

RESEARCH ARTICLE

Potential effect of managing connectivity to contain disease spread among free-ranging wild boar (*Sus scrofa*) in disparate landscapes

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Abstract

1. Landscape connectivity is a major factor shaping the spread of pathogens in wildlife populations. By managing connectivity, transmission pathways can be broken and disease spread be contained, particularly in the early phases of an outbreak. Having witnessed recent outbreaks of African Swine Fever in free-ranging wild boar (*Sus scrofa*) in Belgium, Germany and Italy, offices for disease control are on the alert also in other western European countries.
2. This study investigates the potential effect of managing landscape connectivity to contain disease spread among free-ranging wild boar in disparate landscapes. It involves research into (1) the ease with which wildlife corridors can be blocked for wild boar, (2) the connectivity of wild boar habitat and (3) the impact of landscape fragmentation on connectivity management. This is addressed by carrying out GIS analyses and performing graph operations on the wild boar networks in different biogeographical regions of Switzerland.
3. The results of doing research into the three above-mentioned objects show that, regarding the first, most wildlife corridors are hard to block for wild boar, because their features or location make fencing difficult. Regarding the second, the wild boar habitat is connected. Opening wildlife passages that are currently under construction may allow wild boar to disperse to hitherto uncolonized areas. Regarding the third, all wild boar networks could be partially decomposed by blocking the easy to block corridors and closing the passages. Network decomposition would be easiest to achieve in the region where the built infrastructure is most abundant. All over Switzerland, the potential epidemic size could be reduced by 25% when blocking the minimal set of corridors and passages that cut the networks to non-decomposable components.
4. This study suggests that (a) combining connectivity analysis with fragmentation analysis is key to explaining why a specific measure of disease containment is more effective in one landscape than in the other, (b) complementing the permeability

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model with a species distribution model is essential to identify connected habitat patches for the species of concern and (c) connectivity metrics should consider also the surface area of occupied habitat patches and relative abundance of the species of concern.

KEYWORDS

African Swine Fever, disease management, habitat connectivity, landscape configuration, wild boar

1 | INTRODUCTION

The movement of wildlife in the landscape is important for many ecological processes to preserve genetic diversity and resilience (Keeley et al., 2021). However, such movement can also provide ecosystem disservices such as facilitating invasive species expansion and disease spread (Mitchell et al., 2013; White et al., 2018). Connected landscapes may exacerbate the spread of a pathogen in a population, because infected hosts can come in contact with susceptible hosts more easily than in disconnected ones (Fountain-Jones et al., 2021; Nobert et al., 2016). This is particularly true if one of the hosts is a generalist species, which can travel long distances in both natural and anthropogenic environments (Boitani et al., 1994; Kotulski & König, 2008). For disease management it is important to know whether and to what extent connectivity can be managed to break transmission pathways and contain disease spread when needed. Managing connectivity may be particularly powerful in the early phases of an outbreak, suggesting there should be a readiness to act already before a disease emerges (Rahel, 2013; Silk et al., 2019).

In western Europe, the recent outbreaks of African Swine Fever (ASF) in wild boar (*Sus scrofa*) in Belgium, Germany and Italy have put offices for disease control on the alert. ASF is a highly lethal haemorrhagic disease in both wild and domesticated suids. The ASF virus can be transmitted by direct contact with infected animals or indirectly via contaminated food, bedding, clothes or equipment. Indirect transmission gives rise to the 'human factor' which was regarded key to the transmission path in the Belgium outbreak (Morelle et al., 2019). Conversely, direct contact with wild boar at the German-Polish border was considered the dominant transmission mode of the outbreak in Germany (Landwirtschaftsverlag, 2020). Some suggested strategies to contain ASF include fencing and wild boar eradication (Mysterud & Rolandsen, 2019), zoning (Giacometti, 2003), increasing surveillance and biosecurity measures in farms (Stauffer et al., 2022) and carcasses removal (Morelle et al., 2019).

This study adds to related work by investigating the potential effect of managing landscape connectivity to contain disease spread among free-ranging wild boar in disparate landscapes. This involves research into (1) the ease with which *wildlife corridors* can be blocked for wild boar, (2) the connectivity of the *wild boar habitat* and (3) the impact of *landscape fragmentation* on connectivity management. To manage landscape connectivity, it first is fundamental to know which corridors can be blocked easily and which ones cannot. Second, only

if wildlife passages connect the habitat of wild boar can their closing be expected to have an effect on the spread of a disease. Finally, the effect of managing landscape connectivity to contain disease spread may interact with the degree of fragmentation by artificial surfaces, for instance. Wildlife corridors and wildlife passages are two key terms used in this study. *Wildlife corridors* are undisturbed land that connect natural habitats separated by barriers, often motorways where these lead over a viaduct or through a tunnel (Lindenmayer & Nix, 1993). *Wildlife passages* are man-made under- or overpasses constructed in such a way that wildlife is encouraged to use them, for instance, to cross motorways (Hirschi, 2021). There is limited research on managing connectivity to prevent the spread of non-native species or diseases in ecosystems (Mysterud et al., 2020; Rahel, 2013). In Norway, conservation efforts to restore connectivity were frozen and fragmentation was increased by erecting wildlife fences on roads to strengthen the barrier effect (Mysterud et al., 2020). This was meant to save reindeer after an outbreak of Chronic Wasting Disease in 2016.

To debate on the above subjects (1–3), three research questions (RQs) are proposed and one or more hypotheses are provided for each question:

1.1 | Wildlife corridors

Blocking wildlife corridors is not as straightforward as closing wildlife passages (Giacometti, 2003). The ease with which wildlife corridors can be blocked depends on the surrounding landscape. In this study, the *ease* of blocking refers to the effort (in terms of working hours and equipment) required to effectively prevent wildlife from moving across a corridor. In Switzerland, landscapes are well-represented by the biogeographical region in which they are located (Figure 3). Investigating the ease with which wildlife corridors can be blocked for a species of concern requires knowledge about which features are relevant and how they are shaped in different biogeographical regions (RQ-1).

In the study here, the focus is on landscape features, such as topography. Presumably, motorways can be sealed for potentially crossing wild boar much easier in a region with a flat surface (such as the *Central Plateau* [CP] in Switzerland) than in mountainous regions where animals can pass under the many viaducts and pass over the tunnels.

H1.1. Blocking corridors for wild boar is easier in the Central Plateau than outside of the Central Plateau.

1.2 | Habitat connectivity

In densely inhabited regions where the building activity is high, landscape is increasingly fragmented by the built infrastructure. Particularly, motorways are important barriers that disconnect wildlife networks. When wildlife networks are disconnected, connectivity can be re-established to some extent by constructing wildlife passages. Given that species differ in the habitat they prefer and the distance they cover, it is not a priori clear whether the structurally re-connected landscape and the functionally connected habitat are coextensive in area for a species of concern (Kindlmann & Burel, 2008): Which variables determine whether a structurally connected landscape has an impact on the functional connectivity of the habitat of a species of concern and how do they operate on the wild boar network in Switzerland (RQ-2)?

Whether a habitat is connected or not depends on the features of the landscape and the *dispersal capability* of the species of concern (Urban & Keitt, 2001). Relevant landscape features include *distance between fragments* and *availability of suitable habitat* for a species. Wild boar are known to cover long distances for foraging (Boitani et al., 1994). This also applies to Switzerland (Holzgang et al., 2001), where the occupied habitat for wild boar has been mapped only recently (Vargas Amado et al., 2021).

H2.1. Most existing wildlife passages actually connect the habitat of wild boar in Switzerland.

Previous work found habitat suitable for wild boar in areas which are not yet colonized (Vargas-Amado et al., 2020).

H2.2. Constructing new wildlife passages will connect habitat suitable for wild boar in areas that are not yet colonized.

