in degraded remnant areas, with the degree of degradation mostly depending on the remnant area isolation and size (Saunders et al., 1991). Small areas in particular are

Table 2
The assigned ENV factor values for the World Database on Protected Areas classes, complemented with national datasets of different Alpine countries.

Legal protection status	Factor value (0–10)	Country	Protected area type(s)
Strict conservation status, no economic use	10	Austria	Primary forests, wilderness areas, natural monuments (IUCN Cat. Ib), special protection areas (IUCN Cat. Ib), Nature protection areas (IUCN Cat. Ia)
		France	Forest Nature Reserves (IUCN Cat. Ia), Nature Reserve in National Parks
		Germany	Bavaria: natural forest reserves
		Italy	Regional/Provincial Nature Reserves (IUCN Cat. Ia), State Nature Reserves (IUCN Cat. Ia)
		Liechtenstein	Nature protection areas, Ramsar Sites, forest reserves
		Slovenia	Nature reserves, strict nature reserves, natural monuments, Forest reserves (category I)
		Switzerland	Swiss National Park, Federal Inventory of Raised and Transition Bogs of National Importance
Protected areas with strictly regulated economic use	9	Austria	National Parks (core zone, special protection zone), steppingstones (natural forest network)
		France, Germany	National Parks (core zone)
		Italy	National Parks
		Slovenia	Triglav National Park zone 1 + 2, Forest reserves (category II)
		Switzerland	Nature discovery parks
Protected areas with legal restraints I	7	Austria	Protected natural areas (IUCN Cat. IV), protected landscape features (IUCN Cat. IV), plant sanctuary (IUCN Cat. IV), sanctuary, special protection area (IUCN Cat. IV), natural monument (IUCN Cat. IV), protected habitat, ecological development area
		France	Areas established under the Arrête de protection de biotope, Biological reserve (IUCN Cat. IV), National nature reserve, land acquired by the Conservatoire du littoral, land acquired by the Conservatoire d'espaces naturels
		Germany	Nature Conservation areas, Natural Forest reserves
		Italy	Other Protected Natural Regional Areas (IUCN Cat. IV), Int. significance

(continued on next page)

Table 2 (*continued*)

Legal protection status	Factor value (0–10)	Country	Protected area type(s)
			Natural Marine Area, Regional/Provincial Nature Park (IUCN Cat. IV), Ramsar Site, Natural Marine Reserve and Natural Protected Marine Area, Regional/ Provincial Nature Reserve (IUCN Cat. IV), State Nature Reserve (IUCN Cat. IV), Natura 2000 (Habitat & Bird)
		Liechtenstein	Forest reserves
		Slovenia	Regional Parks, Landscape Parks, Triglav National Park zone 3, Protective forests
		Switzerland	Federal Inventories of Swiss Game Reserves, Reserves for Waterbirds and Migratory Birds of international and national importance, Floodplains of National Importance, Fens of National Importance, Amphibian Spawning Sites of National Importance, Dry Grasslands of National Importance, Emerald sites, Pro Natura: Nature Preserves
Protected areas with legal restraints II	6	Austria	Natura 2000, protected landscape features (IUCN Cat. III), Nature monument (IUCN Cat. III), protected natural formations of local importance, protected biotopes
		France	National hunting and wildlife reserves, Natura 2000
		Germany	Specially Protected Habitats under Section 30 of the Federal Nature Conservation Act, Natura 2000, Biosphere reserve
		Italy	Other Protected Natural Regional Areas (IUCN Cat. V), Regional/ Provincial Nature Park (IUCN Cat. V), Regional/ Provincial Nature Reserve (IUCN Cat. V), World Heritage Site
		Slovenia	Natura 2000
Protected areas without legal restraints AND / OR Protected areas where the management serves the sustainable development of natural ecosystems	5	Austria	Protected landscape areas, protected nature and landscape areas, nature parks, protected landscape features (IUCN Cat. V), biosphere reserves, Ramsar Site, local reserves, protected areas for scenery
		France	National Park buffer zones, regional nature parks, Ramsar Site,

Table 2 (*continued*)

Legal protection status	Factor value (0–10)	Country	Protected area type(s)
			Specially Protected Areas of Mediterranean Importance (Barcelona convention), UNESCO MAB Biosphere Reserves
		Germany	Landscape Protection Areas, Nature Parks, Nature Monuments, Protected Landscape Elements (Bavaria)
		Italy	Other Protected Natural Regional Areas (IUCN Cat. III),
		Liechtenstein	Plant nature reserves, landscape protection areas
		Slovenia	Ecological important areas
		Switzerland	Ramsar Sites, World Heritage Sites, regional nature parks, Federal Inventory of Landscapes and Natural Monuments, Federal Inventory of Mire Landscapes of Particular Beauty and National Significance, Biosphere reservation
No protection	0		

Table 3
The assigned POP factor values for eleven human population density classes.

