Spatial Aspects of Potential Disease Spread and Its Containment Among Free-Ranging Wild Boar in Switzerland Considering Possible Spillover to Domestic Pigs

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von
Maria Elena Vargas Amado

aus
Mexiko

Promotionskommission
Prof. Dr. Ross Purves (Vorsitz)
Prof. Dr. Maria J. Santos
PD Dr. Rolf Grütter

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Summary

Wild boar (*Sus scrofa*) are susceptible to a range of diseases that can be transmitted to domestic pigs. African Swine Fever (ASF) has become of great concern to swine producers and government disease control agencies because of its severe consequences to animal health and the pig industry. Having witnessed recent outbreaks of ASF in free-ranging wild boar in Belgium, Germany, and Italy, offices for disease control are on alert in Switzerland as well. To help these offices set their scope of action, it is essential to assess the potential risk of disease introduction and of transmission-related events in wildlife and livestock populations. Similarly, it is important to explore the extent to which disease spread can be contained by managing landscape connectivity after an outbreak.

In the first part of the work presented here, the potential risk of transmission-related events was assessed by identifying (i) where wild boar occur in Switzerland, (ii) where they could still potentially colonize, and (iii) where piggeries are dense. The distribution of wild boar in Switzerland was projected from a grid of hunting data and casual observations as probabilities of presence, using an approach based on statistical modeling. This analysis was completed separately for the closed and open seasons for hunting. The predicted probabilities of wild boar presence were related to the density of piggeries in the six agricultural zones of Switzerland. The resulting maps show how the potential risk of transmission-related events, as a proxy for disease transmission, is distributed in Switzerland. The probability of wild boar occurrence was high (> 0.7) in the Jura region, the valleys of the Southern Alps, the Rhone Valley down the river from Martigny, and the Rhine Valley down the river from Bündner Herrschaft; it was fair (0.5–0.7) in the Central Plateau. These regions broadly overlap agricultural zones with a high density of piggeries. Patches of perennially suitable, but currently not colonized, habitat were found in the cantons of Bern, Obwalden, Uri, Schwyz, Glarus, and Grisons. The probability of wild boar occurrence across the entire study area, including the Alps, increased by 12% during closed season for hunting.

In the second part of this work, a method was developed to estimate and map the risk of introducing ASF into the domestic pig population via wild boar. This method considered data about hunted wild boar, rest areas along motorways connecting ASF-affected countries to Switzerland, outdoor piggeries, and forest cover. These data were used to compute relative wild boar abundance and to estimate the risk of both (i) disease introduction into the wild boar population and (ii) disease transmission to domestic pigs. The method used to calculate relative wild boar abundance is novel in that it considers the effect of beech mast on hunting success and the probability of wild boar occurrence when distributing relative abundance values among individual grid cells. The risk of ASF introduction into the domestic pig population via wild boar was highest near the borders of France, Germany, and Italy. On the north side of the Alps, areas of high risk were located on the unshielded side of the main motorway crossing the Central Plateau, which acts as a barrier for wild boar. The estimation of the risk of disease introduction into the domestic pig population without considering wild boar suggested that dispersing wild boar may play a key role in spreading the risk to areas

remote from motorways. The results of this study can be used to focus surveillance efforts on high-risk areas to achieve early disease detection. The developed method could potentially be used to inform policies to control other diseases that are transmitted by direct contact from wild boar to domestic pigs.

The third part of this work was an investigation of the potential effect of managing landscape connectivity on disease spread in free-ranging wild boar in Switzerland. This involved research into (i) how easily wildlife corridors can be blocked, (ii) the connectivity of the wild boar habitat in Switzerland, and (iii) the impact of landscape fragmentation on connectivity management. This was addressed by carrying out GIS analyses and performing graph operations on the wild boar networks in different biogeographical regions of Switzerland. The results showed that (Re 1) most wildlife corridors were hard to block because their features or location make fencing difficult. (Re 2) The wild boar habitat is connected. Opening wildlife passages that are currently under construction may allow wild boar to disperse to hitherto uncolonized areas. (Re 3) 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 Central Plateau where the built infrastructure is most extensive. All over Switzerland, the potential epidemic size could be reduced by 25% by blocking the minimum set of corridors and passages that divide the networks into non-decomposable components. These results suggest that connectivity and fragmentation analyses are important tools for wildlife disease management. Findings that are also relevant outside of the spatial context of Switzerland are spelled out. Finally, general conclusions of this thesis work are provided.

List of acronyms

Acronym	Meaning
Diseases and pathogens	
ADV	Aujeszky's Disease Virus
APP	Actinobacillus pleuropneumoniae
ASF	African Swine Fever
ASFV	African Swine Fever Virus
CSF	Classical Swine Fever
CSFV	Classical Swine Fever Virus
EP	Enzootic Pneumonia
PR	Pseudorabies
PRRS	Porcine Reproductive and Respiratory Syndrome
PRRSV	Porcine Reproductive and Respiratory Syndrome Virus
PPV	Porcine Parvovirus
Population estimation	
CMR	Capture-Mark-Recapture
CR	Capture-resights
General	
BTS-Programm	Besonders tierfreundliche Stallhaltungssysteme / Specialized animal-friendly housing systems
CP	Central Plateau
DNA	Deoxyribonucleic Acid
GPS	Global Positioning System
mtDNA	mitochondrial DNA
RAUS-Programm	Regelmässiger Auslauf im Freien/Regular outdoor exercise
Institutions	
FAO	Food and Agriculture Organization of the United Nations
FiBL	Research Institute of Organic Agriculture
FLI	Friedrich-Loeffler Institute
FOEN/BAFU	Federal Office for the Environment / Bundesamt für Umwelt
FOAG/BLV	Federal Office of Agriculture / Bundesamt für Landwirtschaft
FSO/BFS	Federal Statistical Office / Bundesamt für Statistik
FSVO/BVET	Federal Food Safety and Veterinary Office/ Bundesamt für Lebensmittelsicherheit und Veterinärwesen
Calculations	
GAM	Generalized Additive Model
LCC	Largest Connected Component
MLR	Multivariate Logistic Regression
PES	Potential Epidemic Size
RF	Random Forest
SDM	Species Distribution Model
SLCC	Second Largest Connected Component
TPR	True Positive Rate

Glossary

Relevant to population estimation	
Direct hunting methods	"It is a method to estimate density or relative abundance that is based on the direct observation of animals, also with statistical calibration" (ENETWILD-consortium, et al., 2018, p. 38).
Distribution of a species	It refers to the geographic space where a species can be found (Guisan, Thuiller, & Zimmermann, 2017).
Distance sampling method	"Density estimation method based on the decrease in the detectability of the animals as distance increases. It calculates the detectability for a series of distance intervals with respect to observer" (ENETWILD-consortium, et al., 2018, p. 38).
ENETWILD	"A consortium composed of leading Institutions on wildlife ecology and health will run a European Food Safety Authority (EFSA) project whose main objective is to collect information on the geographical distribution, abundance and structure of selected wildlife species populations relevant for livestock and human health" (ENETWILD PROJECT https://enetwild.com/the-project/).
Genetic data analysis	"Determines the effective population size by genetics (individuals or pellets)" (ENETWILD-consortium, et al., 2018, p. 20).
Home range	"The home range of an animal is the area where it spends its time; it is the region that encompasses all the resources the animal requires to survive and reproduce" (ENETWILD-consortium, et al., 2018, p. 39).
Hunting bag (aka hunting bag statistics)	"Total number of animals (game species) hunted in a given event, hunting area and period of time. Hunting bag may result in an indicator of population density, which requires standardized sampling effort" (ENETWILD-consortium, et al., 2018, p. 39).
Indirect hunting methods	"It is a method to estimate density or relative abundance that is based on the detection of presence signs, but not on living animals" (ENETWILD-consortium, et al., 2018, p. 39).
Occurrence	"Presence or absence of a wild species in a certain area" (ENETWILD-consortium, et al., 2018, p. 39).

Pellet counts	"Record the number / frequency of wild boar droppings per unit of effort to calculate local density or a relative abundance" (ENETWILD-consortium, et al., 2018, p. 19).
Population density	"It is a measurement of population size per area unit, i.e., population size divided by total land area. The absolute density usually is expressed in heads per 100 ha. Multiplying the population density by the studied surface, we obtain the population size" (ENETWILD-consortium, et al., 2018, p. 40).
Presence data	Refers to the observations/records of a species of concern (Guisan, Thuiller, & Zimmermann, 2017).
Relative abundance (aka abundance index)	"Relative abundance or abundance index: It refers to the relative representation of a species in a particular ecosystem. Relative abundance can be calculated by different methods. The relative abundance reflects the temporal or spatial variations of the size (N) or density (d) of a population, but does not directly estimate these parameters" (ENETWILD-consortium, et al., 2018, p. 40).
Snow tracks	Direct method used to estimate wildlife populations. Its objective is "to record the number / frequency of snow tracks (footprint dimension) per unit of effort to calculate an abundance index for a local population" (ENETWILD-consortium, et al., 2018, p. 19).
Relevant to connectivity	
Connectivity, functional	"It considers organisms' behavioral responses to individual landscape elements (patches and edges) and the spatial configuration of the entire landscape" (Kindlmann & Burel, 2008, p. 880).
Connectivity, structural	"occurs where connectivity is based entirely on landscape structure with no direct link to any behavioral attributes of organisms" (Kindlmann & Burel, 2008, p. 880).
Landscape connectivity	"It is defined as the degree to which a landscape facilitates or impedes movement of organisms among resource patches" (Tischendorf & Fahrig, 2000, p. 8)
Wildlife corridors	Undisturbed land that connects natural habitats separated by barriers, often motorways where these lead over a viaduct or through a tunnel (Lindenmayer & Nix, 1993).
Wildlife passages	Man-made under- or overpasses constructed in such a way that wildlife is encouraged to use them, for instance, to cross motorways (Hirschi, 2021).

Contents

Chapter 1: Introduction

1.1. Motivation

Even though wild boar[1] have been shown to have some useful effects on ecosystems (Risch, Busse, Page-Dumroese, & Schütz, 2010; Wirthner, Beat, Busse, Schütz, & Risch, 2011), they are generally considered a pest because of the environmental damage they cause and the massive economic losses that emerge from human–wild boar interactions (Köppel, et al., 2007). These losses include damage to crops (Honda & Kawauchi, 2011; Rutten, et al., 2019), damage to cars and/or passengers resulting from collisions with wild boar (Morelle, Lehaire, & Lejeune, 2013; Gren & Jägerbrand, 2019), and the health threat that this species represents to domestic pigs (Laddomada, et al., 1994; Fritzemeier, Greiser-Wilke, Staubach, Schlüter, & Moennig, 2000; Ruiz-Fons, Segalés, & Gortázar, 2008; Wu, et al., 2011). Wild boar and domestic pigs are susceptible to the same range of diseases, the most common being: classical swine fever, Aujeszky's disease, and pig brucellosis (Köppel, et al., 2007; Ruiz-Fons, et al., 2008b). In Switzerland, the number of outdoor piggeries has grown in recent years due to a greater demand for ethical husbandry, resulting in an increase in the probability of contact between wild boar and pigs (Köppel, et al., 2007). One disease that has concerned the government, due to its high lethality, is African Swine Fever (ASF). ASF first appeared in Portugal in 1957, from where it spread across Europe until its final official clearance in 1993, except for Sardinia, where the disease became endemic (Boinas, Wilson, Hutchings, Martins, & Dixon, 2011). ASF re-appeared in Eurasia in 2007 (Vergne, Gogin, & Pfeiffer, 2017), jumped to Eastern Europe in 2014 (Gallardo, et al., 2018). It spread to Belgium where the first cases appeared in 2018 (Morelle, Jezek, Licoppe, & Podgorski, 2019). The first case of ASF in Germany was documented in 2020 in wild boar (Deutscher Landwirtschaftsverlag, 2020), and in 2021 the virus was detected in piggeries (Federal Ministry of Food Agriculture, 2022). In 2022, the virus was detected in Italy (Stauffer, Polansek, & Alves, 2022), and the most recent case was reported in Greece in 2023 (ter Beek, 2023) . ASF has a high mortality rate, and it affects domestic pigs (BLV, 2019). In Switzerland, pork is the most consumed meat. If ASF (or another infectious disease) emerges in the country, it will cause considerable loss for the producers. In order to effectively contain the disease and prevent it from being transmitted to domestic pigs, the Swiss authorities require information on the distribution and abundance of wild boar, as well as on the connectivity and potential compartmentation of their habitat.

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[1] In this thesis, the term 'wild boar' refers to the taxon, that is, the same spelling is used in the singular and in the plural.

The objective of the thesis presented here is to analyze the spatial aspects related to the dispersal and colonization of free-ranging wild boar in Switzerland. Understanding these aspects is necessary to improve early disease detection and disease containment within the wild boar population and to reduce the risk of disease transmission to domestic pigs. To complete this task, the mechanisms and factors that can potentially play a part in the introduction and spread of an infectious disease within the wild boar population have to be defined. Similarly, it is important to consider and analyze how an infectious process can spread from wild boar to similar species (e.g. domestic pigs). In this thesis, the objective is addressed by (i) identifying the potential areas or suitable habitat where wild boar can colonize; (ii) computing their relative abundance, identifying potential entry points of ASF into the wild boar population, and detecting risk areas where direct contact between wild boar and domestic pigs can occur; and finally (iii) exploring the effect of managing landscape connectivity on disease spread within the wild boar population.

1.2. Related Work

1.2.1. Wild boar in their natural environment

Wild boar is a diurnal animal, but under human pressure (e.g. hunting) its habit switches to nocturnal (Russo, Massei, & Genov, 1997; Johann, Handschuh, Linderoth, Dormann, & Arnold, 2020; Keuling, Stier, & Roth, 2008). Wild boar is a social mammal, which can even show empathic behavior towards other individuals (Masilkova, et al., 2021). It is a very prolific species (Graves, 1984; Rosell, Fernández-Llario, & Herrero, 2001). Females can farrow twice a year with a mean of five piglets per litter (Rosell, Fernández-Llario, & Herrero, 2001). Their social interactions begin soon after birth, since a female and its offsprings usually get mixed with other females and their litters. There are also groups with a single sow and its litters (Graves, 1984). A group of wild boar is sometimes called a sounder (Graitson, Barbraud, & Bonnet, 2019), and it is usually composed of females, piglets and some subadults that can include males. Males in these groups will remain until they are old enough to leave it. Mature males are normally lone wanderers (Boitani, Mattei, Nonis, & Corsi, 1994; Spitz & Janeu, 1995); however, adult males might be present around a sounder when a female is in estrus (Graves, 1984). Each sounder and each adult male have a home range, which can be shared with other groups, but the core is mostly shared by family members of the main group. The core area is used for farrowing, rest and other basic activities (Janeau, Cousse, Cargnelutti, & Spitz, 1995), and it is considered a place that offers protection to the group. The home range differs depending the sex (Spitz & Janeu, 1995), hunting season (Morelle & Lejeune, 2015), season of the year, and food availability (Boitani, Mattei, Nonis, & Corsi, 1994; Drimaj, et al., 2021). In the case of females, the home range reduces after farrowing (Graves, 1984).

In a natural environment, the diet of wild boar is seasonal (Graves, 1984; Massei, Genov, & Staines, 1996). In fall their diet is based on vegetables, tree-nuts (e.g. acorn, beechnuts), and berries, while in summer they feed of tubers, roots, and worms (Graves, 1984; Massei, Genov, & Staines, 1996; Schley & Roper, 2003). However, their diet is driven by the availability of food and their environment (Cahill, Llimona, & Cabañeros, 2012; Oja, Kaasik, & Valdmann, 2014), and their adaptation capacity drives them to switch food sources when needed. They can eat animal matter (Schley & Roper, 2003; Ballari & Barrios-García, 2014), eggs (Graves, 1984; Bengsen, Gentle, Mitchell, Pearson, & Saunders, 2014), and mushrooms (Baubet, Bonenfant, & Brandt, 2004), and they can even develop scavenger behavior (Ballari & Barrios-García, 2014).

Wild boar natural habitat is in forested areas, swamps, and marshes (Graves, 1984). They have managed to adapt to urban sprawl and can be seen in abandoned parcels, agro-silvo-pastoral landscapes, and even urban areas (Cahill, Llimona, & Cabañeros, 2012; Johann, Handschuh, Linderoth, Dormann, & Arnold, 2020).

Wild boar enhance soil ventilation through grubbing or rooting activities (Risch, Busse, Page-Dumroese, & Schütz, 2010; Barrios-Garcia & Ballari, 2012). Wild boar act as spore dispersers for some tree species when rubbing trees. This is beneficial for the conservation and propagation of these plants within forests (Heinken, Schmidt, Von Oheimb, Kriebitzsch, & Ellenberg, 2006). On a local scale, wild boar serve as a dispersal vector for some aquatic invertebrate species when wallowing (Vanschoenwinkel, Waterkeyn, Vandecaetsbeek, Grillas, & Brendonck, 2008).

Wild boar is, nevertheless, considered as an invasive species due to the negative impact it has on the environment (Ballari & Barrios-García, 2014; Bengsen, Gentle, Mitchell, Pearson, & Saunders, 2014; McClure, Farnsworth, J., & Miller, 2018). Some authors have proposed that wild boar act as ecosystem engineers (Boughton & Boughton, 2014; McClure, Farnsworth, J., & Miller, 2018), given their capacity to modify soil properties through rooting and grubbing (Singer, Swank, & Clebsch, 1984; Barrios-Garcia & Ballari, 2012). Rooting impacts soils by reducing the litter layer and favoring soil erosion (Singer, Swank, & Clebsch, 1984). Wild boar remove parasites by wallowing, rubbing and tusking. The last two activities are performed against trees (in some cases on poles), which damages the bark and sometimes the wood of the trees. In the worst case, the tree dies as a result of the severe damage (Graves, 1984). Additionally to this, the food habits of wild boar (i.e. omnivorous) are a source of stress for other co-inhabiting species, in the form of predation and domination of common areas. For instance, in Belgium *Vipera berus*, a native snake species is being pushed toward extinction by wild boar, which not only prey on the snake but also affect its habitat (Graitson, Barbraud, & Bonnet, 2019). Similarly, in areas where wild boar were introduced, such as Australia, several turtle species are endangered due to egg predation (*Chelodina rugose, Lepidochelys olivacea, Chelonia mydas*, and *Natator depressus*), suffering population declines of up to 90% (Bengsen, Gentle, Mitchell, Pearson, & Saunders, 2014).

1.2.2. Wild boar and humans

Urban sprawl and expansion of the built infrastructure reduce wildlife habitat, exposing animals to forced encounters with humans (Jaeger, Soukup, Schwick, Madriñán, & Kienast, 2016). Although most wildlife try to avoid it, there are some species that have learned to live near or among humans (Beisner, et al., 2015). The high degree of plasticity of wild boar enables them to overcome the landscape of fear (Stillfried, et al., 2017). In other words, they adapt their movements according to human disturbances. Disturbances can be direct, like hunting, or indirect, like timber work and peasant activity in the woods (Ohashi, et al., 2013). Sightings of wild boar in urban areas are being reported around the world, and their frequency has increased over the years. This has occurred in countries like Germany, Spain, Norway, China, and Poland (Kotulski & König, 2008; Cahill, Llimona, & Cabañeros, 2012; Licoppe, et al., 2013; Johann, Handschuh, Linderoth, Dormann, & Arnold, 2020). The most frequent complaints about encounters with wild boar among inhabitants of these areas include: damage to backyards and public parks, attacks on pets (or humans), and car collisions (Kotulski & König, 2008; Cahill, Llimona, & Cabañeros, 2012; Licoppe, et al., 2013).

One of the most common and negative impacts of wild boar reported worldwide is damage to crops (Massei, Genov, & Staines, 1996; Schley & Roper, 2003; Geisser & Reyer, 2004; Herrero, García-Serrano, Couto, Ortuño, & García-González, 2006; Ohashi, et al., 2013; Li, et al., 2013). Such agricultural damage causes large economic losses per year in most European countries and in the USA (Geisser & Reyer, 2004). Car collisions are another issue resulting in large economic losses, as well as injury or death to the animals and humans (Morelle, Lehaire, & Lejeune, 2013).

Intensive breeding of wild boar for hunting was suggested in a study conducted in 2010 and proven to be a potentially profitable business (Iarca, et al., 2011), but the side effects of this activity can also cause considerable damage. For instance, if the fencing is not adapted to keep the animals within the desired area (The Deer Initiative, 2009), some individuals could escape. Downsides also exist with wild boar farming for human consumption. For example, the prevalence of *trichinellosis* has been found to be higher in wild boar than in domestic pigs (Sukura, Näreaho, Veijalainen, & Oivanen, 2001). *Trichinellosis* is a zoonotic disease that can seriously affect humans if they eat insufficiently cooked meat from infested animals.

The control of invasive species, like wild boar, is an extremely expensive and management-demanding measure (McClure, Farnsworth, J., & Miller, 2018). This management and control include techniques including Judas pigs (i.e. wild boar that is caught, collared, released to be tracked in order to find a bigger group and exterminate them), poisoning (Barrios-Garcia & Ballari, 2012), fertility control (Jori, et al., 2021), and in some cases fencing. Fencing areas is a technique that is being used for the conservation of some species (Taylor & Martin, 1987), to restrain roaming individuals that might be infected with diseases (Taylor & Martin, 1987; Jo & Gortázar, 2021), and to reduce car collisions with wildlife (McInturff, Xu, Wilkinson, Dejid, & Brashares, 2020).

Building fences for wild boar can be very expensive due to the requirements that need to be fulfilled for the fences to be completely effective. Once built, the fences must have regular maintenance to remain effective (The Deer Initiative, 2009; Jori, et al., 2021). However, it is important to mention that fencing also affects other species, as it contributes to the separation of wildlife habitat (Mysterud & Rolandsen, 2019; McInturff, Xu, Wilkinson, Dejid, & Brashares, 2020).

1.2.3. Wild boar in Switzerland

Wild boar is one of the most wide-spread ungulates in the world, occurring on every continent except Antarctica (Barrios-Garcia & Ballari, 2012) . There are several factors that contribute to the species' expansion, especially toward northern territories (Jori, et al., 2021). Global warming, far from placing this species in danger, contributes to its dispersal. Specifically, winters are becoming milder, meaning that food resources for wild boar are available for longer (Melis, Szafrańska, Jędrzejewska, & Bartoń, 2006). Some other factors that favor the species' expansion are: the cultivation of agricultural land in the form of monocultures (e.g. maize) (Fattebert, Baubet, Slotow, & Fischer, 2017), the reduction in hunting pressure (Massei, et al., 2015; Keuling, Strauß, & Siebert, 2016), the lack of natural predators, and the species' high reproduction rate (Keuling, et al., 2013).

In the twentieth century, wild boar numbers were highly reduced across almost all of Europe (Leuenberger, 2004; Acevedo, Escudero, Muńoz, & Gortázar, 2006; Schlageter & Haag-Wackernagel, 2011; Massei, et al., 2015; Jori, et al., 2021). After being eradicated in Switzerland, wild boar started to be present again in this country approximately during the 1970s (Leuenberger, 2004; Schlageter & Haag-Wackernagel, 2011). The re-colonization of wild boar in Switzerland is the result of the immigration of this species from neighboring countries: France, Germany, and Italy (Merli & Meriggi, 2006; JagdSchweiz, 2018). In Ticino, for instance, the first observations were recorded in the early 1980s (Moretti, 2014). After the 1980s, the population started spreading fast, recolonizing areas which were suitable for them (Sáez-Royuela & Tellería, 1986; Geisser & Reyer, 2005; Massei, et al., 2015; Jori, et al., 2021). This phenomenon was observed not only in Switzerland but also in other parts of the continent where wild boar was no longer a common species (Acevedo, et al., 2007; Rutten, et al., 2019). Currently, there are two wild boar populations in Switzerland, one in the north of the country, from Geneva to Saint Gallen, and the other in the south, in the canton of Ticino (Meier & Ryser-Degiorgis, 2018).

In Switzerland, like in many other countries, the natural environment of wild boar is in the forest (Geisser & Reyer, 2005), but they are also present in cultivated areas (Fattebert, Baubet, Slotow, & Fischer, 2017). Over the last decades, the main changes to the Swiss landscape have been the intensification of road network and the extension of urban areas (urban sprawl). This situation has led to the continuous fragmentation of wildlife habitat, reducing the number of several species, and it has affected the space requirements of large mammals like wild boar, lynx and red deer (Holzgang, et al., 2001; Jaeger, Soukup, Schwick, Madriñán, & Kienast, 2016). Switzerland has a very rugged terrain, which makes areas above 2000 m.a.s.l. difficult for wild boar to live in or to cross (Giacometti, 2003), and hence are rarely colonized.

Knowing the distribution and density of wild boar is of paramount importance for the management and control of populations (Pittiglio, Khomenko, & Beltran-Alcrudo, 2018). A considerable amount of research has been carried out to assess the density, abundance and distribution of wild boar. Calculating wild boar abundance or density represents a great challenge, due to the nocturnal habits of this species (Boitani, Mattei, Nonis, & Corsi, 1994), its preference for wooded areas (Cahill, Llimona, & Gràcia, 2003), and its alertness to situations that could represent a threat, including the presence of hunters or observers (Chapman & Trani, 2007; Marini, Franzetti, Calabrese, Cappellini, & Focardi, 2009).

Two main method types are typically used to collect the data needed to estimate wild boar population estimators: direct and indirect methods. Hunting statistics, counts, capture-mark-recapture, distance sampling, and camera traps are considered direct methods. Pellet counts, snow tracks, genetic data, impact on the environment, and life-trails are considered indirect methods (ENETWILD-consortium, et al., 2018). Hunting statistics are one of the most widely used data sources for population estimations. This low-cost data source enables comparisons across countries (ENETWILD-consortium, et al., 2018). Depending on the recording methodology (e.g. coordinates of hunted animal per day), it is possible to assess abundance and density at different scales, including the national level (Leuenberger, 2004; Bosch, et al., 2012; Acevedo, Quirós-Fernández, Casal, & Vicente, 2014; Meier, Fischer, & Ryser-Degiorgis, 2015).

Hunting statistics have been the dominant method used for wild boar population estimation in Switzerland. The probability of wild boar occurrence was predicted at the country level for the first time in 2004 (Leuenberger, 2004). In that study, occurrence probability was predicted based on a multivariate logistic regression of the estimated wild boar population density on various landscape characteristics. Wild boar population density was estimated using hunting statistics from a two-year period (2001–2002), applying assumptions regarding (i) the annual wild boar population increment and (ii) the percentage of wild boar killed by hunters out of this annual population increment. The results indicated high occurrence probabilities near the borders with France and Germany in northern Switzerland, and near the borders with Italy in southern Switzerland. Additionally, the model underpredicted probabilities near the border but overpredicted probabilities in the interior regions of the country. The latter finding suggests, according to the authors, that there is some suitable habitat for wild boar in these interior regions that has not been colonized yet.

In the canton of Geneva, wild boar hunting was forbidden in 1974, and the harvesting of wild boar has been performed only by game keepers since then (Fischer, Gourdin, & Obermann, 2004). This has led to (i) a lack of hunting statistics in this canton, which limits the possibility of comparing wild boar population estimates with other cantons, and (ii) the need to look for alternatives when trying to calculate the density or relative abundance of wild boar. One alternative used in this canton has been the capture-resight (CR) method in combination with culling statistics (Hebeisen, Fattebert, Baubet, & Fischer, 2008). CR is a reliable and accurate source of data that is widely used for density/abundance estimations. It consists of detailed tracking data of the marked animal, which includes spatio-temporal information of fine granularity (i.e. coordinates of the location of the animal several times per day). However, it is too expensive to apply it on a national scale. In 2007, this technique was used to estimate not only the population size but also the density of wild boar in the canton (Hebeisen, Fattebert, Baubet, & Fischer, 2008). Wild boar were captured and marked in 2002–2005. The resightings were recorded using camera traps (either marked or unmarked animals). From these data, population size estimators, total population and density of wild boar were calculated. The culling bags were used to calculate the culling index (Cind) (number of culled animals divided by culling hours per day). The trends from Cind were compared to the total populations to understand culling effects on the population. Although the sampling areas and methods applied in this work differed from those reported in other countries (Melis, Szafrańska, Jędrzejewska, & Bartoń, 2006), the authors claimed that the population density was the highest in Western Europe, at 10.6 ± 0.8 (SD) individuals per sq. km (Hebeisen, Fattebert, Baubet, & Fischer, 2008).

In 2015, another study included population estimations of wild boar calculated using distinct methods: hunting statistics, counting pellets, and thermal cameras (Meier, Fischer, & Ryser-Degiorgis, 2015). Hunting statistics (hunted, culled and found dead) from the period 1992–2012 were used to calculate the dead wild boar density per 100 ha at the national level. The density of dead wild boar increased by almost 10% over the two decades, which was interpreted as an expansion of wild boar. Pellet (feces) counts and camera traps (night vision counts) were additional methods used to estimate the density and relative abundance of wild boar at a local scale. The observation period for these methods was 2014–2015. The results based on these two methods were inconclusive.

1.2.4. The pig industry in Switzerland

An analysis of the pig production network in several countries of the European Union (EU) showed similarities in their topology (Relun, et al., 2016). The regular model of pig industries in Europe consists of diverse holdings that handle different production processes, for instance farrowing or feeding farms (Früh, et al., 2014). Each holding is handled in a different way, and in many cases the pigs are transported from one place to another, such as from farrowing farms to feeding farms. Switzerland has a slightly different production scheme. The main difference lies in how pig trade happens within the country: it is organized in a hierarchical way with many small farms, which makes this network highly decentralized. This might be an advantage for disease prevention (Sterchi, et al., 2019).

In the European Union and in Switzerland, increased awareness of what we eat has led to a boom in the demand for more ethical food production overall. This includes organic pork products (Früh, et al., 2011; Früh, et al., 2014).

Switzerland has implemented two types of animal-friendly husbandry: Regelmässiger Auslauf im Freien (RAUS-Programm; regular outdoor exercise), implemented in 1993, and Besonders tierfreundliche Stallhaltungssysteme (BTS-Programm; particularly animal-friendly housing systems), implemented in 1996. These programs were developed to improve the quality of livestock by incentivizing the farmers to increase their production standards, which in turn would be reflected in better remuneration for the final pork products. These programs are not mandatory but are contributing to fairer livestock production nationally (Früh, et al., 2011; Bundesamt für Landwirtschaft (BLW), 2021). In Switzerland there are basically three types of pig housing systems: indoor without run area, indoor with run area, and outdoor with pasture (Figure 1) (Früh, et al., 2011). The latter two are subsidized by the RAUS and BTS programs. In the last two housing systems, pigs are particularly at risk of having direct contact with wild boar. Observations of hybrids (domestic pig × wild boar) among the piglets farrowed in some farms in Switzerland have confirmed that such contact actually occurs (Meier & Ryser-Degiorgis, 2018).
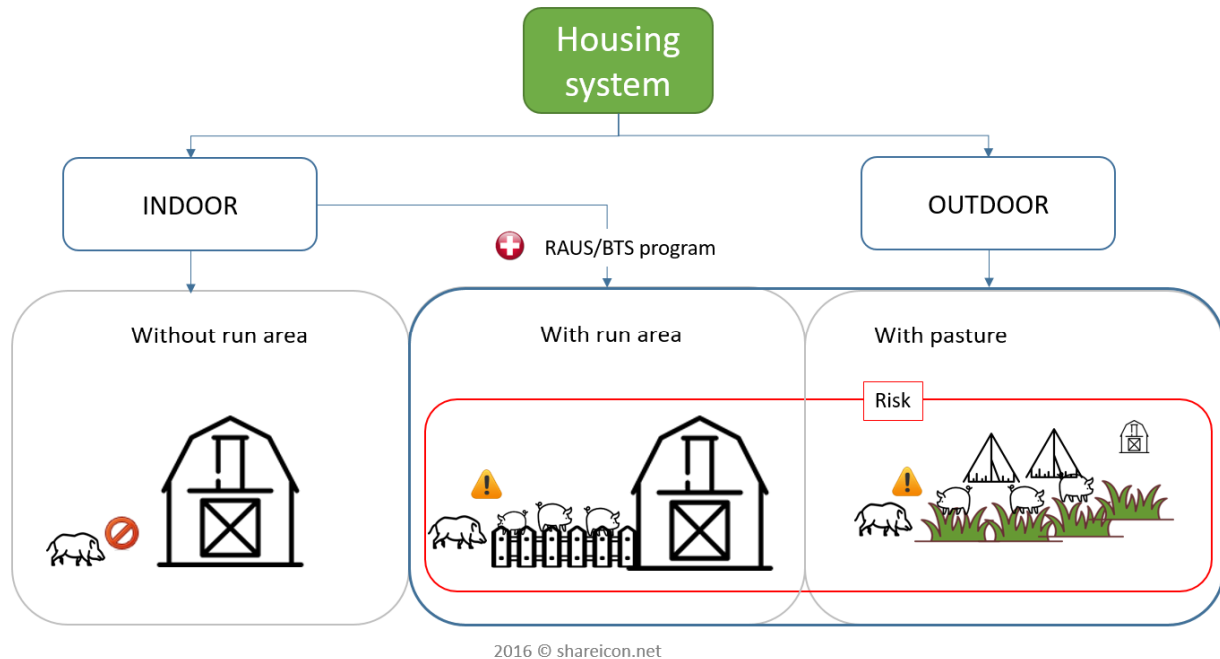
Figure 1². Pig housing systems in Switzerland.

Domestic pigs in Switzerland benefit from good health conditions compared with pigs farmed in other European countries. Thanks to the implementation of a systematic control of respiratory diseases in 1996 in Switzerland, it was possible to drastically reduce cases of enzootic pneumonia (EP) and pleuropneumonia (Stärk, Miserez, Siegmann, Ochs, & Infanger, 2007). There are still cases of EP, where a seroprevalence has been found in some Swiss farms (Scalisi, et al., 2022). An outbreak of PRRSV happened in 2012, but it was controlled in January 2013, at which point Switzerland gained the disease-free status for this disease (Nathues, et al., 2016). A study in 2006 found a low prevalence of *Escherichia coli* (*E. coli*) in pigs in Switzerland, but the combination of strains that was found are considered harmless to humans (Kaufmann, et al., 2006). Domestic pigs in Switzerland have been free of pseudorabies (Aujeszky's disease) since 1983 (Wittmann & Rziha, 1989; Müller, et al., 2011).

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² Prepared by the author based on Köppel, et al., 2007, Früh, et al., 2011, Jori, et al., 2017; BLW, 2021. The icons were downloaded from https://www.shareicon.net/. 2016 © shareicon.net is a website to share and free download icon.

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1.2.5. Wild boar as a reservoir of diseases and transmission to domestic pigs

Wild boar are hosts of various zoonotic agents that can affect other mammals and humans: bacteria such as *Mycobacterium tuberculosis*, *Salmonella*, *Yersinia*, and *Brucella* (Fredriksson-Ahomaa, et al., 2020); parasites such as *Toxoplasma gondii* (Rostami, et al., 2017) and *Trichinella spiralis* (Sukura, Näreaho, Veijalainen, & Oivanen, 2001); viruses such as *Herpesvirus* (Kukielka, Rodriguez-Prieto, Vicente, & Sánchez-Vizcaíno, 2016); and ticks that can also carry pathogens, including *Anaplasma phagocytophilum* (Hrazdilová, et al., 2021).

Pathogens hosted by wild boar that are a threat to domestic pigs include: Aujeszky's Disease Virus (ADV) or pseudorabies (PR) (Lee & Wilson, 1979; Ruiz-Fons, et al., 2008b), African Swine Fever Virus (ASFV) (Sánchez-Vizcaíno, Mur, & Martínez-López, 2013), Classical Swine Fever Virus (CSFV), Porcine Reproductive and Respiratory Syndrome Virus (PRRSV), Porcine Parvovirus (PPV) (Meng & Sriranganathan, 2009), Enzootic Pneumonia (EP), and pleuropneumonias caused by the bacteria *Mycoplasma hyopneumoniae* and *Actinobacillus pleuropneumoniae (APP)*, respectively.

The transmission process depends on the agent (Nelson & Williams, 2014), and an infectious agent can be acquired through air, food, water, ticks, or mating events. Once an infectious agent enters a wild boar population, it is transmitted and often persists within the population. This persistence is related not only to the size of the population and the contact rates derived from it (Ruiz-Fons, Segalés, & Gortázar, 2008; Fredriksson-Ahomaa, 2019), but also to the long life cycle that a pathogen can develop among the wildlife hosts. This persistence is what makes wild boar a reservoir for diseases (Ruiz-Fons, Segalés, & Gortázar, 2008).

The genetic similarity between wild boar and pigs was proven with a molecular analysis of mitochondrial DNA (mtDNA) sequences performed on domestic pigs. With this analysis it was possible to date a common ancestor of wild boar, domestic pigs and Asian pigs from about 500,000 years ago (Giuffra, et al., 2000). This genetic similarity makes domestic pigs and wild boar susceptible to the same range of diseases (Meng & Sriranganathan, 2009; Fredriksson-Ahomaa, 2019). Therefore, it is considered that wild boar is a threat to domestic pigs.