1.3 | Landscape fragmentation

Landscape variables, including land cover-based indices of fragmentation, were the primary drivers of wild boar ranging patterns in a human-dominated agro-ecosystem (Fattebert et al., 2017). This brings up the question of how fragmentation influences the effectiveness of disease containment measures in a landscape (RQ-3)?

Exploring fragmentation in dissimilar landscapes may explain why a specific measure of disease containment is more effective in one than in the other. In Switzerland, the densely inhabited CP is expected to be more fragmented than the other biogeographical regions.

H3.1. Closing wildlife passages and blocking corridors is a more effective measure of disease

containment in the Central Plateau than in any other biogeographical region.

How effective the closing of wildlife passages and blocking of corridors in a given biogeographical region is, can be estimated by measuring the change in the connectivity of the respective network. Connectivity can be summarized in the form of (1) the number of components, (2) the number of nodes in the largest connected component (LCC) and (3) the diameter of the LCC (Urban & Keitt, 2001). The LCC was given an epidemiological interpretation in terms of the maximal *potential epidemic size* (PES; Dubé et al., 2011; Kao et al., 2006). In wildlife networks, where nodes are occupied habitat patches, the PES can be estimated by summing up the area-weighted abundances of a species of concern in the LCC (cf. Equation 5). The change in the PES, thus, is an additional metric (4) to estimate the effectiveness of closing wildlife passages and blocking corridors.

Finally, identifying those passages and corridors that decompose the wild boar networks on a large scale upon closure may help authorities to prioritize the spots where construction measures should be taken in case of a disease outbreak, particularly if resources are scarce.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out in Switzerland, a country that covers a total surface area of 41,285 km² ranging from 193 to 4634 m above sea level (Swiss Confederation, 2020). Settlement areas cover 7.5% of Switzerland's territory. Around 40% of the territory is used for agriculture, while roughly 30% is covered by forest and woodland. Switzerland has three main geographical regions: The Alps, covering around 60% of the country's total surface area, the CP (30%) and the Jura (10%). Based on the patterns of distribution of the flora and fauna, the main geographical regions were subdivided into six *biogeographical* regions, namely Northern Alps, Western Central Alps, Eastern Central Alps, Southern Alps, CP and Jura (Gonseth et al., 2001). The first three were considered a single region 'Northern Alps' in this study, because they are similar in the relevant features and only sparsely populated by wild boar (Figure 3).

2.2 | Data collection and preparation

The data collected for this study together with their sources and dates are summarized in Table 1. The *wildlife network system* and the *interregional wildlife corridors* originate from a study in which wildlife networks were established for the most common species, such as wild boar, red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and chamois (*Rupicapra rupicapra*), by interviewing gamekeepers, modelling landscape permeability in a GIS system, and looking up the hunting statistics (Holzgang et al., 2001). The corridors and the

Data	Source	Date	Hypothesis			
			H1.1	H2.1	H2.2	H3.1
Wildlife network system	FOEN	2012	x	x	x	x
Interregional wildlife corridors	FOEN	2012	x			x
Wildlife passages	FOEN	2012		x	x	x
Wildlife passages' state	Federal Roads Office	2021		x	x	x
Motorways	Federal Roads Office	2020	x			x
CORINE land cover	Copernicus Program	2018				x
Probability of wild boar occurrence	Vargas-Amado et al. (2020)	2020			x	
Relative abundance of wild boar	Vargas Amado et al. (2021)	2021	x	x		x
Compartments	Giacometti (2003)	2003	x			x
Biogeographical regions	FOEN	2019	x			x

Abbreviation: FOEN, Federal Office for the Environment.

connecting axes were modified in 2012 by the Federal Office for the Environment (FOEN) based on the information of the cantonal hunting agencies (cantons represent the third level in the Nomenclature of Territorial Units for Statistics, NUTS). The data consisted of the 2012 update packing together georeferenced data of 304 corridor objects (https://data.geo.admin.ch/ch.bafu.fauna-wildtierkorridor_national/, https://data.geo.admin.ch/ch.bafu.fauna-vernetzung_sachsen_national/).

Wildlife passages. Forty-five wildlife passages were obtained along with the interregional wildlife corridors. Up-to-date information about the state of the passages ('constructed', 'under construction' or 'planned') was obtained from the Federal Roads Office (FEDRO; Hirschi, 2021) as was the 2020 update of the national routes.

CORINE land cover. The data consisted of version of 2018 with a pixel size of 100m (<https://land.copernicus.eu/pan-european/corine-land-cover/clc2018>).

Probability of wild boar occurrence. Area-covering 1 km² data grids with probabilities of wild boar occurrence of 0.5–1.0 were produced for open and closed season for hunting in previous work (Vargas-Amado et al., 2020).

Relative abundance of wild boar. An area-covering 1 km² data grid with the relative abundance at the time in the year when wild boar is most abundant (i.e. after reproduction in spring and before hunting in autumn/winter) was produced by collecting data over a 7-year-period in previous work (Vargas Amado et al., 2021).

The networks for wild boar in Switzerland, consisting of occupied habitat patches, corridors and passages, were established based on the wildlife network system and the data grid representing the relative abundance of wild boar (Figure 2). Habitat patches were considered 'occupied' if the Federal hunting statistics (<https://www.jagdstatistik.ch/>) report shots of wild boar for them. This does not imply

that there always is a viable population in these patches. The networks were overlaid with the *compartments* defined in related work (Giacometti, 2003), the boundaries of which consisted of mountain ridges, lakes and national motorways that cannot be crossed easily by wild boar. Compartments were refined by considering also more recent motorways. Refined compartments contained zero, one or more occupied habitat patches. Only the 45 corridors plus 45 passages (numbers are equal by chance) that are located on a compartment boundary were considered for the analyses, because map-based inspection showed that those inside the compartments (mostly corridors without a passage) could not be blocked, because the natural landscape features and artificial surfaces they are cutting across are no barriers for wild boar (they may be barriers for other species).

There are two independent networks for wild boar in Switzerland, one connecting the northern population and the other connecting the southern population (Figure 1). The northern wild boar population occupies parts of the biogeographical regions of Jura, CP, Northern Alps (including Western Central Alps and Eastern Central Alps), and is contiguous with the wild boar populations in neighbouring Germany and France. The southern wild boar population occupies the biogeographical region of Southern Alps and is contiguous with the northern Italian wild boar population (Meier & Ryser-Degiorgis, 2018; Vargas Amado et al., 2021).

2.3 | Data analysis

Wild boar networks were established for (1) the northern population, (2) the southern population and (3) the CP (Figure 2). The latter is a sub-network in the most densely inhabited biogeographical region of the north. Three different states of the networks were investigated: *present-day* (i.e. state of July 2021), *near future* (i.e. with new

TABLE 1 Data used to test the hypotheses.