Inhabitants per hectare	Factor value
≤ 2	10
2–5	9
5–9	8
9–16	7
16–26	6
26–43	5
43–67	4
67–106	3
106–172	2
172–300	1
> 300	0

increasingly affected over time by decreasing essential ecosystem functions (Haddad et al., 2015).

To measure the fragmentation, the effective mesh or an equivalent index like the Landscape Division Index (Jaeger, 2000) size are widely used. To omit boundary problems and mitigate the impact of the investigated areas' size, the cross-boundary concept proposed by Moser et al. (2007) should be applied. The cross-boundary concept can be adapted to a regular grid instead of administrative units. In ALPBIONET2030, FRA factor values were assigned to ten classes of effective mesh density (Table 4). The mesh sizes were calculated on a regular grid with a cell size of four square kilometres and by considering the fifty square kilometre area surrounding the cell. To define the fragmenting elements, the EuroGlobalMap dataset (IGN, 2016) including railways, motorways and trunks at primary, secondary and tertiary levels was used. The four square kilometre area was used to optimize the alpine-wide processing.

2.2.5. *Topography factor (TOP)*

Even though it is a non-anthropogenic factor, topography was

Table 4
The assigned FRA factor values to eleven effective mesh density classes.

Effective mesh density	Factor value (0–10)
≤ 1	10
1–6	9
6–20	8
20–37	7
37–60	6
60–98	5
98–170	4
170–340	3
340–960	2
960–10,000	1
$>$ 10,000	0

Table 5
The assigned TOP factor values for altitude and slope classes.

Altitude (m a.s.l.)	Factor value (0–10)	Slope (°)	Factor value (0–10)
$\leq$ 1500	10	$\leq$ 30°	10
1500–1675	9	30-40°	7
1675–1850	8	40-45°	5
1850–2025	7	$>$ 45°	3
2025–2200	6		
2200–2375	5		
2375–2550	4		
2550–2725	3		
2725–2900	2		
$>$ 2900	1		

considered because high alpine areas act as a barrier for many species, and steep rock walls may be insurmountable obstacles (Meyer and Thaler, 1995; Bertuzzo et al., 2016). Furthermore, opportunities for life are scarcer with increasing altitude (Körner, 2007). Overall, the TOP factor highlights the potential of lower elevations for stronger ecological connectivity and accounts for possible obstacles in movement processes given to steep terrains.

To calculate the TOP factor, slope and altitude information can be derived from a digital elevation model and reclassified according to the classification scheme developed for mountainous ranges in Table 5. The TOP is the mean of both slope and altitude values. A freely available ASTER Global Digital Elevation Model Version 2 (NASA et al., 2011) resampled at 100 m was used for the TOP factor in ALPBIONET2030. In flatter study areas, the TOP could be neglected as it was primarily introduced to mitigate the issue of very high and remote mountain peaks having excessively high CSI values, despite their marginal significance for ecological connectivity.

2.2.6. The CSI for a strategic connectivity area approach

The overall CSI value for each cell in a raster grid was calculated as the expert-defined weighted mean of the five factor values transposed into raster grids (Eq. (1)):

$$CSI = \frac{2*LAN + 2*POP + ENV + FRA + TOP}{7} \quad (1)$$

The decision to assign double weight to both LAN and TOP emerged as a result of the expert workshops, recognizing their substantial impact on ecological connectivity. The CSI was further classified into three qualitative classes for pinpointing priority areas for ecological connectivity on a macro-regional level, i.e., the Strategic Alpine Connectivity Area (SACA) approach. As proposed by Haller (2016), CSI thresholds were identified by the experts and areas were grouped into three categories accordingly. This approach follows the concept of global conditions for biodiversity conservation by Locke et al. (2019) which stipulates the three categories of “cities and farms”, “shared lands” and “large wild areas”. Categories were differentiated according to the status of their ecological connectivity and the type of action required for biodiversity conservation and sustainable use:

- **SACA 1:** Ecological conservation areas with considerable space for connectivity. They should be protected to avoid negative impacts on ecological functioning. SACA 1 were defined as areas having a CSI $\geq$ 8 and a size of at least 100 ha.
- **SACA 2:** Ecological intervention areas that represent important links between SACA 1. In these areas, improvement and restoration measures are needed. SACA 2 have been modelled using the electric circuit theory-based simulator Circuitscape (Shah and McRae, 2008; McRae et al., 2008), with the inverse CSI as the landscape resistance, SACA 1 as the electric source and SACA 3 as resistance to ground (see Appendix Section A2 for a detailed description of the method). Hence, SACA 2 may exhibit a CSI value ranging from higher than five to typically smaller than eight.
- **SACA 3:** Connectivity restoration areas. In these areas, the fragmentation has already progressed so far that only mitigation is possible. They represent important barriers between SACA 1 and were defined as areas having CSI $\leq$ 5.