The transmission of diseases between wild boar and domestic pigs can occur directly or indirectly. Direct transmission occurs vertically and horizontally. Vertical direct transmission occurs when the disease is transmitted from mother to piglet. Horizontal transmission happens when there are encounters between wild boar and domestic pigs because they co-occur in an area (Ribbens, Dewulf, Koenen, Laevens, & de Kruif, 2004). In the past few years, outdoor farming has become a trend due to a greater demand for more ethical pig farming (Köppel, et al., 2007; Jori, et al., 2017). Outdoor farming is meant to improve animal welfare, but it also increases the chance of direct contact between wild boar and pigs.

Indirect routes of transmission include biological vectors (e.g. mosquitoes or bats), mechanical transmission (e.g. artificial insemination), mechanical vectors (e.g. ticks), contaminated food or illegal food trade, and humans (Ribbens, Dewulf, Koenen, Laevens, & de Kruif, 2004). Indirect contact was the most common transmission route of Classical Swine Fever (CSF) between wild boar and domestic pigs (Ribbens, Dewulf, Koenen, Laevens, & de Kruif, 2004). Activities where humans were indirectly involved in disease transmission included: contact of contaminated hunting equipment with domestic pigs, improper carcass handling, lack of hygiene management in holdings (Fredriksson-Ahomaa, 2019), and feeding pigs with contaminated food waste (Ribbens, Dewulf, Koenen, Laevens, & de Kruif, 2004; Niederwerder, 2021).

1.2.6. African Swine Fever (ASF)

African Swine Fever (ASF) is a disease caused by the virus with the same name (ASFV). ASF was first diagnosed in 1909 and described in 1921 in Kenya (Montgomery, 1921). It is a disease endemic to sub-Saharan countries, where some hogs and ticks act as a reservoir (Guinat, et al., 2016; Borca, et al., 2020). The symptoms of ASF include high fever, loss of appetite, and signs of hemorrhage on the skin of pigs (ears and flanks) (Anonymous, 2014). Mortality is high among animals that develop an acute form of the disease (Borca, et al., 2020). A high survival rate was found among individuals infected experimentally by a naturally occurring low virulent isolate, and the pigs did not develop symptoms (Martins & Leitão, 1994).

ASFV attacks the macrophage cells in the target organism. These are the white blood cells responsible for the consumption/digestion of pathogens. Unlike in swine, macrophages in humans and other mammals have not shown vulnerability to this virus. This means that the virus cannot be transmitted to humans (Enjuanes, Cubero, & Viñuela, 1977; Trotta, et al., 2022). Further, due to its low mutation rate, a mutation compatible with humans is unlikely to happen in the short term (Trotta, et al., 2022). However, this disease is a topic of concern due to its considerable impact on the pig farming (Penrith & Vosloo, 2009; Guinat, et al., 2016). China, one of the largest pork producers worldwide, lost between 50% and 70% of its pig population in two years (2018–2020) due to an ASF outbreak (Mason-D'Croz, et al., 2021). This situation is particularly devastating in countries where production is not high enough to satisfy the local demand, like in Madagascar (Randrianantoandro, Kono, & Kubota, 2015).

Conventional vaccines induce the production of macrophages. In the case of ASF these vaccines have an adverse effect on the health status of the recipients because they indirectly accelerate the replication of the virus. Promising results with a non-conventional vaccine have been reported in the USA (Röhrlich, 2022). More recently, in June 2022, the health minister of Vietnam announced the first commercial vaccine against ASF. This was developed by the company NAVET-ASFVAC (Vietnam Plus, 2022), and its effectiveness and safeness were confirmed by the Agricultural Research Services (USDA) (Herrmann, 2022). Before a vaccine is approved by the European Medicines Agency (EMA) it has to undergo a series of close examinations. Up to today (i.e. July 2022) no vaccine against ASF has passed all exams or been put to use in European countries (Röhrlich, 2022).

1.2.7. Routes and mechanisms of ASF transmission

There are four main routes of introduction of ASF into the wild boar population (Figure 2): (i) direct contact, (ii) environmental transmission, (iii) contact with individuals that survived the disease (O'Neill, White, Ruiz-Fons, Gortázar, & Christian, 2020), and (iv) indirect routes (Rowlands, et al., 2008; FASFC, 2019).
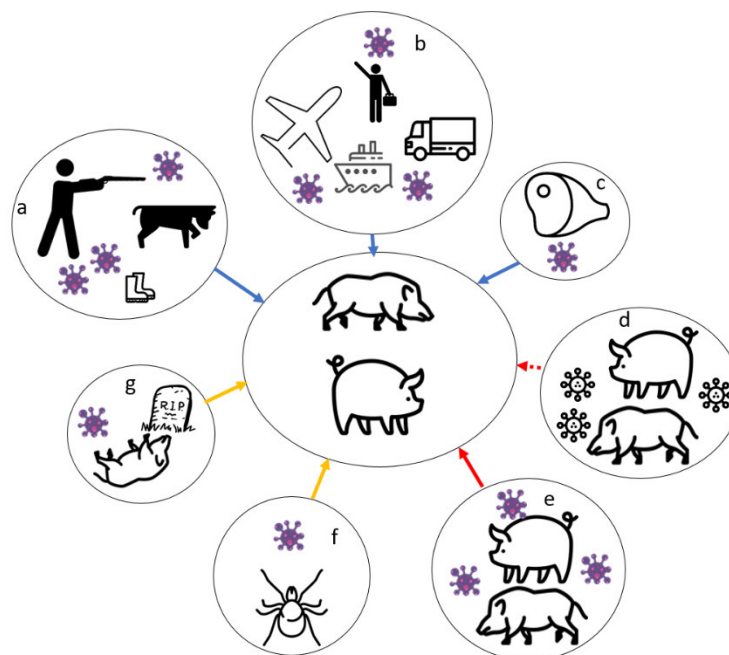
2016 © shareicon.net

Figure 2[3]. Routes of introduction of African Swine Fever. The red solid line corresponds to direct contact, the yellow lines to environmental factors, the blue lines to indirect routes of transmission, and the red dotted line to transmission via surviving individuals. (a) Hunting fomite, (b) travel/trade fomite, (c) contaminated food, (d) surviving individuals, (e) infected individuals, (f) soft ticks, and (g) infected carcasses.

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[3] Prepared by the author for illustrative purposes. The icons were downloaded from https://www.shareicon.net/. 2016 © shareicon.net is a website to share and free download icon.

Direct contact (Figure 2, *red solid arrows*): this form of introduction occurs when an infected subject has contact with a susceptible one. Transmission occurs through secretions, excretions. This can occur in common meeting places like wallowing areas and drinking or feeding places (O'Neill, White, Ruiz-Fons, Gortázar, & Christian, 2020).

Environmental transmission (Figure 2, *yellow arrows*): when an individual succumbs to the disease, the virus can remain in the carcass for a prolonged period (Mazur-Panasiuk & Woźniakowski, 2020; O'Neill, White, Ruiz-Fons, Gortázar, & Christian, 2020), which contributes to the persistence of the virus in the region (Morelle, Jezek, Licoppe, & Podgorski, 2019). The opportunistic feeding behavior of wild boar includes feeding on carcasses when no other food source is available (Ballari & Barrios-García, 2014). In a study performed in the Netherlands, where carcasses were placed on different sites to monitor their depletion time, wild boar was the dominant scavenger compared with other species, i.e. carcass depletion time reduced if wild boar were present. The species of the carcasses included wild boar, deer (roe, reed and fallow), European badger, and sheep (Wenting, Rinzema, & van Langevelde, 2022). Scarce food in winter makes wild boar especially prone to consuming carcasses, included their dead fellows (i.e. cannibalism) (Ballari & Barrios-García, 2014; Cukor, et al., 2020). Carcasses available in winter can present a higher risk of transmission because the virus has a longer period of activation in colder environments (Mazur-Panasiuk & Woźniakowski, 2020; Cukor, et al., 2020). In 2020, a carcass was found in Brandenburg, Germany that tested positive for ASFV, becoming the first case of the disease in wild boar or pigs in Germany. It is believed that the virus came with wild boar migration from Poland to Germany, since the carcass was found 30 km from the nearest case of ASF in Poland (Pacey, Perrin, & Gauntlett, 2020).

ASFV can be transmitted through parasites, including soft ticks (Penrith & Vosloo, 2009; O'Neill, White, Ruiz-Fons, Gortázar, & Christian, 2020; Cwynar, Stojkov, & Wlazlak, 2019). These *Ornithodoros* species are believed to carry the disease in Africa, together with the warthogs. In Europe, the soft tick *Ornithodoros erraticus* was linked to the transmission of ASFV in the Iberian Peninsula during the first wave of ASF in Europe (Pietschmann, et al., 2016; Cwynar, Stojkov, & Wlazlak, 2019). However, in a recent study in Germany, no traces of the virus were found among the collected exemplars, which means that the risk of introduction of the disease to Germany through ticks is quite low (Pietschmann, et al., 2016).

Surviving individuals (Figure 2, *red-dotted arrows*): a study *in vivo* with a low-virulent strain of ASFV suggested that animals that recover from the disease could still transmit the virus to other individuals (Gallardo, et al., 2015).

Indirect routes of introduction (Figure 2, *blue arrows*): these routes play a very important role in the introduction of the disease. This was the case with the reintroduction of ASF to Europe in 2007. An analysis of the virus strain proved that it corresponded to an endemic one from Southeast Africa. It was hypothesized that the disease had entered Europe on a transcontinental ship where contaminated food was disposed of in the Port of Poti (Georgia) in the Black Sea (Rowlands, et al., 2008). The introduction responsible for the emergence of this disease in Belgium in 2018 might have had a similar origin. It is believed that a careless driver disposed of contaminated food somewhere along a motorway, which was afterwards consumed by a wild boar (FASFC, 2019). In many countries there is an awareness of this type of introduction (Bundesministerium für Ernährung und Landwritschaft, 2022). To encourage appropriate disposal, special containers are placed at rest areas along motorways. These containers are accompanied by posters written in several languages, which aim to raise awareness about the danger of introducing ASF into the wild boar population if food waste is not disposed of properly (Figure 3).

Figure 3. Poster warning about risk of introduction of ASF within wild boar population (BMEL, 2019).

ASF can be introduced to domestic pigs by contaminated feed ingredients, which may have a transboundary origin. Crops can be visited by infected wild boar that have left biological traces (i.e. feces or urine); afterwards these crops are harvested and then used in food for pigs (Niederwerder, 2021). After testing several feed ingredients (e.g. soy bean), it was found that, depending on the ingredient, the virus can survive for up to 30 days which often exceeds the feed transport period (Dee, et al., 2019). Infectious food can also come from other sources including pork products (McKercher, Hess, & Hamdy, 1978; Guinat, et al., 2016; Dee, et al., 2019).

Contact with contaminated equipment is also a potential transmission route. This is extended to any device or material (e.g. hunting equipment, clothing) that has had contact with the virus (i.e. the fomite) and can touch susceptible individuals (Penrith & Vosloo, 2009).

Another means of transmission of ASF and other diseases is through pig trade, where pigs are transported from places where the disease is already present in domestic pigs. Live trade is a common practice in countries in the European Union and the Russian Federation. Introduction can also come from trucks used to transport infected individuals and then not properly disinfected after use (Mur, Martínez-López, & Sánchez-Vizcaíno, 2012). This trade is not limited to pigs, but also to biological compounds, such as semen. An outbreak of PRRSV occurred in Switzerland in 2012, when semen was imported from infected boars from Germany (Nathues, et al., 2016). It is important to emphasize that in almost all the ways in which ASF has been introduced into the pig industry, human activity has been involved. It is also important to mention that some authors believe that the rapid increase in the wild boar population could contribute to future disease outbreaks, not only in domestic pigs but also in humans (Müller, et al., 2011).

1.2.8. ASF in Europe

In 2007, an ASF outbreak was detected on pig farms in Georgia (WOAH, World Organization for Animal Health, 2007). In order to identify the source of this outbreak, the DNA of the virus was sequenced. The results showed that this virus was related to a strain from Mozambique, Madagascar, and Zambia. Therefore, it was believed that the virus was introduced to Georgia via contaminated food brought by ship (Rowlands, et al., 2008). After the introduction to the European continent, the disease began to spread further. In 2014 the first outbreaks in Eastern Europe were reported, in Belarus, Latvia, Lithuania, Poland, Estonia, and Ukraine. During that year, cases of infected wild boar and of infected pigs in some holdings were confirmed. In 2017 the first case of wild boar infected with ASF was reported in the Czech Republic, and in the same year the first case at a pig holding appeared in Romania (Smith, Wright, & Robert, 2017). The first case in Central Europe occurred in Belgium in 2018 (Morelle, Jezek, Licoppe, & Podgorski, 2019) In 2020 there were cases in Germany (Deutscher Landwirtschaftsverlag, 2020), and a case in January 2022 made Italy the most recent addition to the list of affected countries (Stauffer, Polansek, & Alves, 2022).

1.3. Study area

The thesis considers all of Switzerland, a country that covers a total surface area of 41,285 sq. km, ranging from 193 to 4634 m a.s.l. (Swiss Confederation, 2020a). Switzerland borders with the countries of France to the West, Germany to the North, Italy to the South, and Austria and Liechtenstein to the East (Figure 4).
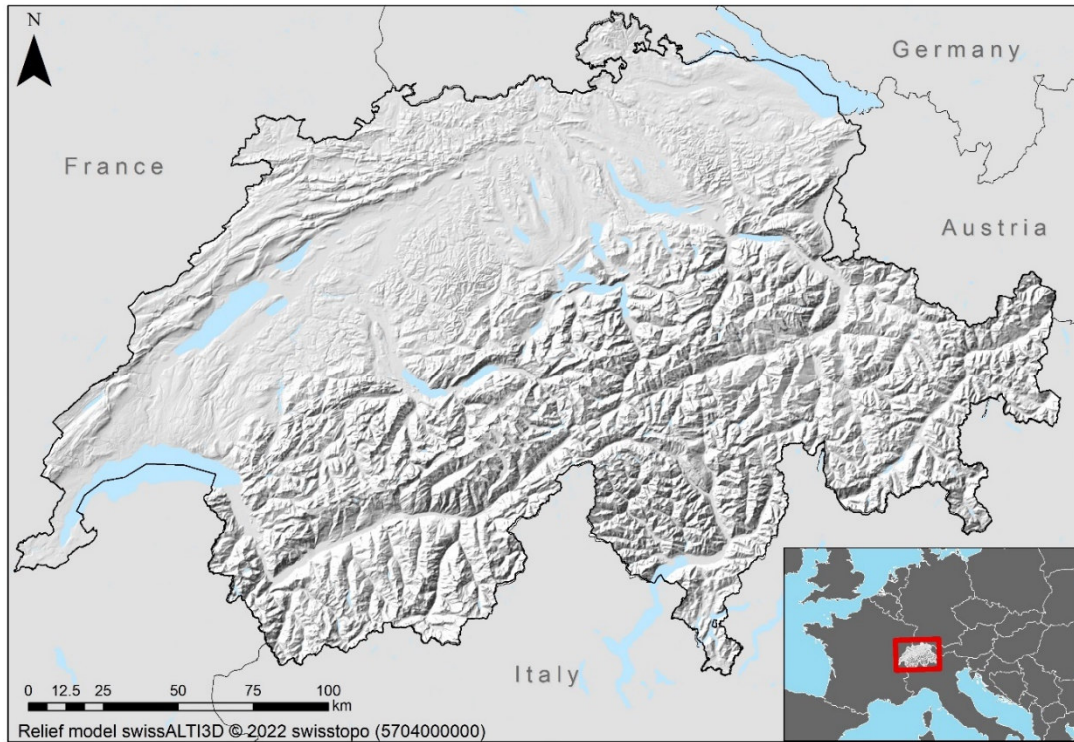
Figure 4[4]. Location of Switzerland.

Settlement areas cover 7.5% of Switzerland's territory. These include areas given over to housing, infrastructure (trade, industry and transport), water and energy supply, wastewater disposal, and green and recreational spaces. Around 40% of Swiss land is used for agriculture, while roughly 30% is covered by forest and woodland. Switzerland has three main geographic regions: the Alps, covering around 60% of the country's total surface area, the Central Plateau (30%) and the Jura (10%). The Alps act as a prominent climatic barrier between northern and southern Switzerland (Swiss Confederation, 2020b). The climate of northern Switzerland is heavily influenced by the Atlantic Ocean. Winters in the northern Swiss Plateau are mild and damp, whereas higher elevations experience arctic temperatures. At elevations above 1200–1500 m a.s.l., precipitation in winter mainly falls as snow. Southern Switzerland is strongly affected by the Mediterranean Sea, making winters mild and summers humid and warm or hot.

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[4] Prepared by the author based on the layers: 1) "World Countries". Downloaded from http://tapiquen-sig.jimdo.com. Carlos Efraín Porto Tapiquén. Orogénesis Soluciones Geográficas. Porlamar, Venezuela 2015. Based on shapes from Enviromental Systems Research Institute (ESRI). Free Distribuition. 2) Swiss Boundaries from *"Bundesamt für Landestopografie"* swisstopo (SwissBOUNDARIES[3D], 2020).

For the computation of the wild boar probability distribution, relative abundance, and risk of ASF introduction and transmission, the time frame considered was 2011–2018. For the establishment of the wild boar network system two time frames were considered, the present time (2021) and the near future, which includes information relevant to planning for 2021–2026.

1.4. Research gaps

As shown in related work, understanding the spatial aspects of potential disease spread among free-ranging wild boar and knowing how to contain it, considering a possible spillover to domestic pigs, requires information about relevant phenomena and knowledge of the respective domains. Much of this information and knowledge were initially unavailable on the required spatial scale for the period of observation, indicating specific research gaps. In particular, there was a lack of:

1) high-resolution and up-to-date information about the potential distribution and abundance of wild boar in Switzerland;
2) knowledge of where an epidemic disease like ASF could be introduced into the Swiss wild boar population and where it could be transmitted to domestic pigs, lack of methods to locate these areas;
3) up-to-date information about the ways in which natural and artificial barriers for wildlife divide Switzerland's surface into compartments, knowledge of the extent to which the wild boar habitat in Switzerland is connected and how far landscape connectivity can be managed to contain disease spread, lack of methods to acquire this knowledge.

The Chapters 2-4 expand on the work done to fill the research gaps previously mentioned.

1.5. Tools used

The following tools were used for the development of this work according to its specific research gap.

ArcMap™ 10.8.2 from ArcGIS[5] was used in every stage of this work. The license was provided by the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL). From this software, several geoprocessing tools were utilized, including the Model Builder. This tool is very useful to establish workflows and to automatize many processes. In Chapter 2, workflows like data alignment, data preparation, data calculations, data extraction, mass reprojection, and resampling were set to achieve the main objective. The arranged layers were used in combination of code lines adapted from (Guisan, Thuiller, & Zimmermann, 2017) for RStudio©[6]. With the layers and the code, it was possible (i) to select the predictors that could explain best the spatial structure from the species data, (ii) to fit a model with the species dataset, (iii) to evaluate the performance of the model, (iv) to build an assembled model, (v) and to calculate the spatial correlation.

For Chapter 3, Model Builder was used to clean and prepare the data used as input for different calculations including: the Euclidean distance to rest areas, the proximity to forest and the combined risk. The geotools used involved: point to raster, feature to point, intersects, reclassification, erases, merges, spatial joins, queries, and map algebra. The calculation of wild boar relative abundance was performed through a self-developed python code (version 2.7.14) through *the web-based interactive developed environment* "Jupyeter Notebook[7]", using libraries like arcpy, pandas, numpy, and math. The python code was adapted according to the spatial and temporal resolution available of the hunting data per canton. These availability gave origin to 5 possible combinations: (i) coordinates per day, (ii) commune/*reviere* or *bezirik* per day, (iii) a mixture between coordinates per day and commune/*reviere* or *bezirik* per day, (iv) commune per year, and (v) canton per year. The steps developed for the sets of codes (Jupyter Notebooks), varied according these combinations. However, the code structure (i.e. the steps) was the same for each data-case: (i) Import the hunting data, (ii) perform the firsts calculations, (iii) export the data to ArcMap to assign the calculated values to the centroids of the pre-created grid, (iv) once the assignment was performed, import the data back into the Jupyter Notebooks to finalize the calculations, and (v) run some verifications on the final data.

The ArcMap tools used in Chapter 4 included the definition of several workflows (i.e. model builder) for the preparation of the layers to calculate the landscape fragmentation. In this workflow, the Corine Land Cover Layer was reclassified, and iterations set to extract the new reclassification per bioregion. The fragmentation analysis ran through the Fragstats software version 4.2.1.603 from Kevin Mcgarigal & Eduard Ene[8].

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[5] Copyright © 1995-2021 Esri. All rights reserved. Published in the United States of America.
[6] 2009-2021 RStudio, PBC.
[7] https://jupyter.org/
[8] https://fragstats.org/

Experimental version of Google Earth[9] was used to explore at high level of detail the landscape around the intersections between Motorways (i.e. barriers) and the wildlife networks.

The network analysis was performed through a self-developed python code (version 3.6.5) ran through "Jupyter Notebook". These codes allowed much more versatility and flexibility when making calculations and specifying connectivity between nodes and edge removal (i.e. present day and after containment). The libraries used for the correct execution of the code were: csv, operator, networkx, matplotlib, pandas, numpy, PIL, and sys. The code was set to query from master source (i.e. the adjacency matrix), define the network on the present day (i.e. query A_0), create the network after containment (i.e. query A_{-1}) and calculate the different network metrics, including the PES.

The portal Mapgeoadmin.ch[10] is an official Swiss geoportal to download geodata from the country from diverse governmental agencies. The downloaded data was useful for Chapters 2, 3 and 4.

All the maps showed in this synthesis were created using ArcMap and projected under the parameters developed by the *"Bundesamt für Landestopografie"* Swisstopo for Switzerland (Table 1) (EPSG, 2022).

Projection CH1903_LV03	
WKID	21781 Authority EPSG
Projection	Hotine Oblique Mercator Azimuth Center
False Easting	600000
False Northing	200000
Scale Factor	1
Azimuth	90
Longitude Of Center	7.439583333
Latitude Of Center	46.95240556
Linear Unit	Meter (1.0)
Geographic Coordinate System	GCS_CH1903
Angular Unit	Degree (0.0174532925199433)
Prime Meridian	Greenwich (0.0)
Datum	D_CH1903
Spheroid	Bessel_1841
Semimajor Axis	6377397.155
Semiminor Axis	6356078.963
Inverse Flattening	299.1528128

Table 1. Projection used and specifications of parameters.

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[9] https://earth.google.com/web (Version 9.185.0.0 Web Assembly).
[10] Karten der Schweiz - Cartes de la Suisse : map.geo.admin.ch | das Geoportal des Bundes - le géoportail fédéral : www.geo.admin.ch | Copyright.

Chapter 2: Free-ranging wild boar (*Sus scrofa*) in Switzerland: casual observations and model-based projections during the open and closed season for hunting[11]

2.1. Introduction

Since wild boar and pigs are susceptible to the same range of diseases, contact among these two species is unwanted in the pig industry (Ruiz-Fons, Segalés, & Gortázar, 2008; Fredriksson-Ahomaa, 2019). Identifying the spots where direct or indirect contact between wild boar and domestic pigs can take place is critical to develop risk-based surveillance systems for improving early disease detection and control. To have control over these encounters, it is of paramount importance to know where wild boar is currently present and areas it could potentially colonize. Research on the abundance and density of wild boar has been conducted previously at the European level (Alexander, Massei, & Wint, 2016; Pittiglio, Khomenko, & Beltran-Alcrudo, 2018) and in some European countries like Spain (Bosch, et al., 2012; Acevedo, Quirós-Fernández, Casal, & Vicente, 2014) and Great Britain (Croft, Chauvenet, & Smith, 2017). In Switzerland, work on the distribution and density of wild boar was done in 2004 using hunting statistics as a source (Leuenberger, 2004). In 2007, a finer grain study was then performed in the canton of Geneva with data derived from the capture-resights technique (Hebeisen, Fattebert, Baubet, & Fischer, 2008). Finally, in 2015 the abundance of wild boar across Switzerland was calculated using counting pellets, hunting statistics and thermal cameras (Meier, Fischer, & Ryser-Degiorgis, 2015).

The aim of this study was to model the potential distribution of free-ranging wild boar in Switzerland at a high level of detail and to relate it to the density of piggeries in different agricultural zones. Since the hunting season has an influence on wild boar's behavior (Keuling, Stier, & Roth, 2008), the potential distribution of wild boar was computed separately for the open and closed seasons for hunting. The two resulting maps were used to find piggeries at potential risk of disease transmission.

2.2. Data collection (material)

Species data: species data from the years 2011–2018 were requested from diverse sources. Hunting data (12,693 records) were obtained from all 16 Swiss cantons maintaining a license hunting system, covering roughly two thirds of Switzerland, plus Solothurn (for 2017) and Zurich. Causal observations (11,430 records) were obtained from Info fauna[12], and GPS-tracking data came from private sources. The latter data were used to validate the model. The data structure consisted of x and y coordinates and the date of the observation event. The data were split into summer (March through August) and winter (September through February), according to the closed and open seasons for hunting. A 1-km grid of Switzerland was developed. The hunting data and the observations were aggregated according to the 1-km grid to reduce spatial autocorrelation. The cells with one or more observations were considered as 'presence' data. For the 'pseudo-absence' dataset, the same number of cells as the presence cells were randomly selected, sampling twice as densely in zones where wild boar occur only sporadically, for instance at elevations above 2000 m a.s.l. Figure 5 depicts the workflow of the species data collection process.
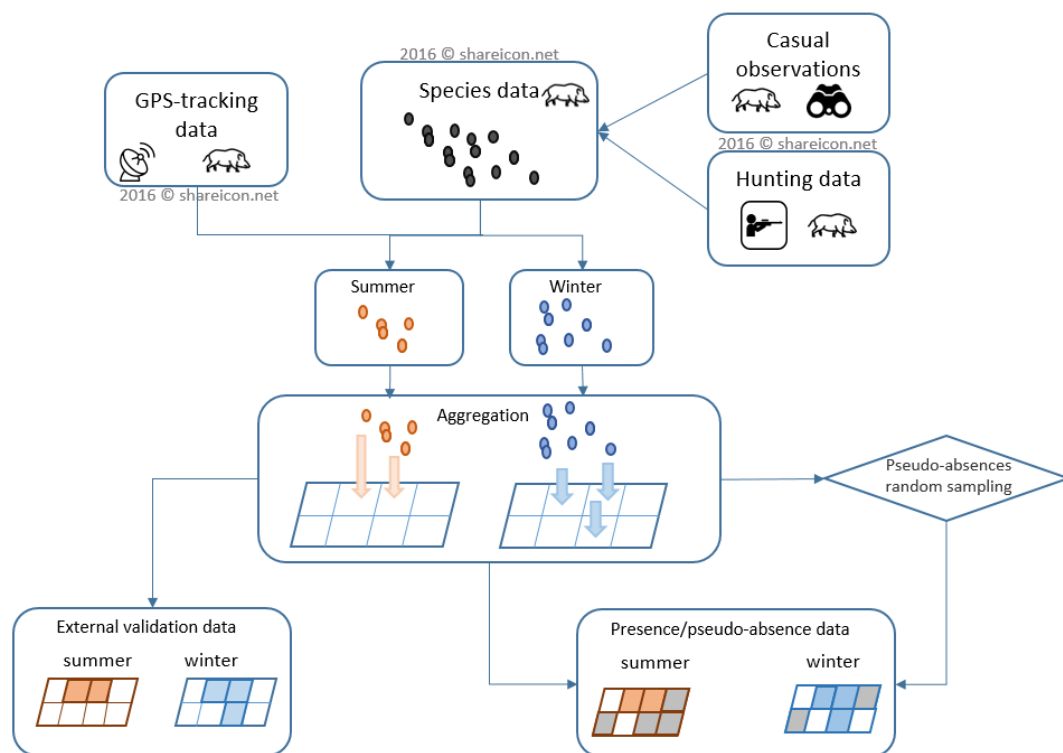
Figure 5[13]. Workflow from species data to presence/pseudo-absence data.

Predictor variables: after a literature review of wild boar's environmental preferences, 26 predictors were pre-selected (Table 2). The corresponding raster layers were obtained and spatially aligned with the presence/pseudo-absence layer from the previous step (Figure 5). The predictors that had a temporal reference (e.g. monthly precipitation) were averaged according to a time-span defined for summer (i.e. closed hunting season) and winter (i.e. open hunting season) (Table 2). The computation included the use of random forests (RF) (Breiman, 2001) in a stepwise backward elimination process as a method to identify the predictors that explained the presence data best. Predictors that showed a correlation of 0.7 or more, with predictor that had already been selected, were eliminated to avoid collinearity. Figure 6 shows a simplified version of the workflow used to determine the final predictors (Table 2 in bold text).

Variable	Definition	Unit	Type	Summer	Winter
Bio 1	**Annual Mean Temperature**	**°C**	**Bioclimate**	✓	✗
Bio 2	**Annual Mean Diurnal Range**	**°C**	**Bioclimate**	✗	✓
Bio 4	**Temperature Seasonality (Standard Deviation)**	**°C**	**Bioclimate**	✓	✓
Bio 5	Max. Temperature of Warmest Month	°C	Bioclimate	✗	✗
Bio 6	Min. Temperature of Coldest Month	°C	Bioclimate	✗	✗
Bio 7	**Annual Temperature Range**	**°C**	**Bioclimate**	✓	✗
Bio 12	Annual Precipitation	mm	Bioclimate	✗	✗
Bio 13	**Precipitation of Wettest Month**	**mm**	**Bioclimate**	✗	✓
Bio 14	**Precipitation of Driest Month**	**mm**	**Bioclimate**	✓	✓
Bio 15	**Precipitation Seasonality (CV)**	**percentage**	**Bioclimate**	✓	✓
Mbal	Yearly Moisture Balance	mm	Bioclimate	✗	✗
Mind	Yearly Moisture Index	unitless	Bioclimate	✗	✗
PET	Yearly Potential Evapotranspiration (PET)	mm	Bioclimate	✗	✗
SrelM	**Rel. Sunshine Duration**	**percentage**	**Bioclimate**	✓	✓
DEM_Aspc_1	Aspect	degree	Topography	✗	✗
DEM_Relief	Terrain Relief		Topography	✗	✗
slp	**Slope**	**degree**	**Topography**	✓	✗
tpi_8c_s81	Topographic position Index	m	Topography	✗	✗
TWI_M01K_1	SAGA Wetness Index		Topography	✗	✗
TWI_SAGA_1	Wetness Index		Topography	✗	✗
ForestTy	Percentage of Mixed Forest (broad-leaved/coniferous)	percentage	Vegetation	✗	✗
ddeg0	**Growing degree days above 0°C**	**°C days**	**Vegetation**	✗	✓
ddeg5	Growing degree days above 5°C	°C days	Vegetation	✗	✗
ForestMa	Forest mask from the Swiss National Forest Inventory (NFI)	yes/no	Land Fragmentation	✗	✗
NOAS04	**Land Use (4 classes)**	**4 classes**	**Land Fragmentation**	✗	✓
STATPOP	**Population density**	**n/ha**	**Socio-economics**	✓	✓

Table 2. Preselected and selected predictors. The bold text indicates the selected ones. Summer/Winter refer to the season for which the predictors were selected.
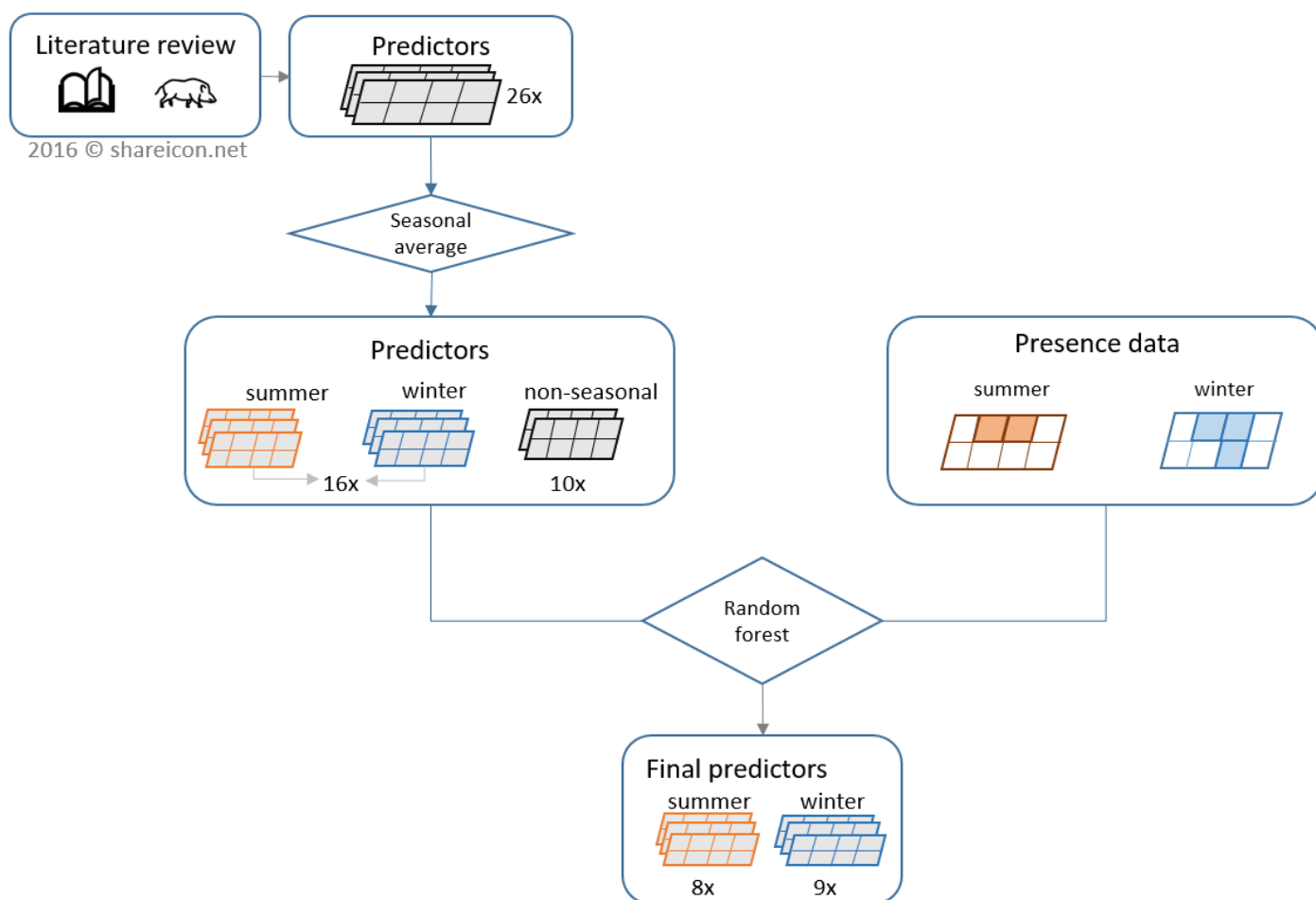
Figure 6[14]. Workflow for the computation of the final predictors.

Other data: the density of piggeries was downloaded from the website of the Federal Statistical Office (*Bundesamt für Statistik*) [15]. The downloaded data describe the farm structure and includes the numbers of farm animals per agricultural zone. The shape file for the 6 agricultural zone boundaries used here was developed by the Federal Office of Agriculture (*Bundesamt für Landwirtschaft BLW*). The shape file of biogeographical regions was defined by the Federal Office for the Environment (*Bundesamt für Umwelt BAFU*). These two files were downloaded from the Swiss portal 'geo.admin.ch'[16].

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[14] Prepared by the author based on the workflow defined for this analysis. The icons were downloaded from https://www.shareicon.net/. 2016 © shareicon.net is a website to share and free download icon.
[15] https://www.bfs.admin.ch/bfs/en/home/statistics/catalogues-databases.assetdetail.2041588.html
[16] https://map.geo.admin.ch/

2.3. Modeling

The final predictors obtained for the different seasons (Table 2, *in bold text*), as well as the presence and pseudo-absence data, were used to build an ensemble spatial distribution model. This ensemble included five different modeling approaches. The computed values were weighted according to the predictive performance of the respective models and averaged to yield a single probability value. To produce the final layer, this probability value was assigned to one of three ranges, 0–0.5, 0.5–0.7, or 0.7–1. Values between 0.5 and 0.7 were used to define areas with a potential presence of wild boar. Thresholds above 0.5 to 0.6 are suggested to tansform probability to presences (Guisan, Thuiller, & Zimmermann, 2017). Those equal to or above 0.7 defined areas likely to have presence of wild boar, which is in line with common practice (Araújo, Pearson, G., Thuiller, & Erhard, 2005). However, these values can be tuned according to the overal result of the ensemble modeling (Guisan, Thuiller, & Zimmermann, 2017). The same procedure previously described was carried out separately for winter and for summer.