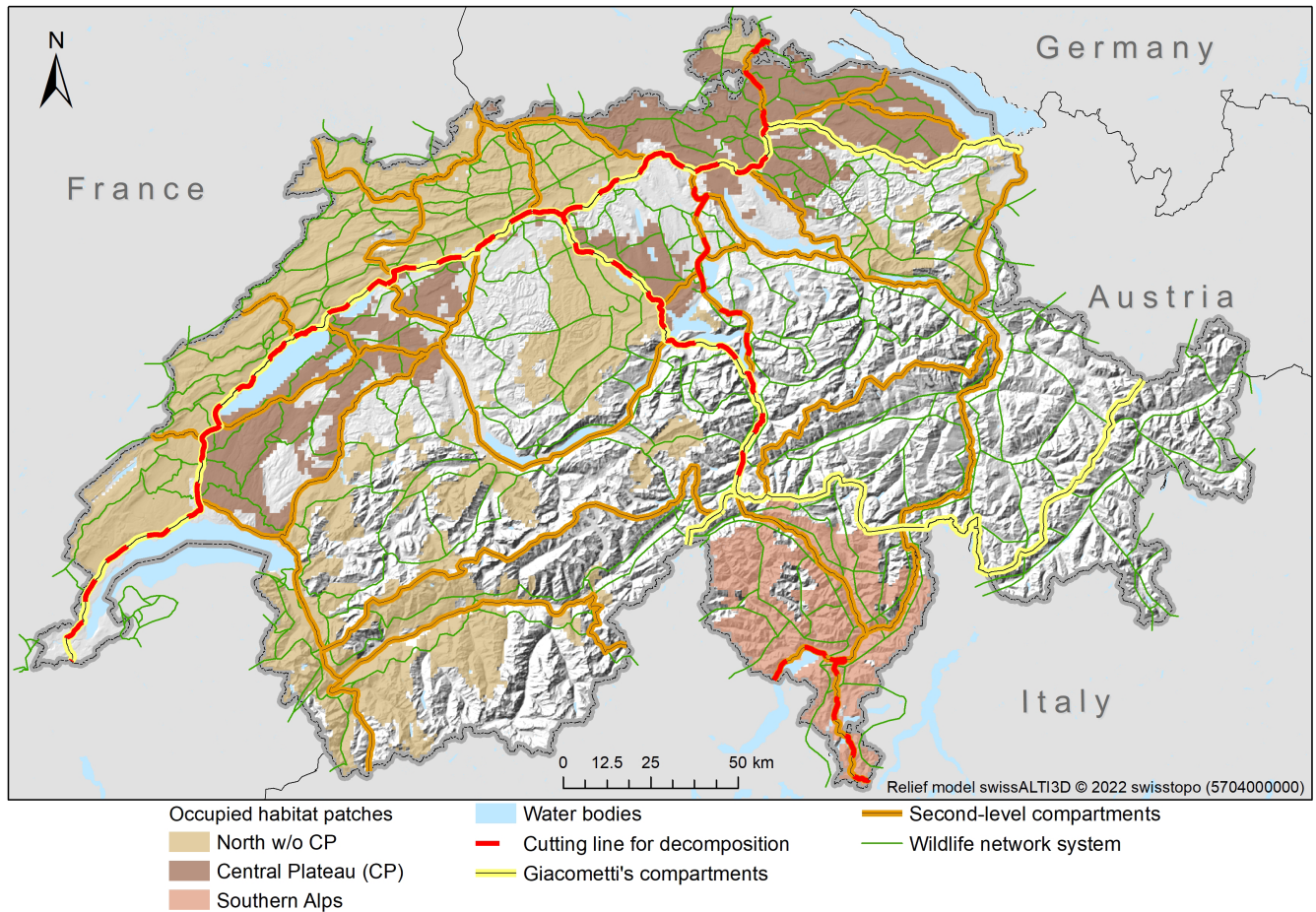


FIGURE 1 Wildlife network system, compartments and habitat patches occupied by wild boar in different biogeographical regions of Switzerland; red-dotted lines link stretches of motorways A1, A2, A4, A5 in the north and A2, A13 in the south; they indicate where the networks can be decomposed on a large scale; second-level compartments refine Giacometti's (2003) compartments by considering more recent motorways.

passages built until 2026) and *contained* (i.e. after closing passages and blocking easy to block corridors). The established networks were represented as matrices (adjacency, dispersal distance and dispersal probability) before carrying out the analyses. Table 2 gives an overview of the elements of the framework in Figure 2 that were considered when testing the hypotheses.

Dispersal probability was approximated as negative-exponential decay, $p_{ij} = \exp(-\theta \times d_{ij})$ (Urban & Keitt, 2001). Thereby, d_{ij} is the path-respecting distance between the edges of patches i and j , and θ is a distance-decay coefficient that determines the steepness of the relationship. This coefficient was computed based on the observation that the threshold distance for a species corresponding to a dispersal probability of 0.05 equals $-\ln(0.05)/\theta$. A threshold distance of 20,000m was chosen in this study, which corresponds to the radius of the connected habitat occupied in Switzerland by a viable wild boar population consisting of 50 sounders with 10 animals each (Holzgang et al., 2001). It does not factor in solitary individuals (usually adult males) that may disperse farther. Accordingly, the coefficient θ equals $-\ln(0.05)/20,000 = 0.150 \times 10^{-3}$. Table 3 summarizes the equations used for data analyses.

2.3.1 | Wildlife corridors

To test whether blocking corridors for wild boar would be easier in the CP than outside of the CP (H1.1), each corridor for wild boar on a compartment boundary was qualified independently by two observers as either 'easy to block' or 'hard to block', assuming fencing, based on a map analysis and on the observers' knowledge of the Swiss landscape.

The map analysis consisted in inspecting the compartment boundaries starting from the intersection of the wild boar network and the barriers. Where there was a disagreement between observers, the issue was discussed and a common qualification was sought. In order to be as specific as possible regarding 'easy to block' corridors, unclear cases were qualified as 'hard to block'. The qualification considered the following features:

- *Width of the corridor*: Corridors of a width of a few 100m or less were considered easier to block than wider corridors.
- *Topography*: Flat terrain was considered easier to block than rising or sloping terrain.