Areas without classification are characterized by CSI $>$ 5 but are not classified as SACA2 or SACA 1. These areas do not represent ecological corridors between SACA 1, are too far away from SACA 1 (i.e., no current flow in the Circuitscape modelling), or are too small for being a SACA 1. For the EUSALP perimeter (Fig. 2), most of SACA1 areas identified in the ALPBIONET project were located within the inner Alpine Space in higher altitudes, while in the flatlands on the outer Alpine Space, they were smaller and less present. SACA1 areas covered 11,1% of the perimeter, SACA2 areas corresponded to 58,6% and SACA3 areas to 9,7%. 91 % of the SACA1 areas overlaid with protected areas from any category specified in Table 2.

The SACA approach is an example of how the CSI can be used to model connectivity, offering an area-wide overview of the ecological connectivity and support tool in landscape planning, i.e., zoning (Plassmann et al., 2019). For a more targeted approach to prioritize conservation and restoration actions, the CSI can be further used in combination with a least-cost path model to identify existing and potential corridors (Favilli et al., 2023).

2.3. Sensitivity, plausibility and consistency analysis of the CSI

All three projects (Appendix Table A2) used to test the sensitivity, plausibility and consistency of the CSI, calculated the CSI following Eq. (1). However, the projects differed in data sources, spatial precision, calculation of FRA and the classifications of CSI values for the definition of SACA areas. The sensitivity and plausibility analyses were performed to identify the most influential factors on the CSI and test the robustness of the approach. In particular, we: (1) performed a single-parameter sensitivity analysis; (2) compared the CSI to red-list species presence data; and (3) compared the spatially overlapping CSI results between the projects.

2.3.1. Sensitivity analysis of the CSI

We performed a sensitivity analysis by varying the input factors for the 100-metre resolution ALPBIONET2030 CSI one at a time and subsequently analysed the model output. The so-performed sensitivity analysis is suited to single-parameter evaluations such as factor weight changes (Chen et al., 2010; de Brito et al., 2019, Fildes et al., 2022). The method consisted of a series of model runs, where the weight of the factor under investigation was altered using a small increment and the weights of the other factors adjusted proportionally (i.e., all factor weights had to sum up to 1). We refer to Fildes et al. (2022) for a detailed method description. We used a small incremental change of ±2 % and a range of percent change of ±100 %. Thus, the total number of model runs was 501 (100 runs for each of the five factors, plus the base run represented in Eq. (1). For each model run, we tracked the number of CSI

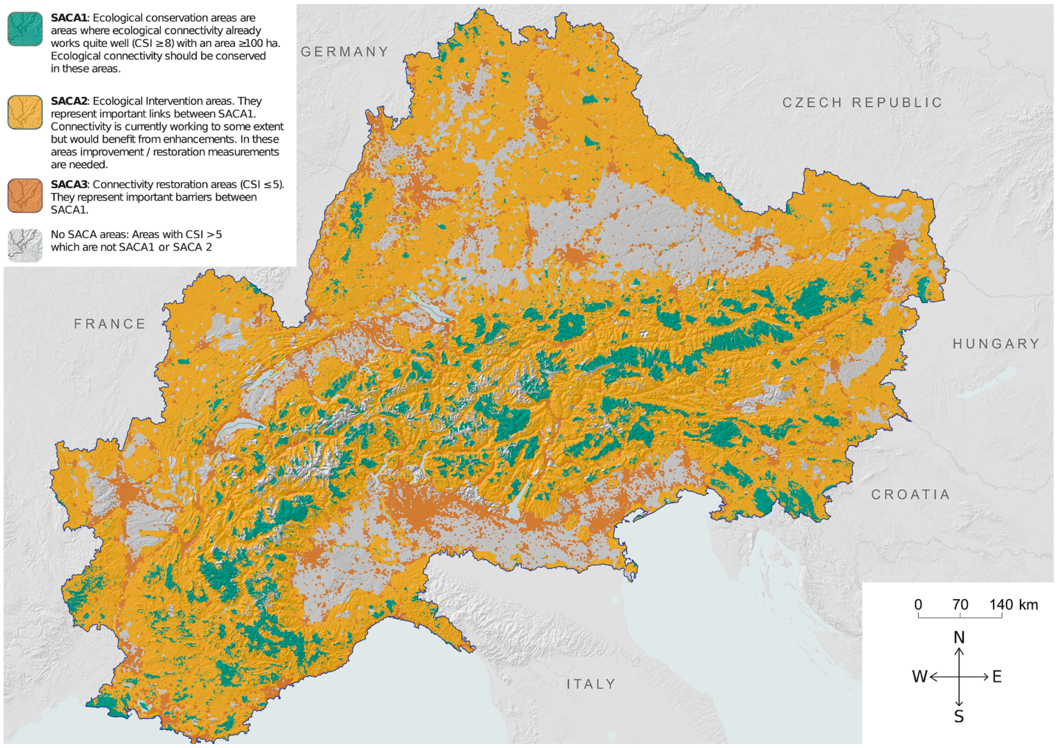

Fig. 2. Strategic Alpine Connectivity Areas (SACA) based on the Continuum Suitability Index (CSI) and circuit theory (optimistic approach in Appendix A2) over the EU Strategy for the Alpine Region perimeter, resulting from the ALPBIONET2023 project. Data Source JAXA, SNP.

values per cell differing from the base weight run. The sensitivity analysis was implemented in R *4.2.0* (R Core Team, 2022) using the terra package *v1.7.3* (Hijmans et al., 2022).