The data resulting from the probability computation and the density of piggeries per agricultural zone, averaged over 2011–2018, were used to calculate the potential risk of disease transmission. This workflow is depicted in Figure 7.
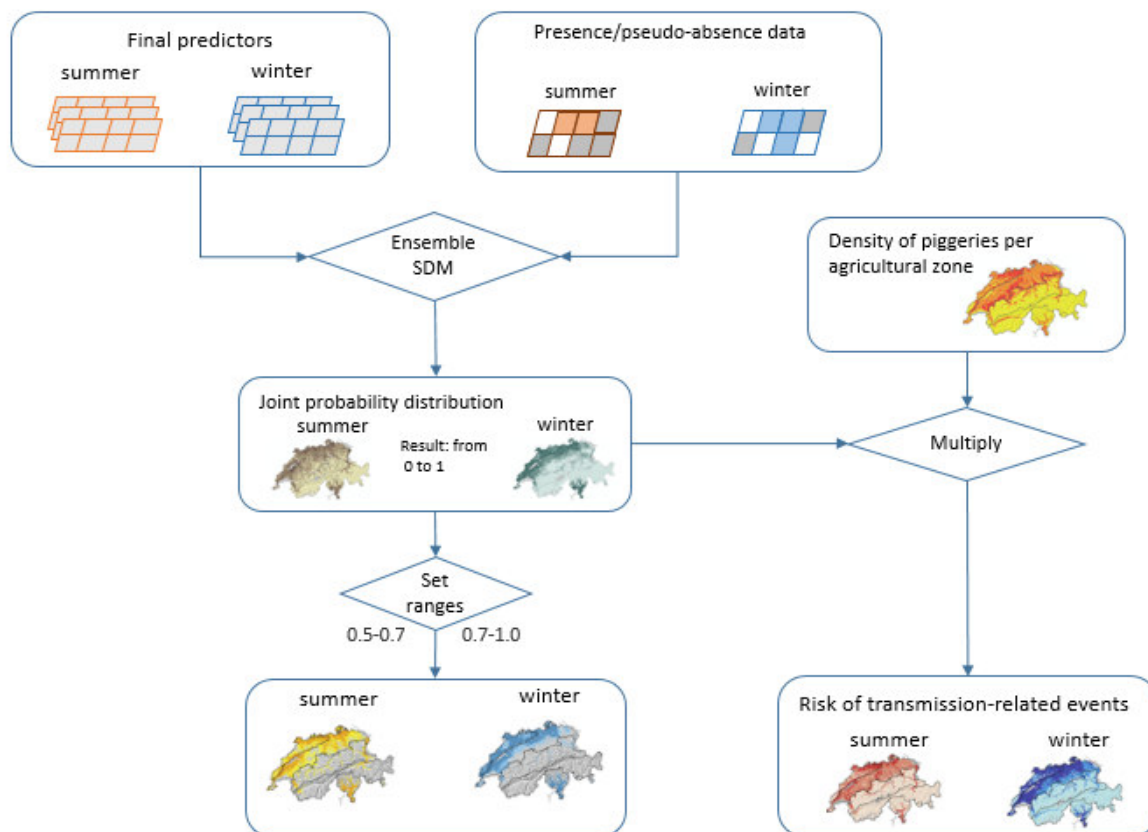
Figure 7[17]. Modeling workflow.

2.4. Evaluation

To identify the amount of spatial structure in the species data that was not explained by the predictors (Guisan, Thuiller, & Zimmermann, 2017), the global Moran's I was computed for a summer GAM (generalized additive model) and a winter GAM (Moran, 1950). This involved deriving a distance matrix from all observations and testing the distance effect against the residuals. In this way, the residuals were tested for spatial autocorrelation. Figure 8 shows a simplified scheme of this validation step.

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[17] Prepared by the author based on the workflow defined for this analysis. The icons were downloaded from https://www.shareicon.net/. 2016 © shareicon.net is a website to share and free download icon. The maps showed in this workflow are snapshots taken from (Vargas-Amado, Grütter, Fischer, Suter, & Bernstein, 2020).
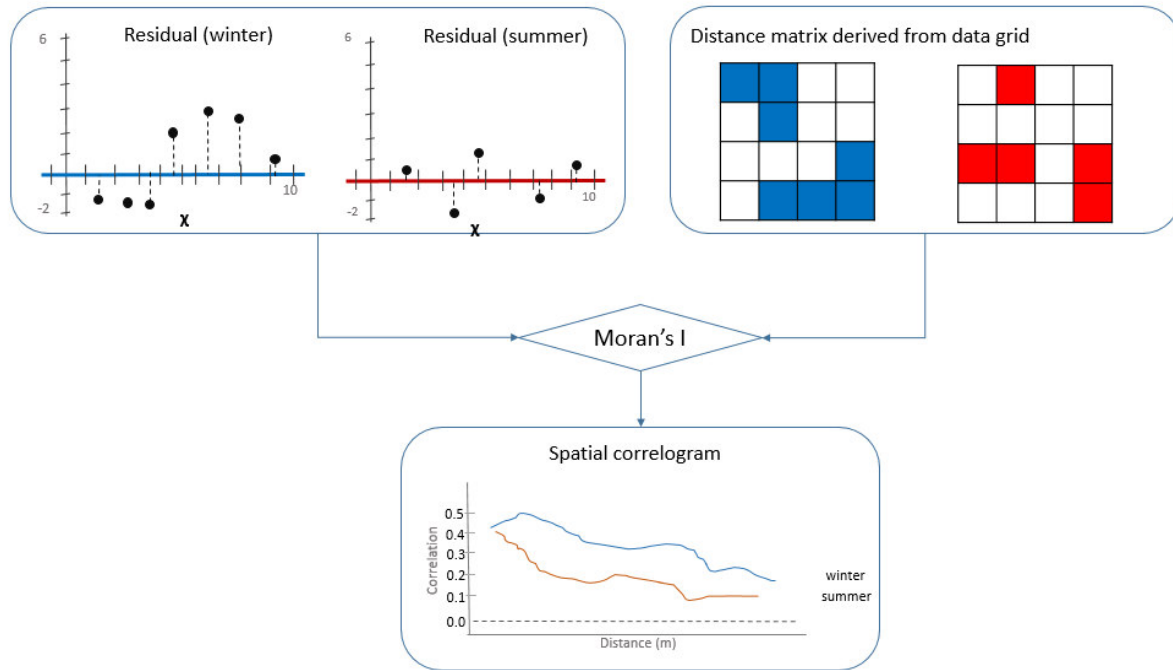
Figure 8[18]. Workflow for the evaluation of Moran's I.

To test how accurately wild boar presences were predicted with the model (i.e. the sensitivity of the classification), the true positive rates (TPRs) were calculated as Clopper-Pearson confidence intervals (Clopper & Pearson, 1934) at a level of 95% for both seasons. The true positive rates were computed for the presence data (internal validation) and for an independent dataset (external validation), namely the GPS-tracking data, at two different threshold levels (i.e. 0.5, 0.7). Figure 9 depicts this validation step in a diagram.

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[18] Prepared by the author based on a synthetized computation of Morans' I described in this section. The residual graphs and the distance matrix were plotted for ilustrative purposes. The spatial correlogram was taken from (Vargas-Amado, Grütter, Fischer, Suter, & Bernstein, 2020).
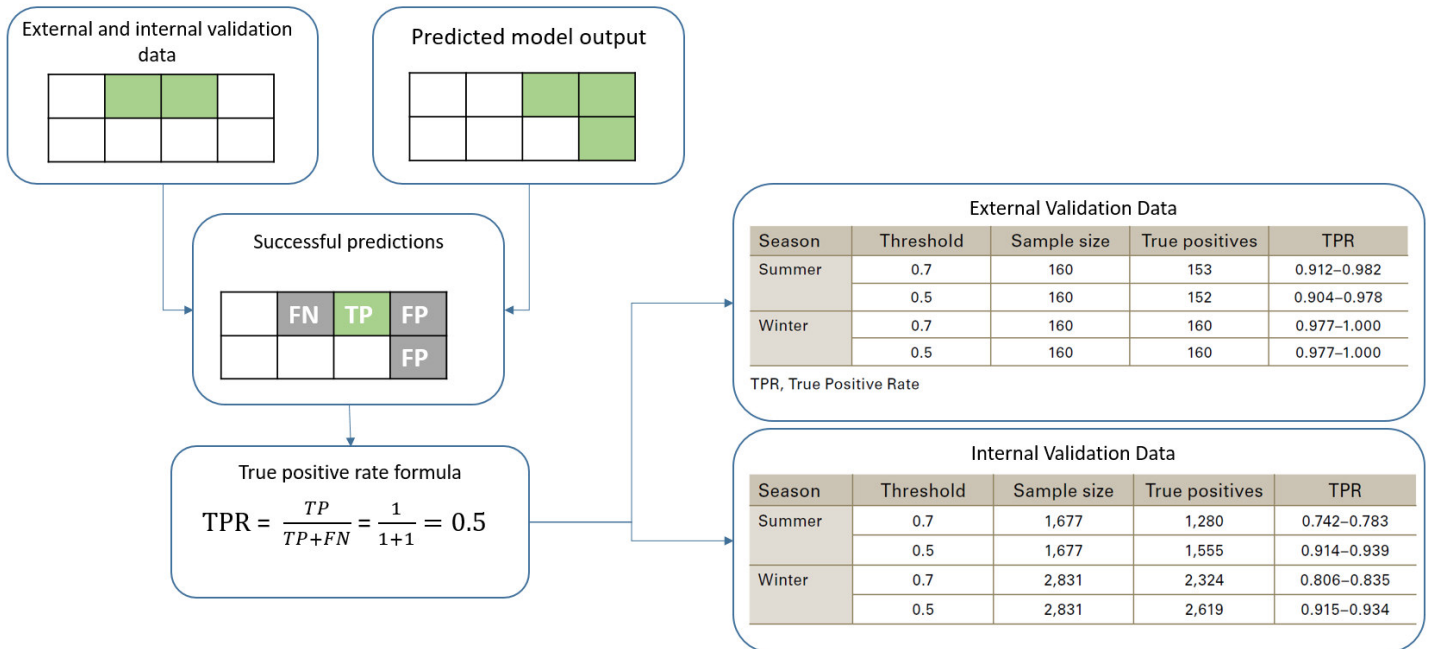
Figure 9[19]. True positive rate (TPR) calculation. TP refers to 'true positives', FN refers to 'false negatives', and FP refers to 'false positives'.

2.5. Results

The model predictions showed a high probability of wild boar presence (>0.7) during both seasons in the Jura, the valleys of the Southern Alps, the Rhone valley down the river from Martigny, and the Rhine Valley down the river from Bünder Herrschaft. During summer the probability was also high in the upper Rhine valley. A potential presence (0.5–0.7) was found in the Swiss Plateau and, especially in summer, in the valleys of the Northern Alps. The probability of wild boar occurrence across the country, including the Alps, increased by 12% during the closed season for hunting. Patches of perennially suitable but currently uncolonized habitat were found in the cantons of Bern, Obwalden, Uri, Schwyz, Glarus, and Grisons. The potential risk of transmission-related events was highest in the Jura, the Swiss Plateau, the Rhône valley, the valleys of the Southern Alps, and the Rhine valley.

The computation of Moran's I revealed significant, albeit weak, positive relationships, particularly at short distances and in winter, thereby implying that most of the spatial structure in the species data was explained by the predictor variables. The true positive rates suggested that the projections tend to underpredict the occurrence of wild boar, meaning that the areas of suitable habitat may actually be larger than suggested by the projections.

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[19] The matrices showing the external validation, predicted model, and successful predictions were plotted for ilustrative purposes. The positive rate formula was taken from (Yerushalmy, 1947). The external and internal validation tables were taken from (Vargas-Amado, Grütter, Fischer, Suter, & Bernstein, 2020).

Chapter 3: Towards risk-based surveillance of African Swine Fever in Switzerland[20]

3.1. Introduction

African Swine Fever (ASF) has emerged as a disease of great concern to swine producers and government disease control agencies because of its severe consequences for animal health and the pig industry. Early detection of an ASF introduction is considered essential for reducing the impact of the disease. Risk-based surveillance approaches have been used as enhancements to early disease epidemic detection systems in livestock populations (Snow, et al., 2007; Prattley, 2009; Reist, Jemmi, & Stärk, 2012; Taylor, et al., 2020). Such approaches may consider the role wildlife plays in hosting and transmitting a disease. In this study, a method was presented to estimate and map the risk of introducing ASF into the domestic pig population via wild boar. This involved (i) estimating the risk of disease introduction into the Swiss wild boar population, (ii) estimating the risk of disease transmission from wild boar to domestic pigs, and (iii) estimating the combined risk of disease introduction and transmission.

3.2. Data collection (material)

The data used in the analyses were either time series or snapshots. Time series data were collected for the period 2011–2018 if available. In the case of snapshots, the most recent ones were collected.

The areas ranged by wild boar computed in analysis A-0 (Table 3) were used, together with information on the national motorways, to identify exposed rest stops in analysis A-1. The relative abundances computed in analysis A-0 and the layer with the Euclidean distances to the nearest rest area produced in analysis A-1 were used together with other data to estimate the combined risk of disease introduction and transmission in analysis A-3.

Data	Source	Analysis			
		A-0	A-1	A-2	A-3
Hunting data	cantonal authorities	X	X	X	X
Hunting calendar	jagdstatistik.ch	X	X	X	X
Beech mast index	Nussbaumer et al. 2016	X	X	X	X
Probability of wild boar occurrence	Vargas-Amado et al. 2020	X	X	X	X
Forest cover	Waser, Fischer et al. 2015				X
National motorways	geo.admin.ch		X		X
Rest areas	geo.admin.ch, swisstopo		X		X
Outdoor piggeries	Federal Office for Agriculture (FOAG)			X	X

Table 3. Data collected from the indicated sources used to calculate relative wild boar abundance (analysis A-0) and to estimate the risk of disease introduction (analysis A-1), disease transmission (analysis A-2), and disease introduction and transmission (analysis A-3).

3.3. Data analysis (methods)

Computation of relative wild boar abundance (A-0 in Table 3). The estimation of the combined risk of disease introduction and transmission (see below) required the computation of relative wild boar abundance. The latter was computed based on the hunting index as defined by ENETWILD, namely the number of animals shot per area (ENETWILD-consortium, et al., 2018). In addition to hunting index, the number of hunting days (as a proxy for hunting effort) was considered, as well as mast index (as a proxy for food availability) and occurrence probability (as a proxy for suitable habitat). Weather conditions influencing the effectiveness of hunting were accounted for by averaging relative wild boar abundance over seven consecutive years. The Figure 10 shows the workflow for this estimation.
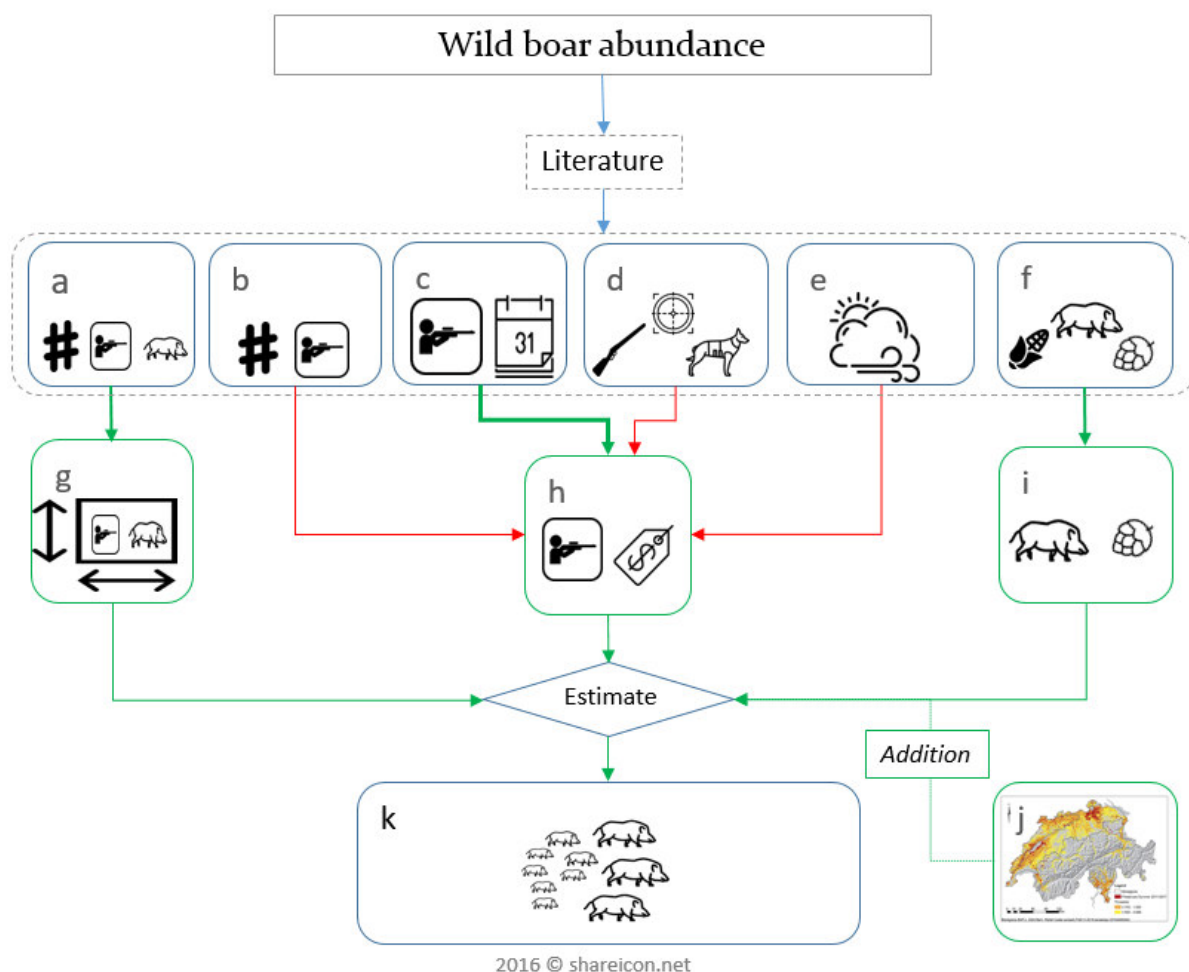
Figure 10[21]. Workflow for the estimation of the wild boar abundance: (a) hunting bag, (b) number of hunters, (c) hunting days, (d) hunting methods, (e) weather conditions, (f) food availability, (g) hunting index, (h) hunting effort, (i) mast index, (j) relative occurrence probability of wild boar in Switzerland, (k) wild boar abundance index. The red arrows correspond to the suggested variables by the literature. The green arrows represent the variables considered in this estimation.

Estimation of the risk of disease introduction (A-1 in Table 3). The highest risk of ASF introduction into the wild boar population in Switzerland is posed by the careless disposal of contaminated food waste (Bundesamt für Lebensmittelsicherheit und Veterinärwesen (BLV), 2020a). ASFV can remain infectious for a long time in processed pork products, which may be consumed by humans without fatal consequences. This happens in many countries where the disease is already present. People traveling from these countries to Switzerland may bring with them pork products that are contaminated with the virus. If leftover food is carelessly discarded at a rest stop on a motorway in an area ranged by wild boar, then wild boar can come into contact with the contaminated food and become infected.

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[21] Prepared by the author based on ENETWILD-consortium, et al., 2018. The icons were downloaded from https://www.shareicon.net/. 2016 © shareicon.net is a website to share and free download icon. The map showed in this workflow is a snapshot taken from (Vargas-Amado, Grütter, Fischer, Suter, & Bernstein, 2020).

To detect these possible entry points, motorways that connect Switzerland to countries where ASF is present (e.g. Poland, Romania) were identified (Figure 11a), as well as rest areas on the identified motorways in areas ranged by wild boar (considering also driving direction) (Figure 11b). Once these points were identified, the Euclidian distance at different ranges was calculated. The ranges were determined based on the ranging behavior of wild boar in Switzerland (Figure 11c) (Holzgang, et al., 2001; Fattebert, Baubet, Slotow, & Fischer, 2017). The result was a ring-shaped layer with decreasing values as the rings moved away from the centroids or entry points (Figure 11d).
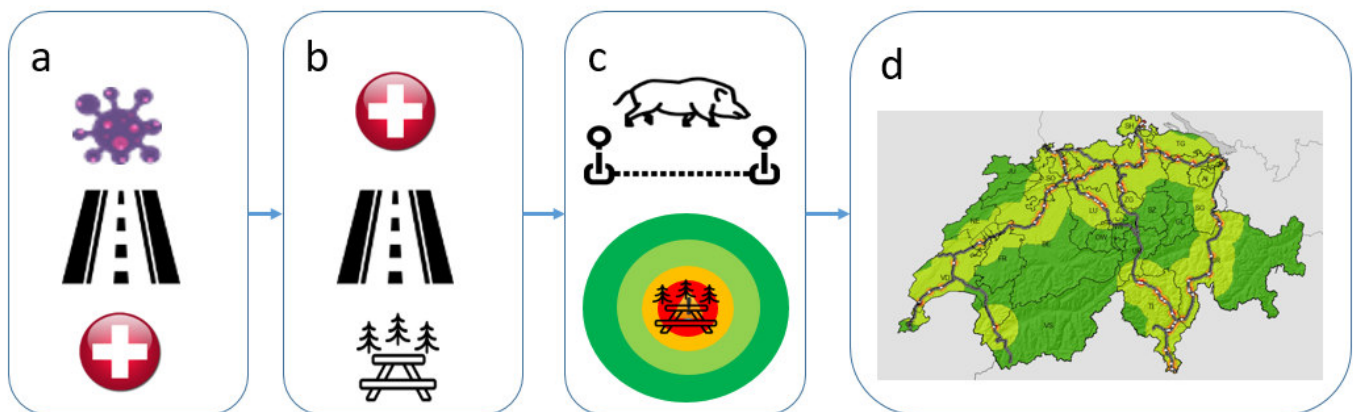
Figure 11[22]. Workflow for the estimation of the risk of disease introduction: (a) selection of motorways connecting Switzerland with ASF countries, (b) identification of rest areas on motorways, (c) Euclidian distance from the detected rest areas (the ranges are based on the movement behavior of wild boar), and (d) resulting map for Switzerland.

Estimation of the risk of disease transmission (A-2 in Table 3). A previous study of the risk factors for a contact between wild boar and outdoor pigs in Switzerland showed that mating events were reported for holdings with a pure pasture or mixed run-out, but not for piggeries with a solid run area (Wu, et al., 2012). This suggests that the type of husbandry system can also be a risk factor for the transmission of ASF from wild boar to domestic pigs. Accordingly, the risk of disease transmission in the research presented here was estimated separately for piggeries with pasture and for piggeries with a solid run area (Figures 12a and 12b). The data obtained about these piggeries were normalized by the communities' surface (Figures 12c). This resulted in the density of piggeries per commune. Figure 12 shows the workflow for the analysis. The resulting layers were combined with areas roamed by wild boar to identify the risk of disease transmission from wild boar to domestic pigs (not shown in Figure 12).

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[22] Prepared by the author based on the workflow defined for this analysis. The icons were downloaded from https://www.shareicon.net/. 2016 © shareicon.net is a website to share and free download icon. The map showed in this workflow is a snapshot taken from (Vargas-Amado, et al., 2022).

The densities at the communal level were classified using the natural breaks classification (Jenks, 1967). This classification is frequently used on choropleth maps with epidemiological purposes (Brewer & Pickle, 2002). This method clusters the data maximizing the variance between groups and minimizing it within the group (National Center for Health Statistics, 2022).

2016 © shareicon.net
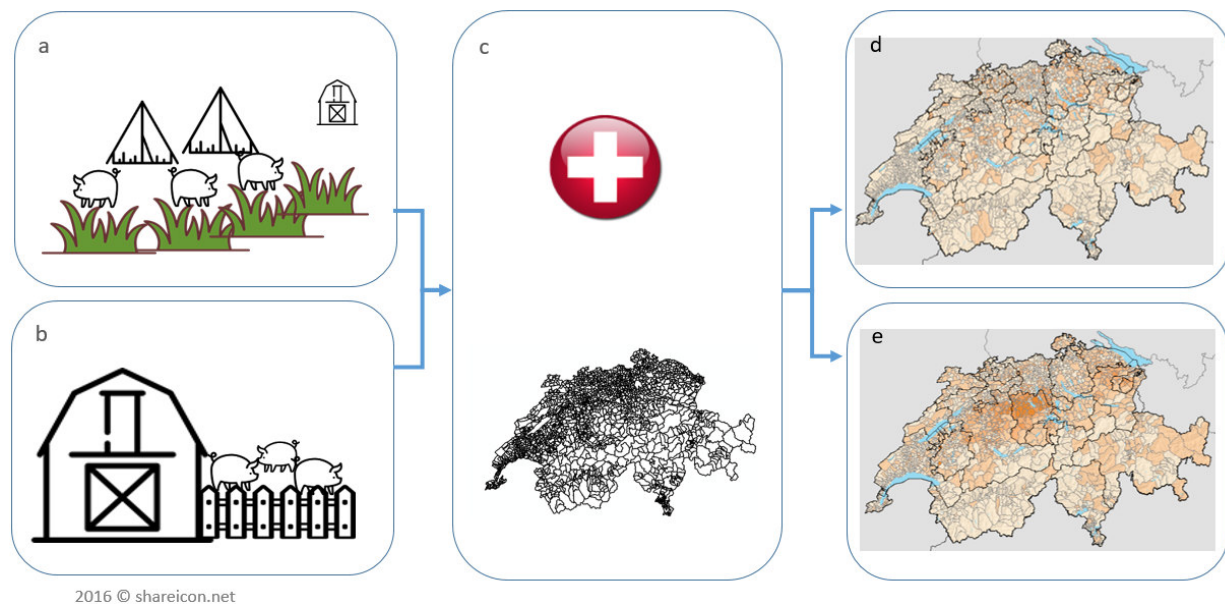
Figure 12[23]. Workflow for the estimation of the risk of disease transmission: (a) piggeries with pasture, (b) piggeries with run area, (c) communities in Switzerland, (d) density of piggeries with pasture (e) density of piggeries with run area.

Estimation of the combined risk of disease introduction and transmission (A-3 in Table 3). This parameter was estimated by multiplying the values of relative wild boar abundance (scores 0–4) (Figure 13a), Euclidean distance to the nearest rest area (scores 1–4) (Figure 13b), density of outdoor piggeries (scores 0–4) (Figure 13 d and e), and proximity to a forest (scores 1–2) (Figure 13c).

The scores for Euclidean distance were based on expert's opinion and by the literature (Holzgang, et al., 2001; Fattebert, Baubet, Slotow, & Fischer, 2017). Score 4, ranges from 0 to 2000 m (i.e. related to the seasonal home range of females). Score 3, ranges from 2001 to 4000 m (i.e. related to seasonal movements of males). Score 2, ranges from 4001 to 20,000 m (i.e. related to distances traveled by dispersers). Score 1, are distances longer than 20,000 m (i.e. related to some individuals that disperse farther).

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[23] Prepared by the author made for illustrative purposes. The icons were downloaded from https://www.shareicon.net/. 2016 © shareicon.net is a website to share and free download icon. The maps showed in this figure are snapshots taken from (Vargas-Amado, et al., 2022).

The same number of scores (i.e. four) were given to wild boar abundance, and to the density of piggeries. However, in this, case the scores were based on classes were the cut-off values were set by natural brakes' classification. Respecting the proximity to forest, since two option were possible (e.g. woods or not woods), wooded cells were given a score of 2, and score of 1 was given for areas without woods.

To assess the extent to which free-ranging wild boar contribute to the risk of disease introduction and transmission, estimates were recomputed without consideration of relative wild boar abundance, but with all other factors remaining the same (Figure 13h). This was computed for outdoor piggeries with pasture only, where the chances that pigs escape from the fenced area are much higher than in piggeries with a solid run area (usually equipped with iron railings). The procedure and the resulting three layers are shown in Figure 13.
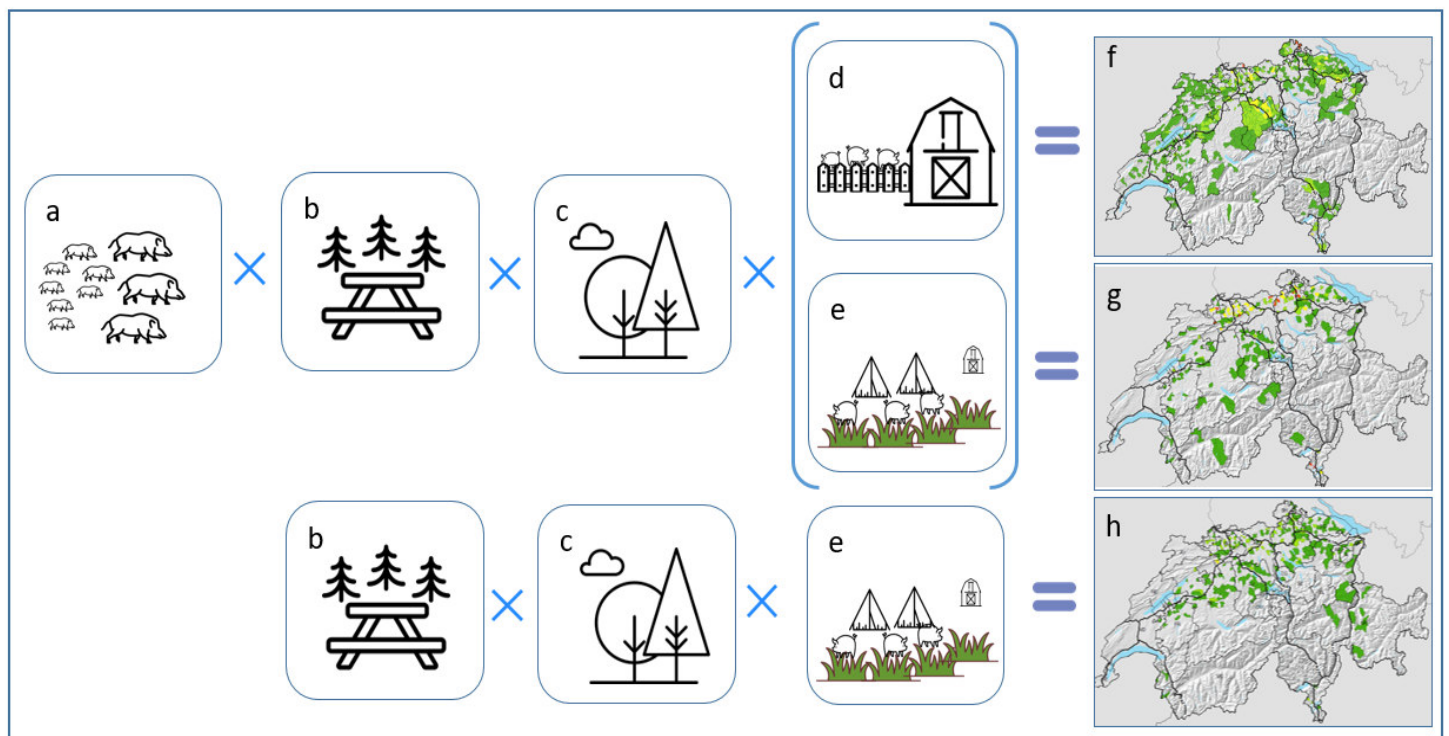
Figure 13[24]. Workflow for the estimation of areas with a combined risk of disease introduction and transmission: (a) areas ranged by wild boar, (b) Euclidian distance to rest areas, (c) proximity to forest, (d) density of piggeries with a run area, (e) density of piggeries with a pasture, (f) result for piggeries with a run area, (g) result for piggeries with a pasture, and (h) result for piggeries with a pasture without considering wild boar as a means of disease introduction.

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[24] Prepared by the author based on the workflow defined for this analysis. The icons were downloaded from https://www.shareicon.net/. 2016 © shareicon.net is a website to share and free download icon. The maps showed in this workflow are snapshots taken from (Vargas-Amado, et al., 2022).

3.4. Results

Wild boar abundance was high in areas near the borders of France, Germany, and Italy. They were also abundant in the south-east of Lake Neuchâtel (Figure 14).
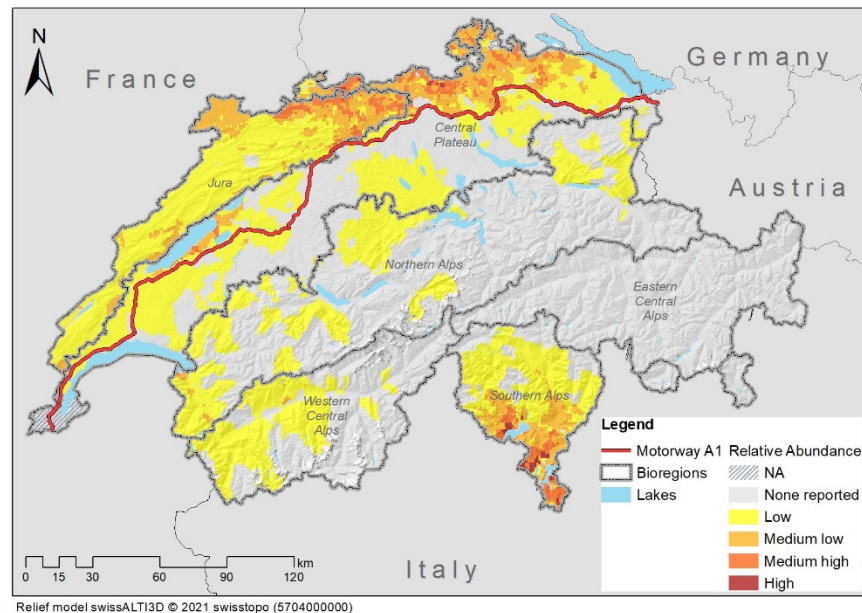

Figure 14[25]. Relative abundance of wild boar in Switzerland. The numerical values underlying the nominal index values are not shown to avoid these are mistaken as (absolute) wild boar 'densities'.

The risk of ASF introduction into the domestic pig population by wild boar was highest near the borders of France, Germany, and Italy (Figure 15 a and b). On the northern side of the Alps, areas of high risk were located on the unshielded side of A1, the main motorway crossing the Central Plateau, which acts as a barrier for wild boar. When the risk of disease introduction into the domestic pig population was estimated without consideration of wild boar relative abundance, risk areas were more consistently located alongside motorways and extended to areas where no wild boar were reported (Figure 15 c). This suggests that dispersing wild boar may play a key role in spreading the risk of ASF to areas remote from motorways. It was concluded that the results of this study could be used to focus surveillance efforts for early disease detection on high-risk areas. The developed method might also inform policies to control other diseases that are transmitted by direct contact from wild boar to domestic pigs.

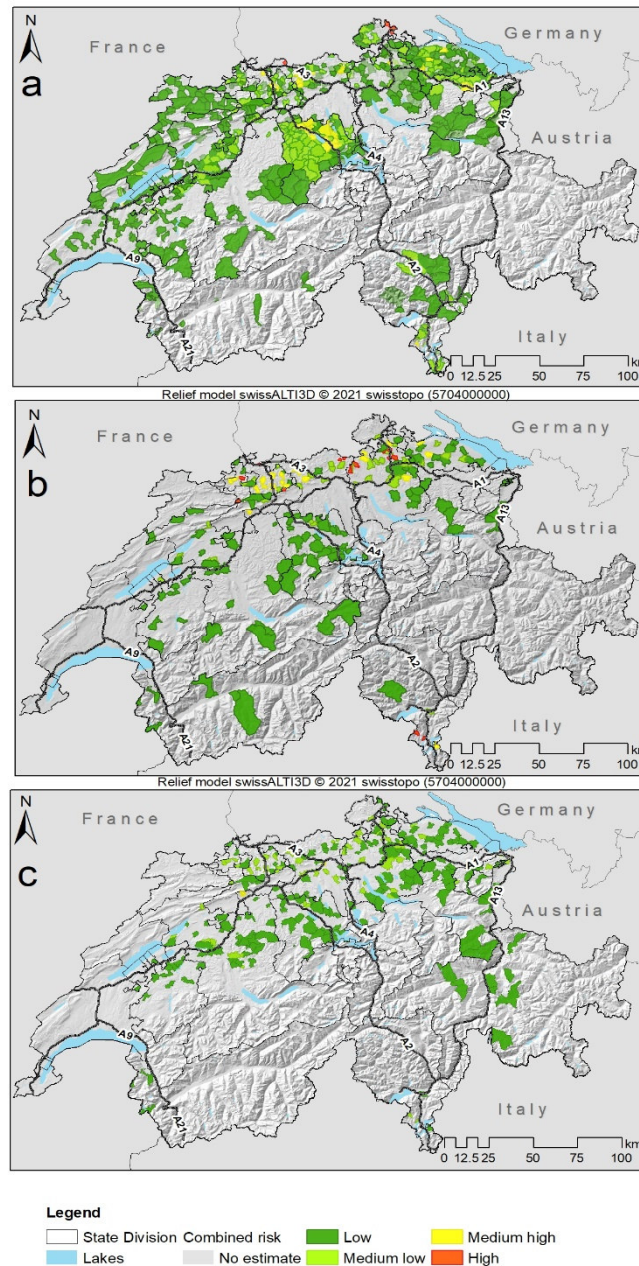[25] The map was taken from (Vargas-Amado, et al., 2022).