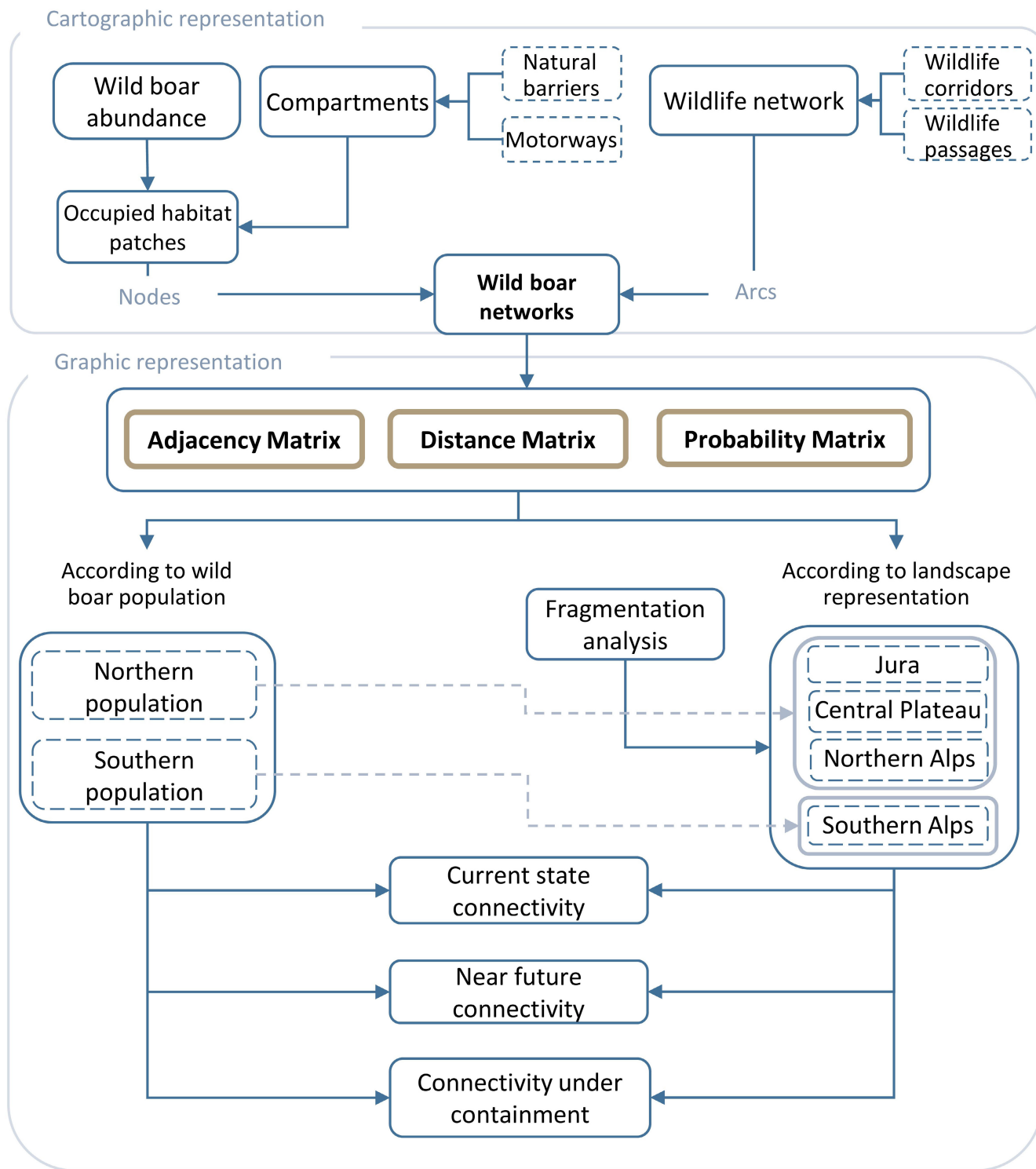


FIGURE 2 Analytical framework showing (upper part) how the wild boar networks in Switzerland were established from geographical features, (lower part) their representation as matrices according to the wild boar populations and the biogeographical regions as well as the states of the networks investigated.

- *Configuration of the ground*: Clear ground was considered easier to block than ground abounding in rocks and stones.
- *Land cover*: Semi-natural areas and agricultural land were considered easier to block than settlements, undeveloped forest, wetlands and water bodies.

- *Built and green infrastructure*: Stretches of land were considered easier to block along roads and rails than over hedges and ditches.

These features were established in the course of the analysis based on the heterogeneity of the inspected corridors.

TABLE 2 Elements of the framework in Figure 2 considered when testing the hypotheses.

Hypothesis	Feature	Matrix	Representation	Connectivity	Fragmentation
H1.1	Corridor	Adjacency	Landscape	Current state	No
H2.1	Passage	Distance	Population	Current state	No
H2.2	Passage	Probability	Population	Near future	No
H3.1	Corridor, passage	Adjacency	Landscape, population	Current state, under containment	Yes

TABLE 3 Equations used for data analysis.

Equation	Variables
(1) $\forall (i, j) \in A_0 \cdot \frac{\#\{d_{ij} \mid 0 < d_{ij} \leq 20,000\}}{\#\{d_{ij} \mid d_{ij} > 0\}} > 0.500$	A_0 is the set of all wildlife passages (i, j) that are open at present d_{ij} is the path-respecting distance between adjacent patches i and j # indicates a count operation on { ... }
(2) $\forall (i, j) \in (A_1 \setminus A_0) \cdot \#\{d_{ij} \mid 0 < d_{ij} \leq 20,000\} > 0$	A_1 is the set of all wildlife passages that are open at present or will be (re-) opened in the near future For # and d_{ij} see (1)
(3) $P_i = a \times \sum_j p_{ij} \times s_j \times k_j$	P_i is the number of propagules (i.e. wild boar) arriving in a new patch i a is a scale factor ^a p_{ij} is the probability that an individual in patch j will disperse to new patch i s_j is the surface area of patch j k_j is the relative abundance of wild boar averaged over patch j
(4) $\text{DIVISION} = \left[1 - \sum_{j=1}^m \left(\frac{s_j}{S} \right)^2 \right]$	S is the total area of the landscape s_j is the surface area of the j -th patch in the i -th land cover class
(5) $\text{PES} = a \times \sum_{i=1}^n s_i \times k_i$	PES is the potential epidemic size in terms of number of wild boar n is the number of patches in the LCC. For a , s_j and k_j see (3)
(6) $(\Delta \text{mtrc} / \text{mtrc}_0)_{\text{CP}} > (\Delta \text{mtrc} / \text{mtrc}_0)_{\text{not(CP)}}$	$\Delta \text{mtrc} / \text{mtrc}_0$ is the change in connectivity metric mtrc CP is the Central Plateau

^aThe scale factor a is unknown. However, a is factored out in the analysis, because the non-negative change $\Delta \text{mtrc} / \text{mtrc}_0$ is computed for each metric mtrc , rather than the absolute value.

2.3.2 | Habitat connectivity

To test whether most existing wildlife passages actually connect the habitat of wild boar in Switzerland (H2.1) the proportion of distances below 20,000m (Holzgang et al., 2001) between pairs of occupied patches connected by a wildlife passage was calculated. The hypothesis was considered corroborated if the proportion was greater than 0.500 (cf. Equation 1 in Table 3). This analysis was carried out on the present-day wild boar networks of the northern and the southern population.

To test whether constructing new wildlife passages will connect habitat suitable for wild boar in areas that are not yet colonized (H2.2), it was explored whether there is some perennially suitable habitat for wild boar within the threshold distance of any newly connected landscape fragment (cf. Equation 2 in Table 3). To this end, the estimated spatial distributions of wild boar in Switzerland during open and closed season for hunting, computed in previous work, were used (Vargas-Amado et al., 2020). This analysis was carried out on the near-future wild boar networks of the northern and the southern population.

Connecting new habitat does not necessarily imply colonization. Colonization probability depends, among other things, on the number

P_i of propagules arriving in a new patch (Urban & Keitt, 2001). This number was computed for every new patch in order to identify areas where colonization is more probable than elsewhere (cf. Equation 3 in Table 3). In order to get an estimate for colonization probability, the number P_i was related to the maximum possible number which was obtained by setting $p_{ij} = 1$.

2.3.3 | Landscape fragmentation

DIVISION was computed as an easy understandable metric of landscape fragmentation (Jaeger, 2000) for the CP, the other regions occupied by the northern wild boar population, and the Southern Alps using Fragstats 4.2 and adopting the 8-cell neighbourhood rule (McGarigal et al., 2002). DIVISION is based on the cumulative patch area distribution and is interpreted as the probability that two randomly chosen pixels in the landscape are not located in the same patch of the corresponding land cover class. The closer the metric is to 1 in the unit interval, the more fragmented is the landscape.

DIVISION was computed for a potential *habitat* land cover class (Figure 3). This land cover class was established by reclassifying (i)