2.3.2. Comparing the CSI to red-list species presence

True validation of the CSI would have required movement data to assess how well species move through the landscape. Lacking this, we conducted a plausibility-check by comparing the CSI indicators to species presence data. The aim of the plausibility-check was to find connections between the CSI indicators and the actual species presence and not the potential habitat suitability (Wade et al., 2015). To do so, we modelled species presence data with the CSI factors 100-metre resolution from the ALPBIONET2030 project. We used the presence data of threatened species (i.e., red-listed) in Switzerland for 15 years (2003–2018), obtained from the Swiss national data centres 'Swissbryophytes', 'Info Flora' and 'Info Fauna'. The individual data centres consist of systematic monitoring data and occasional observations from various projects. Together, they are part of the national data centre for biodiversity initiated by the Federal Office for the Environment (FOEN). All plants and animals with a red-list priority of four and higher and more than ten presence data points were used. We specifically used red-list species given their increased vulnerability, making them a valuable indicator of ecosystem integrity. After filtering, the dataset included 710 species with 88,895 presence records. We generated absence data per species according to the number of presence points times ten randomly distributed inside Switzerland. A binomial generalized linear model was created for each species with species presence or absence as the response variable and the CSI individual factors as predictors. We calculated the proportion of deviance explained by each model (D^2, Dsquared function of the modEvA *v3.5* package in R) and the relative variable importance of each predictor (varImp function of the caret *v6.0-93* package in R).

2.3.3. Consistency and robustness analysis of the CSI

To check the CSI's ability to maintain consistency across different data sources, we compared the CSI of the DINALPCONNECT and ALPBIONET2030 projects within their overlapping region. These areas included Slovenia and the north-western part of Italy including the regions of Friuli–Venezia Giulia, Veneto and Trentino–Alto Adige. Both datasets considered a spatial resolution of 100 m, but the CSI values of the two different projects were calculated by starting from different data sources and the revised FRA factor in the DINALPCONNECT project (Laner and Favilli, 2022a).

To compare the values of CSI with two different levels of spatial data precision, we used the area of Switzerland in the ALPBIONET2030 and the ABCH projects: The ALPBIONET2030 project harmonised the raster dataset of each factor to the level of detail of the Corine Land Cover, which has a scale of 1:100,000, with a minimum cartographic unit of 25 ha and a cell size of 100 by 100 m. The level of detail for the ABCH project was based on the large-scale topographic landscape model SwissTLM with a scale of 1:10,000, and a cell size of five by five metres. Within Switzerland, each 100 by 100 m CSI pixel from the ALPBIONET2030 project was resampled with the nearest neighbour technique into five by five metre pixels and compared to the ABCH project. The resampling and difference between the CSI values were calculated using the *Raster Calculator* tool in ArcGIS desktop *v10.7*. To compare the CSI layers of the different projects, we also calculated the Pearson correlation with the "Band Collection Statistics" tool in ArcGIS desktop *v10.7*.

3. Results

3.1. Sensitivity of the CSI to its different factors

The results from the weight changes showed different results per factor (Fig. 3). The POP had the largest influence on the CSI with respect to weight changes. Only 6 % of the cells remained unchanged when the POP weight was changed by ±100 % compared with the base run. FRA had the lowest influence on the CSI results, with over 70 % of the cells showing the same CSI value when its weight was changed by ±100 %. Weight changes of the ENV, LAN and TOP showed an intermediate influence on the CSI values.