Figure 15[26]. Areas with a combined risk of disease introduction into the wild boar population and transmission to domestic pigs identified based on relative wild boar abundance, Euclidean distance to the nearest rest area, density of outdoor piggeries, and proximity of a forest. (a) Piggeries in the RAUS program (i.e., run area without pasture), (b) piggeries with pasture, (c) piggeries with pasture without considering relative wild boar abundance.

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[26] The map was taken from (Vargas-Amado, et al., 2022).

Chapter 4: Potential effect of managing connectivity to contain disease spread among free-ranging wild boar in disparate landscapes[27]

4.1. Introduction

Landscape connectivity facilitates gene flow, which is important for the preservation of wildlife species (Keeley, Beier, & Jenness, 2021). This connectivity, however, can have negative effects like proliferation of invasive species and disease spread (Mitchell, Bennett, & Gonzalez, 2013; White, Forester, & Craft, 2018). Reducing landscape connectivity to disease-transmission-vectors is likely to slow down the spread of pathogen (Mysterud, Strand, & Rolandsen, 2020). Maintaining or restoring connectivity after an outbreak can have grave consequences. This situation can be particularly worrisome, if one of the disease-transmission-vectors is a generalist species such as wild boar. Wild boar can travel long distances in natural and anthropogenic environments (Boitani, Mattei, Nonis, & Corsi, 1994; Kotulski & König, 2008) driven by food availability (Cahill, Llimona, & Cabañeros, 2012; Oja, Kaasik, & Valdmann, 2014), or due to human pressure (e.g. hunting) (Keuling, Stier, & Roth, 2008), and it is genetically similar to a domesticated species (e.g. pigs) (Acevedo, Quirós-Fernández, Casal, & Vicente, 2014).

A disease that have drawn authorities' attention due to its lethality is African Swine Fever (ASF). New cases of ASF in wild boar were reported in countries where the disease was not present: Belgium (FASFC, 2019), Germany (Deutscher Landwirtschaftsverlag, 2020), Italy (Stauffer, Polansek, & Alves, 2022), and more recently Greece (ter Beek, 2023). Managing connectivity can be a useful strategy in the early stages of a disease. 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 (Figure 16).

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[27] This chapter is based on Vargas Amado, M. E., Vidondo, B., Fischer, C., Pisano, S.R.R., & Grütter, R., Potential "Effect of Managing Connectivity to Contain Disease Spread Among Free-Ranging Wild Boar in Disparate Landscapes". Submitted on December 8, 2022 in the *Journal of Applied Ecology*.
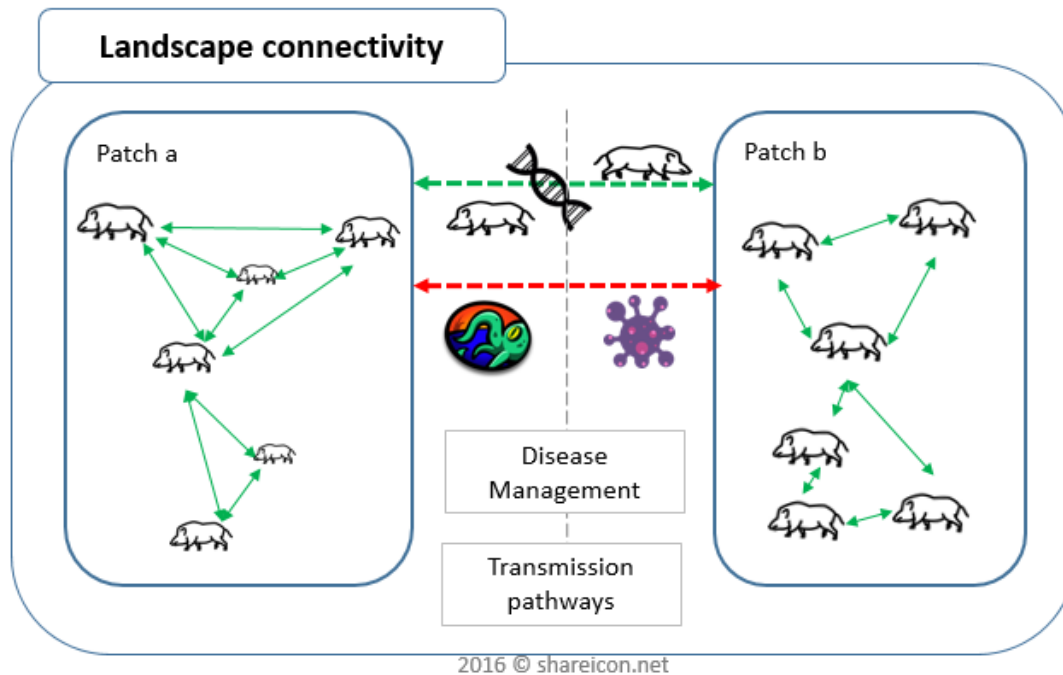
Figure 16[28]. Habitat connectivity and landscape management for disease containment.

Some strategies implemented by some countries to contain ASF include fencing and wild boar eradication (Mysterud & Rolandsen, 2019), zoning (Giacometti, 2003), increasing surveillance and biosecurity measures in farms (Stauffer, Polansek, & Alves, 2022), and carcasses removal (Morelle, Jezek, Licoppe, & Podgorski, 2019).

Research on connectivity management has been done on the prevention of the spread of non-native species in ecosystems (Rahel, 2013). In Norway, conservation efforts to restore connectivity were paused due to an outbreak of Chronic Wasting Disease on reindeer in 2016. To counteract the spread of this disease, fragmentation was increased by erecting wildlife fences on some roads and increasing surveillance to prevent the animals from crossing open roads (Mysterud, Strand, & Rolandsen, 2020).

The objective of the study summarized here was to investigate the potential effect of managing landscape connectivity on the containment of disease spread in free-ranging wild boar in Switzerland. This involved research into (i) how easily wildlife corridors can be blocked (by fencing), (ii) the (functional) connectivity of the wild boar habitat, and (iii) the impact of landscape fragmentation on connectivity management.

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[28] Prepared by the author for illustrative purposes. The icons were downloaded from https://www.shareicon.net/. 2016 © shareicon.net is a website to share and free download icon.

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4.2. Data collection (material)

The wildlife network system was the basic data structure upon which all computations in this study were performed. From this source, the interregional wildlife corridors were analyzed cartographically to see how easily they can be blocked. The 'easy to block' corridors were used to investigate the influence of landscape fragmentation on the effectiveness of closing wildlife passages and blocking corridors as a disease containment measure.

In Switzerland, wildlife networks were established for the most common species (Holzgang, et al., 2001). These networks describe the action space of a species in which the animals may move between patches of habitat that are connected by wildlife corridors, some of which are equipped with passages.

There are two independent networks for wild boar in Switzerland, one connecting the northern population and the other connecting the southern population. The northern wild boar population occupies most of the Jura, important parts of the Central Plateau, and parts of the Northern Alps and the Western Central Alps (Meier & Ryser-Degiorgis, 2018; Vargas-Amado, et al., 2022). This population is contiguous with the wild boar populations in neighboring Germany and France. The southern wild boar population occupies important parts of the Southern Alps and is contiguous with the northern Italian wild boar population.

Wildlife passages were used to determine the extent to which the habitat of wild boar is connected. They were also used to investigate the influence of landscape fragmentation on the effectiveness of closing wildlife passages and blocking corridors as a measure of disease containment.

The wildlife network system, the wildlife passages, and the national motorways where some of the passages are located were downloaded from the Swiss Federal geoportal[29].

CORINE land cover was used in this study to investigate the influence of landscape fragmentation on the effectiveness of closing wildlife passages and blocking corridors as a measure for disease containment. It was downloaded from the Copernicus Web site[30].

Probability of wild boar occurrence. In a previous study, area-covering 1 sq. km data grids with probabilities of wild boar occurrence of 0.5–1.0 were produced for the open and closed seasons for hunting (Vargas-Amado, Grütter, Fischer, Suter, & Bernstein, 2020). These data grids were used in this study to explore whether constructing new wildlife passages would connect habitat suitable for wild boar in areas that are not yet colonized.

Relative abundance of wild boar. This data grid was used to compute a metric to estimate colonization probability and to investigate the influence of landscape fragmentation on the effectiveness of closing wildlife passages and blocking corridors as a measure for disease containment. This layer was the result of previous work (Vargas-Amado, et al., 2022).

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[29] https://www.geo.admin.ch/
[30] https://land.copernicus.eu/

The networks for wild boar in Switzerland, consisting of occupied habitat patches (i.e. the nodes in the network), wildlife corridors and passages were established based on the wildlife network system (i.e. the arcs in the network) and the data grid representing the relative abundance of wild boar (Figure 17). Habitat patches were considered 'occupied' in this study if the 'Federal Hunting Statistics' reported shots of wild boar for them (Figures 17a). The wildlife interregional networks (Figures 17c) were overlayed with the compartments defined in related work (Giacometti, 2003), which were refined by additionally considering more recent motorways (Figures 17b). These refinements are called 'second-level compartments' in Figures 18, 21, and 22. Two different representations resulted from this analysis: cartographic (Figure 18) and graphic (Figure 19).
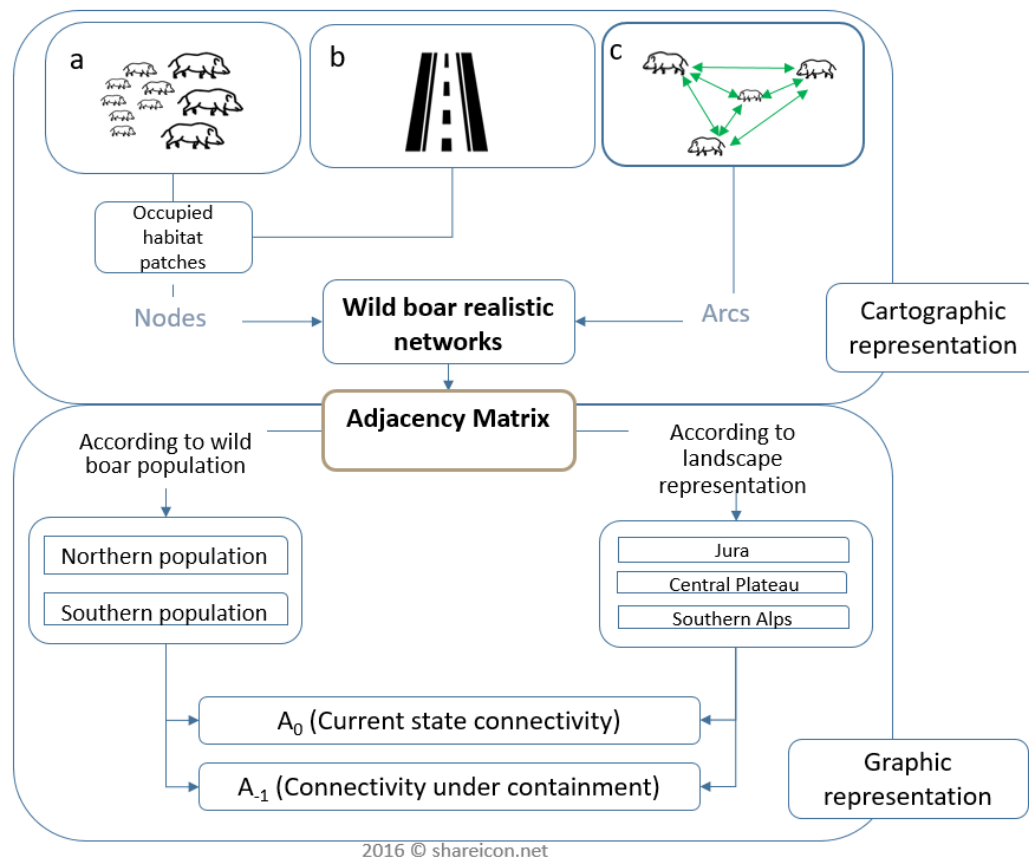
Figure 17[31]. Definition of realistic wild boar networks. Input data: (a) wild boar relative abundance, (b) barriers (i.e., motorways), (c) wild boar interregional networks.

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[31] Prepared by the author based on the workflow defined for this analysis. The icons were downloaded from https://www.shareicon.net/. 2016 © shareicon.net is a website to share and free download icon.

Legend

⬛ Water bodies		🟩 1, undisturbed		🟨 Low	

Wild boar corridors   Relative abundance

- ⬛ Water bodies
- 🟥 Axis of national routes
- 🟧 Second-level compartments
- ▨ Wild boar patches
- — National wildlife network
- —·— Regional wildlife network

Wild boar corridors
- 🟩 1, undisturbed
- 🟨 2, impaired
- 🟥 3, interrupted

Relative abundance
- 🟨 Low
- 🟧 Medium low
- 🟧 Medium high
- 🟫 High
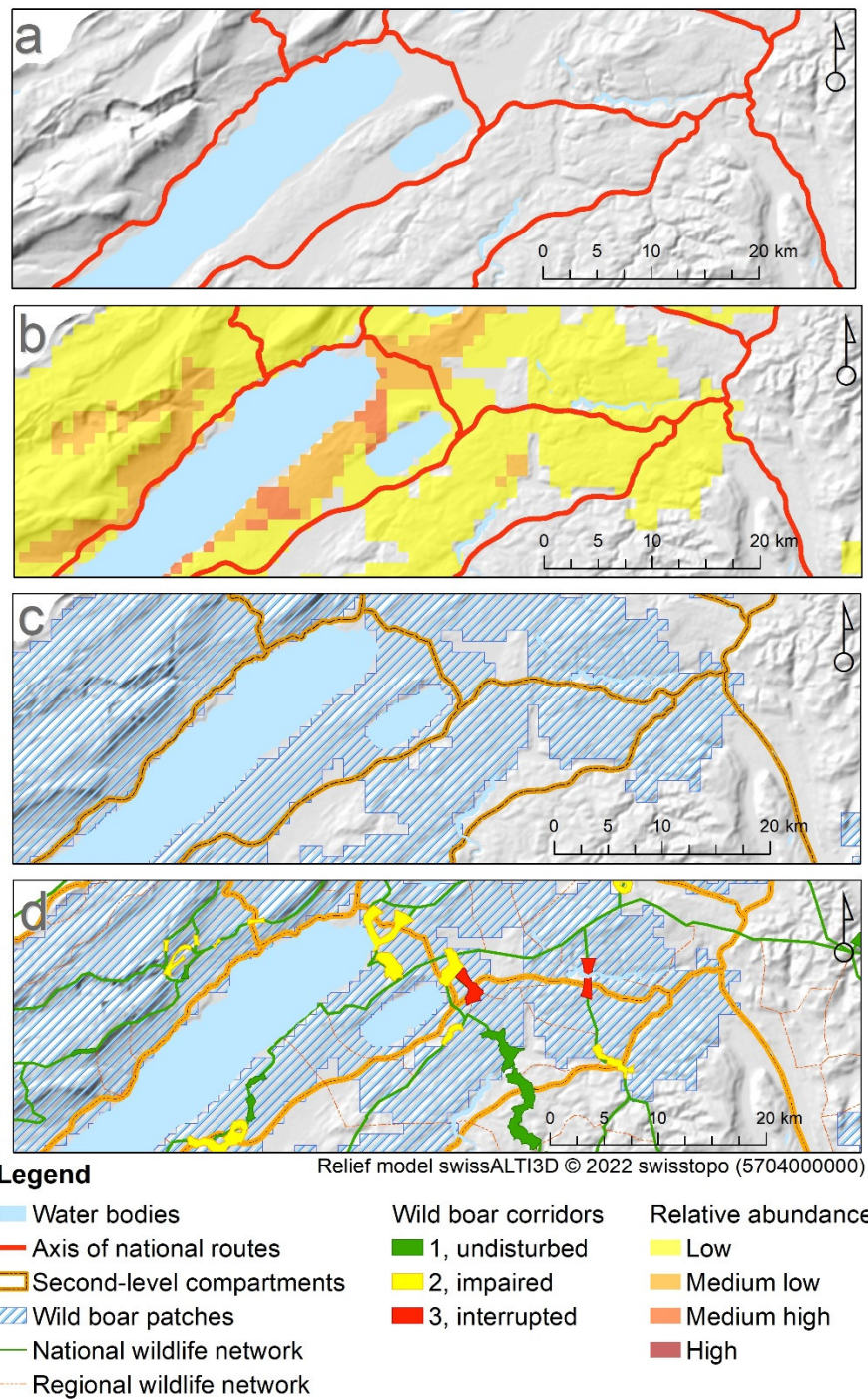
Figure 18[32]. Cartographic representation of wild boar realistic networks with: (a) barriers (motorways), (b) relative wild boar abundance, (c) wild boar patches (derived from a and b), and (d) wild boar corridor's status and wild boar network.

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[32] Prepared by the author based on the sources described on the chapter 4.2. of this synthesis. The map was produced using ArcGIS Desktop 10.8.2.
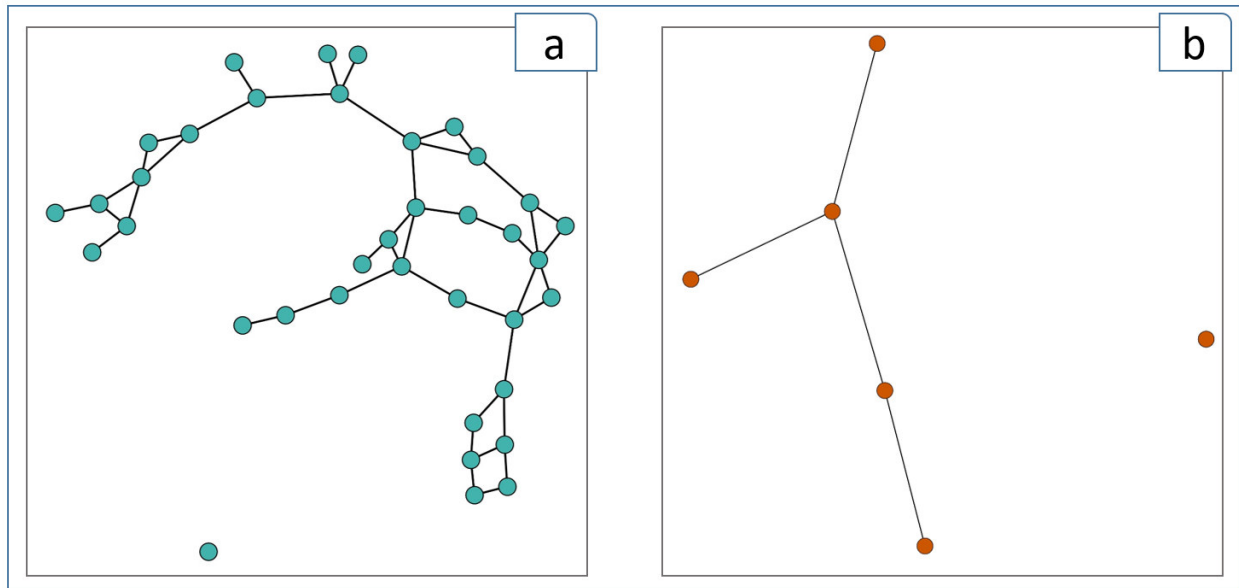
Figure 19[33]. Graphic representation of the wild boar networks of (a) the northern population and (b) the southern population. Isolated nodes represent (a) the city of Zurich, for which it is unclear where it connects with the northern network, and (b) the west side of the district of Mendrisio, which only connects with the Italian wild boar network (not represented here).

4.3. Data analysis (methods)

Wild boar networks were established (i) according to the wild boar population and (ii) according to the landscape representation (Figure 17). Three different states of the networks were investigated: *present-day* (i.e. state in July 2021), *near-future* (i.e. with new 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 (Figure 17).

Wildlife corridors. In order to test whether blocking corridors (by blocking we assume fencing) for wild boar would be easier in the Central Plateau than outside of the Central Plateau, each corridor for wild boar on a compartment boundary was qualified as either 'easy to block' or 'hard to block'. The analysis consisted of inspecting the areas around the intersection of the wild boar network and the barriers and qualifying them according to five features (Figure 20).

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[33] Prepared by the author as a result of the network analysis presented in this chapter. The network analysis was performed with the library networkx, pandas, numpy and matplotlib using python version 3.6.5.
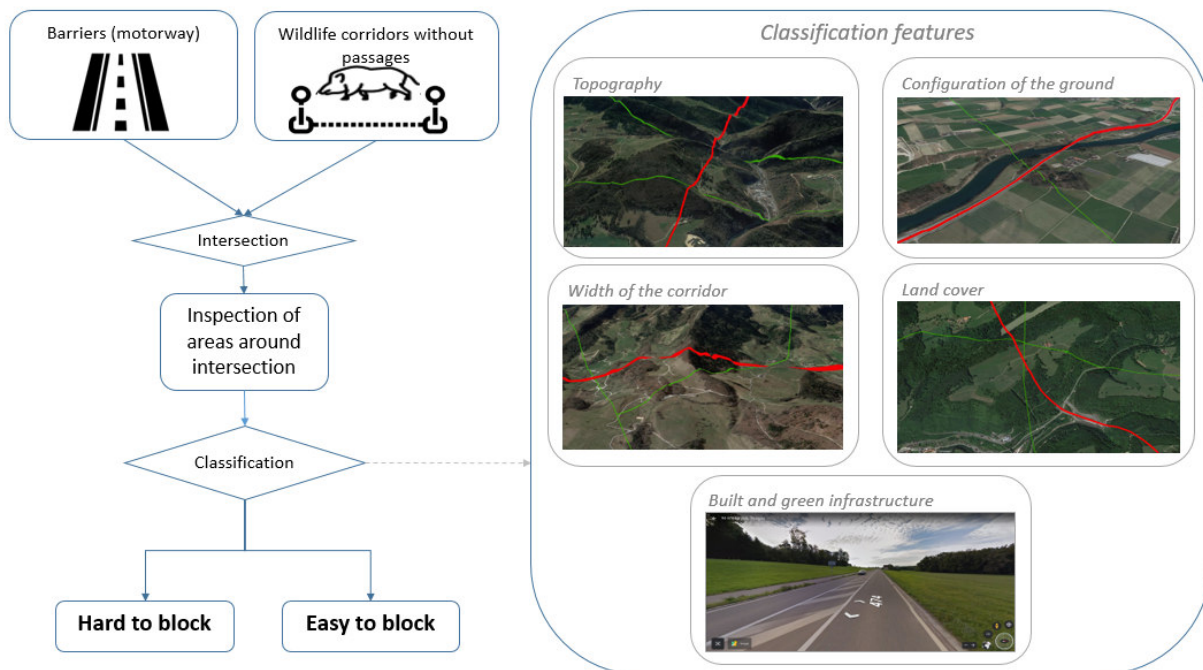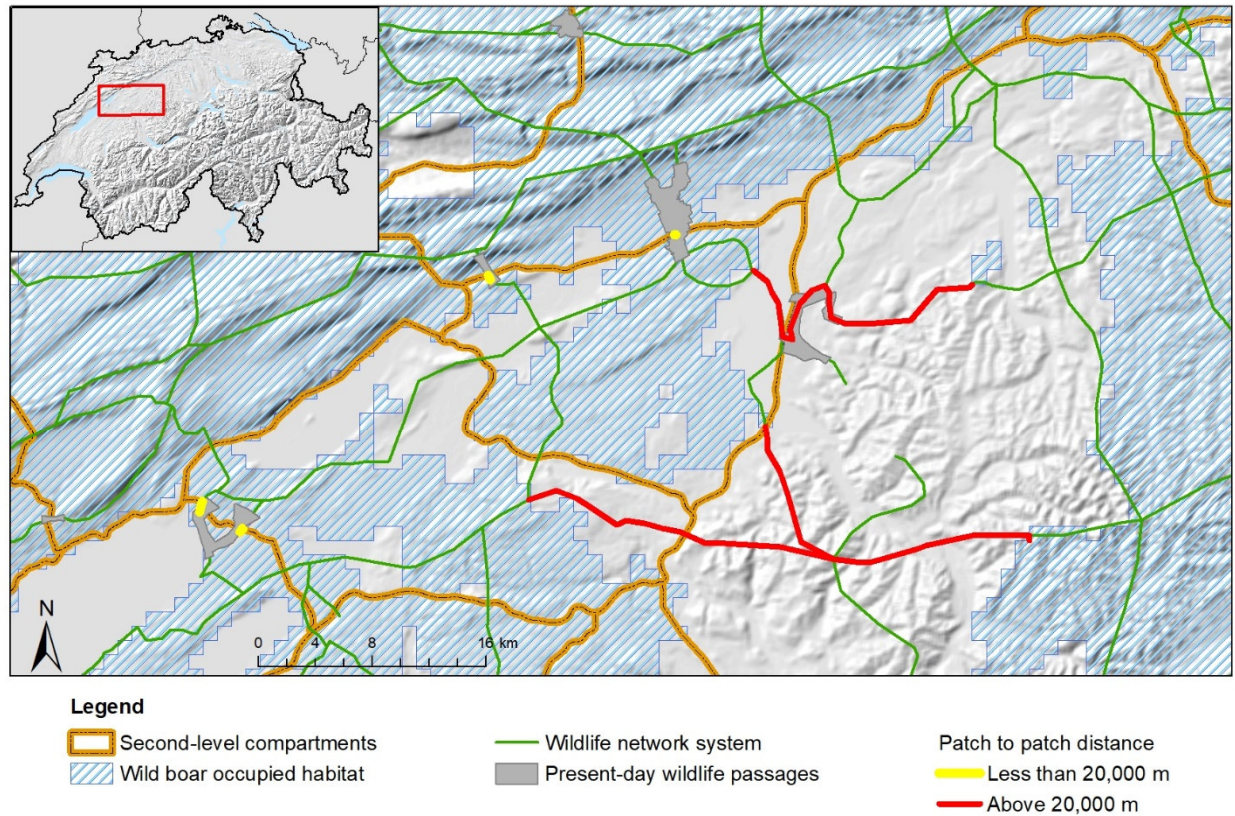
Figure 20[34]. Workflow for the definition of hard or easy to block corridors and visual examples of the features used for their qualification. Motorways are outlined in red, and wildlife corridors in green.

Habitat connectivity. In order to test whether most existing wildlife passages actually connect the habitat of wild boar in Switzerland, the proportion of distances between pairs of occupied patches connected by a wildlife passage below a given threshold was calculated. A distance of 20,000 m was chosen as a threshold, which is how far wild boar disperse in Switzerland, notwithstanding that some individuals disperse (much) farther (Figure 21) (Holzgang, et al., 2001).

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[34] Prepared by the author based on the workflow defined for this analysis. The icons were downloaded from https://www.shareicon.net/. 2016 © shareicon.net is a website to share and free download icon. The images showed in this workflow are snapshots taken from experimental version of Google Earth.

Legend

▭ Second-level compartments	— Wildlife network system	Patch to patch distance
▨ Wild boar occupied habitat	▨ Present-day wildlife passages	— Less than 20,000 m
		— Above 20,000 m

Relief model swissALTI3D © 2022 swisstopo (5704000000)

Figure 21[35]. Current wild boar habitat connectivity.

To test whether constructing new wildlife passages would connect habitat suitable for wild boar in areas that are not yet colonized, it was explored whether there is some perennially suitable habitat for wild boar within the threshold distance of any newly connected landscape fragment. To this end, the estimated spatial distributions of wild boar in Switzerland during the open and closed seasons for hunting, computed in previous work (Chapter 3), were reused (Vargas-Amado, Grütter, Fischer, Suter, & Bernstein, 2020). This analysis was carried out on the near-future wild boar networks of the northern and the southern populations (Figure 22).

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[35] Prepared by the author based on the sources described on the chapter 4.2. of this synthesis. The map was produced using ArcGIS Desktop 10.8.2.

Legend

▨ Wild boar occupied habitat	── Wildlife network system	Near-future wildlife passages	▬ Oftringen
▨ Wild boar potential habitat	── Distance: patch to potential habitat	▬ Wangen a.d. Aare	▬ Suret
▭ Second-level compartments	┈ Motorway A1	▬ Oberbuchsiten-Kestenholz	
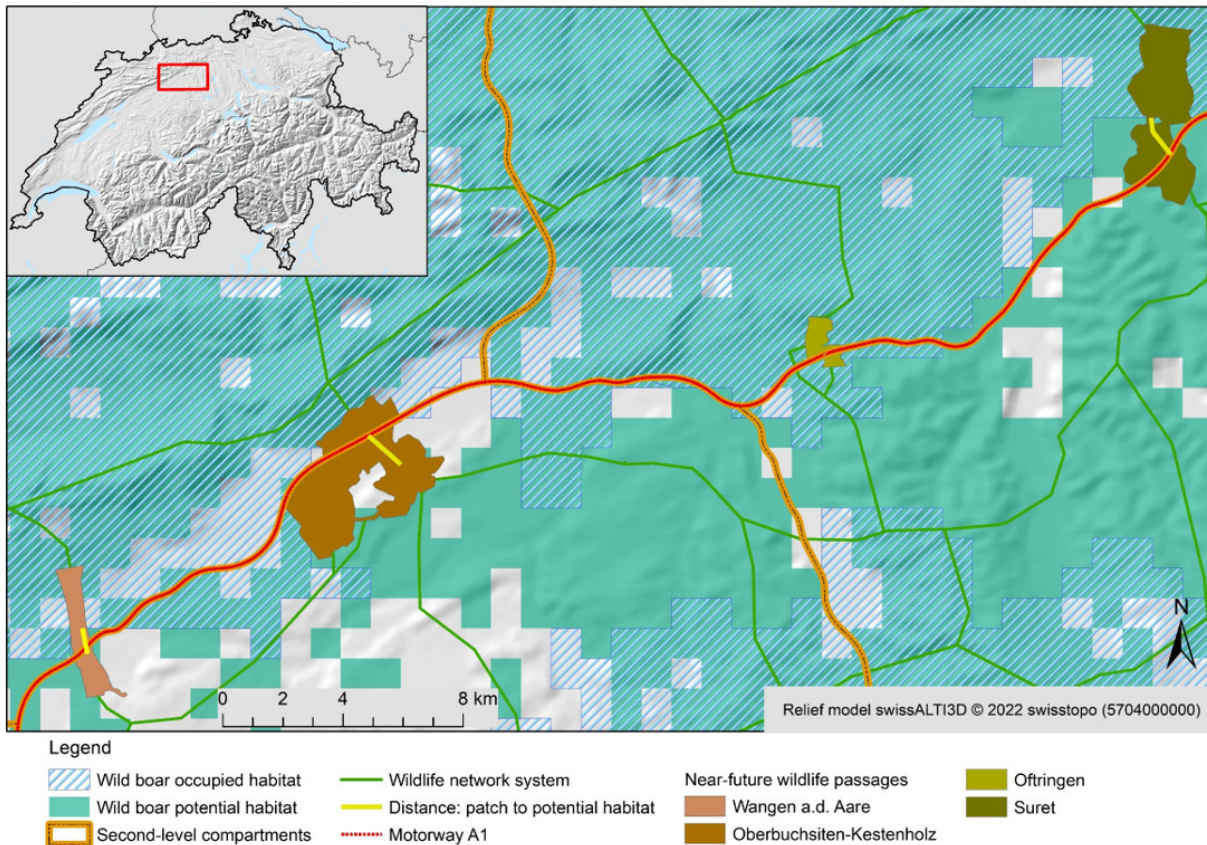
Figure 22[36]. Future connectivity of wild boar habitat. Habitat occupied by wild boar northwest of motorway A1 will be connected with potential habitat southeast of A1.

To test whether closing wildlife passages and blocking corridors is a more effective measure for disease containment in the highly fragmented Central Plateau than in any other biogeographical region in Switzerland, the following parameters were computed: (i) the number of components, (ii) the number of patches in the largest connected component (LCC) and in the second largest connected component (SLCC), (iii) the diameter of the LCC and the SLCC, and (iv) the potential epidemic size (PES) for the LCC and the SLCC. These metrics were computed before (Matrix A_0 Figure 23) and after (Matrix A_{-1} Figure 23) closing all wildlife passages and blocking all 'easy to block' corridors in the wild boar networks of the Central Plateau (CP), the other regions occupied by the northern population, and the Southern Alps (Figure 23).

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[36] The maps showed was taken from "Vargas Amado, M. E., Vidondo, B., Fischer, C., Pisano, S.R.R., & Grütter, R., "Potential Effect of Managing Connectivity to Contain Disease Spread Among Free-Ranging Wild Boar in Disparate Landscapes". Submitted on December 8, 2022 in *the Journal of Applied Ecology*.
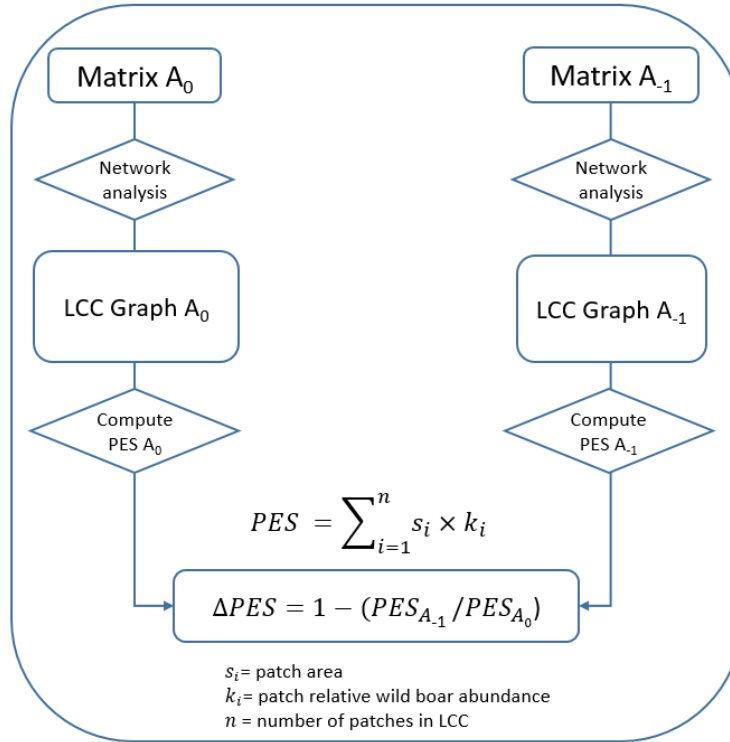
$$PES = \sum_{i=1}^{n} s_i \times k_i$$

$$\Delta PES = 1 - (PES_{A_{-1}} / PES_{A_0})$$

s_i = patch area
k_i = patch relative wild boar abundance
n = number of patches in LCC

Figure 23. Workflow to analyze the effectiveness of a disease containment measure.

4.4. Results

The results showed that (i) most wildlife corridors are hard to block because their features or location make fencing difficult. (ii) The wild boar habitat is connected. Opening wildlife passages that are currently under construction may allow wild boar to disperse to hitherto uncolonized areas. (iii). 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 Central Plateau where the built infrastructure is most abundant. All over Switzerland, the potential epidemic size could be reduced by 25%. It was concluded that connectivity and fragmentation analyses are important tools for wildlife disease management.

Chapter 5: Discussion

5.1. Contributions and limitations

This chapter comprises a discussion of how this thesis helped to address the existing research gaps mentioned in Chapter 1.4.

To deal with the lack of high-resolution and up-to-date information about the actual and potential distribution and abundance of wild boar in Switzerland, two high-resolution and up-to-date layers were produced in this thesis work: (i) the joint probability distribution of wild boar for summer and winter, and (ii) the relative wild boar abundance. The first layer was used, along with other variables, to produce the second one. Both layers were developed with a detail level (cell size) of 1 sq. km.

The approach adopted to project the occurrence of wild boar in Switzerland reflects the state-of-the-art of species distribution modeling (SDM) in conservation biology and ecology (Guisan, Thuiller, & Zimmermann, 2017). Statistical models were fitted and evaluated in an initial dataset of wild boar presences and (pseudo-) absences. They were then used to predict the probabilities of presence across Switzerland for winter and summer.

The way relative wild boar abundance was calculated adds to the current state of the art by considering the effect of beech mast on hunting success (Bozzuto & Geisser, 2019) and the probability of wild boar occurrence when distributing relative abundance values among individual grid cells.

Three main limitations were found when computing the joint probability distribution: (i) limited availability of input data (i.e. presence data), (ii) potential bias of input data, and (iii) spatially correlated input data. The following solutions were found to minimize the effect of these issues on the result obtained.