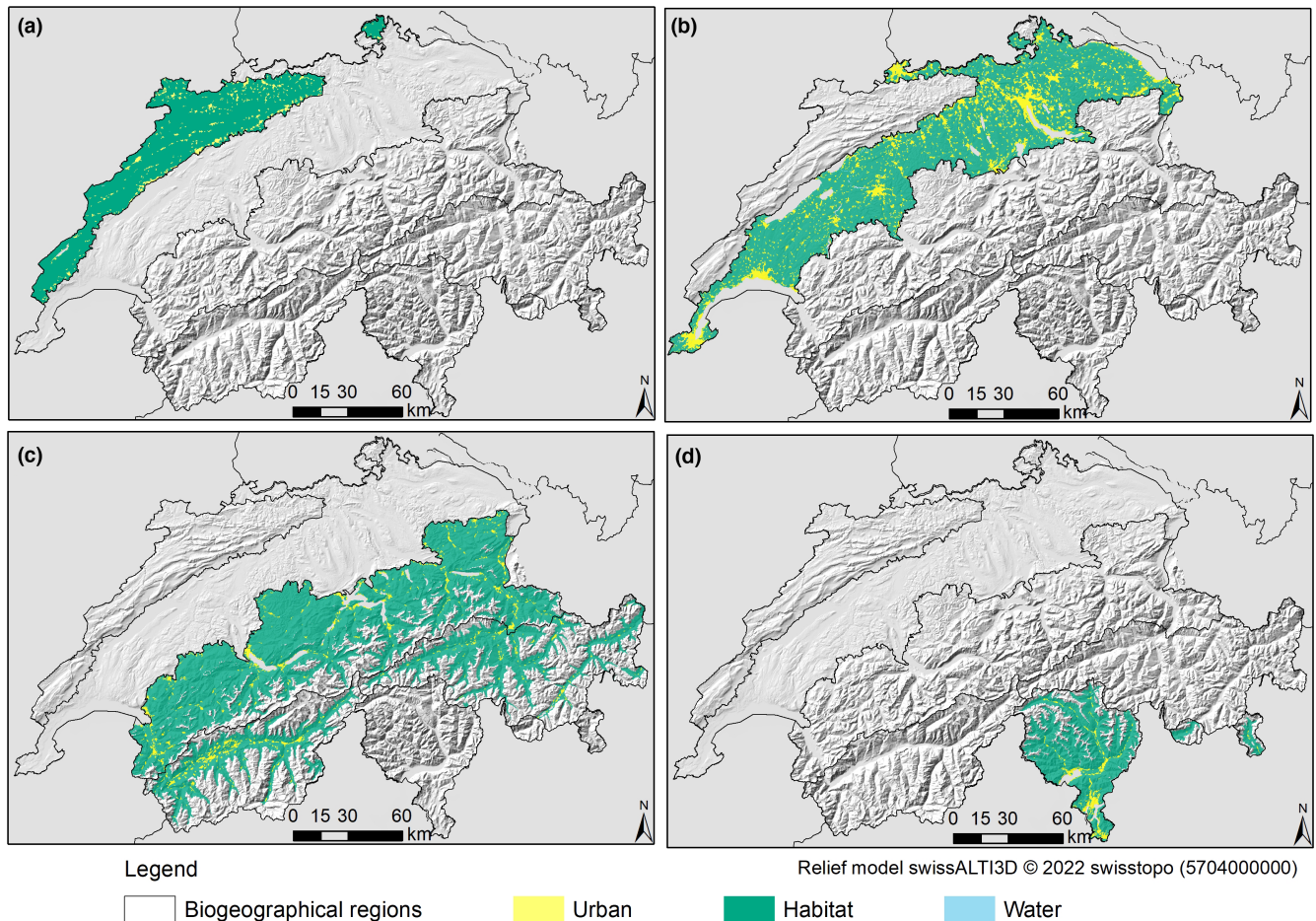


FIGURE 3 Wild boar potential habitat and artificial surfaces resulting from the reclassified CORINE land cover in different biogeographical regions of Switzerland; (a) Jura, (b) Central Plateau, (c) Northern Alps (including Western Central Alps and Eastern Central Alps), (d) Southern Alps.

forest and semi-natural areas, (ii) agricultural areas and (iii) wetlands. The proportions of both matrix land cover classes (iv) artificial surfaces and (v) water bodies, were calculated to find out which of the two classes drives the difference in fragmentation between the different regions.

To test whether closing wildlife passages and blocking corridors is a more effective measure of disease containment in the CP than in any other biogeographical region (H3.1), the connectivity metrics introduced in the introduction were computed. Metrics (2–4) were computed for both the LCC and the second largest connected component (SLCC; cf. Equation 5 in Table 3). All metrics were computed before (subscript '0') and after (subscript '-1') closing all wildlife passages and blocking all 'easy to block' corridors in the wild boar networks of the CP, the other regions occupied by the northern population, and the Southern Alps (the latter two are referred to as not[CP]) using the Python package 'NetworkX', version 2.5. The hypothesis was considered corroborated if for each metric $mtrc$, the non-negative change $\Delta mtrc / mtrc_0 = |1 - mtrc_{-1} / mtrc_0|$ in the estimate was larger in the CP than in any other biogeographical region (cf. Equation 6 in Table 3).

The passages and corridors decomposing the wild boar networks of the northern and the southern population on a large scale upon closure were identified by discontinuing in turn every combination of cuttable connections and selecting the minimal set of passages and corridors cutting the network to a non-decomposable LCC and non-decomposable component with maximum PES (Figure 4).

3 | RESULTS

3.1 | Wildlife corridors

Forty of 45 corridors for wild boar in Switzerland are functional (i.e. traversable by wild boar) at present. In the CP, 7 of 16 functional corridors (0.438) were qualified as 'easy to block' (Figure 5), while outside of the CP, 4 of 24 functional corridors (0.167) were qualified as 'easy to block'. All over Switzerland, 5 of 10 viaducts for motorways were qualified as 'easy to block'. Among the functional corridors that are 'hard to block' in Switzerland was all land covering the seven tunnels for motorways that intersect the wild boar network (Figure 6).

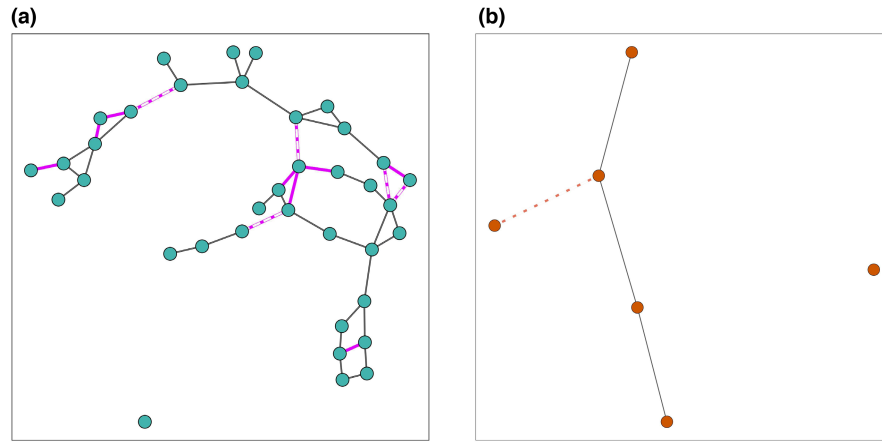


FIGURE 4 Graph representation of the wild boar networks of (a) the northern population and (b) the southern population. Emphasized links show corridors/passages that can be blocked/closed; dashed links indicate where the networks were decomposed to reduce the potential epidemic size on a large scale, they correspond to the cutting lines in Figure 1; isolated nodes represent (a) the city of Zurich for which it is unclear where it connects with the northern network, (b) the west of the district of Mendrisio which only connects with the Italian wild boar network not represented here.