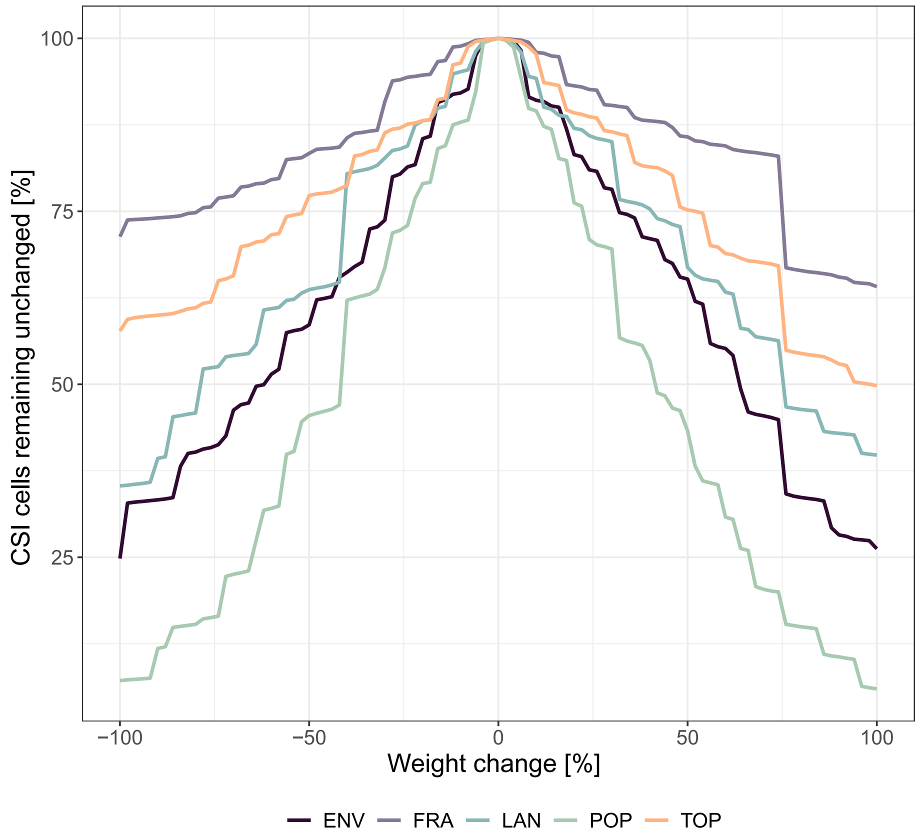

Fig. 3. Percentage of the Continuum Suitability Index cells that remained unchanged after each weight increment per factor starting from the main base weight (LAN and POP with a weight of 2/7 and the other factors with a weight of 1/7).

3.2. Amount of red-list species presence explained by CSI factors

On average, the models built using the CSI factors explained 32 % of the deviance in the distribution of red-list species. Similar levels of deviance were explained on average for the taxonomic kingdom of *Plantae* ($D^2 = 0.33$, species n = 630) and *Animalia* ($D^2 = 0.27$, species n = 80). The lowest deviance was found for the taxonomic class of *Leucodontaceae* ($D^2 = 0.11$, species n = 1) and the highest for *Sphagnopsida* ($D^2 = 0.48$, species n = 5, Fig. 4a). On average, the relative variable importance was the highest for ENV (31 %) followed by FRA (22 %), LAN (20 %), TOP (15 %) and POP (12 %, Fig. 4b).

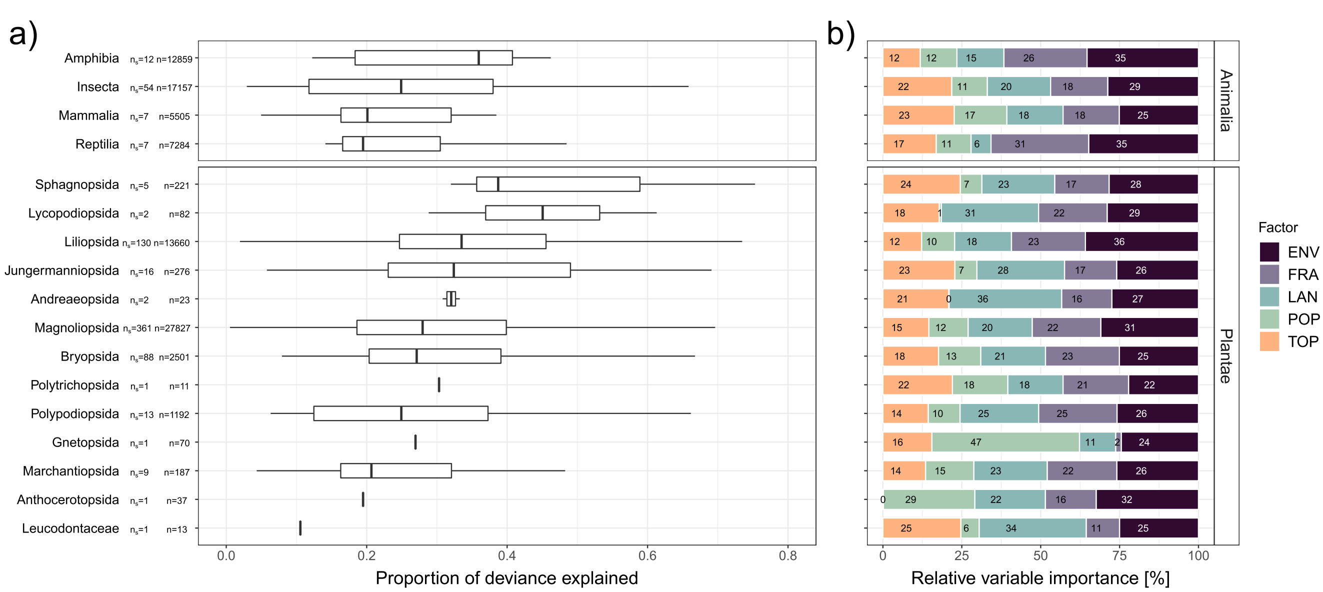

Fig. 4. (a) Model proportion of explained deviance grouped by taxonomic class with n indicating the presence records in the dataset and n_s indicating the number of species. Each box shows the middle 50% of the data points, the whiskers represent the range of the rest of the data points excluding outliers, and the vertical line in each box indicates the data median. Outliers defined as values that are larger than 1.5 times the interquartile range away from the top or bottom edges of each box are not displayed. (b) Average proportions of relative variable importance for each CSI factor, grouped by taxonomic class.