The limited availability of input data is one of the main problems scientists face when modeling. In 1991 a formula was developed regarding the minimum amount of data that should be used for regression analysis (Green, 1991). The amount of data used for the present analysis greatly exceeded the number suggested by the formula.

Data are biased according to their origin. Causal observations are mostly made in easily accessible areas (Phillips, et al., 2009), while hunting data tend to come from the forests where the battues are carried out. As a result, areas that have suitable environmental conditions for wild boar but are difficult to access are underrepresented or, in the worst case, not represented at all. The work presented here dealt with a possible bias in the presence data by sampling pseudo-absences in potentially unsuitable (and less accessible) areas twice as densely as in potentially suitable ones. Doing so resulted in better predictions than if pseudo-absences were sampled regularly across the study area.

Species data are almost always spatially autocorrelated. This may occur if species presence data are based on samples located close together. To deal with this, the observations made in hectares were aggregated to presences in sq. km. In this way the imprecision of the original data was accounted for and the species data were thinned.

Two main limitations were found in the computation of relative abundance: (i) the lack of factors available to calculate the relative abundance and (ii) short-term variations in hunting data. These issues were addressed as follows, to minimize the impact on the output data: The formula developed by ENETWILD (ENETWILD-consortium, et al., 2018) only considers the hunting bag (i.e. the number of hunted wild boar) and the surface area of the hunting district (or equivalent). Hunting bags are likely to be biased because the circumstances under which they are filled vary across time and place. To reduce the bias derived from hunting bags, the formula was expanded by including additional factors relevant to relative wild boar abundance. ENETWILD suggested variables that were not included in the information obtained from the cantonal hunting authorities (e.g. number of hunters, hunting method, weather conditions). Therefore, to reduce the bias, the number of hunting days (as a proxy for hunting effort), mast index (as a proxy for food availability), and occurrence probability (as a proxy for suitable habitat, not mentioned by ENETWILD) were considered here when estimating relative wild boar abundance. To deal with short-term variations in the spatial distribution and number of wild boar hunted annually, e.g. due to varying weather conditions, the data were averaged over an observation period of seven years.

A first result to identify areas where piggeries are at risk of disease introduction via wild boar, resulted in two maps. These show the potential risk of transmission-related events, as a proxy for disease transmission in Switzerland, and were produced in the Chapter 3, one for summer and one for winter. To create these maps, the predicted probabilities of wild boar occurrence for the two seasons were related to the density of piggeries in the six agricultural zones[37].

According to the Bundesamt für Lebensmittelsicherheit und Veterinärwesen (BLV), contaminated food waste discarded carelessly is considered the most probable route of ASF introduction into Switzerland. Therefore, assuming this as means of introduction, a list with 57 exposed rest areas was compiled in the work presented here (Table 4). These rest areas are located along motorways connecting places in ASF-affected countries to five urban centers in Switzerland in areas ranged by wild boar.

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[37] https://map.geo.admin.ch/?layers=ch.blw.landwirtschaftliche-zonengrenzen

Canton	Name and directions of the rest area
AG	Walterswil, Würenlos
BE	Lindenrain, Oberbipp-Nord
BL	Mühlematt (both directions), Pratteln-Süd, Sonnenberg (both directions)
FR	Rose de la Broye
GR	Campagnola (both directions)
LU	Chilchbüel, Inseli, Knutwil-Nord, Knutwil-Süd, Neuenkirch (both directions)
SG	Rheintal Ost, Rheintal West, Thurau Nord, Wildhus Nord
SH	Berg, Moos
SO	Eggberg, Gunzgen-Nord, Teufengraben
TG	Hexentobel Nord
TI	Bellinzona Nord, Bellinzona Sud, Bodio, Coldrerio (both directions), Giornico, Lavorgo (both directions), Moleno Nord, Moleno Sud, Motto, Muzzano (both directions), San Gottardo-Sud, Sasso, Segoma (both directions)
VD	Bavois, Crans-près-Céligny, St-Prex
VS	Dents de Morcles
ZH	Baltenswil-Nord, Büsisee, Chrüzstrass, Forrenberg Nord, Kemptthal, Stegen, Weinland (both directions)

Table 4. Identified rest areas as hot spots for ASF introduction.

Relevant motorways were identified by searching for the fastest routes using Google Maps' route planner and by looking up the main transit roads for heavy goods traffic through Switzerland on 'map.geo.admin.ch'. The points of departure were selected based on a map from the Friedrich-Loeffler Institute (FLI), where all cases of ASF in Europe are cumulatively displayed for every calendar year. Areas ranged by wild boar were identified by the layer with relative abundances, selecting all values above zero (Vargas-Amado, et al., 2022). In this way, it was possible to obtain a representation of occupied areas. Once this was defined, methods to locate these areas, and to identify the spatial units in which piggeries are at risk of disease introduction were derived. This resulted in two additional maps that were produced in the Chapter 4. These show the risk of ASF introduction into the domestic pig population via wild boar at the level of communes, one for piggeries with a solid run area and the other for piggeries with a pasture. These maps were the result of multiplying the density of piggeries with a run area or the density of piggeries with a pasture by the scores from the layers corresponding to (i) the relative abundance of wild boar, (ii) the Euclidian distance to rest areas, and (iii) the proximity to a forest (Figure 13).

To describe the extent to which the wild boar habitat in Switzerland is connected, representations of realistic wild boar networks, consisting of connected habitat patches that are occupied, of the northern and southern populations as maps and graphs (networks, resp.) were developed (Chapter 4). These were established through a GIS analysis with the following input data: (I) the wildlife network developed in related work (Holzgang, et al., 2001), (ii) the national motorways, and (iii) the map with the relative wild boar abundances developed in previous work (Vargas-Amado, et al., 2022). A network analysis was carried out on the wild boar networks established this way, using a threshold distance from the literature (Holzgang, et al., 2001) that considers the local conditions in Switzerland.

An updated map of the division of Switzerland's surface into compartments was produced. This new map was based on previous work carried out in 2003 (Giacometti, 2003). In his work, Giacometti established different levels on which the habitat of wild boar was divided due to human and natural barriers. Compartments were the largest areas defined by these barriers. The aim of compartmentalization is to 'divide and rule'. This means that making use of the environmental and human barriers that already exist can ease the process of cutting selected connections to avoid the spread of diseases. In the work presented in the Chapter 4, the compartments were updated to also consider the motorways that were built after 2003. In addition, some of the mountain ridges were redefined.

In order to contain a disease spread (e.g. ASF), in the Chapter 4 of this thesis, it was established which connections in the networks of the northern and the southern population could be easily cut and which cannot. It was shown that network decomposition would be easier to achieve in the Central Plateau than in any other biogeographical region. The maximum possible reduction of the potential epidemic size was calculated in both networks. To achieve this, the first step was to establish a qualitative method to define whether a corridor without passage was easy to block. The 'easiness to block' a corridor was defined according to well-defined features. The next step was to determine the extent to which the potential epidemic size (PES) could be reduced by closing wildlife passages and blocking the 'easy-to-block' corridors. In this study, PES was calculated using (i) the size of the node (the area of the patch ranged by wild boar), (ii) the relative abundance of wild boar in the patch, and (iii) the number of nodes in the LCC. This differs from related work, where PES was calculated using (i) the out-degree distribution, (ii) the infection chain, and (iii) the size of strong and (iv) weak components (Dubé, Ribble, Kelton, & McNab, 2008).

5.2. Recommendations for policy makers

Hunting data are the source most often used to perform calculations of the abundance and density of wild boar (ENETWILD-consortium, et al., 2018). The relative abundance of wild boar is an example of a result derived from hunting statistics.

In Switzerland, each canton is autonomous, which means that every canton decides on procedures for different tasks of concern. These tasks include the hunting proceedings and thus the way that the hunting data are reported. When reports based on hunting data are produced at the cantonal level, the results are framed to the level of detail required by each canton. The resulting heterogeneity in the data complicates the comparison of results within and beyond the country. Therefore, it would be desirable that all cantons in Switzerland report hunting data in a standardized way and agree on a common set of variables for which data should be collected. New variables, such as unsuccessful hunting days and the number of hunters hunting wild boar, should also be considered. This would greatly enhance the outcomes of further work.

The abundance layer developed in previous work (Vargas-Amado, et al., 2022) was one of the main types of input data used for the representation of realistic wild boar networks. This population estimator was calculated using hunting statistics from different cantons. As mentioned previously, the heterogeneity of the data had an impact on the output of the calculations. This problem was exemplified by the 'occupied' patch covering the entire canton of Luzern (Figure14). The data from this canton were available at a very low spatial and temporal granularity (i.e. canton per year). Luzern reported 14 wild boar hunted between 2011 and 2018 (BAFU, 2022). The low granularity of the area for which this number was reported led to a spatial overrepresentation of wild boar in the canton. To avoid this issue in future work, the cantonal authorities should collect and report the data with a fine spatial and temporal granularity (recommended, coordinates per day).

As mentioned in Chapter 3, the highest risk of disease introduction comes from food carelessly disposed. To run one of the analysis in that chapter (*Estimation of the risk of disease introduction)*, two variables were considered of interest to develop the model on the risk of disease introduction were (i) the use of traffic density from countries affected by ASF, and (ii) the number of users per day (or any time unit) of the rest areas. Unfortunately, this information was not available for Switzerland. Therefore, given the importance of the topic, it would be a recommendation to collect more data on this matter.

Given that there is a high probability of the pathogen being brought into the country via roads, the inhabitants around the 57 exposed rest areas (Table 4) should be informed about the risk of ASF. They should be asked to be vigilant for dead wild boar and report them to the cantonal authorities for carcass pick up and testing. Garbage management could be improved at rest stops on high-risk routes. For example, animal proof garbage containers could be installed in these rest stops. The frequency of garbage container emptying could be increased to ensure there is always room in the garbage containers for people to put their garbage in. Rest stop cleaners could be trained to detect and report signs of wild boar activity at these rest stops. Pig farmers in these areas could be informed about the risk and asked to ensure there, domestic pigs do not have outdoor access, or if they do, the barrier between domestic pigs and wild boar should be strengthened. Farmers and veterinarians in high risk areas should be informed of the risk and asked to report any disease occurrences that could potentially be ASF.

Estimating the changing risk of disease transmission at different times of the year would require temporal (or seasonal) data about wild boar abundance, which are currently not available. The relative abundance data in the study presented in this thesis were only for the summer. The seasonal variation in transmission risk might also be driven by the dynamics of the husbandry system (i.e. summer grazing of pigs on Alpine pastures). To consider these in the model, it was recommended that the disease control agency in Switzerland should maintain a country-wide record of Alpine pastures with domestic pigs in the future.

Chapter 6: Conclusions and further work

The objective of this thesis was to analyze spatial aspects related to the dispersal and colonization of free-ranging wild boar in Switzerland. Given that disease spread within a population is a spatial phenomenon, understanding these aspects was considered a prerequisite to improve early disease detection in wild boar and to reduce the risk of disease transmission to domestic pigs. Spatial aspects are also critical for containing a disease after an outbreak.

To meet the stated thesis objective, areas of suitable habitat for wild boar (Chapter 2) and areas already colonized by this species (Chapter 3) were identified and mapped. Additionally, precise information was provided about which areas are at risk of being polluted with contaminated food waste, which the competent authorities consider to be the most likely route of disease introduction. In addition, communes with outdoor piggeries, in which pigs are at risk of coming into contact with potentially infected wild boar, were detected (Chapter 3). Two complementary representations (i.e. cartographic and graphic) were developed of the wild boar networks in the northern and the southern population connecting occupied habitat patches in Switzerland (Chapter 4). Moreover, an understanding was established in the same chapter of how this connectivity could be managed to contain disease spread among free-ranging wild boar. Based on the work presented here, unaffected spatial clusters of compartments could be isolated from the affected one in case of a disease outbreak. In this way the pathogen could be prevented from spreading across the country, and the overall chance of transmitting the pathogen from wild boar to domestic pigs could be reduced.

To reduce the potential bias associated with the hunting bag, ENETWILD (ENETWILD-consortium, et al., 2018) suggests that the hunting effort should be properly defined, and the use of quotas or targets should be fully described. Hunting effort includes factors such as the number of hunting days, number of hunters, and method of hunting (Figure 10). Counting the number of calendar days in the open season for hunting, as done here, is a rough proxy for the hunting effort. A better approach might be to identify 'good hunting days' based on a model of successful hunting days. The success of hunting days depends, among other things, on the weather conditions on these days. Temperature and precipitation values are widely used to study different kinds of phenomena. In Switzerland, interpolated data are available on different spatial (e.g. area-covering 1-km grids) and temporal (e.g. daily) scales (MeteoSwiss, 2022). The temperature and precipitation values on successful hunting days could be extracted and related to those on all hunting days in the same climatic region to identify 'good hunting days' that were not successful. Still, it is an open issue whether hunting days can be described sufficiently well by these (or additional) variables to achieve better results.

The experience that other European countries acquired from the introduction of ASF into their wild boar population should be a starting point for other countries. For instance, in Belgium in 2019, it was determined that ASF was introduced through contaminated food discarded somewhere along a motorway (FASFC, 2019), confirming that this could be a route of ASF introduction to Switzerland (Bundesamt für Lebensmittelsicherheit und Veterinärwesen (BLV), 2020a). In many Eastern European countries, the ASF virus is prevalent in domestic pigs. Romania, for instance, was in the news because of its tradition of slaughtering pigs in the time before Christmas (MDR, 2019). Products made from pork are traditional Christmas gifts in that country. Since a quarter of the total stock is held in backyard farms, slaughtering events often escape the notice of the public authorities. Romanians working in Western European countries thus could bring contaminated pork with them and dispose of leftover food in the places where they work and rest in their host country. If this happens in the agricultural industry, domestic pigs could incidentally be infected without the intermediary of wild boar. Romania and Bulgaria are countries where hunting tourism is allowed. This means that people outside the country are permitted to go to these countries and hunt game species. ASF is already present in these countries (EFSA, et al., 2019). Without consideration of biosecurity measures, hunters returning from affected countries could bring the virus back to Switzerland on their clothes or equipment.

The qualitative method used in this work to determine whether a wildlife corridor was easy to block (Chapter 4.3: *Wildlife corridors*) was limited by several factors: (i) a lack of literature on the topic, (ii) a lack of participation of experts on the topic (e.g. game keepers, wildlife biologists), and (iii) the cartographic analysis was limited to the area where the motorways and the wildlife network intersected. A deeper analysis on leaking points along motorways on a regional scale could contribute to enhance the management, since these animals can roam for several kilometers driven by food (Cahill, Llimona, & Cabañeros, 2012; Oja, Kaasik, & Valdmann, 2014) or to escape from hunters (Chapman & Trani, 2007; Marini, Franzetti, Calabrese, Cappellini, & Focardi, 2009), and the influence area can go further than these intersections. It is important to consider that a qualitative evaluation of the results by experts would be especially helpful to develop a standardized set of features that could be used elsewhere.

The threshold distance used in the GIS analysis to decide on habitat connectivity (Chapter 4.3: *Habitat connectivity*) corresponds to the radius of some 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, and considering these individuals may change the conclusions.

Given the importance that compartmentalization has for landscape connectivity management, an automatic process could be established to periodically develop new versions of these compartments. The definition of compartments includes barriers that affect landscape connectivity (e.g. motorways). However, compartments are increasingly connected through wildlife passages. Therefore, an automatized process that considers these updates would result in a more timely information access.

The management of landscape connectivity was framed in a way that only considered wild boar as a target species. Given that other species use the same passages and corridors as wild boar, the effect of connectivity management on other species should be analyzed as well. This work could also be extended by studying how managing connectivity would modify the risk of disease transmission from wild boar to domestic pigs.

The degree of connectedness of piggeries to the rest of the domestic pig production network could be added to the analysis to assess the consequences of disease introduction. Such an extension should expand on previous work investigating the structure and patterns of the pig transport network in Switzerland (Sterchi, et al., 2019).

Finally, epidemic disease spread could be explored in a more realistic setting by linking the approach presented here with state-of-the-art epidemic modeling (Nelson & Williams, 2014). This would make it possibly to set a time limit for the closing of wildlife passages and the blocking of corridors in case of an epidemic disease outbreak. 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. Expanding the analysis in such a way would require temporal data about wild boar dispersal on Swiss conditions, which were not available on the required scale in this study.

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Publications

CRediT author statement

The author contributions per paper are summarized according to the CRediT taxonomy (Allen, O'Connell, & Kiermer, 2019).

Term	Free-ranging wild boar (*Sus scrofa*) in Switzerland: Casual observations and model-based projections during open and closed season for hunting	Towards risk-based surveillance of African Swine Fever in Switzerland	Potential effect of managing connectivity to contain disease spread among free-ranging wild boar in disparate landscapes
Conceptualization	✓	✓	✓
Methodology	✓	✓	✓
Software	✓	✓	✓
Validation	✓	✗	✗
Formal analysis	✓	✓	✓
Investigation	✓	✓	✓
Resources	✗	✗	✗
Data Curation	✓	✓	✓
Writing - Original Draft	(✓)	✓	✓
Writing - Review & Editing	✓	✓	✓
Visualization	✓	✓	✓
Supervision	✗	✗	✗
Project administration	✗	✗	✗
Funding acquisition	✗	✗	✗

Table 5. Author's Contributions where ✓ means fully contributed, (✓) means partly contributed, and ✗ no contribution.

First Publication

Free-ranging wild boar (*Sus scrofa*) in Switzerland: casual observations and model-based projections during open and closed season for hunting

M. E. Vargas Amado[1,2], R. Grütter[1], C. Fischer[3], S. Suter[4], A. Bernstein[2]

[1] Swiss Federal Research Institute WSL, Birmensdorf, Switzerland; [2] Department of Informatics, University of Zurich, Switzerland; [3] Haute école du paysage, d'ingénierie et d'architecture HEPIA, Geneva, Switzerland; [4] ZHAW School of Life Sciences and Facility Management, Wädenswil, Switzerland

Abstract

Wild boar (i.e., Sus scrofa) are susceptible to a range of diseases that can be transmitted to domestic pigs. Assessing the potential risk of transmission-related events involves identifying where wild boar occur in Switzerland and where they still can colonize. It also involves identifying zones where piggeries are dense. In the work presented here, the distribution of wild boar in Switzerland was projected from grid data as probabilities of presence using an approach based on statistical modeling, separately for closed and open season for hunting. The predicted probabilities of wild boar presence were related to the density of piggeries in the six agricultural zones. The resulting maps show how the potential risk of transmission-related events, as a proxy for disease transmission, is distributed in Switzerland. Wild boar presence data consisted of hunting data and casual observations recorded from September 2011 to February 2018 at the coordinate level. They were obtained from all 16 Swiss cantons maintaining a license hunting system plus Solothurn (for 2017) and Zurich, as well as from info fauna. The probability of wild boar occurrence was high (> 0.7) in Jura, the valleys of the Southern Alps, the Rhone Valley down the river from Martigny, and the Rhine Valley down the river from Bündner Herrschaft; it was fair (0.5–0.7) in the Swiss Plateau. These regions broadly overlap agricultural zones with a high density of piggeries. Patches of perennially suitable, but currently not colonized habitat were found in the cantons of Berne, Obwalden, Uri, Schwyz, Glarus, and Grisons. The probability of wild boar occurrence across the entire study area, including the Alps, increased by 12% during closed season for hunting. The results were discussed with reference to similar studies.

Keywords: Colonization, habitat suitability, risk assessment, spatial projection, species distribution, *Sus scrofa*

Wildschweine (*Sus scrofa*) in der Schweiz: Beobachtungen und modellbasierte Projektionen während der Jagd- und Schonzeit

Eine Reihe von Krankheiten, für welche das Wildschwein (*Sus scrofa*) empfänglich ist, können auf das Hausschwein übertragen werden. Zur Abschätzung des potenziellen Risikos von übertragungsrelevanten Ereignissen muss herausgefunden werden, wo das Wildschwein in der Schweiz vorkommt und welche Gebiete es noch besiedeln kann. Ebenso müssen Zonen mit einer hohen Dichte von Schweinehaltungen bestimmt werden. In der vorliegenden Arbeit wurde das beobachtete Wildschweinvorkommen während der Jagdsaison und in der Schonzeit als Auftretenswahrscheinlichkeiten in ein landesweites Datenraster projiziert. Das so vorhergesagte Auftreten wurde zur Anzahl an Schweinebetrieben pro Quadratkilometer in Beziehung gesetzt. Die resultierenden Karten zeigen, wie das potenzielle Risiko von übertragungsrelevanten Ereignissen, stellvertretend für eine Krankheitsübertragung, in der Schweiz verteilt ist. Die Datenbasis bestand aus Jagddaten und beiläufigen Beobachtungen, soweit diese zwischen September 2011 und Februar 2018 koordinatengenau aufgezeichnet wurden. Sie wurden von allen 16 Patentjagdkantonen, plus Solothurn (2017) und Zürich, sowie von info fauna für die Studie bereitgestellt. Im Jura, in den Alpensüdtälern, im Rhônetal unterhalb von Martigny und im Rheintal unterhalb der Bündner Herrschaft war die Wahrscheinlichkeit des Wildschweinvorkommens hoch (> 0.7); im Mittelland war die Wahrscheinlichkeit mittel bis hoch (0.5–0.7). Diese Regionen decken sich weitgehend mit Zonen mit einer hohen Schweinebetriebsdichte. Ganzjährig für das Wildschwein geeigneter, aber noch unbesiedelter Lebensraum wurde in den Kantonen Bern, Obwalden, Uri, Schwyz, Glarus und Graubünden

gefunden. Schweizweit erhöhte sich die Auftretenswahrscheinlichkeit in der Schonzeit um 12%. Die Resultate wurden unter Bezugnahme auf ähnliche Studien im In- und Ausland diskutiert.

Introduction

Wild boar are susceptible to a range of diseases that can affect also domestic pigs. Examples are Enzootic Pneumonia (EP) and African swine fever (ASF).[6,12] ASF is currently spreading in European wild boar populations, though Switzerland is still free from the disease. ASF can be transmitted to domestic pigs via contact with infected animals, or contaminated carcass remains and equipment.[12] It has a high mortality rate and is a major threat for the pig industry, particularly in Switzerland where the proportion of outdoor piggeries is high. Identifying the spots where a direct or indirect contact between wild boar and domestic pigs can take place is critical to develop risk-based surveillance systems for improving early disease detection and control. This involves, identifying where wild boar occur in Switzerland and where they still can colonize. It also involves identifying zones where piggeries are dense.

The abundance and density of wild boar in Switzerland has already been investigated in related work. The probability of wild boar occurrence per hunting area and *sq km* was predicted using a set of landscape composition variables and the annual hunting statistics per hunting area as a surrogate of population data.[31] Wild boar abundance and density were also estimated based on capture-resights in the canton of Geneva.[28] The spatial overlap between areas roamed by free-ranging wild boar and outdoor piggeries was mapped at the level of municipalities.[59] Information on wild boar, in that study, originated from qualitative reports to the Centre Suisse de Cartographie de la Faune (CSCF) and from a questionnaire survey among pig farmers.[60] Lately, wild boar occurring in Switzerland were mapped by density class as an aggregate of wild boar hunted or found dead in municipalities or hunting grounds.[34,35] The distribution and abundance of wild boar has been mapped also in Europe and Eurasia, including Switzerland, in terms of rasters of 10 km, 5 km and, as of recently, 2 km based on very heterogeneous data from various sources.[3,46,1,16]

The work presented here extends beyond the above cited by *cumulatively* satisfying the requirements listed below. The distribution of wild boar (i.e., *Sus scrofa*) in Switzerland was projected

– From *grid data* as probabilities of presence using an approach based on *statistical modeling* (an approach based on statistical modeling was also taken in other studies);[31,3,46,1,16]
– with a *fine-grained* spatial resolution of 1 *sq km* (a raster map of 1 *sq km* was also produced in other work, albeit unpublished);[31]
– separately for *summer* (closed season for hunting) and winter (open season for hunting). Summer (March–August) and winter (September–February) were distinguished in accordance with the hunting season rather than with vernal and autumnal equinoxes. In the hunting season, there are more carcasses available (i.e., wild boar shot but not retrieved). Since the species is to some extent scavenging on carcasses and, in the case of ASF, the virus survives well in them, the risk of being infected is then increased.[12]

The approach adopted here to project the occurrence of wild boar in Switzerland reflects the state-of-the-art of species distribution modeling (SDM) in conservation biology and ecology.[25] Thereby, the term 'projection' refers to a model-based spatial prediction in a data grid. Statistical models were fitted and evaluated in an initial dataset of wild boar presences and (pseudo-) absences.
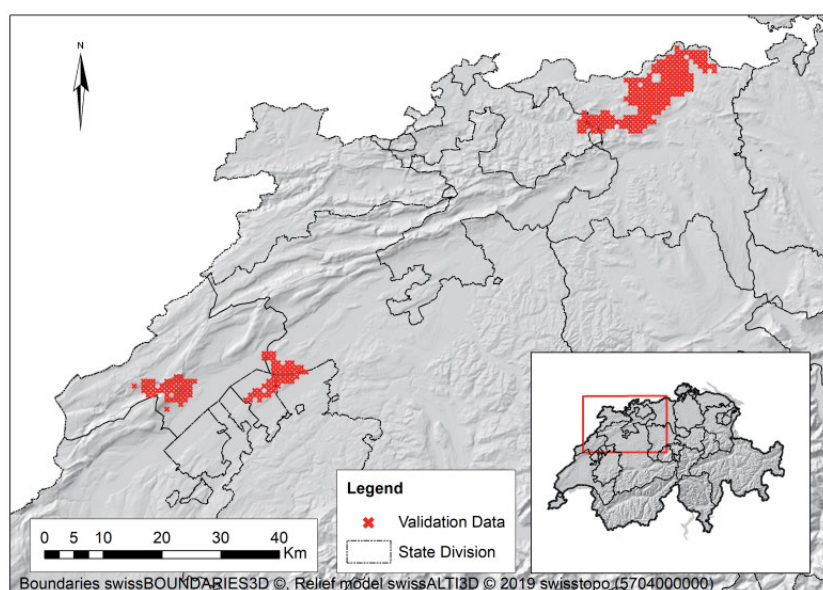
Figure 1: Areas in the cantons of Neuchâtel, Vaud, Fribourg, Berne, Basel-Country, and Aargau where the wild boar (*Sus scrofa*) presence data used for external validation of the summer and winter model have been collected.

They were then used to predict the probabilities of presence in the entire study area, namely, all of Switzerland. The predicted probabilities of wild boar presence for the two seasons were related to the density of piggeries in the six agricultural zones. The resulting maps show how the potential risk of transmission-related events, as a proxy for disease transmission, is distributed in Switzerland.

Material and methods

Study area

The study considers all of Switzerland. Switzerland is located in Western and Central Europe and covers a total surface area of 41,285 *sq km* ranging from 193 to 4,634 meters above sea level. It has three main geographic regions: the Alps, covering around 60% of the country's total surface area, the Swiss Plateau (30%) and the Jura (10%). Of Switzerland's surface area, 7.5% is used for settlements and urban areas, trade, industry and transport, energy supply and waste disposal or recreational areas and parks, while agricultural land occupies 35.9%, and forests as well as woodlands 31.3%.[54]

The Alps act as a prominent climatic barrier between Northern and Southern Switzerland. The climate of Northern Switzerland is heavily influenced by the Atlantic Ocean. Winters in the Northern Plateau are mild and damp, whereas higher altitudes experience arctic temperatures. At altitudes above 1,200–1,500 meters, precipitation in winter mainly falls as snow. Southern Switzerland is strongly affected by the Mediterranean Sea, and so winters are mild and summers warm and humid, and sometimes hot. All along the Alpine ridge there are frequent thunderstorms in the summer.[55]

Species data

Wild boar *presence* data consisted of 12,693 hunting data and 11,430 casual observations recorded from September 2011 to February 2018 at the coordinate level. They were obtained from all 16 Swiss cantons maintaining a license hunting system, covering roughly two thirds of the overall area, plus Solothurn (for 2017) and Zurich, as well as info fauna (copyright by the data providers). A short description of license hunting and a map showing all cantons implementing this system can be looked up on the web site of *Eidgenössische Jagdstatistik*. In order to account for the inaccuracy of locating observations, all data were aggregated to a 1 *sq km* grid. Doing so resulted in 1,702 data cells with reported wild boar presence in summer and 2,882 data cells with reported wild boar presence in winter. Info fauna records observational data on a *ha* basis of which, according to them, only +/– 20% were correctly located by the observers. They recommended to use the *sq km* data which are sufficiently precise.
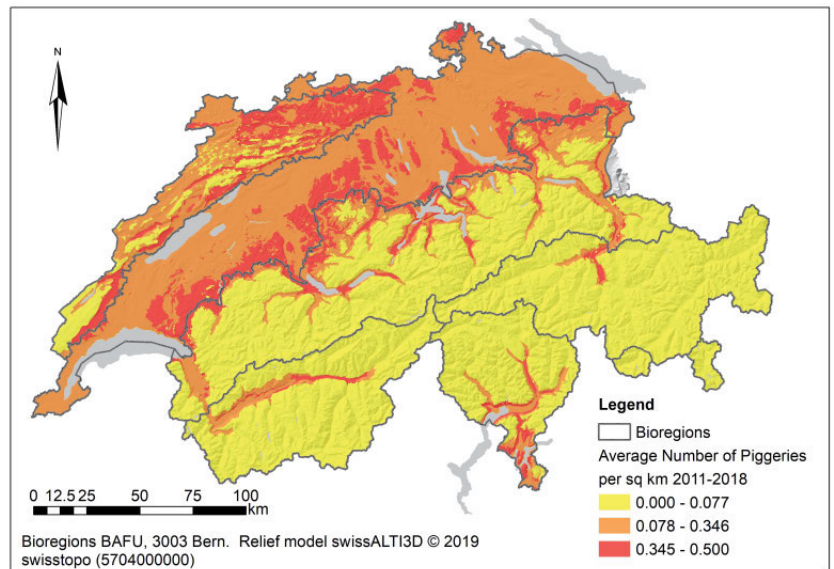
Figure 2: Piggeries per *sq km* in Switzerland, averaged across 2011–2018. Data source: Landwirtschaftliche Zonengrenzen der Schweiz, Bundesbehörden der Schweizerischen Eidgenossenschaft.

For each season, *pseudo-absences* were collected by sampling a number of data cells, equal to that of presence data, at random from the 1 *sq km* grid of Switzerland. Samples that are unbalanced with respect to presences/pseudo-absences have been demonstrated to reduce the accuracy of the models.[25] When sampling at random, (1) the sites of recorded presences and (2) waters and glaciers were not considered. The former were omitted in order not to introduce noise into the data by sampling pseudo-absences from presence data. The latter were omitted in order to constrain the study area to a realistic realm by factoring out areas that are from the outset unsuitable.[25] Areas above 2,000 meters above sea level (which corresponds roughly to the tree line), where wild boar occur only sporadically, were sampled twice as densely.[31,34] The intention was to outweigh the initial bias in the presence data towards environmental conditions in easily accessible areas below 2,000 meters.[45] Figure 3 and 4 (top) show the locations of the presence data cells for summer and winter.

For external validation the presence records from a published and an unpublished study were used (cf. Figure 1). In the former, data came from GPS-collared wild boar, recorded from 2014 to 2017 in the cantons of Vaud, Fribourg, Berne, Basel-Country, and Aargau.[52] In the latter study, occurrence data were recorded based on capture-resights from 2011 to 2014 in the canton of Neuchâtel. Together presence data were recorded in 160 grid cells in each season.

Predictor variables

Twenty-six predictor variables were manually pre-selected using the current ecological understanding of the

system as reported in related work on wild boar: 14 related to bioclimate, 6 to topography, 3 to vegetation, 2 to land fragmentation, and 1 to socio-economics.[36,8,2,7,41,3,46,1,16] In agreement with what is considered a typical wild boar habitat, namely, forested areas and mosaics of forests and agricultural areas,[58] also three categorical variables were among the pre-selected predictors: land use, forest mix rate Swiss National Forest Inventory (NFI), and the forest mask NFI. The sources of the predictor variables are listed in the *Appendix*. For each seasonal variable, namely each bioclimatic variable and two vegetation variables, two raster maps were produced, one for summer (March–August), another for winter (September–February), using average values

across 2011/12–2017/18. For all other variables, a single raster map was produced. All raster maps had the same spatial resolution, namely, 1 *sq km*, which fitted with the uncertainty of the position coordinates for the point observations (cf. section *Species data*). They had the same lower-left coordinate and the same spatial extent, namely, all of Switzerland.

The final variables were identified in a repeated (20 times) 5-fold cross-validation procedure as explained below.[10] For each repetition the variables were selected in a stepwise backward elimination process carried out by growing at each step 1,000 trees with at least 20 terminal nodes using the random forest algorithm.[9] The predictive accuracy of the selected variables was estimated by joining the predictions of the 5 cross-validation subsets and computing the area under the Receiver Operating Characteristic (ROC) curve.[48,53] The set of variables maximizing the AUC was returned, and strongly correlated variables ($|r| > 0.7$) with a low mean decrease in the Gini coefficient were removed.[22,23] The R packages used for variable selection are listed in the *Appendix*. Random forests are built from multiple regression trees, which classify data by clustering rather than by linear separation. Accordingly, they do not assume that the values of the predictor variables and those of the response variable have a linear relationship.[21] Being non-parametric models, they further do not assume independence and, hence, are not affected by spatial-autocorrelation, unless sampling is biased from the source to target scale.[17] The latter was demonstrated in a simulation experiment with gridded data.[50] The predictor variables selected by this procedure for summer and winter are shown in Table 1.

Modeling

An ensemble approach was adopted to model the potential distribution of wild boar in Switzerland.[25] For each season, the ensemble consisted of two regression-based approaches, one classification approach, and two approaches based on machine learning: *generalized additive model* (GAM) with default settings; *multivariate adaptive regression splines* (MARS) without interaction terms; *flexible discriminant analysis* (FDA) using MARS as the fitting method; *random forest* (RF), parameterized to grow 1,000 trees; and *support vector machine* (SVM) with default settings.[27,19,26,14,9] These five approaches outperformed in a pre-test (not shown) the generalized linear model (GLM) with a binomial distribution and a logit link function, artificial neural networks (ANN) using a cross-validation procedure to select the optimal size of the hidden layer and weight decay, and Naive Bayes with priors of 0.5 for presence and absence.[33,32,43] The R packages used for ensemble modeling are listed in the *Appendix*. The five approaches were ensembled as (continuous) *joint probability distributions* and *discretized*
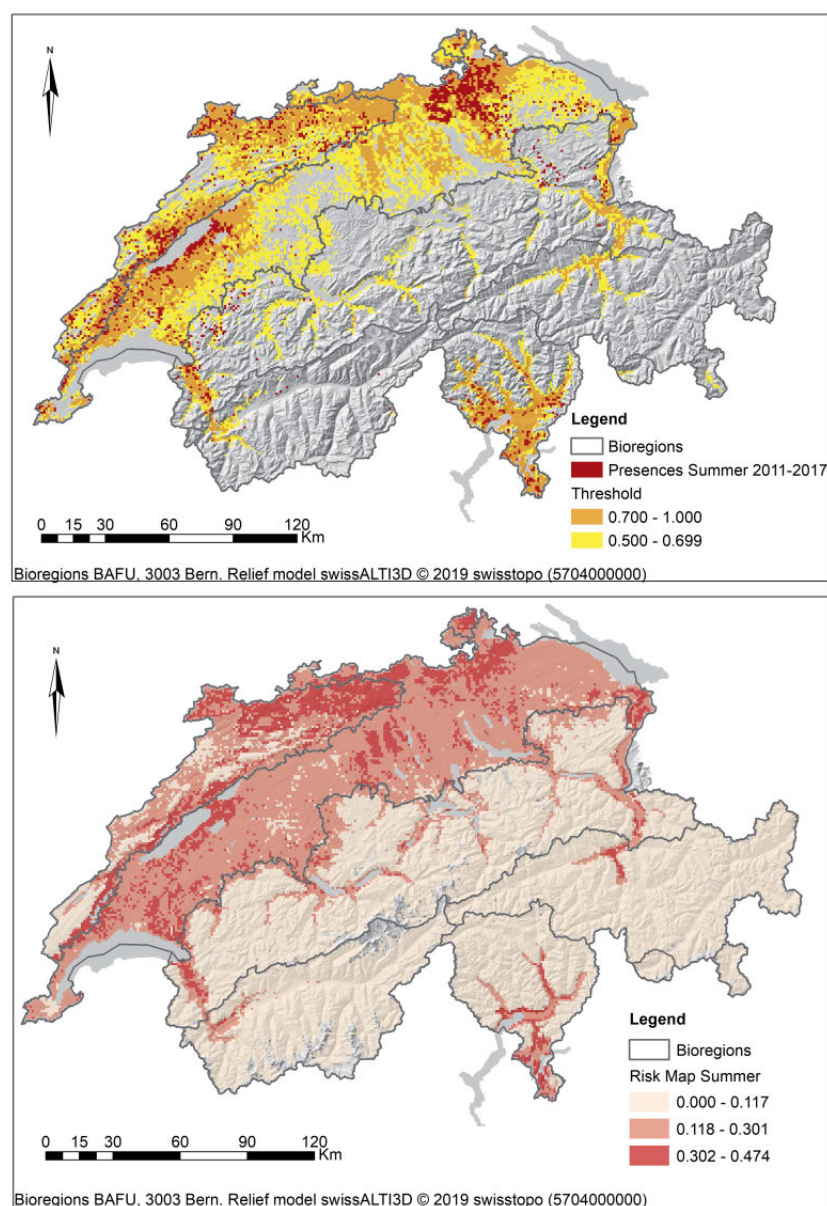
Figure 3: Top Projected *Sus scrofa* occurrence with probabilities of 0.5–0.7 and > 0.7, and actual observations (summer). **Bottom** Potential risk of transmission-related events in summer calculated as *wild boar probability × piggery/sq km*.

maps (presences at two different levels of probability) to serve researchers and decision makers alike. The ensemble predictions were obtained by calculating a weighted average of the predictions from all models, according to the formula:

$$\bar{p} = \sum_{i=1}^{n} (w_i \times p_i)$$

where $w_i \times p_i$ was the predicted probability from model i, weighted by its weight of evidence, and n the number of models considered. The weights were obtained by repeatedly (100 times) running a balanced (i.e., equal numbers of presence and pseudo-absence cells) split-sample cross-validation (80% training, 20% testing) and computing the areas under the ROC curves. Accordingly, models showing a good predictive performance were upweighted in the averaged prediction. Discretized maps were produced using the following classifier:

$$Sus\ scrofa\ is \begin{cases} likely\ present & if\ \ \bar{p} \geq 0.7 \\ potentially\ present & if\ 0.5 \leq \bar{p} < 0.7 \end{cases}$$

The value of 0.7 used as a threshold for likely presence is in line with current practice.[4,49] A value of 0.5 used as a threshold for potential presence is also used occasionally.[20]

Evaluation

Model predictions were validated in the gridded presence data and in independent data (cf. section *Species data*). When fitting the habitat suitability models, the residuals were tested for spatial autocorrelation to identify the amount of spatial structure in the species data that was not explained by the predictors.[25] To this end, global Moran's I was computed for summer GAM and winter GAM.[39] This involved deriving a distance matrix from all observations, and testing the distance effect against the residuals.[25]

Limitations of the modeling approach

The literature discusses a number of theoretical and methodological assumptions that a species distribution model should meet.[25] However, meeting all assumptions is rarely feasible, and assumptions that are not fully met reflect the limitations of the model. The most relevant for the study presented here are (1) limited availability of presence data, (2) possibly biased presence data, and (3) possibly spatially correlated observations.