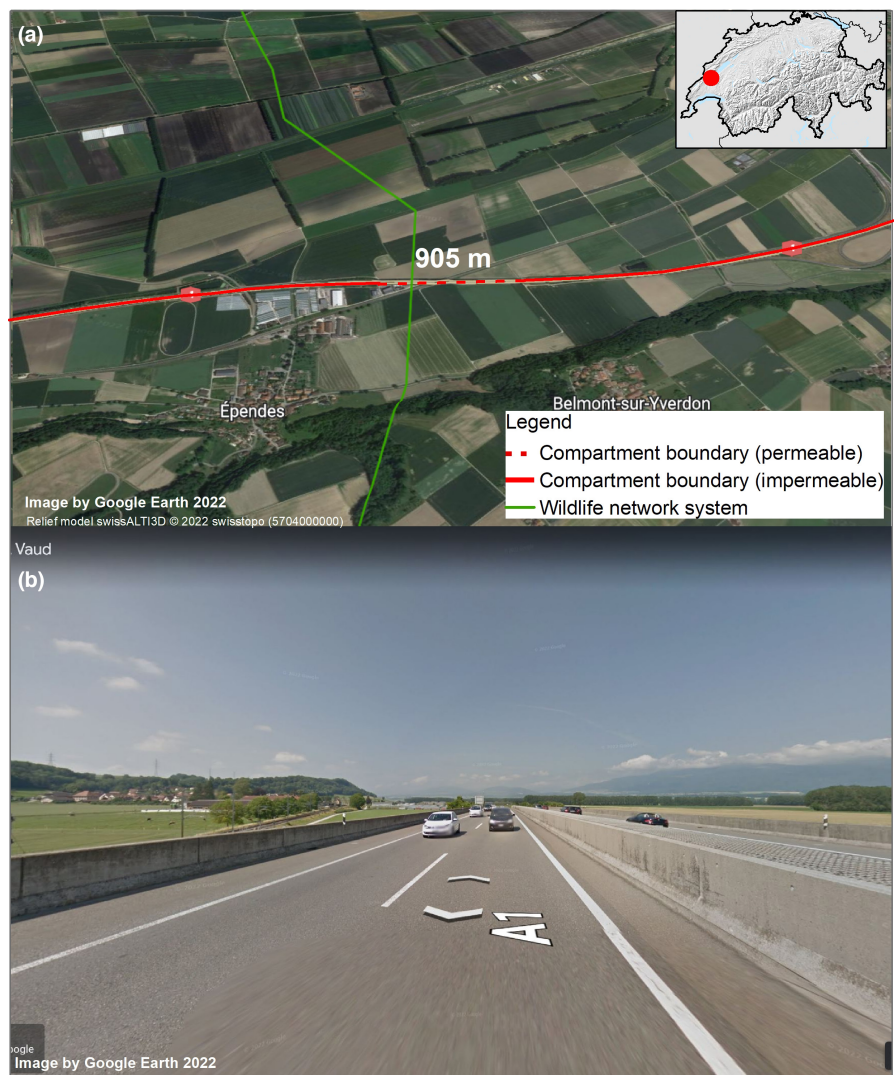


FIGURE 5 Easy to block wildlife corridor connecting habitat patches underneath a viaduct in the Central Plateau; (a) bird's eye view, (b) close-up view.

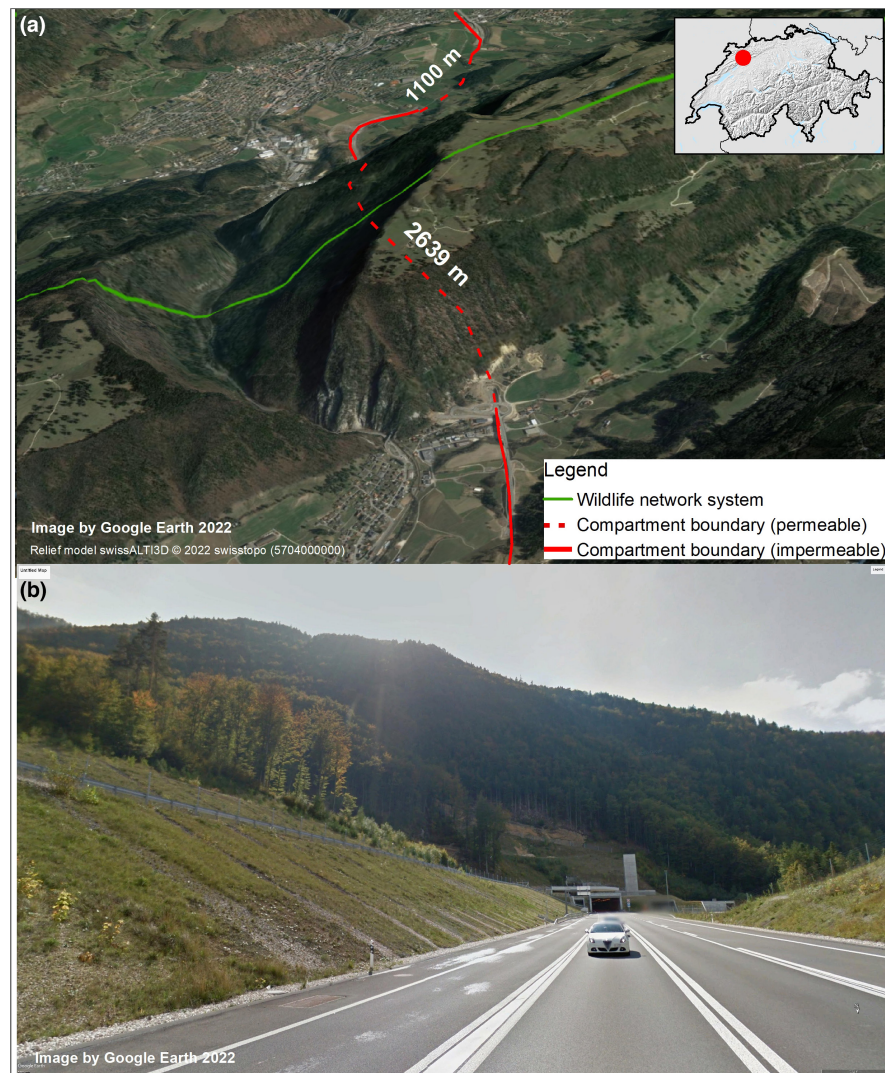


FIGURE 6 Hard to block wildlife corridor that consists of land covering a tunnel outside of the Central Plateau; (a) bird's eye view, (b) close-up view.

3.2 | Habitat connectivity

For 16 of 20 open wildlife passages in the wild boar network of the northern population were the adjacent patches within a distance of 20,000m. Accordingly, the proportion of distances below the threshold was 0.800. Four open wildlife passages did not connect the habitat of wild boar when using the fixed threshold. The occupied patches connected by the open wildlife passage in the southern network (a single one) were within the threshold distance.

Four of 17 wildlife passages that are currently under construction connect habitat suitable for wild boar in areas that were not colonized so far. These passages are part of the northern network and are located along motorway A1 in Oftringen AG, Wangen a.d. Aare BE, Suret AG and Oberbuchsiten/Kestenholz SO (Figure 7). The remaining 13 wild life passages either connect habitat that is already colonized by wild boar or they are located in uncolonized areas where the probability of wild boar occurrence is below 0.5. For wild boar to disperse to new areas in the cantons of Aargau (AG), Berne (BE) and Solothurn (SO) the probabilities were 0.999, 0.879 and 0.804 respectively. Another seven wildlife passages are planned for the far future (i.e. after 2026) and were not considered here.

3.3 | Landscape fragmentation

The potential habitat of wild boar was almost twice as fragmented in the CP than in the other regions occupied by the northern population (referred to as 'North w/o CP' in Table 5; Table 4). The fragmentation seems to be driven by artificial surfaces, the percentage of which in the CP was more than twice the percentage in the other regions of the north. The potential habitat in the Southern Alps was almost as fragmented as in the CP, even though the percentage of artificial surfaces was in the low range of those in the Jura and the Northern Alps. The percentage of the water bodies class was below 0.5% in all four biogeographical regions.

After closing all wildlife passages and blocking all 'easy to block' corridors the change in the three connectivity metrics was consistently larger in the CP than in the other regions occupied by the northern population and in the Southern Alps (Table 5; Figure 8). In contrast, the change in the PES (Equation 5 in Table 3) was smaller in the LCC of the CP than in the Southern Alps. The small relative decrease in the surface area in the Southern Alps suggests that the change in the PES was driven by the relative abundance of wild boar, whereas in the CP the size of the patches was also a driver.