3.3. Difference in CSI and connectivity areas between applications

When comparing the CSI of the DINALPCONNECT with the ALPBIONET2030, roughly 60 % of the CSI values demonstrated consistency across the two projects, whereas 96 % of the cells only exhibited a variation of one unit (Table A3 in Appendix). Furthermore, there was a nearly equal distribution of positive and negative differences among cells.

The analysis revealed a strong positive linear relationship, with a Pearson correlation coefficient of 0.83 ($p < 0.001$) between the two layers.

When comparing the SACA1 areas of the two projects, it was evident that in the DINALPCONNECT project, these areas were typically larger (Fig. 5). The SACA 1 areas from the ALPBIONET2030 project were found to overlap by 85 % with those of the DINALPCONNECT project. Only in Slovenia, the SACA1 of the ALPBIONET2030 project covered larger areas. Overall, the SACA1 areas of the DINALPCONNECT project had a 65 % overlap with those of the ALPBIONET2030 project.

When comparing the CSI of the ABCH with the ALPBIONET2030, approximately 90 % of the values fell within the range of minus one to plus one, while 99 % fell within the range of minus two to plus two (Table A4 in Appendix). Hence, CSI values from the ALPBIONET2030 project and the ABCH project varied by no more than two values while comparing the same cell. CSI values of the ALPBIONET2030 project were generally higher and with a higher level of detail than those of the ABCH project. The correlation matrix for the two layers of the ALPBIONET2030 and ABCH projects showed a Pearson correlation value of 0.78 ($p < 0.001$), indicating a strong positive linear relationship.

The comparison of SACA1 areas of the ALPBIONET2030 project and the C1 areas of the ABCH project showed significant differences in the overlap, while they have almost the same total size, ranging from 4,710 (ABCH) to 4,798 square kilometres (C1). Only 46 % of C1 overlapped with SACA1 areas.

4. Discussion

4.1. CSI methodology for ecological connectivity

Consistent with previous studies, the CSI approach employed the level of human pressure as an indicator of ecological connectivity and habitat condition (Dickson et al., 2017; Kennedy et al., 2019). The factors used in the CSI methodology are in line with the three ecological objectives of connectivity proposed by Ferretti and Pomarico (2013), including minimization of human pressure, consideration of biotic factors and physical environment. In particular, the first objective is considered by the factors POP and LAN, the second one is considered by ENV and the third one is considered through the FRA and TOP. In line with the methodology proposed by Kennedy et al. (2019), the CSI includes human stressors, such as human settlement and land use to delineate spatial categories with different levels of landscape permeability. Using such factors also enables the calculations of the CSI for future scenarios, involving changes in land use intensity, along with a potential increase in population density.

Similar to the connectivity areas derived from the CSI, previous studies have used the resistance matrix to model landscape connectivity. For example, Dickson et al. (2017) applied circuit theory between protected areas in the western United States utilizing a resistance matrix derived from human stressors. Specifically, their model is based on the human modification factors of Theobald (2013), who developed a "parsimonious set of stressors using an existing framework to minimize redundancy and overlap" (p. 1859). The CSI approach also employs a minimal set of human stress factors but was used to model the ecological connections that extend beyond the boundaries of protected areas.

4.2. Practical suggestions for the CSI factors

Our sensitivity and plausibility analyses offer practical suggestions and considerations for CSI application. First, FRA was partially related