In a widely cited study some support for a minimum sample size in multiple regression (two of the approaches adopted here are regression-based) of $n = 50 + 8 \times m$ was obtained with m the number of predictor variables.[24] This number increases with the number of categories if categorical variables are used. Thus, in

the study presented here the minimum sample size is $50 + 8 \times (12 + 4) = 178$. This number is clearly outmatched by the 1,702 data cells with reported wild boar presence in summer and the 2,882 data cells in winter. However, more important than the absolute number of observations is the extent to which these cover the whole range of environmental conditions suitable for a species, which is discussed in the next paragraph.

Presence data are often biased towards easily accessible areas.[45] When delivering the data, info fauna made clear that their data are biased towards areas usually visited by observers (e.g., ornithologists) and towards sightings in the open field. Hunting data, on the other hand, are

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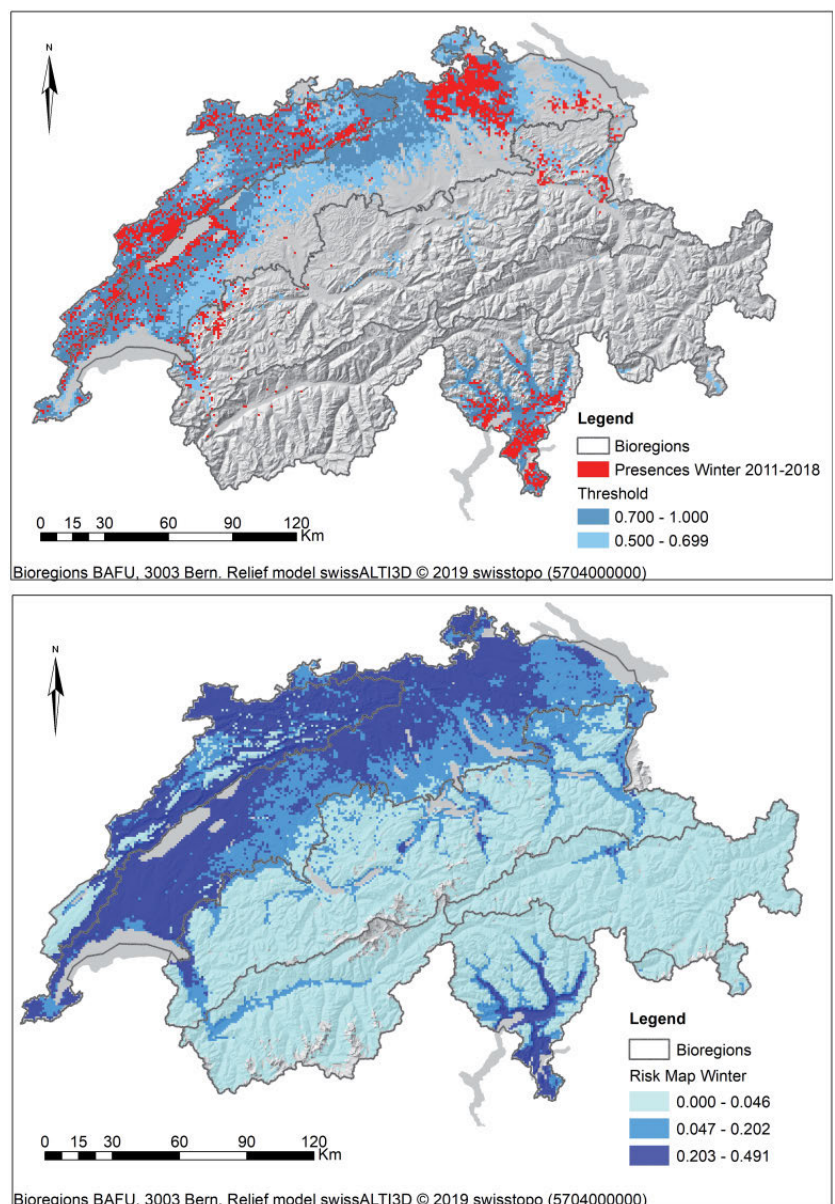
Figure 4: Top Projected *Sus scrofa* occurrence with probabilities of 0.5–0.7 and > 0.7, and actual observations (winter). Bottom Potential risk of transmission-related events in winter calculated as wild *boar probability × piggery/sq km*.

Table 1: Predictor variables selected for statistical modeling in a stepwise backward elimination process using random forest in summer and winter. n/a = variable not selected for this season. Predictor variables: Bioclimatic (*Bio 1–Bio 15, SrelM*), topographic (*slp*), vegetation (*ddeg0*), land use (*NOAS04*), (human) population density (*STATPOP*).

Variable	Definition	Unit	MDGS	MDGW
Bio 1	Semi-annual mean temperature	°C	144.299	n/a
Bio 2	Semi-annual mean diurnal range	°C	n/a	51.432
Bio 4	Temperature seasonality	°C	43.416	83.162
Bio 7	Semi-annual temperature range	°C	37.170	n/a
Bio 13	Precipitation of wettest month	mm	n/a	87.894
Bio 14	Precipitation of driest month	mm	43.208	82.515
Bio 15	Precipitation seasonality	%	58.285	164.472
ddeg0	Growing degree days above 0°C	°C days	n/a	232.448
SrelM	Rel. sunshine duration	%	45.461	134.011
slp	Rate of change of elevation	deg	30.400	n/a
NOAS04	Land use	4 classes	n/a	41.454
STATPOP	Population density	n/ha	31.543	37.335

MDGS, mean decrease in Gini coeffcient (summer); MDGW, mean decrease in Gini coeffcient (winter)

Table 2: Internal validation: True Positive Rates (= rates of presence data cells from this study that were correctly predicted) for summer and winter.

Season	Threshold	Sample size	True positives	TPR
Summer	0.7	1,677	1,280	0.742–0.783
	0.5	1,677	1,555	0.914–0.939
Winter	0.7	2,831	2,324	0.806–0.835
	0.5	2,831	2,619	0.915–0.934

TPR, True Positive Rate

Table 3: External validation: True Positive Rates (= rates of presence data cells from two independent studies that were correctly predicted) for summer and winter. Data came from GPS-collared wild boar, recorded 2014–2017 in the cantons of Vaud, Fribourg, Berne, Basel-Country, Aargau, and from capture-resights, recorded 2011–2014 in the canton of Neuchâtel.

Season	Threshold	Sample size	True positives	TPR
Summer	0.7	160	153	0.912–0.982
	0.5	160	152	0.904–0.978
Winter	0.7	160	160	0.977–1.000
	0.5	160	160	0.977–1.000

TPR, True Positive Rate

biased towards the woods where the battues are carried out. The problem with biased observations is that the environmental conditions in suitable areas that are difficult to access are underrepresented or, in the worst case, not represented at all. The work presented here dealt with a possible bias in the presence data by sampling psedo-absences in potentially unsuitable areas twice as densely as in potentially suitable ones. Doing so resulted in better predictions when compared to sampling pseudo-absences regularly across the study area (not shown). However, as the *true positive rates* for a threshold of 0.7 in Table 2 suggest, the projections still tend to underpredict the occurrence of wild boar in Switzerland.

Species data are almost always spatially autocorrelated.[25] Spatial autocorrelation may occur if species presences are taken from samples in overly close proximity. When species data are autocorrelated the degrees of freedom used in many statistics associated with the models no longer correspond to the number of observations.[30] As a result, some statistics may be inaccurate or even wrong.[15] In the study presented here observations in *ha* were aggregated to presences in *sq km*. In this way not only the imprecision in the original data was accounted for, but also were species data thinned, in some areas almost hundredfold. As Figure 6 shows, there is still some weak spatial correlation (< 0.4) in the residuals, particularly at short distances and in winter. An attempt to further thin the data using the respective toolset in a geographic information system did not decrease the correlation in the residuals (not shown). This may point to the presence of ecological or environmental processes that are not fully captured by the predictor variables.[25]

Results

Modeling

Figure 3 and 4 (top) show the discretized maps for summer and winter, overlayed by the presence data used for modeling (cf. section *Species data*) and the six biogeographical regions in Switzerland. These regions subdivide the three geographic regions mentioned in section *Study area* into smaller ones based on their faunistic and floristic potential. It is worth noting that in Valais wild boar has since been observed also in Lötschental, Mattertal, Gantertal, and Goms, according to info fauna.

In both seasons, the probability of wild boar occurrence is high (> 0.7) in Jura, the valleys of the Southern Alps, the Rhone Valley down the river from Martigny, and the Rhine Valley down the river from Bündner Herrschaft. In summer it is also high in the upper Rhine valley. The probability is fair (0.5–0.7) in the Plateau and, particularly in summer, in the valleys of the Northern Alps.

The *true positive rates* (TPRs), computed as Clopper-Pearson confidence intervals at a level of 95%, are shown in Table 2.[13] The probability of wild boar occurrence across the entire study area, including the Alps, increased by 12% in summer when compared with winter. Figure 3 and 4 (bottom) show the potential risk of transmission-related events, calculated as *wild boar probability × piggery / sq km*, for both seasons in Switzerland. It is important to see, that this potential cannot be fully realized because of a number of natural and artificial barriers, the effects of which are discussed in Section Discussion.

Figure 5 shows patches of perennially suitable habitat in the cantons of Berne, Obwalden, Uri, Schwyz, Glarus, and Grisons that are currently not colonized. For the rest of Switzerland, the joint probability distributions were similar to the discretized maps shown in Figure 3 and 4 (top). It is worth noting that a high probability of occurrence does not necessarily indicate a high density of wild boar. A more detailed analysis should be based on the estimated density of wild boar, which is outside the scope of this article.

Evaluation

The values of the areas under the ROC curves (AUC), averaged across 100 split-sample cross-validation runs for summer and winter (cf. section *Modeling*), are shown below. These values were the weights used to compute the joint probability distributions from the predictions of the individual approaches in the ensemble.

	GAM	MARS	FDA	RF	SVM
AUC_Summer	0.872	0.860	0.861	0.919	0.883
AUC_Winter	0.898	0.884	0.883	0.937	0.891

The results of the validation in the external dataset (cf. section *Species data*) are shown in Table 3. The tests for spatial autocorrelation in the residuals of the GAM model revealed significant, but weak positive relationships, particularly at short distances and in winter, thereby implying that the major part of the spatial structure in the species data was explained by the predictor variables (cf. Figure 6).

Discussion

The risk maps in Figure 3 and 4 (bottom) show for both seasons patterns similar to the density of piggeries in Figure 2. The reason is that there is a broad overlap between piggeries and areas where wild boar are potentially or likely present (cf. Figure 3 and 4, top). Accordingly, the potential risk of transmission-related events is currently highest in Jura, the Swiss Plateau, the Rhône valley, the valleys of the Southern Alps, and the Rhine valley. *Transmission-related events* refer to a range of conditions that encourage the transmission of diseases, such as ASF, from wild boar to domestic pigs. Examples are a direct contact with infected animals in outdoor piggeries, an indirect contact via contaminated clothes or equipment, or using straw from cropland ranged by wild boar as litter in piggeries.[12] Indirect contacts are more likely where farmers are themselves hunters or welcome hunters on their farm, and where farmers and hunters have access to dead animal disposal plants on the same

weekday. Not only are wild boar likely to occur where piggeries are dense, but also where the human population is dense (cf. STATPOP in Table 1). This supports the hypothesis that wild boar are a synanthropic species.[42]

The joint probability distributions suggest that the (re-) colonization of Switzerland by wild boar from France, Germany, and Italy is not yet completed. Particularly, in the cantons of Berne, Obwalden, Uri, Schwyz, Glarus, and Grisons the models predict perennially some suitable habitat that is currently not populated. In Obwalden, Uri, Schwyz, and Glarus none or only a few animals were observed or shot in years 2009 through
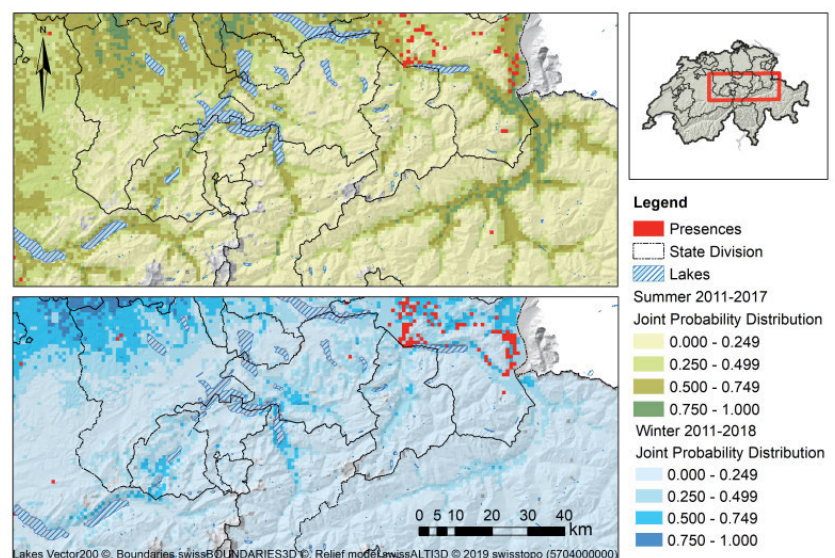
Figure 5: Joint probability distribution of *Sus scrofa* showing patches of perennially suitable, but currently not colonized habitat in the cantons of Berne, Obwalden, Uri, Schwyz, Glarus, and Grisons.
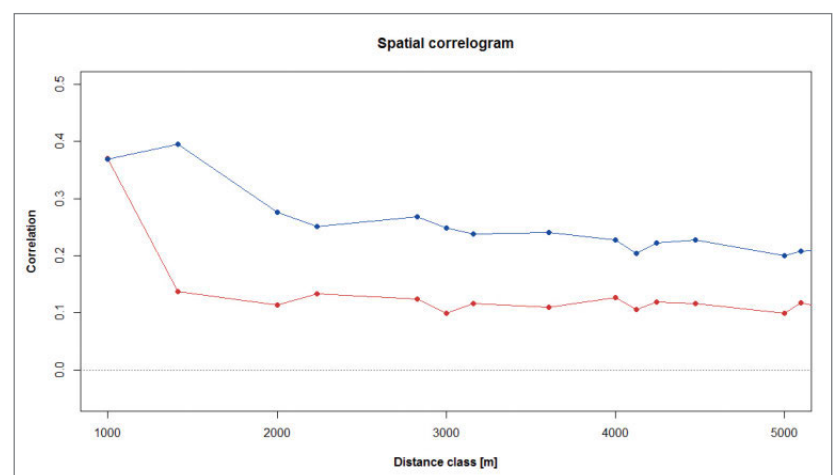
Figure 6: Spatial correlation of model residuals at increasing distances between sample locations in summer (red) and winter (blue) using the predictor variables in Table 1. It shows some significant, but weak positive relationships, particularly at short distances and in winter.

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2018 (cf. Figure 5). It seems that these cantons are hard to colonize by wild boar because of natural and artificial barriers. As suggested by the TPRs in Table 2, the projections tend to underpredict the occurrence of wild boar. Accordingly, the areas of suitable habitat may actually be larger than suggested by the projections. Wild boar have been observed in the Rhine valley of Saint Gall. The projections suggest that they are likely to colonize the (anterior) Rhine valley (and side valleys) of Grisons unless gamekeeping prevents them from doing so. In the future wild boar may benefit from climate change, range in even higher altitudes in summer, and overwinter in the Prealps.

A study on surveilled wildlife passages at the junction between the Jura and the Swiss Plateau as well as in the Swiss Plateau identified highway A5 at the south foot of Jura between Yverdon-les-Bains and Luterbach as a potential barrier for wild boar[59]. The spatial distribution of presence records in the study presented here suggests that this barrier has since been overcome in the Neuchâtel area and wild boar on march got stuck at highway A10 between Neuchâtel and Kerzers, and highway A1 between Kerzers and Berne (cf. Figure 7). The projections in Figure 5 suggest that, without these barriers, wild boar would colonize areas along the Aare river, Lake Thun, Lake Brienz, in the Hasli valley and the other valleys of the Bernese Oberland to the extent that these are predominantly covered with deciduous forest. These are areas where piggeries are dense (cf. Figure 2) and where the risk of transmission-related events is high (cf. Figure 3 and 4, bottom). Wild boar prefer deciduous

forests, where the fruits of the oak and beech trees provide a basic food resource, particularly during the cold season, over coniferous forests.[42,29] A further barrier is highway A2 between Härkingen and Lucerne. Highway A3 between Zurich and Sargans is a barrier for wild boar colonizing Switzerland from the north. There the natural barriers of Walensee lake and Lake Zurich might also have prevented wild boar from colonizing Glarus and Schwyz. The migratory pressure onto Swiss cantons shielded by highways is expected to increase in the future: wildlife passages have to be built by law in order to increase the connectivity of the natural habitat.

The proportion of forest was found to be one of the main drivers of wild boar population expansion into unoccupied agroecosystems.[40] This was attributed to the role forests play in providing wild boar with food resources and year-round protection, but also in constituting an important corridor facilitating wild boar population movement. In a study in the Geneva Basin, landscape fragmentation variables were the primary drivers of wild boar ranging patterns in a human-dominated agroecosystem with range size best explained by a model including landscape variables only.[18] As mentioned above there is currently no viable population of wild boar in central Switzerland, despite the fact that there is some suitable habitat for this species. Hence, in addition to barriers, the remarkable patchiness of the predominantly coniferous forest together with a high fragmentation of landscape in general and the absence of hunting-free zones in the Oberaargau, Lucerne foreland, and Lucerne hinterland, which are regions in the Swiss Plateau, might also have limited the expansion of wild boar into suitable habitat. This is of relevance, since the piggeries in the canton of Lucerne are strongly connected with holdings in other cantons.[51] There a potential contact between domestic pigs and wild boar could have severe consequences.

In the study presented here, the probability of wild boar occurrence across the study area was larger in summer than in winter. This is in line with the findings in the south of Belgium where the suitable habitat almost doubled in the growing season when compared to the hunting season.[41] In Belgium this was explained by the cover and food provided by the agricultural area in the growing season. The computation of the mean probability of wild boar occurrence per land use class in Switzerland did not show any significant shift among the classes between summer and winter. This might be explained by the agricultural practice of yearly crop rotation on a small spatial scale. Accordingly, information on the type of crop grown, used as predictor variables in the Belgium study, was not available on the required scale in Switzerland.
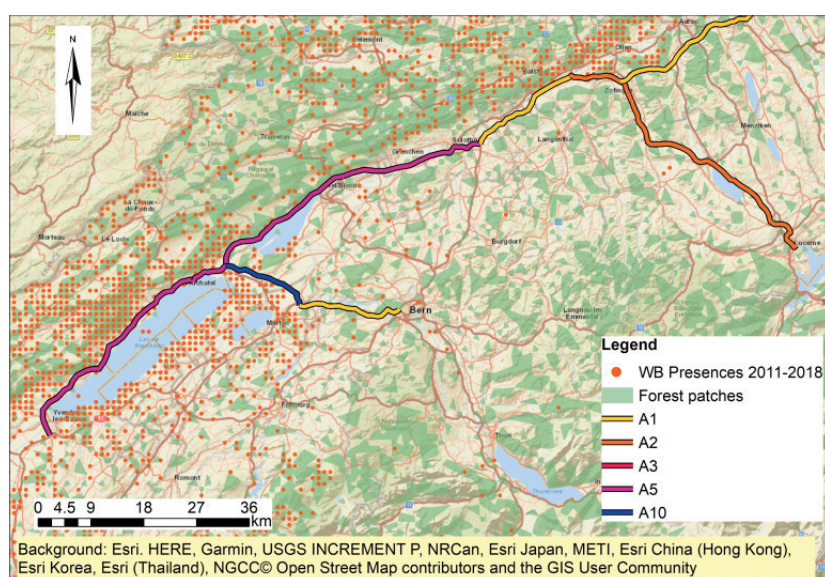
Figure 7: Natural and artificial barriers at the junction between Jura and the Swiss Plateau, and wild boar presences. A1–A10: Swiss national highways. This suggests that highway A5 has been overcome by wild boars in the Neuchâtel area. However, highway A10 between Neuchâtel and Kerzers, highway A1 between Kerzers and Berne, and highway A1 between Luterbach and Birrfeld seem to be effective barriers.

Appendix

Software tools and packages

All modeling and evaluation were carried out in RStudio Version 1.2.1335 running R x64 3.5.3. The following packages were used:

Ensemble modeling	Variable selection	Moran's I
library(biomod2)	library(AUCRF)	library(ape)
library(MASS)	library(tidyverse)	library(ncf)
library(mgcv)	library(rcompanion)	library(gam)
library(earth)	library(reshape)	
library(rpart)		
library(mda)		
library(Hmisc)		
library(e1071)		

ArcGIS for Desktop 10.4.1 was used to prepare the input data to RStudio and to draw the maps.

Predictor variables

The predictor variables were fed from the following sources:

Bioclimate
Bioclimatic predictors (e.g., *Bio 1–Bio 15* and *SrelM* in Table 1) were computed according to the formulas provided by the U.S. Geological Survey using grid data from the Federal Office of Meteorology and Climatology MeteoSwiss.[37,38,44]

Topography
Topographic predictors (e.g., *slp* in Table 1) were derived prior to this work from the Digital Elevation Model (swissALTI3D) of swisstopo.[5,11]

Vegetation
Seasonal vegetation predictors (e.g., *ddeg0* in Table 1) were computed according to the formula provided in related work using the grid data from the Federal Office of Meteorology and Climatology MeteoSwiss (cf. above).[47] The forest mix rate of the National Forest Inventory (NFI) was computed prior to this work using multispectral aerial images and a Digital Terrain Model (DTM) developed from Airborne Laser Scanning (ALS) data.[57]

Land fragmentation
Land use (*NOAS04* in Table 1) was computed based on the statistics of the Federal Statistical Office (BFS GEOSTAT). The forest mask was computed prior to this work based on Digital Surface Models (DSMs) from image-based point clouds of Airborne Digital Sensor (ADS) data.[56]

Socio-economics
The population density (*STATPOP* in Table 1) was computed based on the population and households statistics of the Federal Statistical Office (BFS).

Free-ranging wild boar (*Sus scrofa*) in Switzerland: casual observations and model-based projections during open and closed season for hunting

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Free-ranging wild boar (*Sus scrofa*) in Switzerland: casual observations and model-based projections during open and closed season for hunting

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Sanglier (*Sus scrofa*) en Suisse: observations occasionnelles et projections basées sur des modèles d'ouverture et fermeture de chasse

Le sanglier (*Sus scrofa*) est sensible à plusieurs maladies qui peuvent être transmises au cochon domestique. Afin d'estimer le risque potentiel de transmission, il est important d'identifier les zones occupées par le sanglier en Suisse ainsi que celles qu'il pourrait encore coloniser. De plus, cela implique également de pouvoir situer les secteurs où les élevages de cochons sont les plus abondant. Dans le présent travail, la distribution du sanglier a été projetée selon une grille à l'échelle de la Suisse à partir des présences confirmées en utilisant des méthodes statistiques, ceci en considérant la période d'ouverture de chasse d'une part et la période de fermeture d'autre part. Les probabilités de présence calculées ont été misent en relation avec la densité des porcheries dans les différentes zones agricoles. Les cartes résultant de cet exercice montrent comment le risque potentiel de transmission de maladies est distribué en Suisse. La base de données utilisée contenait des informations sur les sangliers tirés lors de la chasse, ainsi que des observations occasionnelles, rapportées à l'échelle de la coordonnée entre Septembre 2011 et Février 2018. Ces données ont étés obtenues de l'ensemble des 16 cantons maintenant un système de chasse à patente, plus Soleure (2017) et Zurich, et des données disponibles sur info fauna. La probabilité de trouver des sangler est élevée (> 0.7) dans le Jura, les vallées du sud des Alpes, la vallée du Rhône en aval de Martigny et la vallée du Rhin en aval de Bündner Herrschaft. Elle est modérée (0.5–0.7) pour le Plateau Suisse. Ces régions correspondent à peu près aux zones agricoles possédant les plus grandes densités de porcheries. Des secteurs offrant des conditions favorables toute l'année, mais encore inoccupés par le sanglier ont été trouvés dans les cantons de Berne, Obwald, Uri, Schwyz, Glaris et les Grisons. Sur l'ensemble de la zone d'étude, la probabilité de présence des sangliers était supérieur de 12% en dehors de la période de chasse. Les résultats ont été discutés en les comparant à des études similaires.

Mots-clés: Colonisation, adéquation de l'habitat, évaluation des risques, projection spatiale, distribution des espèces, *Sus scrofa*

Cinghiale libero (*Sus scrofa*) in Svizzera: osservazioni casuali e proiezioni basata su modelli durante la stagione della caccia aperta e chiusa

I cinghiali (i.e., *Sus scrofa*) sono sensibili a molte malattie che possono essere trasmesse ai suini domestici. Per la valutazione del rischio di trasmissione potenziale, è importante identificare le aree in cui i cinghiali vivono in Svizzera e quali possono ancora colonizzare. Si tratta inoltre di individuare le zone in cui la densità degli allevamenti di suini è molto densa. Nello studio qui presentato, la distribuzione dei cinghiali selvatici è stata proiettata sulla base di una griglia a livello svizzero a partire dalla presenza confermata utilizzando dei metodi statistici, considerando il periodo di apertura della caccia da una parte e di chiusura dall'altra. Le probabilità della presenza di cinghiali calcolate sono state messe in relazione con la densità degli allevamenti di suini nelle differenti zone agricole. Le carte che ne sono risultate mostrano come il rischio potenziale di trasmissione delle malattie sia distribuito in Svizzera. I dati utilizzati sulla presenza di cinghiali erano costituiti da dati provenienti dalla caccia e da osservazioni casuali registrate a livello di coordinate da settembre 2011 a febbraio 2018. Questi dati provenivano da tutti i 16 Cantoni svizzeri che mantengono un sistema di caccia con autorizzazione, più Soletta (per il 2017) e Zurigo, nonché da infofauna. La probabilità di avvistamento di cinghiali era alta (> 0,7) nel Giura, nelle valli delle Alpi meridionali, nella valle del Rodano sotto Martigny e nella valle del Reno sotto la Bündner Herrschaft (Signoria Grigionese); era moderata (0,5-0,7) nell'Altipiano svizzero. Queste regioni si sovrappongono ampiamente alle zone agricole ad alta densità di allevamenti di suini. Nei Cantoni di Berna, Obvaldo, Uri, Svitto, Glarona e Grigioni sono state identificate zone di habitat adatte, ma attualmente non ancora popolate dai cinghiali. La probabilità della presenza di cinghiali in tutta l'area di studio, è aumentata del 12% durante la stagione di chiusura della caccia. I risultati sono stati discussi e comparati a studi simili.

Parole chiavi: Colonizzazione, habitat adatto, valutazione del rischio, proiezione spaziale, distribuzione delle specie, Sus scrofa

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Corresponding author

R. Grütter, DVM, MBA
Swiss Federal Research Institute WSL
Zürcherstrasse 111
8903 Birmensdorf
Switzerland
Phone +41 44 739 2509
E-Mail: rolf.gruetter@wsl.ch

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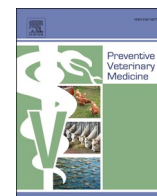
Towards risk-based surveillance of African Swine Fever in Switzerland

Maria Elena Vargas-Amado [a,b], Luís Pedro Carmo [c], John Berezowski [c], Claude Fischer [d], Maria João Santos [b], Rolf Grütter [a,*]

[a] *Swiss Federal Research Institute WSL, Birmensdorf, Switzerland*
[b] *University of Zurich, Department of Geography, Zurich, Switzerland*
[c] *Veterinary Public Health Institute, Vetsuisse Faculty, University of Bern, Bern, Switzerland*
[d] *Haute école du paysage, d'ingénierie et d'architecture HEPIA, Geneva, Switzerland*

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ABSTRACT

African Swine Fever (ASF) has emerged as a disease of great concern to swine producers and government disease control agencies because of its severe consequences to animal health and the pig industry. Early detection of an ASF introduction is considered essential for reducing the impact of the disease. Risk-based surveillance approaches have been used as enhancements to early disease epidemic detection systems in livestock populations. Such approaches may consider the role wildlife plays in hosting and transmitting a disease. In this study, a method is presented to estimate and map the risk of introducing ASF into the domestic pig population through wild boar intermediate hosts. It makes use of data about hunted wild boar, rest areas along motorways connecting ASF affected countries to Switzerland, outdoor piggeries, and forest cover. These data were used to compute relative wild boar abundance as well as to estimate the risk of both disease introduction into the wild boar population and disease transmission to domestic pigs. The way relative wild boar abundance was calculated adds to the current state of the art by considering the effect of beech mast on hunting success and the probability of wild boar occurrence when distributing relative abundance values among individual grid cells. The risk of ASF introduction into the domestic pig population by wild boar was highest near the borders of France, Germany, and Italy. On the north side of the Alps, areas of high risk were located on the unshielded side of the main motorway crossing the Central Plateau, which acts as a barrier for wild boar. Estimating the risk of disease introduction into the domestic pig population without the intermediary of wild boar suggested that dispersing wild boar may play a key role in spreading the risk to areas remote from motorways. The results of this study can be used to focus surveillance efforts for early disease detection on high risk areas. The developed method may also inform policies to control other diseases that are transmitted by a direct contact from wild boar to domestic pigs.

1. Introduction

Wild boar represent a health threat to domestic pigs (Laddomada et al., 1994; Fritzemeier et al., 2000; Köppel et al., 2007; Ruiz-Fons et al., 2008; Wu et al., 2011), because these two varieties share susceptibility to a similar range of diseases. Diseases found in wild boar that are a significant threat to the swine industry include: classical swine fever, Aujeszky's disease, and porcine brucellosis (Köppel et al., 2007; Ruiz-Fons et al., 2008). In Switzerland, not only has the wild boar population increased in the last decades (Sáez-Royuela and Tellería, 1986; Geisser and Reyer, 2004; Massei et al., 2015), but the number of outdoor piggeries has also grown. With these two developments, the probability of contact between free ranging wild boar and farmed pigs

has increased (Köppel et al., 2007). Recently African Swine Fever (ASF) has emerged as a disease of great concern to swine producers and government disease control agencies because of its health and economic consequences. It re-emerged in Eurasia in 2007 (Vergne, Gogin and Pfeiffer, 2017), jumping to East Europe in 2014 (Gallardo et al., 2018), to Belgium in 2018 (Morelle et al., 2019). In 2020, the first case was reported in Germany (Landwirtschaftsverlag, 2020), and more recently, ASF has been found in a wild boar in Italy's Piedmont region (Stauffer, Polansek und Alves, 2022). In most of the countries affected by the disease it was found that the introduction took place due to a lack of prevention measures on the part of the humans involved in pig production. In countries where biosecurity measures to prevent the introduction/transmission of ASF into/within swine production were

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well-established, the presence of the virus in the wild population still implied a persistent threat to domestic pigs (Jurado et al., 2018; Dellicour et al., 2020). The most evident case was the outbreak of ASF in China, which occurred in 2018. There, 60% of the pig production takes place in backyard farms where the biosecurity is poor (Wang, Sun and Qiu, 2018). This structure of the swine industry favored a rapid increase in outbreaks after the disease was introduced. Accordingly, the susceptibility and the incidence in rural farms were considerably higher compared to suburban areas (Tao et al., 2020).

In Switzerland, domestic pigs have a relatively high health status and are free from many diseases including ASF (Köppel et al., 2007; Nathues et al., 2016). However, ASF outbreaks have occurred quite close to the Swiss borders and ASF poses a substantial threat with potentially extreme consequences to the Swiss pig industry. Early detection of an ASF introduction will be essential for reducing the impact of the disease. Risk-based surveillance approaches have been widely used as enhancements to early disease epidemic detection systems in livestock populations. For instance, in Great Britain risk-based approaches were used to identify high risk areas where surveillance should be focused to identify avian influenza outbreaks (Snow et al., 2007). In New Zealand, risk-based surveillance was used to detect vector-borne causes of ovine and caprine abortion (Prattley, 2009). A risk assessment framework was used to determine the probability of infection of European swine with the ASF virus through wild boar movement and legal trade of pigs and pig meat (Taylor et al., 2020). Risk assessment in that study was performed at a fine spatial scale, allowing the limited surveillance and intervention resources to be focused on high-risk areas and pathways. In Switzerland, the benefits of implementing risk-based surveillance approaches have been reported using the examples of (1) freedom from infectious bovine rhinotracheitis (IBR) and enzootic bovine leucosis (EBL), (2) bluetongue surveillance, and (3) the national residue monitoring program (Reist, Jemmi and Stärk, 2012).

In order to assess the risk of occurrence of an ASF outbreak within the wild boar population in Switzerland, it is important to know the spatial distribution and relative abundance of wild boar. Density and abundance calculations are widely used to monitor, manage, and control wildlife populations (Pittiglio, Khomenko and Beltran-Alcrudo, 2018). This information can be used by authorities (Acevedo et al., 2007) to assess the vulnerability of crops to damage by wild boar (Geisser and Reyer, 2004; Honda and Kawauchi, 2011) or implement population control activities such as fencing, trapping, and hunting (Chapman and Trani, 2007).

Information about potential routes of introduction is also fundamental as it can be used to focus wild boar ASF surveillance activities on geographical areas where there is a high risk of pathogen introduction. One way of introducing the disease is by improper disposal of contaminated food waste in areas where wild boar are known to be present (Mur et al., 2012; EFSA, 2010). This was suspected in Belgium in 2018 (FASFC, 2019). Travelers coming from countries where the disease is currently active can introduce the pathogen through contaminated food that is disposed of in rest areas along motorways. Wild boar are opportunistic scavengers (Penrith and Vosloo, 2009), and if discarded food is improperly contained, they may consume it and become infected, providing a pathway for the pathogen to enter the wild boar population.

If there is an introduction of ASF into the Swiss wild boar population, it is likely that the initial spread of the pathogen will occur locally among wild boar. Because the pathogen can be easily transmitted by direct contact from wild boar to domestic pigs, it is of paramount importance to identify pig holdings in close proximity to wild boar where cross-variety contact could potentially occur. Knowing the location of these holdings is essential for optimizing surveillance for early detection of an ASF introduction into domestic swine. Once the pathogen is introduced into the pig population of a single pig farm, initial spread to other pig farms will be dependent on the contacts between the infected farm and other uninfected farms. The most rapid spread of the pathogen is expected in networks of the most highly connected

piggeries. Because of the severe consequence of an ASF introduction into these networks, they should also be a focus for early epidemic detection surveillance. Early detection is critically important. Once the disease enters one node (farm) of the pig production network, the spread across the entire pig production network can potentially be very fast, compromising the swine production supply chain and Swiss export markets for pigs and pig products (Stärk et al., 2006).