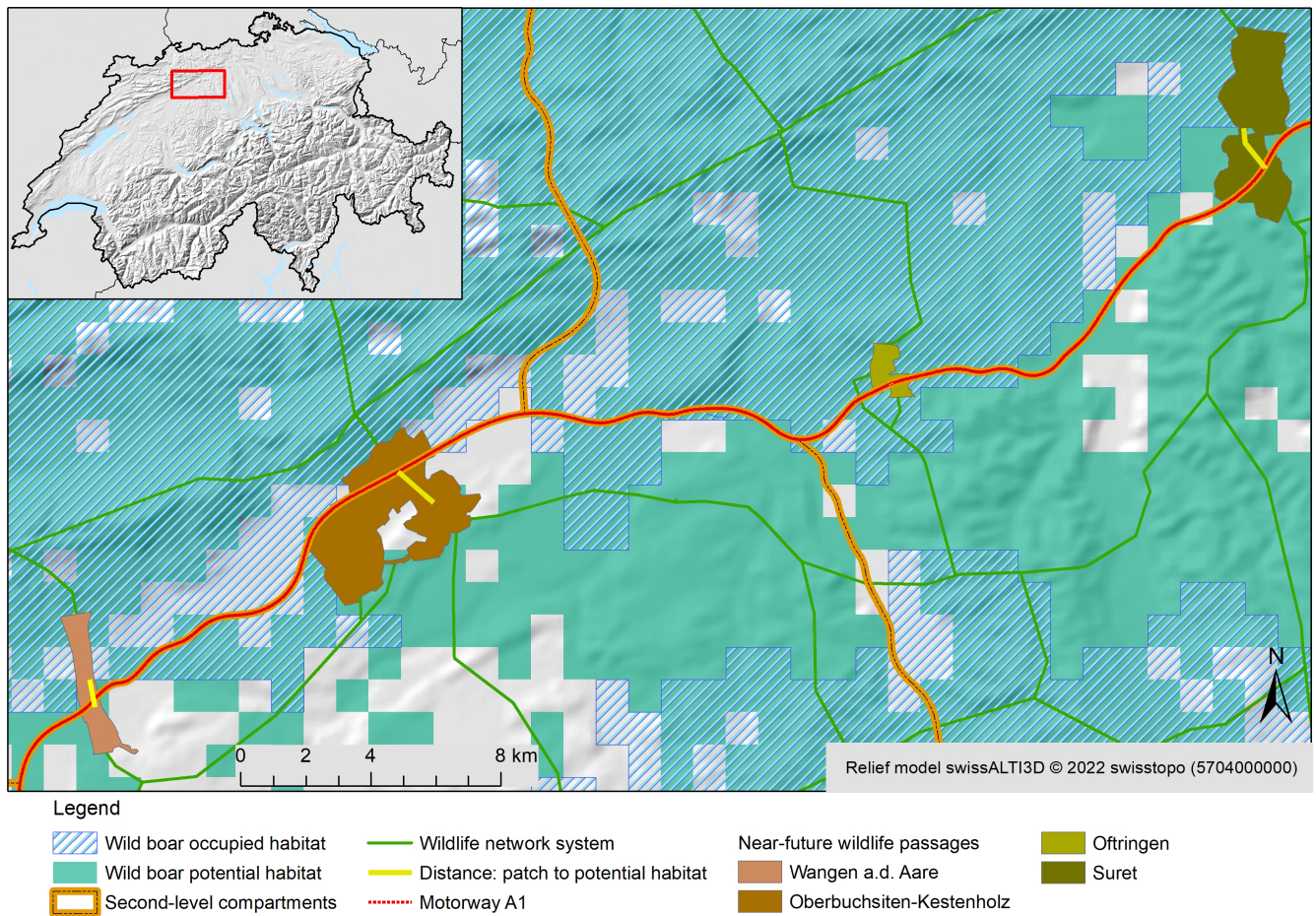


FIGURE 7 Near-future wildlife passages (i.e. to be built until 2026) connecting habitat occupied by wild boar northwest of motorway A1 with potential habitat southeast of A1.

TABLE 4 Fragmentation analysis of reclassified CORINE land cover in different biogeographical regions (DIVISION see Equation 4; PLAND, percentage of landscape).

CORINE class	Metric	Central Plateau	Jura	Northern Alps	Southern Alps
Potential habitat	DIVISION (0, 1)	0.354	0.187	0.159	0.329
	PLAND [%]	82.760	92.765	95.210	93.135
Artificial surfaces	PLAND [%]	16.746	7.136	4.653	6.751
Water bodies	PLAND [%]	0.494	0.099	0.137	0.114

TABLE 5 Changes in connectivity, potential epidemic size (PES) and surface area of the largest connected component (LCC) and the second largest connected component (SLCC) in different biogeographical regions after closing wildlife passages and blocking 'easy to block' corridors; 'North w/o CP' consists of Jura and Northern Alps; SLCC is the component with maximum PES; in the Southern Alps there is only one large connected component; arrows indicate the direction of the changes.

Metric [$\Delta mtrc / mtrc_0$]	Central Plateau (CP)		North w/o CP		Southern Alps
	LCC	SLCC	LCC	SLCC	
Number of components (\uparrow)	0.800	0.800	0.400	0.400	0.500
Number of patches (\downarrow)	0.429	0.333	0.000	0.143	0.200
Diameter of component (\downarrow)	0.500	0.250	0.000	0.200	0.000
Potential epidemic size (\downarrow)	0.068	0.638	0.000	0.083	0.256
Surface area of component (\downarrow)	0.139	0.443	0.000	0.184	0.072