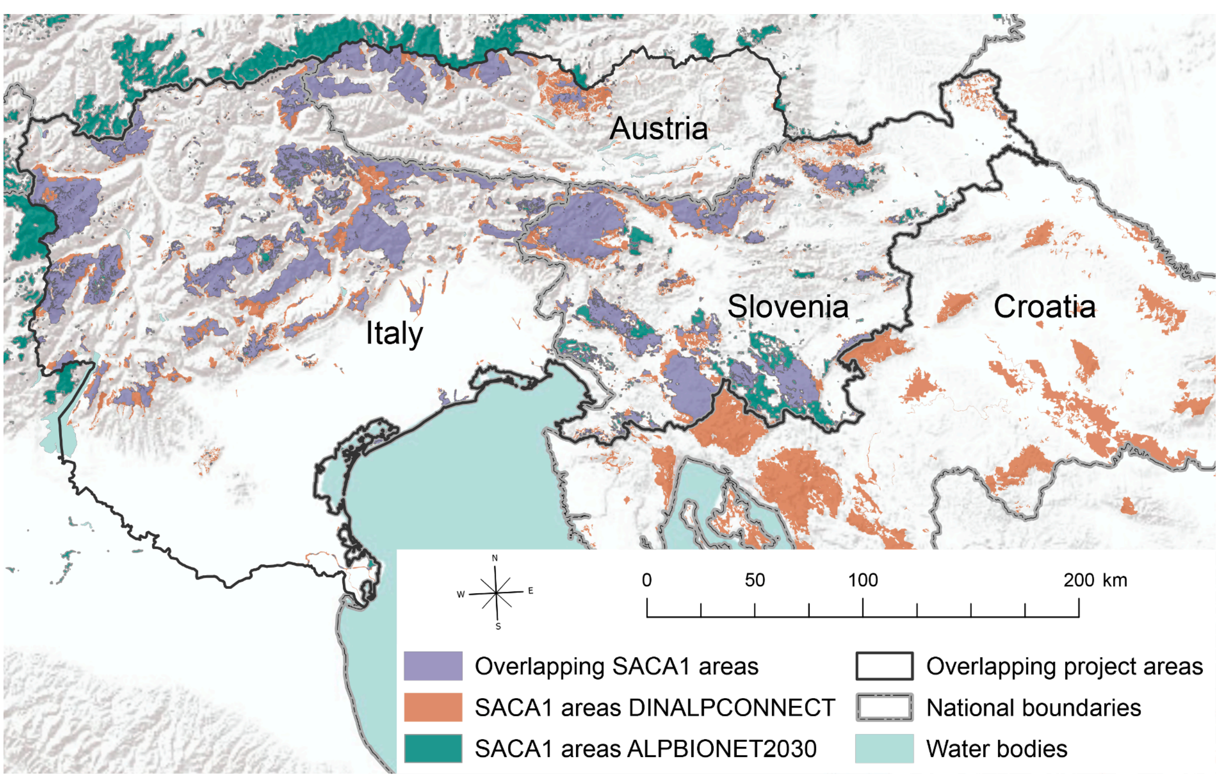

Fig. 5. Strategic Alpine Connectivity Area (SACA) of category one within the overlapping region of the ALPBIONET2030 and DINALPCONNECT projects. Data source for Basemap: Esri, USGS, NOAA.

to the other factors, as suggested by our sensitivity analysis (Section 3.1). While the FRA was an important factor in explaining the presence of red-list species (Section 3.2), changing its weights only marginally influenced the CSI-values. In line with previous studies claiming that land use intensity and population density are significant causes of land fragmentation (Foley et al., 2005; Liu et al., 2016), the highest degree of fragmentation in the Alps occurs within densely populated areas or where intensive agriculture is practised. However, it is worth considering that the marginality of FRA may also be linked to the limited number of fragmenting elements and coarse spatial resolution used in the ALPBIONET2030 project. In future applications, it could be therefore beneficial to use a fragmentation layer with a higher level of detail, such as the now available FGA2-S dataset from the European Environment Agency (EEA, 2019). The dataset provides the effective mesh density with an accuracy of 100 m for 39 European countries, considering not only the road network, but also railway lines and urbanised areas as fragmenting elements. As demonstrated by the moderate correlation of FGA2-S dataset with the FRA of ALPBIONET2030 (Appendix Section A4), using a fragmentation dataset with a higher level of detail could lead to slightly different results. Second, the POP factor implemented in the three analysed projects focused on settlements and their proximity, which may have limited relevance for endangered species, as shown by the low deviance explained for red-listed species. As currently implemented, the POP factor failed to account for human activities in areas with low settlement density (e.g., ski slopes), potentially leading to overestimated CSI values in these areas. To address these limitations, future applications of the CSI should consider expanding the influence of population density to include human recreational activities that occur at varying distances from inhabited areas (Corradini et al., 2021). By doing so, it would be possible to capture the broader impact of human presence and activities on the landscape and better inform conservation planning efforts. Third, the weighting of the ENV factor may have been undervalued during the expert workshops, particularly when considering its ability to predict the presence of red-listed species. However, if the objective of the CSI is to identify areas for protection, it may be preferable to place less emphasis on the existing protection status. Additionally, it is crucial to consider that the management practices of protected areas can vary significantly between countries and regions (Leverington et al., 2010), making the ENV factor challenging to harmonize and inconsistent on large spatial extents. Therefore, careful consideration of the appropriate use and weighting of the ENV factor should be given in future applications of the CSI.

4.3. CSI results are consistent over multiple projects

The comparison of different macro-regional projects showed significant differences in the derived products of the CSI, such as the SACA1 areas. Notably, inconsistencies are particularly evident when comparing studies conducted using varying levels of spatial detail. Upon visually examining the resulting maps, it becomes apparent that C1 areas (i.e., equivalent to SACA 1 for the ABCH project) are less compact and more scattered in space than SACA1 areas from the ALPBIONET2030 project. This discrepancy can be explained by the different definitions of minimum size used in the respective projects. In the ALPBIONET2030 project, SACA1 areas had a minimum size of 100 ha, whereas the ABCH project defined C1 areas with a minimum size of 0.25 ha. Notably, C1 areas often fall outside the boundaries of SACA1 areas. The variation could be due to the availability of more precise barrier data when operating at a higher level of detail. Thus, the selection of suitable levels of detail and thresholds should align with the specific scope of the analysis. Nevertheless, it is important to highlight that the total surface areas of SACA1 and C1 areas within Switzerland are almost identical. The comparison of CSI values showed congruent values with small variations, which highlights the consistent application of the CSI approach, despite slight variations in the fragmentation factor calculation and the use of different datasets to assess population pressure. Collectively, these results demonstrate the robustness of the CSI and its potential for replication in other study regions.