This study provides information that can be useful in the future for the development of a risk-based surveillance system for ASF entering Switzerland by contaminated food waste, including (1) identifying risk areas that could represent entrance points of ASF into the wild boar population by identifying geographic areas where there are high relative abundances of wild boar and rest areas along important motorways, (2) identifying the outdoor piggeries in which domestic pigs may be more likely to be exposed to the ASF virus due to a high relative abundance of wild boar, and (3) identifying areas with a combined risk of introducing ASF into the domestic pig population by wild boar.

In a previous study, the potential distribution of wild boar in Switzerland was modeled (Vargas-Amado et al., 2020). In the current study this information was complemented by modeling the effect of beech mast on hunting success in order to calculate wild boar relative abundance in Switzerland, with a fine-grained spatial resolution using hunting statistics as input data.

2. Material and methods

2.1. Study area

The study considers all of Switzerland, a country that covers a total surface area of 41,285 sq km ranging from 193 to 4634 m above sea level (Swiss Confederation, 2020a). Settlement areas cover 7.5% of Switzerland's territory. These include areas given over to housing, infrastructure (trade, industry and transport), water and energy supply, wastewater disposal, as well as green and recreational spaces. Around 40% of Swiss land is used for agriculture, while roughly 30% is covered by forest and woodland. Switzerland has three main geographic regions: the Alps, covering around 60% of the country's total surface area, the Swiss Plateau (30%) and the Jura (10%). The Alps act as a prominent climatic barrier between Northern and Southern Switzerland (Swiss Confederation. Federal Office of Meteorology and Climatology MeteoSwiss. 2020b. ⟨https://www.meteoswiss.admin.ch/home/climate/the-climate-of-switzerland.html⟩ (accessed October 1, 2020). The climate of Northern Switzerland is heavily influenced by the Atlantic Ocean. Winters in the Northern Plateau are mild and damp, whereas higher altitudes experience arctic temperatures. At altitudes above 1200–1500 m, precipitation in winter mainly falls as snow. Southern Switzerland is strongly affected by the Mediterranean Sea, making winters mild and summers warm and humid, and sometimes hot.

2.2. Data collection

2.2.1. Hunting data

Hunting data from 2011/12–2017/18 were the primary data source for the computation of relative wild boar abundance. They were obtained from the relevant authorities of all cantons in which, according to the Federal Hunting Statistics, wild boar are present, except Basel-Stadt and Luzern. For the latter two cantons, the data reported in the Federal Hunting Statistics were used. The data from Vaud were obtained only for the period of 2012/13–2017/18, those from Fribourg were obtained for the period of 2013/14–2017/18. These longitudinal data made it possible to balance out the strong effects of non-controllable factors on the number of yearly hunted wild boar. For instance, weather conditions such as snow cover and snow depth strongly influence the efficiency of

hunting by making some areas less accessible to hunters (ENETWILD-consortium et al., 2018). The aggregate data used in this study are reported per canton and year in the Federal Hunting Statistics.[1] Both the spatial and the temporal granularity of the data varied widely between different cantons, ranging from daily data with exact geographic location (i.e., coordinates) to yearly data aggregated per canton (see

Table 1

The 26 cantons of Switzerland categorized according to the temporal and spatial granularity of the available hunting data. Category 0 represents cantons where wild boar, according to the hunting authorities, are not yet present. Some communes (value 'Comm'), hunting grounds (value 'Rev'), or districts (value 'District') in categories 2–4 were subject to mergers during the observation period and required particular attention. The canton of Geneva is a special case, because hunting is prohibited throughout the entire year (still between 150 and 200 wild boar are shot every year).

No.	Name	Code	Temporal	Spatial	Hunting Season
0	Schwyz	SZ	N/A	N/A	N/A
0	Obwalden	OW	N/A	N/A	01–09 to 28–02
0	Glarus	GL	N/A	N/A	01–09 to 30–11
0	Uri	UR	N/A	N/A	01–09 to 31–12
0	Zug	ZG	N/A	N/A	01–10 to 31–01
0	Nidwalden	NW	N/A	N/A	01–07 to 28–02
1	Appenzell Innerrhoden	AI	Day	Coord	04–09 to 31–01
1	Neuchâtel	NE	Day	Coord	13–08 to 28–02
1	Vaud	VD	Day	Coord	01–06 to 09–02
1	Graubünden	GR	Day	Coord	01–09 to 20–12
1	Fribourg	FR	Day	Coord	01–07 to 31–01
1	Zurich	ZH	Day	Coord	01–07 to 28–02
1	St. Gallen	SG	Day	Coord	01–07 to 28–02
2	Appenzell Ausserrhoden	AR	Day	Comm	01–08 to 31–01
2	Ticino	TI	Day	Comm	01–09 to 31–01
2	Valais	VS	Day	Comm	17–09 to 27–01
2	Jura	JU	Day	District	15–06 to 28–02
2	Aargau	AG	Day	Rev	01–07 to 31–01
3	Bern	BE	Day	Comm/Coord	02–08 to 31–01
3	Solothurn	SO	Day	Rev/Coord	01–07 to 28–02
4	Basel-Landschaft	BL	Year	Comm	01–07 to 28–02
4	Schaffhausen	SH	Year	Rev	01–07 to 28–02
4	Thurgau	TG	Year	Rev	01–07 to 28–02
5	Basel-Stadt	BS	Year	Canton	01–07 to 28–02
5	Luzern	LU	Year	Canton	01–07 to 28–02
N/A	Geneva	GE	N/A	N/A	N/A

Table 1). This heterogeneity required several preprocessing steps to make the data comparable before computing relative abundance (see Section 'Computation of relative wild boar abundance').

2.2.2. Hunting calendar

The calendar days falling within the hunting period were extracted from the Federal Hunting Statistics for each canton (Table 1). They were used to compute the hunting effort on as granular a spatial level as possible (see Section 'Computation of relative wild boar abundance').

2.2.3. Beech mast index

Available food resources, among them fruits of forest trees, have a strong influence on winter survival and spring reproduction of wild boar (Frauendorf et al., 2016; Gamelon et al., 2017; Geisser and Reyer, 2005; Vetter et al., 2015). Fruit production of tree species such as beech varies from year to year. Years with a high fruit production are called mast years. Based on phenomenological criteria a four-level index is often used to estimate mast (Eichhorn et al., 2016). It covers a range from 'absence of fruits' (0) up to 'abundant fruits' (3). In the study presented here, the beech mast index was used to calculate a factor by which the number of yearly hunted wild boar was adjusted (for details see Section 'Computation of relative wild boar abundance'). The values for the consecutive years 2011–2017 were 3, 0, 2, 1, 0, 3, 0 (Nussbaumer et al., 2016). Including the beech mast index in the computation of relative wild boar abundance was based on the assumption that in rich mast years wild boar are harder to hunt, because they visit hunters' baiting sites less frequently (Bozzuto and Geisser, 2019). *Baiting* refers to the practice of hunters putting out food to attract wild boar in locations where they are known to be frequent.

2.2.4. Probability of wild boar occurrence

An area-covering data grid with the probabilities of wild boar occurrence for all 37,738 sq km raster cells of Switzerland (waters and glaciers were excluded) in summer was produced in previous work (Vargas-Amado et al., 2020). This data grid was used in this study to divide the relative abundance values computed for different areas of wild boar occurrence among the individual grid cells (for details see Section 'Computation of relative wild boar abundance').

2.2.5. Forest cover

The forest cover of the National Forest Inventory (NFI) (Waser, Fischer et al., 2015), together with data about rest areas along motorways and outdoor piggeries, was used to identify the areas where direct transmission of a disease from wild boar to domestic pigs is more likely.

2.2.6. Motorways and rest areas

The national routes were downloaded on September 8, 2020, from the Federal geoportal 'geo.admin.ch'.[2] The shapefiles of all 182 rest areas were obtained from the same source and from the Bundesamt für Landestopografie swisstopo along with the product swissTLM3D 2020.[3]

2.2.7. Agricultural zones boundaries

The agricultural zones boundaries, version from 2017, were downloaded from 'geo.admin.ch' in order to mark off areas for summer grazing of domestic pigs.[4]

2.2.8. Outdoor piggeries

Data about the geographical location and type (solid run area vs. pasture) of outdoor piggeries for years 2011–2019 were obtained from the Federal Office for Agriculture (FOAG). The number of piggeries was

not stable over the observation period. In 2019 there were 3085 holdings in the RAUS program ('Regelmässiger Auslauf im Freien') with a solid run area (without pasture) and 344 holdings with pasture. The two types of outdoor piggeries were accurately described in a related publication (Früh, 2011). In addition, the geographical locations of Alpine pastures, where pigs labeled as 'Alpschwein' graze in summer, were manually extracted from the map on the relevant web site.[5] There is no comprehensive list of such pastures in Switzerland. The extracted ones are examples used to find out whether the dynamics of the husbandry system could be a driver of seasonal variation in transmission risk.

2.3. Data analyses

Fig. 1 shows the model of proposed ASF transmission with risk factors and model variables. The components of the model are described in Section 'Computation of relative wild boar abundance', 'Estimation of the risk of disease introduction', 'Estimation of the risk of disease transmission', and 'Estimation of the combined risk of disease introduction and transmission'. The computation of relative wild boar abundance is given some emphasis, because it refines the state of the art in a way not previously reported.

2.3.1. Computation of relative wild boar abundance

For all cantons with wild boar occurrence, relative abundance was computed as an index value per sq km for summer (i.e., after reproduction and before hunting). *Relative abundance* refers to the "relative representation of a species in a particular ecosystem." It reflects the "temporal or spatial variations of the size or density of a population but does not directly estimate these parameters" (ENETWILD-consortium et al., 2018, 8). In the work presented here, the *spatial* variations of the size or density of the wild boar population in Switzerland were of particular interest. The equation below expands on related work (ENETWILD-consortium et al., 2018) by including factors relevant to relative wild boar abundance. ENETWILD introduce the hunting index $HI =$ number of shot animals (i.e., hunting bag, *HB*) per area, usually 1 sq km, as a basic estimate of relative wild boar abundance. According to them, hunting bags are likely to be biased, because the circumstances under which they are filled vary across time and place. In order to reduce the bias, the hunting effort should be properly defined and the use of quotas or targets should be fully described. Hunting effort, according to ENETWILD, includes factors like hunting days, number of hunters, and method of hunting. Further factors influencing the effectiveness of hunting include weather conditions and food availability. In the study presented here, *number of hunting days*, *mast index* (as a proxy for food availability), and *occurrence probability* (not mentioned by ENETWILD) were considered when estimating relative wild boar abundance. *Weather conditions* were accounted for by averaging relative wild boar abundance over seven consecutive years (see Section 'Data collection'). The number of hunters hunting wild boar was not available in this study, nor was there sufficient information about the hunting method.

$$AI_{i,j} = \frac{1}{|K|}\sum_{k \in K}\left(AI_{i,j}\right)_k \text{ with}$$

$$\left(AI_{i,j}\right)_k = \frac{(HI_i)_k \times (exp(b \times MI))_k \times OP_{i,j}}{(HE_i)_k}$$

$AI_{i,j}$ is the abundance index value of cell j in area i averaged over the observation period; the resulting real number was assigned to one of five index classes ('none reported', 'low', 'low–medium', 'medium–high',

'high') based on the value range in which it fell using the classification method of natural breaks (Jenks) in ArcGIS.[6] Natural breaks are a form of variance splitting based on where the histogram frequencies show drops and increases (it actually calculates which sets of breaks have the smallest within class variance), and have been widely used for classification/display purposes within GIS packages.

$\left(AI_{i,j}\right)_k$ is the abundance index value of cell j in area i for hunting year k. $|K|$ is the number of hunting years; a hunting year is the period between March 1 to February 28 of the following year.

$(HI_i)_k = (HB_i)_k/A_i$ is the hunting index for hunting year k in area i. $(HB_i)_k$ is the hunting bag, i.e., the number of boars shot during hunting year k in area i. It is important to note that most Swiss cantons do not have any quotas for wild boar; Neuchâtel has a quota which, according to the competent authority, has never been exploited so far; the canton of Jura has quotas for boars > 50 kg, but not for lighter ones. A_i is the size of area i in square kilometers.

$(exp(b \times MI))_k$ is a factor adjusting the effect of mast conditions on hunting success in hunting year k (for details see below). $OP_{i,j} = p_{i,j}/\overline{p}_i$ is the (relative) probability of wild boar occurrence of cell j in area i. The probability of wild boar occurrence of cell j in area i (i.e., $p_{i,j}$) was computed for the closed season for hunting in previous work using a number of statistical models of suitable wild boar habitat (Vargas-Amado et al., 2020), $\overline{p}_i$ is the mean probability of wild boar occurrence of all cells in area i.

$(HE_i)_k = (d_i)_k/\overline{d}_k$ is the hunting effort for hunting year k in area i in terms of (relative) number of hunting days, $(d_i)_k$ is the number of hunting days in area i for hunting year k, $\overline{d}_k$ is the number of hunting days for hunting year k averaged over all areas.

Area i was established based on the pooled hunting data for the entire observation period. Data were pooled to balance short-term variations in the spatial distribution of yearly hunted wild boar that were not assumed to be related to colonization/decolonization. How area i was established depended on the spatial granularity of the hunting data available in a canton. For cantons reporting mere counts per commune, hunting ground, or canton, these were the spatial units to which the equation was applied (see Table 1). When the data came with geographic coordinates, the commune, which is the lowest level of administrative division, or hunting ground in which a wild boar was shot was taken as area i. Data with coordinates were handled this way in order to account for the animal's ranging behavior. Overall, 1004 areas were established.

The factor $b \times MI$ was proposed in a state-space model to estimate the (absolute) abundance of wild boar (Bozzuto and Geisser, 2019). For a given hunting effort, $b \times MI$ is the rate by which the instantaneous harvesting mortality rate is adjusted based on mast conditions. Thereby, $MI \in \{0, 1, 2, 3\}$ is the beech mast index and $b = 0.023$ is a scaling factor as estimated in the canton of Thurgau for the period of 1982–2017. Since beech mast in most years is a large-area phenomenon (Nussbaumer et al., 2016), the same factor b was herein also used for other cantons with the same hunting system as Thurgau, namely Zurich, St. Gallen, Aargau, Solothurn, Basel-Stadt, Basel-Landschaft, Schaffhausen, and Luzern. For all other cantons, in which baited hunting is not practiced, the rate $b \times MI$ was set to 0. Given $b \times MI$, the antilogarithm $exp(b \times MI)$ approximates the factor by which the hunting bag must be multiplied to account for mast conditions. It is important to note that this factor only balances the effect of mast on *hunting success*, which is a measure of how efficient hunting with a given effort is. The effect of mast on winter survival and reproduction is directly reflected in the hunting bag of the following year. Fig. 2 summarizes the workflow for the computation of relative abundance from hunting data.

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[5] http://www.alpschweine.ch/

[6] https://pro.arcgis.com/en/pro-app/latest/help/mapping/layer-properties/data-classification-methods.htm
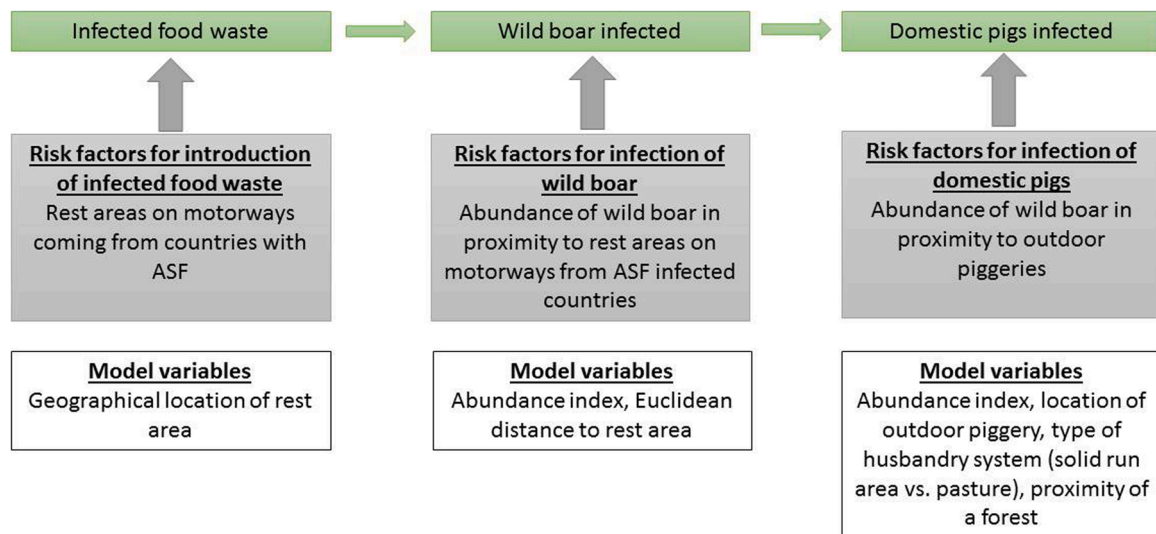
Fig. 1. Model of proposed ASF transmission (green boxes) with risk factors (grey boxes) and model variables (white boxes).

2.3.2. Estimation of the risk of disease introduction

According to the National program for early detection of ASF (Bundesamt für Lebensmittelsicherheit und Veterinärwesen BLV, 2020a), contaminated food waste discarded carelessly pose the highest risk of disease introduction into Switzerland. Rest areas along motorways in wooded areas are considered particularly exposed to this way of introduction, because motorways connect ASF affected countries to the urban centers and wooded areas are the preferred habitat of wild boar. Accordingly, the risk of disease introduction was quantified in terms of Euclidean distance to the nearest rest area along any of the fastest routes from ASF affected countries or main transit roads for heavy goods traffic through Switzerland. Proximity of a forest, which was also identified as a risk factor for a contact between wild boar and outdoor pigs (Wu et al., 2012), was considered when estimating the combined risk of disease introduction and transmission.

Relevant motorways were identified by searching for the fastest routes from Bulgaria (Sofia), Hungary (Budapest), Romania (Bucharest, Cluj-Napoca, Timişoara, Iaşi), Poland (Warsaw, Kraków, Wrocław, Poznań, Gdańsk), Serbia (Belgrade), and Slovakia (Košice) to Switzerland (Zurich, Geneva, Basel, Bern, Lausanne) using Google Maps' route planner and by looking up the main transit roads for heavy goods traffic through Switzerland on 'map.geo.admin'. The points of departure were selected based on the map of the Friedrich-Loeffler-Institut (FLI), where all cases of ASF in Europe are cumulatively displayed for every calendar year.[7] Routes were searched on October 7–8, 2020.

Table 2 shows the number of potentially exposed rest areas along the routes from 13 cities in ASF affected countries to five urban centers and along the main transit roads for heavy goods traffic through Switzerland per canton. Euclidean distance to the nearest rest area was calculated for each cell of a country-wide 1 sq km grid. Distances were classified into classes 1–4 to generate the scores for the calculation of the combined risk of disease introduction and transmission (see below). The cut-off values of the classes were informed by expert opinion and by the literature (Fattebert et al., 2017, Holzgang et al., 2001): class 4 ranges from 0 to 2000 m which is consistent with the seasonal home range of females, class 3 ranges from 2001 to 4000 m which is consistent with seasonal movements of males, class 2 ranges from 4001 to 20,000 m which is consistent with distances traveled by dispersers, class 1 are distances longer than 20,000 m which is consistent with some individuals that disperse farther.

### 2.3.3. Estimation of the risk of disease transmission

Among the measures used for protecting domestic pig populations from a disease like ASF, the Federal Food Safety and Veterinary Office (FSVO) advocates not allowing pigs to have contact with wild boar and, after an ASF outbreak, to avoid outdoor farming in areas affected by the disease (Bundesamt für Lebensmittelsicherheit und Veterinärwesen BLV, 2020b). This is supported by a matched case-control study carried out in Romania in 2019 where wild boar abundance was found a significant risk factor for ASF incursion in backyard farms (Boklund et al., 2020). Accordingly, the risk of disease transmission to domestic pigs was quantified in terms of density of outdoor piggeries in areas ranged by wild boar. How areas ranged by wild boar were established was described in Section 'Computation of relative wild boar abundance'. In order to identify potential risk areas for disease transmission to domestic pigs in the work presented here, communes with piggeries with a solid run area and communes with piggeries with pasture were located separately using the relevant toolset in ArcGIS.[8] For each of the identified communes, piggery density was calculated by dividing the number of piggeries by the surface area of the commune. The resulting values were classified into classes 0–4 for both types of piggeries to generate the scores for the calculation of the combined risk of disease introduction and transmission and to ease the interpretation on the map. How the density values were distributed is described in Section 'Risk areas for disease transmission'.

2.3.4. Estimation of the combined risk of disease introduction and transmission

The combined risk of disease introduction and transmission reflects the risk of introducing a disease into the domestic pig population by the intermediary of wild boar. The combined risk was estimated by multiplying the values of relative wild boar abundance (scores 0–4), Euclidean distance to the nearest rest area (scores 1–4), density of outdoor piggeries (scores 0–4, classified using natural breaks; cf. Footnote 6), and proximity of a forest (not shown). Proximity of a forest was assessed based on the forest cover NFI (Waser, Ginzler and Rehush, 2017), where the pixel size was 25 m. This was transformed to 1 km and wooded cells were given a score of 2, while a score of 1 was given otherwise. The advantage of multiplying the values was that all possible combinations between the mentioned variables were considered. The values resulting from the multiplication were classified into classes 'no estimate', 'low', 'medium low', 'medium high', 'high' based on the

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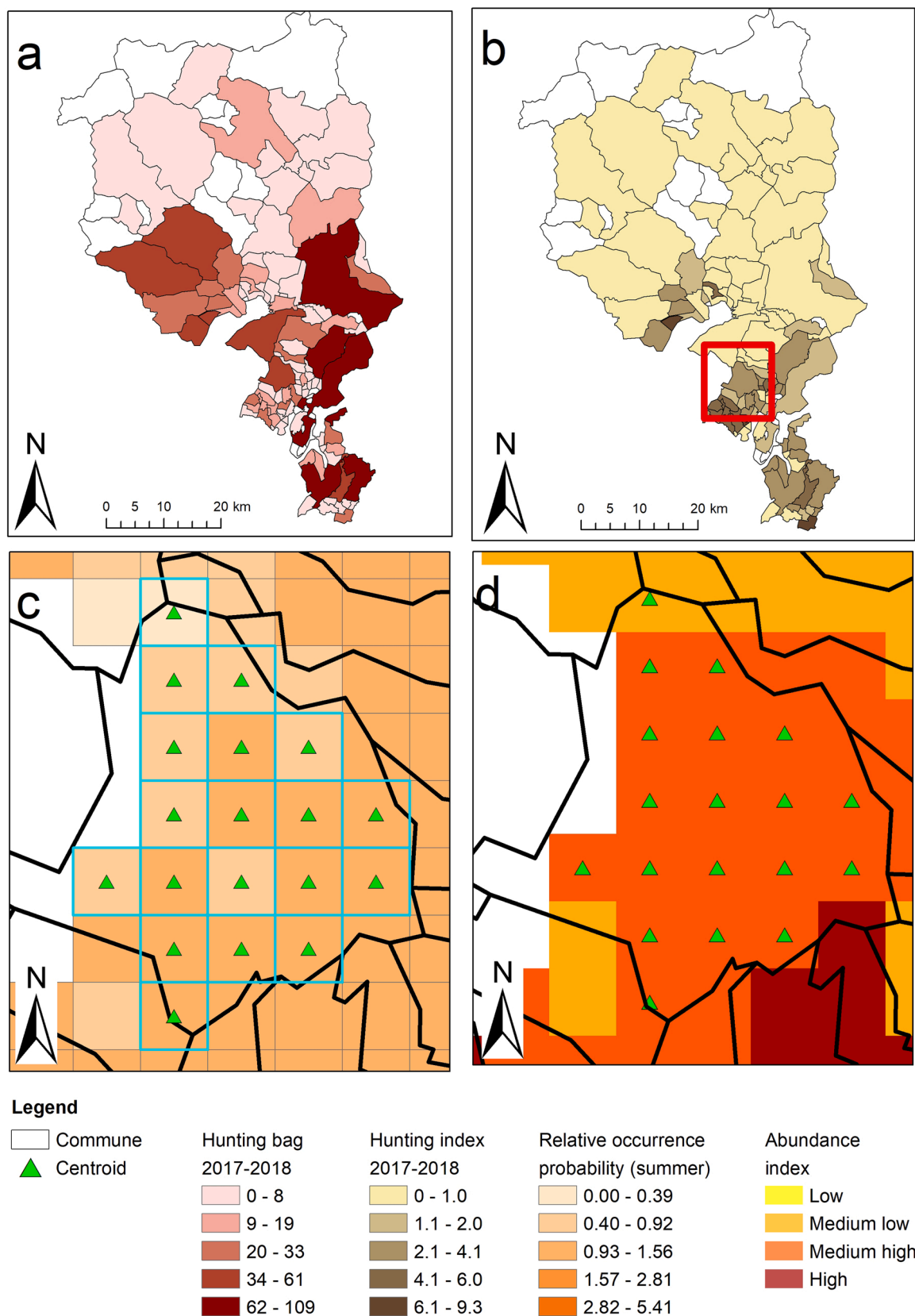
Fig. 2. Step-by-step computation of the abundance index for hunting year 2017/18, which is the seventh year ($k = 7$), in the canton of Ticino. a: hunting bag per commune (i.e., $(HB_i)_k$ in Section 'Computation of relative wild boar abundance'), b: hunting index per commune (i.e., $(HI_i)_k$), c: relative probability of wild boar occurrence in summer (i.e., $OP_{i,j}$) as a country-wide data grid (1 sq km), d: abundance index per grid cell (i.e., $(AI_{i,j})_k$).

Table 2

Number of potentially exposed rest areas along relevant motorways per Swiss canton (86 in all). Destinations in brackets indicate indirect connections. Motorways A1, A3, A9, A21 are traveled in one direction only; motorways A2, A4, A13 are traveled in both directions.

Code	Rest areas	Motorway	Destination
AI	0	n/a	n/a
NE	0	n/a	n/a
VD	4	A1	Lausanne, Geneva
GR	6	A13	transit (north–south)
GR	7	A13	transit (south–north)
FR	1	A1	Lausanne, Geneva
ZH	5	A1	Zurich, (Basel), Bern, Lausanne, Geneva
ZH	3	A4	Zurich, (Bern, Lausanne, Geneva), transit (north–south)
ZH	3	A4	transit (south–north)
SG	4	A1	Zurich, (Basel), Bern, Lausanne, Geneva
SG	2	A13	transit (north–south)
SG	2	A13	transit (south–north)
AR	0	n/a	
TI	9	A2	transit (north–south)
TI	9	A2	(Bern), transit (south–north)
TI	0	A13	transit (north–south)
TI	0	A13	transit (south–north)
VS	0	A21	(Lausanne)
VS	1	A9	Lausanne
JU	0	n/a	n/a
AG	5	A1	(Basel), Bern, Lausanne, Geneva
AG	0	A2	transit (north–south)
AG	0	A2	Bern, transit (south–north)
AG	1	A3	Basel
BE	6	A1	Bern, Lausanne, Geneva
SO	1	A1	Bern, Lausanne, Geneva
SO	1	A2	(Bern, Lausanne, Geneva), transit (north–south)
SO	1	A2	transit (south–north)
BL	0	A3	Basel
BL	3	A2	(Bern, Lausanne, Geneva), transit (north–south)
BL	3	A2	transit (south–north)
SH	1	A4	Zurich, (Bern, Lausanne, Geneva), transit (north–south)
SH	1	A4	transit (south–north)
TG	1	A1	Zurich, (Basel), Bern, Lausanne, Geneva
BS	0	A3	Basel
BS	0	A2	(Bern, Lausanne, Geneva), transit (north–south)
BS	0	A2	transit (south–north)
LU	3	A2	transit (north–south)
LU	3	A2	(Bern), transit (south–north)
GE	0	A1	Geneva

relative distribution of the scores. The resulting raster layer was transformed to a feature layer and the final scores were generalized to yield a single value per commune based on the maximum cell value in that commune. This was carried out in order to identify the political units in which risk areas were found and to facilitate the interpretation on the map. It was accomplished separately for piggeries with a solid run area and for piggeries with pasture. The consideration of proximity of a forest and type of husbandry system (solid run area vs. pasture) was motivated by a related study in which these were identified as risk factors for a contact between wild boar and outdoor pigs (Wu et al., 2012).

To assess the extent to which free-ranging wild boar contribute to the combined risk, estimates were recomputed without consideration of relative wild boar abundance, but with all other factors remaining the same. This was computed for outdoor piggeries with pasture only, where the chances that pigs escape from the fenced area are much higher than in piggeries with a solid run area (usually equipped with iron railings). The model of proposed ASF transmission in Fig. 1 considers *piggeries* rather than individual pigs. Accordingly, the re-computation assumed that escaped (and potentially infected) pigs were recaptured and brought back to their home piggery or to any other piggery with pasture in the same commune.

3. Results

3.1. Relative abundance of wild boar

Fig. 3 shows the relative abundance of wild boar in Switzerland. The northern wild boar population ranges from Geneva to St. Gallen, covering most parts of the Jura and the adjacent regions of the Central Plateau, the Lower Valais, and the Lower Rhine valley. Wild boar occur occasionally also in the Upper Valais, the valleys of the Berner Oberland, and in the canton of Luzern (for the cantonal boundaries see Figs. 4 and 5). This population is contiguous with the wild boar populations in neighboring Germany and France. The southern population is located in the canton of Ticino and in the region of Moesa in Graubünden, but is contiguous with the northern Italian wild boar population.

Wild boar are most abundant in areas near the borders of France, Germany, and Italy. They are also abundant in the south-east of Lake Neuchâtel. A number of reserves for waterbirds and migratory birds are located there, in which hunting is prohibited. In the Alpine canton of Ticino, the spatial pattern of relative wild boar abundance is not only governed by the distance from the border, but also by the meters above sea level: wild boar range in areas above the tree line around 2000 m (not shown) only sporadically.

The spatial pattern of relative wild boar abundance suggests that motorway A1 is a barrier for wild boar colonizing Switzerland from the north in the canton of St. Gallen and parts of Thurgau. It is also a barrier for wild boar colonizing Switzerland from the north-west between Zurich and Bern. Motorway A1 is a leaky barrier between the rest area Hexentobel (TG) and Zurich as well as west of Bern.

3.2. Risk areas for disease introduction

Fig. 4 shows the proximity categories in which the cells of a country-wide data grid fall when classified according to the Euclidean distance to the nearest rest area along one of the relevant motorways. Fifty-seven out of the displayed 86 rest areas are located in areas ranged by wild boar; 96 rest areas are not along motorways connecting ASF affected countries to Switzerland (not shown). The 57 rest areas are the most likely hot spots for disease introduction into the Swiss wild boar population. They are listed by name below.

AG	Walterswil, Würenlos
BE	Lindenrain, Oberbipp-Nord
BL	Mühlematt (both directions), Pratteln-Süd, Sonnenberg (both directions)
FR	Rose de la Broye
GR	Campagnola (both directions)
LU	Chilchbüel, Inseli, Knutwil-Nord, Knutwil-Süd, Neuenkirch (both directions)
SG	Rheintal Ost, Rheintal West, Thurau Nord, Wildhus Nord
SH	Berg, Moos
SO	Eggberg, Gunzgen-Nord, Teufengraben
TG	Hexentobel Nord
TI	Bellinzona Nord, Bellinzona Sud, Bodio, Coldrerio (both directions), Giornico, Lavorgo (both directions), Moleno Nord, Moleno Sud, Motto, Muzzano (both directions), San Gottardo-Sud, Sasso, Segoma (both directions)
VD	Bavois, Crans-près-Céligny, St-Prex
VS	Dents de Morcles
ZH	Baltenswil-Nord, Büsisee, Chrüzstrass, Forrenberg Nord, Kemptthal, Stegen, Weinland (both directions)