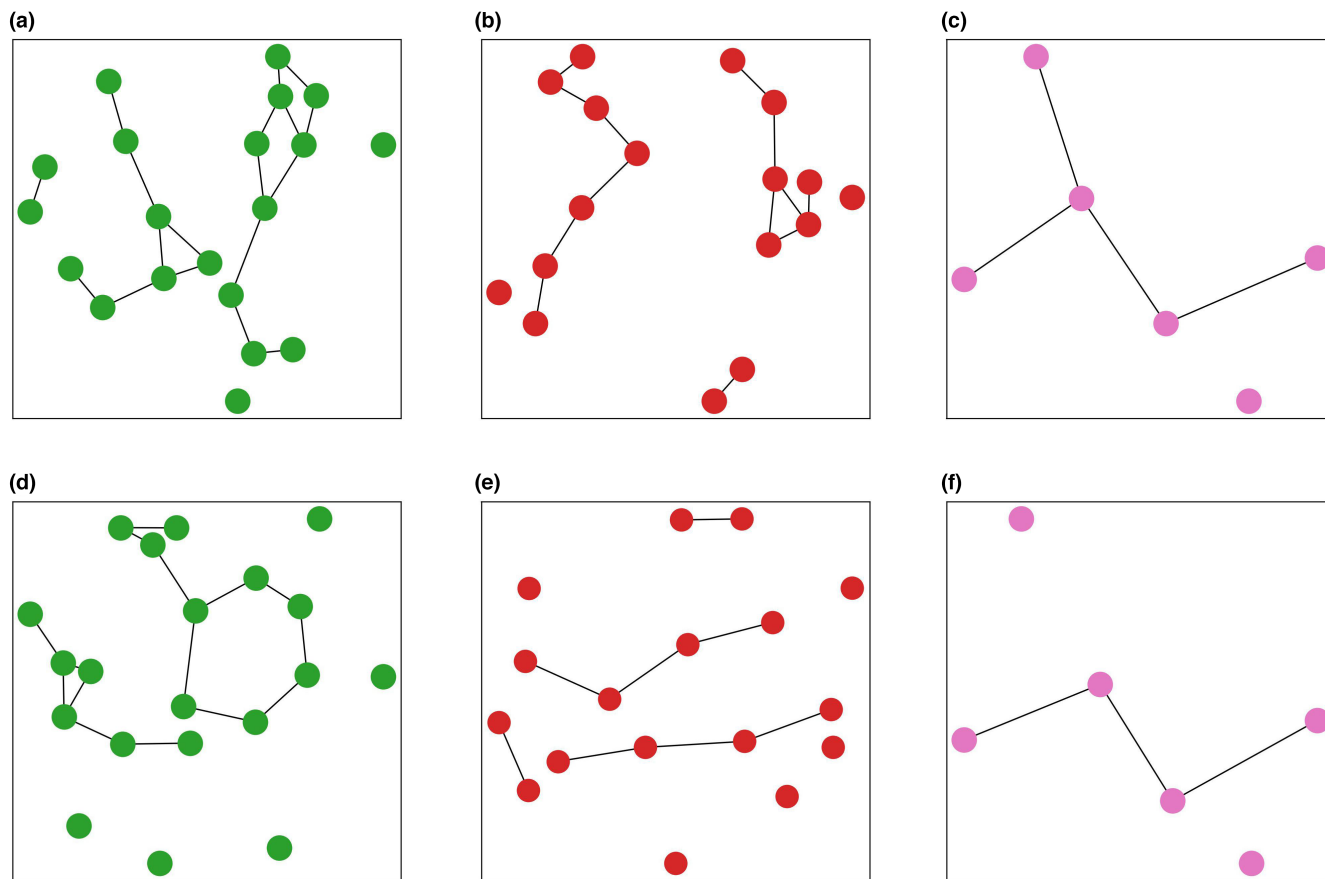


FIGURE 8 Graph representation of the wild boar networks in the Central Plateau (b, e; red), the other regions occupied by the northern population (a, d; green), and the Southern Alps (c, f; pink) before (a–c) and after (d–f) closing all wildlife passages and blocking all ‘easy to block’ corridors; after closing wildlife passages and blocking corridors connectivity decreased more in the Central Plateau than in the other regions occupied by the northern population and in the Southern Alps.

Wildlife passages and corridors that jointly decompose the wild boar network of the northern population on a large scale upon closure are located on motorways A1, A2, A4 and A5 (Figure 1). Their closing resulted in a relative decrease in the PES of 0.258. It cut the network of the northern population to four pieces of 2–10 compartments, three of which bordering France and/or Germany. Two of 25 fully or partly occupied compartments could be isolated by closing wildlife passages and blocking corridors in the northern network. The wildlife passage decomposing the wild boar network of the southern population upon closure is located on motorway A2. The closing of this passage resulted in a relative decrease in the PES of 0.256. It cut the network of the southern population to two pieces of three and one compartments both bordering Italy. None of the four compartments in the southern network could be isolated by closing wildlife passages and blocking corridors.

4 | DISCUSSION

This study investigated in disparate landscapes whether managing connectivity by blocking wildlife corridors and closing wildlife passages could be an effective practice to contain the spread of a

disease like ASF among free-ranging wild boar. This was explored by testing a number of hypotheses on the wild boar networks in different biogeographical regions of Switzerland. Almost half of the wildlife corridors were found easy to block in the flat-surfaced CP, whereas outside of the CP only 17% were easy to block, which supports H1.1. In general, land that passes under a viaduct was more likely to be blocked than land covering a tunnel.

The proportion of occupied patches connected by open wildlife passages that are within a distance of 20,000m was 0.800 in the network of the northern population and 1.000 in the southern network. These results support H2.1: Most existing wildlife passages actually connect the habitat of wild boar in Switzerland. This means that if ASF is to arrive in Switzerland its spread can be extensive, if connectivity is not managed. The four wildlife passages that do not connect the wild boar habitat are located entirely or partly in the Northern Alps. These should not be closed in order not to disturb the dispersal of other species like the red deer.

Four of 17 wildlife passages that are currently under construction connect habitat suitable for wild boar in areas that were not colonized so far which supports H2.2. Still, the majority (i.e. 13) target other species than wild boar. More wildlife passages are to be constructed after 2026 (Hirschi, 2021). Authorities should inform

themselves soon enough about the impact these passages may (or may not) have on colonizing wild boar.

Closing wildlife passages and blocking corridors was found a more effective measure of disease containment in the CP than in any other biogeographical region of Switzerland which supports H3.1. This was related to the potential habitat of wild boar, which is more fragmented in the CP than in the other regions occupied by the northern population (Table 4). A similar relationship could not be observed for the Southern Alps, where the fragmentation metric was inflated artificially. The reason is that the Swiss border cuts the otherwise connected habitat to pieces (Figure 3d), to the effect that some of the pixels chosen randomly by the DIVISION algorithm are no longer located in the same patch of the corresponding land cover class.

In the biogeographical regions of the north, the PES of the SLCC was larger than that of the LCC. Taken alone, some of the standard connectivity metrics, thus, fall short of estimating the effectiveness of blocking corridors and closing passages correctly, particularly, if the abundance of a species of concern is unevenly distributed across habitat patches.

Blocking the minimal set of corridors and passages that cut the networks of the northern and the southern wild boar population to non-decomposable components would reduce the PES in both cases by one quarter. These corridors and passages have to be addressed with priority when a disease must be contained after an outbreak. Even though there are no figures in the current literature to compare with, the reduction potential seems to be rather moderate. However, 'hard to block' does not necessarily mean impossible to block. It would be interesting to explore which of the hard to block corridors could contain disease spread more effectively upon blocking.

The non-decomposable network component with the maximum PES in the north is bordering France and Germany, that with the maximum PES in the south is bordering Italy. Improper disposal of contaminated food waste is considered the most probable way of a potential ASF introduction into Switzerland (Bundesamt für Lebensmittelsicherheit und Veterinärwesen, 2022). Given that wild boar can move over the national border almost without hindrance, attention should be paid also to a possible introduction by dispersing animals. This is even more important, considering that the risk of introducing ASF into the domestic pig population by wild boar was found highest in the same areas in previous work (Vargas Amado et al., 2021).

The approach presented here summarizes the state of a potential disease spread after an unspecified amount of time without consideration of the dynamics of the disease. Even though this summary approach proved to be adequate to test the hypotheses, it would be worth exploring epidemic disease spread in a more realistic setting by linking the approach presented here with state-of-the-art epidemic modelling (Nelson & Williams, 2014). This would allow to fix a time limit for the closing of wildlife passages and the blocking of corridors. Such a time limit is important, because disconnecting the wild boar network is expected to have an impact on other species using the same passages and corridors

(e.g. conservation issues), and can have further side effects, such as shifting human-wildlife conflicts to other areas (Osipova et al., 2018). Considering epidemic modelling presupposes that there are some temporal data about wild boar dispersal on local conditions, which were not available on the required scale in this study.

The range of species to which the presented approach can be applied is limited on those using the same wildlife corridors and passages as wild boar. For a successful transfer, distribution models should be established and abundances be estimated for these species. Similarly, species-specific values should be calculated for dispersal distance and dispersal probability.

This study suggests that combining connectivity analysis with fragmentation analysis was key to explaining why a specific measure of disease containment is more effective in one landscape than in the other. Complementing the permeability model with a species distribution model was essential to identify connected habitat patches for the species of concern. Considering also the surface area of occupied habitat patches and relative abundance of the species made the connectivity analysis more conclusive.

AUTHOR CONTRIBUTIONS

Maria Elena Vargas-Amado and Rolf Grütter were involved in conception and design. Maria Elena Vargas-Amado was involved in acquisition and analysis of data. Maria Elena Vargas-Amado, Beatriz Vidondo, Claude Fischer, Simone Roberto Rolando Pisano and Rolf Grütter were involved in interpretation of data and drafting the article. All authors gave final approval of the manuscript to be published.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data used in this study are accessible from the third-party sources indicated in Section 2.

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