4.4. Limitations associated with the use of the CSI approach

When utilizing the CSI approach, it is imperative to acknowledge that the CSI is susceptible to uncertainties stemming from various sources. These encompass the selection, classification, and weighting of factors, as well as the availability, level of detail and accuracy of the underlying data. In addressing these uncertainties, a multi-step approach involving a prior literature review, as employed in the development of CSI and by previous studies (e.g., Scolozzi and Geneletti, 2012), can help mitigate subjective expert opinions. To further enhance the quantification of uncertainties, future research employing the CSI may consider generating uncertainty maps by computing the standard deviation of multiple runs with altered weighting factors (Section 4.1), as suggested by Fildes et al. (2022).

It is worth noting that the structural approach presented herein does not account for habitat or species distribution data. Specifically, the calculation of SACA2 areas from the CSI, designed to ensure connectivity between SACA1 areas, does not consider the diverse types of habitats and species present within different SACA1 areas. This oversight could potentially lead to the implementation of connectivity measures connecting habitats of lower ecological significance (Van der Sluis et al., 2004). Consequently, the development of precise connectivity measures may necessitate the inclusion of habitats and species information.

Despite the strength of the CSI approach in terms of data accessibility through macro-regional repositories, data availability remains a limiting factor for certain essential variables. For instance, tourism demand and leisure activities significantly contribute to human pressure on ecosystems (Mason, 2003), but complete spatial data coverage for those factors at the macro-regional level is often lacking. The data availability problem arises also when it comes to varying protection levels within national parks. Additionally, the model does not incorporate considerations for water availability, a crucial factor for wildlife species, especially in regions with water scarcity, such as southern regions in Europe. A possible solution was proposed in the DINALPCONNECT project by assigning a higher value to water bodies within the land use factor (Laner and Favilli, 2022a).

4.5. Future perspective: Species movement and remote sensing data

Further research is crucial for validating the CSI or similar landscape permeability methods, expanding beyond the use of species occurrence data to incorporate species movement data. Such validation could provide valuable insights into the reliability of these methods, contributing to a better understanding and management of ecological networks for nature conservation and landscape planning. Additionally, ecological connectivity analyses should also consider the conservation needs of less conspicuous organisms, such as invertebrates, since they significantly impact ecosystem functioning (Risch et al., 2018).

Future applications of the CSI approach should take advantage of the inclusion of additional geographical data, such as land use intensity (e.g., high nature value farming), touristic and leisure activities, light, noise and air pollution. In particular, the CSI approach could benefit from the increasing accessibility of remote sensing data. Spaceborne remote sensing enables more precise estimations of land use, surpassing the limitations of categorical variables like those used with CORINE land cover, by estimating vegetation traits, the frequency of mowing events and anthropogenic forest disturbance (e.g., Senf and Seidl, 2021; Rossi et al., 2020b; Schwieder et al., 2022; Marsoner et al., 2023). Moreover, remote sensing data could facilitate the inclusion of air and land pollution information in the quantification of anthropogenic factors that alter the ecosystems and their ecological connectivity (Holloway et al., 2021).

5. Conclusion

In this study, we presented and assessed the CSI, a landscape permeability model for structural connectivity, which was conceptualized to map important transnational ecological conservation and intervention areas for restoration of ecological connectivity. By elucidating the rationale behind the selection of the CSI main factors, emphasizing their significance in evaluating ecological connectivity, and the results of our plausibility and sensitivity analyses, we contributed to a comprehensive understanding of the potential and limitations associated with the CSI approach in addressing the preservation and restoration of ecological networks.

Collectively, our results indicate the promise of the CSI method and its derived products to offer a simplified approach to pinpoint areas and formulate guidelines for effectively preserving and restoring ecological networks at transnational, national, and regional scales. Therefore, the CSI holds potential for application in various European contexts, extending beyond mountainous regions.

CRediT authorship contribution statement

Peter Laner: Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Christian Rossi:** Writing – original draft, Visualization, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Rachel Luethi:** Writing – review & editing, Funding acquisition, Formal analysis, Conceptualization. **Filippo Favilli:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Irena Bertoncelj:** Writing – review & editing, Funding acquisition, Conceptualization. **Guido Plassmann:** Writing – review & editing, Funding acquisition, Conceptualization. **Rudolf M. Haller:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The datasets generated and analysed in the study are available from the corresponding author upon request. Data from different CSI projects can be visualised at https://www.jecami.eu/.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.112145.

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