3.3. Risk areas for disease transmission

Fig. 5 shows the densities of outdoor piggeries at the level of communes. The spatial distribution of communes with piggeries with a solid run area is the same as that of communes with all types of piggeries (Sterchi et al., 2019), showing high densities in the cantons of Bern, Luzern, St. Gallen, Appenzell Innerrhoden, and Appenzell Ausserrhoden. By contrast, outdoor piggeries with pasture are more evenly distributed across Switzerland. Densities of piggeries were in the same range for both types of husbandry system, namely 0.004–1.880 piggeries with a
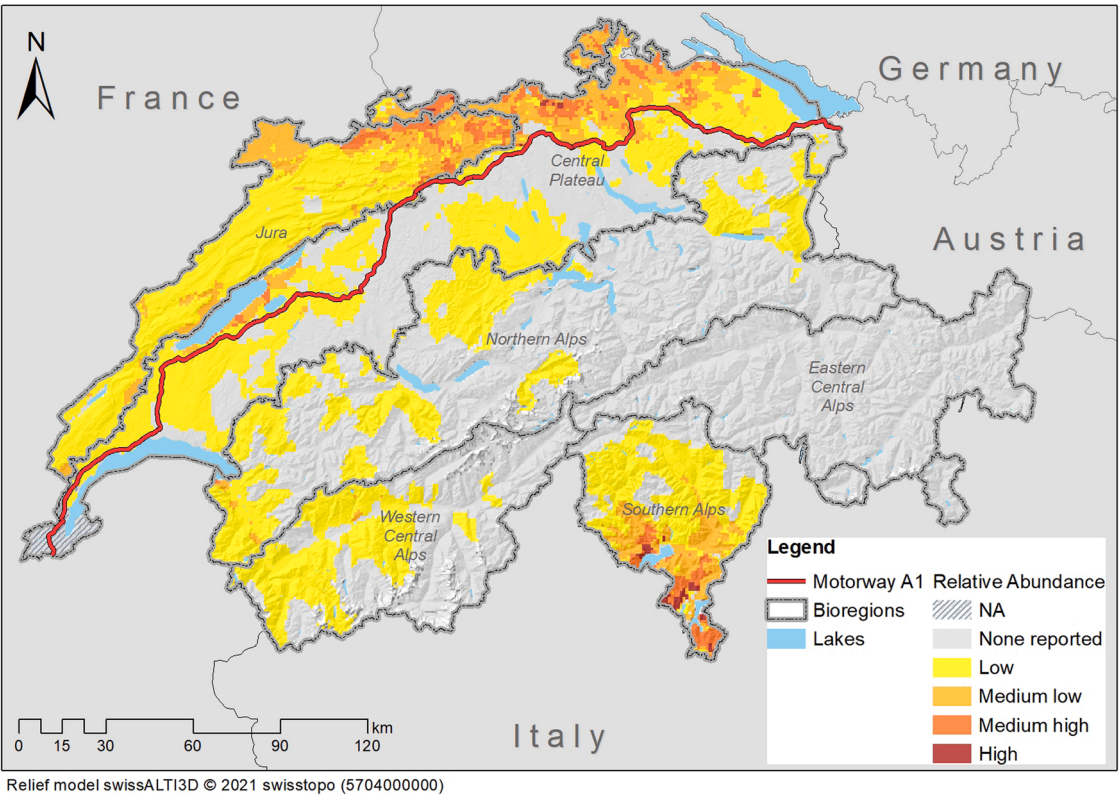
Fig. 3. Relative abundance of wild boar in Switzerland. The numerical values underlying the nominal index values are not shown to avoid these are mistaken as (absolute) wild boar 'densities'.
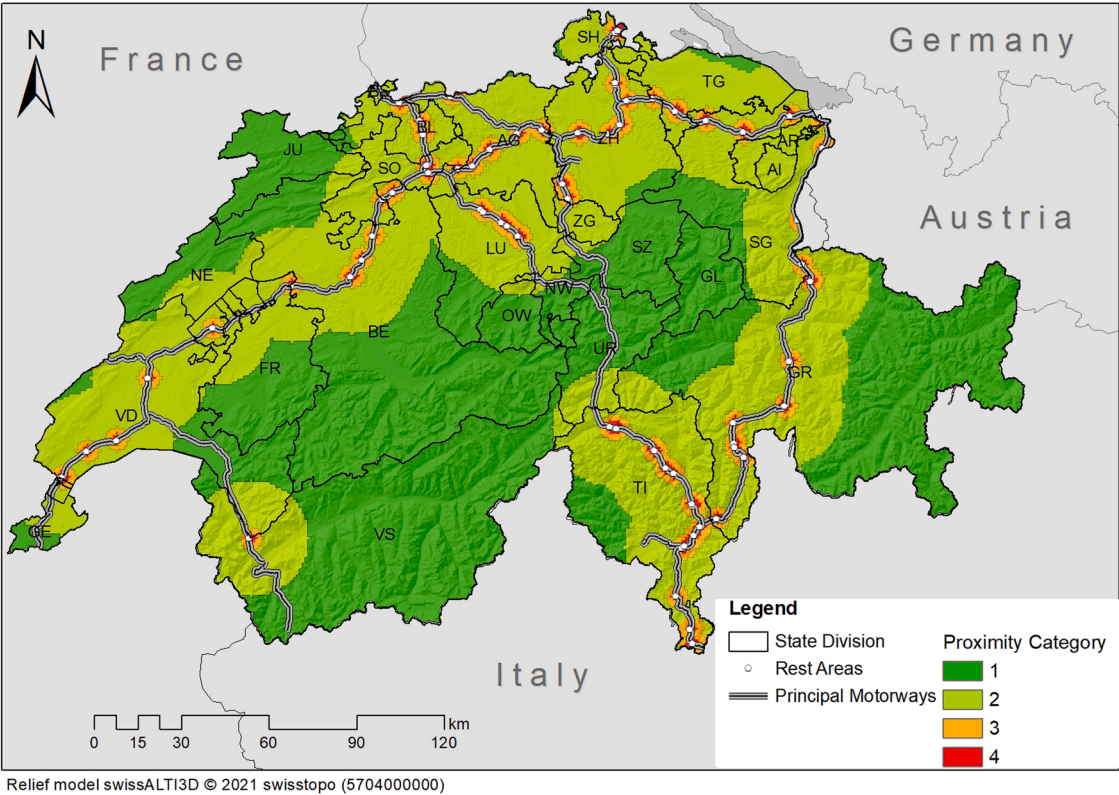
Fig. 4. Euclidean distance to the nearest rest area along one of the routes from 13 cities in ASF affected countries to five urban centers in Switzerland and the main transit roads for heavy goods traffic through Switzerland. Routes were identified using Google Maps' route planner (65 trips in all), they lead to motorways A1, A3, A9, and A21. The main transit roads for heavy goods traffic through Switzerland were motorways A2, A4, A13.
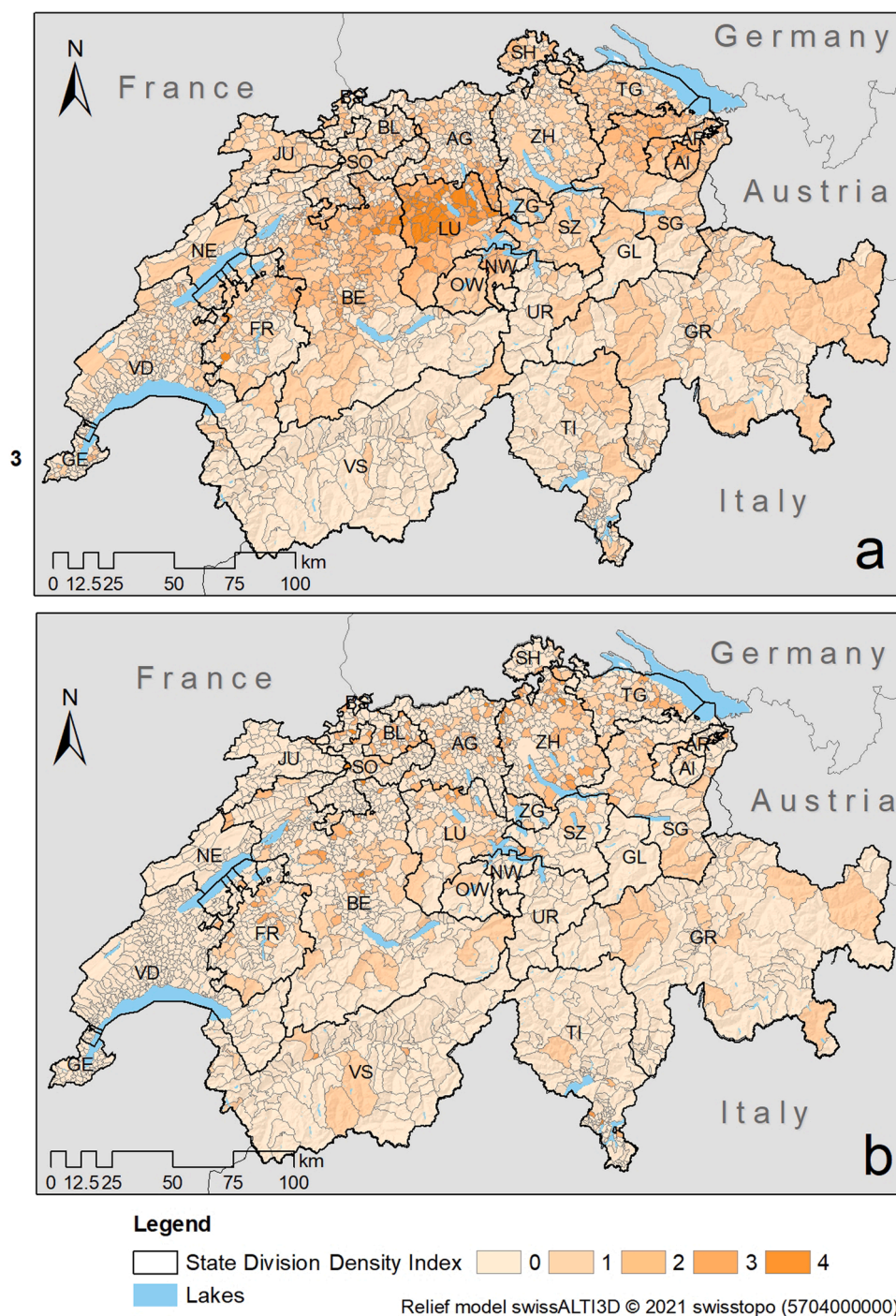
Fig. 5. Density of outdoor piggeries. a: piggeries in the RAUS program (i.e., run area without pasture); RAUS stands for 'Regelmässiger Auslauf im Freien'. b: piggeries with pasture.

solid run area per sq km and 0.004–1.167 piggeries with pasture per sq km, respectively. However, the mean was more than twice as high for piggeries with a solid run area than for piggeries with pasture (0.279 vs. 0.114). Accordingly, the fraction of communes with a low density is higher for piggeries with pasture, which is in line with the observation in Fig. 5 that communes with extensive pig farming are not geographically connected.
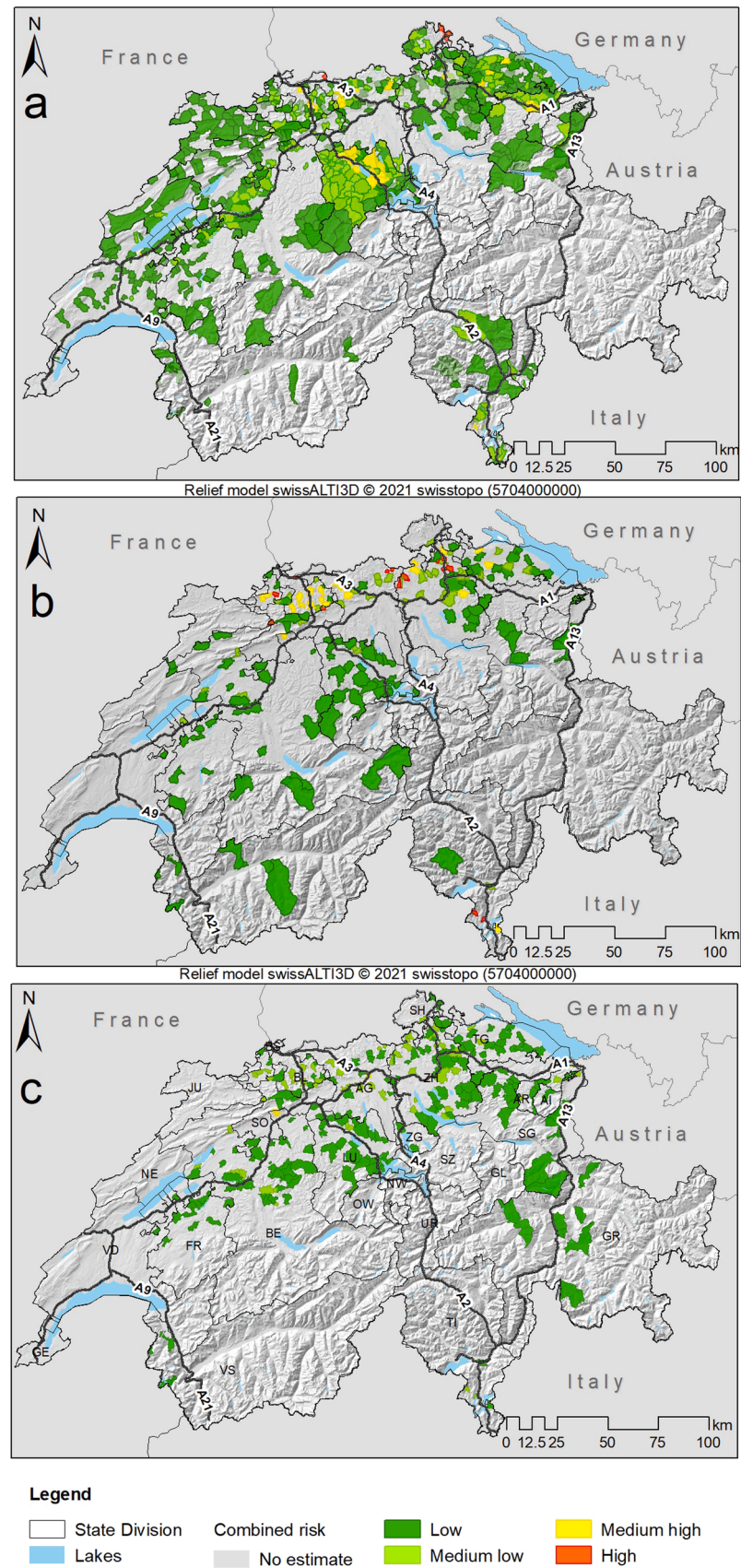
3.4. Areas with a combined risk of disease introduction and transmission

Fig. 6 (a) and (b) show areas with a combined risk of disease introduction into the wild boar population and transmission to domestic pigs.

Accordingly, domestic pigs are most at risk of becoming infected in outdoor piggeries located near the borders of France, Germany, and Italy. On the north side of the Alps, high risk areas are located north of the A1, the main motorway crossing the Central Plateau. Piggeries with a solid run area and piggeries with pasture differ in the size of the risk areas and particularly in the canton of Luzern also in their estimated risk score.

Fig. 6 (c) shows areas with a risk of a direct disease introduction into the domestic pig population, namely, without the intermediary of wild boar. Patches farther away than 20 km from a rest area were greyed out, because it was considered unlikely that escaping pigs surpass this distance. The most striking difference from Fig. 6 (b) is that risk areas are

Fig. 6. Areas with a combined risk of disease introduction into the wild boar population and transmission to domestic pigs identified based on relative wild boar abundance, Euclidean distance to the nearest rest area, density of outdoor piggeries, and proximity of a forest. a: piggeries in the RAUS program (i.e., run area without pasture). b: piggeries with pasture. c: piggeries with pasture without considering relative wild boar abundance.

more consistently located alongside motorways and extend to areas where no wild boar were reported. Another difference is that the risk of disease introduction has a similar degree of intensity on both sides of motorway A1, whereas in Fig. 6 (b) the risk is higher on the north side.
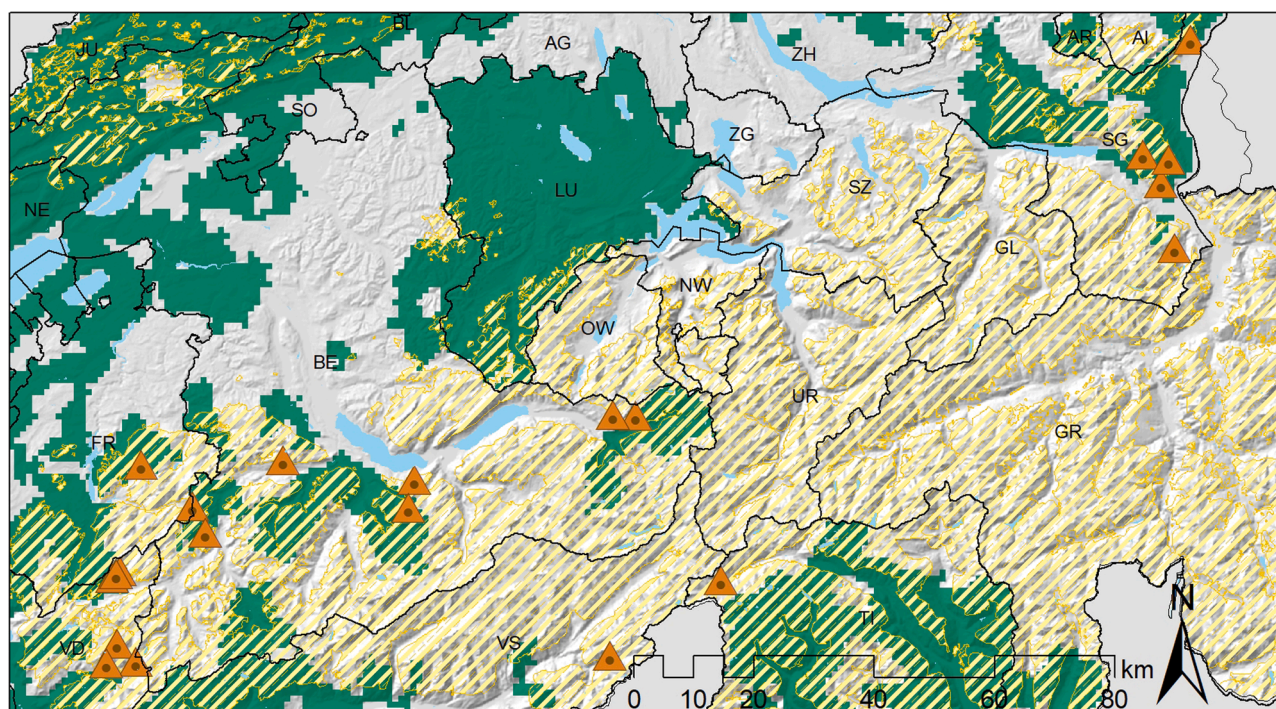
Fig. 7 shows examples of Alpine pastures within or in close proximity of areas ranged by wild boar, where pigs labeled as 'Alpschwein' graze in summer. Pigs are held in these areas in order to use some of the by-products of summer alpine cheesemaking. These pastures are not included in Fig. 5, because a comprehensive list was not available. When compared with Fig. 4, Fig. 7 shows that some pastures in the cantons of St. Gallen and Ticino are located in the proximity of rest areas. The combined risk of disease introduction and transmission is low for all other pastures.

4. Discussion

A method was presented to estimate and map the risk of introducing ASF into the domestic pig population through wild boar intermediate hosts. It makes use of data about hunted wild boar, rest areas along motorways connecting ASF affected countries to Switzerland, outdoor piggeries, and forest cover. These data were used to compute relative wild boar abundance as well as to estimate the risk of both disease introduction into the wild boar population and disease transmission to

domestic pigs. The way relative wild boar abundance was calculated adds to the current state of the art by considering the effect of beech mast on hunting success and the probability of wild boar occurrence when distributing relative abundance values among individual grid cells. The risk of ASF introduction into the domestic pig population by wild boar was highest near the borders of France, Germany, and Italy. On the north side of the Alps, areas of high risk were located on the unshielded side of the main motorway crossing the Central Plateau, which acts as a barrier for wild boar. Estimating the risk of disease introduction into the domestic pig population without the intermediary of wild boar suggested that dispersing wild boar may play a key role in spreading the risk to areas remote from motorways.

The results of this study can be used to focus surveillance efforts for early disease detection on areas where the combined risk of disease introduction into the wild boar population and disease transmission to domestic pigs is high. African Swine Fever is currently at the center of attention in western European countries. Surveillance of wild boar for ASF and biosecurity measures to reduce the probability of virus introduction into wild boar and domestic pigs could be concentrated in areas where there is a higher probability of the pathogen being brought into the country via roads. The local population could be informed about the risk of ASF and asked to be vigilant for dead wild boar and report them to the cantonal authorities for carcass pick up and testing. Garbage
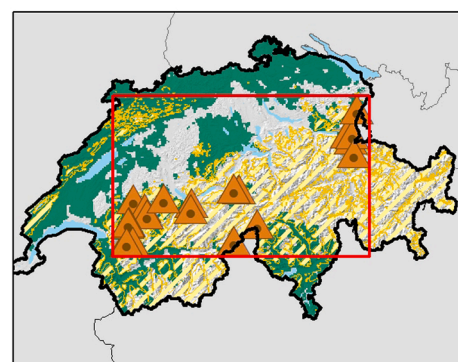

Fig. 7. Alpine pastures, within or in close proximity of areas ranged by wild boar, where pigs labeled as 'Alpschwein' are grazed during summer (http://www.alpsch weine.ch/).

management could be improved at rest stops on high risk routes. For example, animal proof garbage containers could be installed in these rest stops. The frequency of garbage container emptying could be increased to ensure there is always room in the garbage containers for people to put their garbage in. Rest stop cleaners could be trained to detect and report signs of wild boar activity at these rest stops. Pig farmers in these areas could be informed about the risk and asked to ensure there, domestic pigs do not have outdoor access, or if they do, the barrier between domestic pigs and wild boar should be strengthened. Farmers and veterinarians in high risk areas should be informed of the risk and asked to report any disease occurrences that could potentially be ASF.

The results of the analyses carried out in this study may also inform policies to control other diseases that are transmitted by a direct contact from wild boar to domestic pigs. Depending on the transmission route, the results allow for a subtle differentiation. Pigs in both types of outdoor piggeries may be exposed to the risk of a spill-over of infectious agents transmitted by aerosols such as *Mycoplasma hyopneumoniae*. A study based on genotyping of *M. hyopneumoniae* from pig lungs from enzootic pneumonia outbreaks and lungs from wild boar from the close proximity of the affected pig farms confirmed transmission of the pathogen between domestic pigs and wild boar (Kuhnert and Overesch, 2014). By contrast, spill-over of pathogens such as *Brucella suis* that are sexually transmitted is less likely in piggeries with solid run area than in piggeries with pasture. In a study of the risk factors for contact between wild boar and outdoor pigs in Switzerland, mating events were reported for holdings with pure pasture or mixed run-out only (Wu et al., 2012).

Direct contact is not the only way how ASF can be transmitted between wild boar and domestic pigs. In the sequel of the Belgian outbreak in 2018–2019 a panel of 34 national and international experts assessed the risk associated with different transmission routes semi-quantitatively (Mauroy et al., 2021). Among 25 routes for ASF transmission from wild boar to domestic pigs, the experts considered 'farmer', 'bedding material', 'veterinarian', 'professionals from the pig sector', and 'swill feeding' most important in the Belgian epidemiological context. 'Living wild boar' together with 'contaminated vegetal products (feed)' and 'hunter' ranked sixth. This suggests that the 'human factor', which is considered in the study presented here for disease introduction, could potentially play a role in disease transmission also in Switzerland.

The barrier effect of motorway A1, observed in Fig. 3, emphasizes the need to account for landscape configuration and fragmentation when assessing the effect of management regimes on the ranging behavior of wild boar (Fattebert et al., 2017). More fine-grained landscape configuration and fragmentation should be considered when the results of this study are used at the local level.

As stated in Section 'Relative abundance of wild boar', the Swiss wild boar populations are contiguous with those in France, Germany, and Italy. Therefore, a disease like ASF could also be introduced by improper disposal of contaminated food waste in a foreign rest area near the border. Fig. 4 shows that the zones bordering potential risk areas in France, Germany, and Italy usually have a low score of 1 or 2. Accordingly, considering rest areas in neighboring countries, for instance, alongside motorway A36 from Beaune to Mulhouse which passes close by the canton of Jura, could potentially increase the combined risk in Fig. 6 locally. Another important potential way of ASF introduction into the Swiss wild boar population is via hunting tourism. Hunters should be informed properly of the associated risks and of methods of biosecurity by the competent authorities.

There is no viable wild boar population in the canton of Luzern. The canton is ranged by a few dispersed animals only. Nevertheless, the risk of introducing ASF into the domestic pig population by wild boar is estimated as medium in Fig. 6 (a). This is primarily due to Luzern's practice of reporting hunting data as an aggregate for the entire canton (see Table 1), resulting in a positive score also in areas where there are no wild boar. Overestimating the risk of disease introduction in this canton does not have an adverse effect on the recommendations for action derived from Fig. 6. The probability of a wild boar encounter is expected to increase in the future: wildlife passages crossing important motorways, including A1 and A2, that were formerly interrupted are currently repaired and new passages are being built to increase habitat connectivity.

It would be interesting to estimate the changing risk of disease transmission at different times of the year in a future study. This would require that temporal (or seasonal) data about wild boar abundance were available, which is currently not the case. The abundance data in this study were only for the summer. Provided there are no quotas, the hunting bag, in the long run, is proportional to the size of the population before the hunting season starts (ENETWILD-consortium et al., 2018). In this study, data were averaged over many years to avoid strong effects of non-controllable factors, such as weather conditions, on the number of yearly hunted wild boar. Dealing with relative summer abundance does not limit the scope of this research. Summer is the season where the risk of transmission is highest for a number of reasons. First, the wild boar population is most abundant in summer after spring reproduction and before hunting. Second, the area potentially ranged by wild boar is larger in summer than in winter (Vargas-Amado et al., 2020). Third, domestic pigs are grazed on Alpine pastures in summer. The seasonal variation in transmission risk may primarily be driven by the dynamics of the husbandry system, rather than by variations in wild boar abundance. Disease control agencies are well-advised to keep a country-wide record of Alpine pastures with domestic pigs in the future.

A potentially improved model may incorporate traffic density from countries affected by ASF as soon as such data are available. Provided more is known, also the factors may be weighted according to their relative influence on the estimated risk in such a model. In future, the degree of connectedness of piggeries to the rest of the domestic pig production network could be added in order to assess the consequences of a disease introduction. Such an extension should expand on previous work investigating the structure and patterns of the pig transport network in Switzerland (Sterchi et al., 2019).

5. Conclusions

This study has shown that risk-based surveillance for early detection of disease epidemics can benefit from integrating wildlife population data, specifically, high quality hunting statistics. Considering such data is especially advantageous when wildlife reservoirs are important for disease transmission, as the data that are needed for risk estimation are highly variable. Preprocessing methods used in wildlife research may be useful to prepare these data for analysis. Carrying out the analysis may require techniques originating from geographic information science. Involving multiple disciplines is essential for providing the skills and methods needed to deal with the challenges posed by a disease emergence at the livestock-wildlife interface.

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Third paper

Potential effect of managing connectivity to contain disease spread among free-ranging wild boar in disparate landscapes

Maria Elena Vargas-Amado[1, 2], Beatriz Vidondo3[3], Claude Fischer[4], Simone Roberto Rolando Pisano[5], Rolf Grütter[1]

[1] Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

[2] University of Zurich, Department of Geography, Zurich, Switzerland

[3] University of Bern, Veterinary Public Health Institute, Bern, Switzerland

[4] Haute école du paysage, d'ingénierie et d'architecture HEPIA, Geneva, Switzerland

[5] University of Bern, Institute for Fish and Wildlife Health, Bern, Switzerland

Corresponding author Rolf Grütter, rolf.gruetter@wsl.ch

Abstract

1. Landscape connectivity is a major factor shaping the spread of a pathogen 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 (ASF) in free-ranging wild boar 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 easiness with which wildlife corridors can be blocked, (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 show that (Regarding 1) most wildlife corridors are hard to block, because their features or location make fencing difficult. (Regarding 2) 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 3) 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. *Synthesis and applications*. 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 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 Landscape configuration, Habitat connectivity, Disease spread, African Swine Fever, Wild boar

Introduction

The movement of wildlife in the landscape is important for many ecological processes to preserve genetic diversity and resilience (Keeley, Beier, & Jenness, 2021). However, such movement can also provide ecosystem disservices such as facilitating invasive species expansion and disease spread (Mitchell, Bennett, & Gonzalez, 2013; White, Forester, & Craft, 2018). Connected landscapes may exacerbate the spread of a pathogen in a population, because vectors of transmission can come in contact with susceptible hosts more easily than in disconnected ones (Fountain-Jones, et al., 2021; Nobert, Merrill, Pybus, Bollinger, & Hwang, 2016). This particularly holds if one of the vectors is a generalist species, which can travel long distances in both natural and anthropogenic environments (Boitani, Mattei, Nonis, & Corsi, 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. 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, Polansek, & Alves, 2022), and carcasses removal (Morelle, Jezek, Licoppe, & Podgorski, 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 easiness with which *wildlife corridors* can be blocked, (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. 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). Only few research has been carried out on managing connectivity to prevent the spread of non-native species or diseases in ecosystems (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, Strand, & Rolandsen, 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 are proposed and one or more hypotheses are provided for each question:

1. Wildlife corridors

   Wildlife passages can be easily closed, for instance, by installing an artificial barrier (Giacometti, 2003). Here it is assumed that wildlife corridors are much more difficult to block and this depends on the general character of the surrounding landscape. In Switzerland, the general

character of a landscape is well-represented by the biogeographical region in which it is located. The biogeographical classification partitions the surface of Switzerland into six regions based on the patterns of distribution of the flora and fauna (Gonseth, Wohlgemuth, Sansonnens, & Buttler, 2001).

Research question RQ-1: Which features determine how easily a wildlife corridor can be blocked for a species of concern and how do they operate on the wild boar network in different biogeographical regions of Switzerland?

Wildlife corridors are assumed to be blocked by fencing. Factors to be considered when erecting a fence are the targeted species, landscape features, maintenance, seasonality, the placement of the fence, and legal issues (e.g., landownership) (Mysterud & Rolandsen, 2019). 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* in Switzerland) than in mountainous regions where animals can pass under the many viaducts and pass over the tunnels.

Hypothesis H-1.1: Blocking corridors for wild boar is easier in the Central Plateau than outside of the Central Plateau.

2. Habitat connectivity

In densely inhabited regions where the activity in the building line 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. Wildlife passages are the same for a range of species with potentially dissimilar habitat preferences and movement behavior. Accordingly, 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).

Research question RQ-2: 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?

Habitat connectivity is affected by 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, Mattei, Nonis, & Corsi, 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).

Hypothesis H-2.1: 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, Grütter, Fischer, Suter, & Bernstein, 2020).

Hypothesis H-2.2: Constructing new wildlife passages will connect habitat suitable for wild boar in areas that are not yet colonized.

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, Baubet, Slotow, & Fischer, 2017). The extent to which the different land cover classes contribute to fragmentation depends on the biogeographical region in which a landscape is located. Exploring fragmentation in dissimilar landscapes may explain why a specific measure of disease containment is more effective in one than in the other.

Research question RQ-3: How does fragmentation influence the effectiveness of disease containment measures in a landscape?

In Switzerland, the densely inhabited Central Plateau is expected to be more fragmented than the other regions.

Hypothesis H-3.1: 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, Ribble, Kelton, & McNab, 2011; Kao, Danon, Green, & Kiss, 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. The change in the PES, thus, is an additional metric (4) to estimate the effectiveness of closing wildlife passages and blocking corridors.

Finally, it is important to know which passages and corridors decompose the wild boar networks on a large scale upon closure. This will help authorities to prioritize the spots where construction measures should be taken in case of a disease outbreak, particularly if resources are scarce.

Material and methods

Study area

The study was carried out in Switzerland, a country that covers a total surface area of 41,285 km^2 ranging from 193 to 4,634 m above sea level (Swiss Confederation, 2020a). 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 geographic regions: The Alps, covering around 60% of the country's total surface area, the Central Plateau (30%) and the Jura (10%). The Alps act as a prominent climatic barrier between northern and southern Switzerland (Swiss Confederation, 2020b). The climate of Northern Switzerland is heavily influenced by the Atlantic Ocean. Winters in the Northern Plateau are mild and damp, whereas higher altitudes

experience arctic temperatures. Southern Switzerland is strongly affected by the Mediterranean Sea, making winters mild and summers warm and humid, and sometimes hot.

Data collection and preparation

The *wildlife network system* and the *interregional wildlife corridors* were downloaded from the Swiss Federal geoportal (https://www.geo.admin.ch/). They originate from a study in which wildlife networks were established for the most common species by interviewing gamekeepers, modeling landscape permeability in a GIS system, and looking up the hunting statistics (Holzgang, et al., 2001). The corridors and the connecting axes were modified in 2012 by the Federal Office for the Environment (FOEN) based on the information of the cantonal hunting agencies. The download consisted of the 2012 update packing together georeferenced data of 304 corridor objects.

Wildlife passages. Forty-five wildlife passages were downloaded along with the interregional wildlife corridors from the Swiss Federal geoportal (https://www.geo.admin.ch/). 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).

Motorways. The 2020 update of the national routes was downloaded from the Swiss Federal geoportal (https://www.geo.admin.ch/).

CORINE land cover. The version of 2018 with a pixel size of 100 m was downloaded from the Copernicus Web site (https://land.copernicus.eu/).

Probability of wild boar occurrence. Area-covering 1 km^2 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, Grütter, Fischer, Suter, & Bernstein, 2020).

Relative abundance of wild boar. An area-covering 1 km^2 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 seven-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. 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 overlayed with the *compartments* defined in related work (Giacometti, 2003), the boundaries of which consist of mountain ridges, lakes, and national motorways that cannot be crossed easily by wild boar. Compartments were refined by considering also more recent motorways. 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 (Fig. 1). The northern wild boar

population is contiguous with the wild boar populations in neighboring Germany and France. The southern wild boar population is contiguous with the northern Italian wild boar population (Meier & Ryser-Degiorgis, 2018; Vargas Amado, Carmo, Berezowski, Fischer, Santos, & Grütter, 2021).
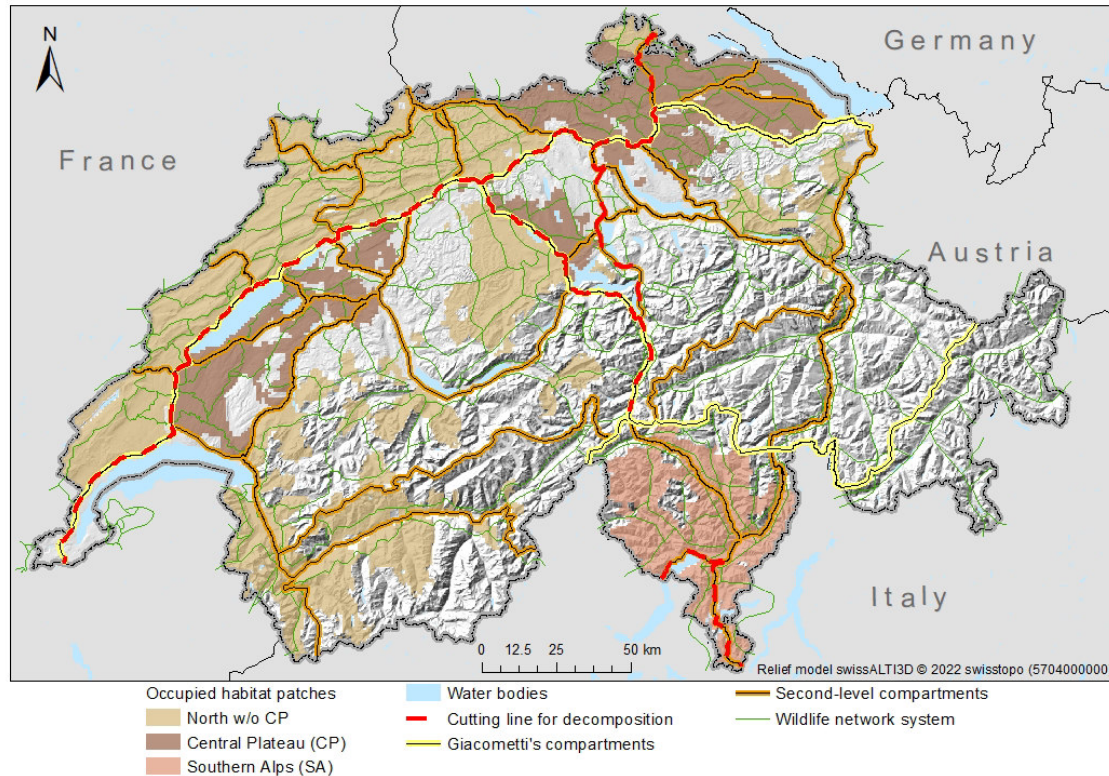
Figure 1. Wildlife network system, compartments, and habitat patches occupied by wild boar in different biogeographical regions of Switzerland; red-dotted lines link stretches of motorways A1, A2, A4, A5 in the north and A2, A13 in the south; they indicate where the networks can be decomposed on a large scale

Data analysis

Wild boar networks were established for (1) the northern population, (2) the southern population, and (3) the Central Plateau. 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 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 (Fig. 2). How dispersal probability was calculated is explained in supplement S1.
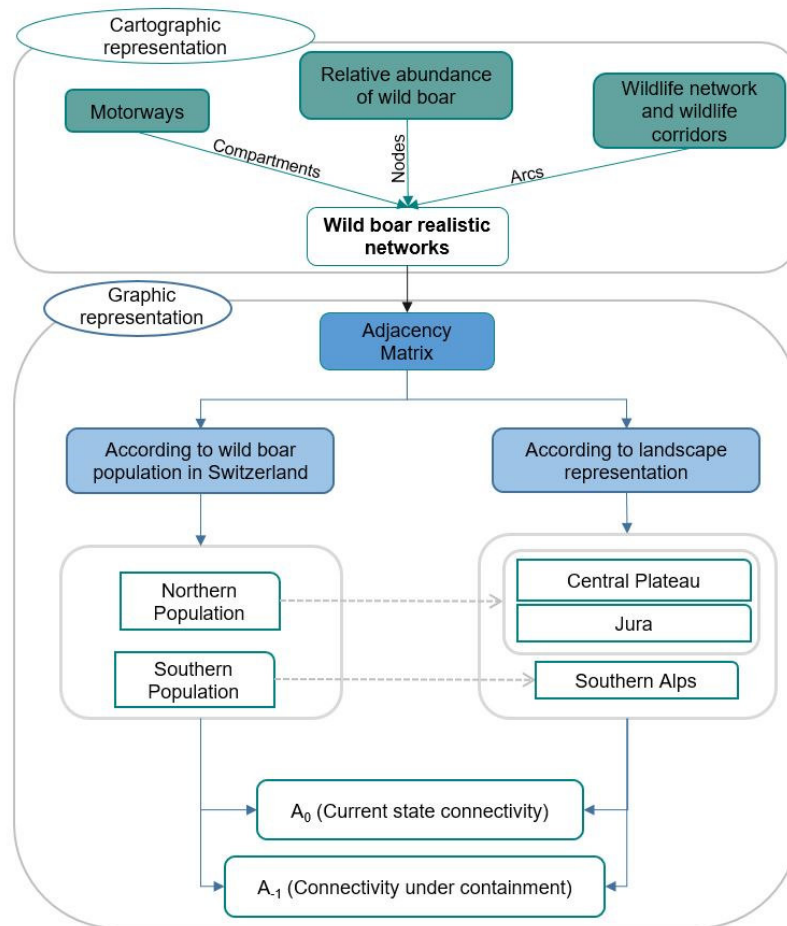
Figure 2. Procedure for the representation of the wild boar networks in Switzerland as maps and graphs

Wildlife corridors

To test whether blocking corridors for wild boar would be easier in the Central Plateau than outside of the Central Plateau (H-1.1), 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 hundred meters or less were considered easier to block than wider corridors.
- *Topography*: Flat terrain was considered easier to block than rising or sloping terrain.
- *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.

Habitat connectivity

To test whether most existing wildlife passages actually connect the habitat of wild boar in Switzerland (H-2.1) the proportion of distances below 20,000 m (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 S1). 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 (H-2.2), 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 S1). To this end, the estimated spatial distributions of wild boar in Switzerland during open and closed season for hunting, computed in previous work, were reused (Vargas-Amado, Grütter, Fischer, Suter, & Bernstein, 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 (wild boar in the case at hand) 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 S1). 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 $p_{ij} = 1$.

Landscape fragmentation

DIVISION was computed as an easy understandable metric of landscape fragmentation (Jaeger J. A., 2000) for the Central Plateau, the other regions occupied by the northern wild boar population, and the Southern Alps using Fragstats 4.2 and adopting the 8-cell neighborhood rule (McGarigal, Cushman, Neel, & Ene, 2002) (cf. description and equation (4) in supplement S1).

DIVISION was computed for a potential *habitat* land cover class (Fig. 3). This land cover class was established by reclassifying (i) forest and semi-natural areas, (ii) agricultural areas, and (iii) wetlands. The shares of both matrix land cover classes (iv) artificial surfaces and (v) water bodies, were calculated to find out what drives the difference in fragmentation between the different regions.
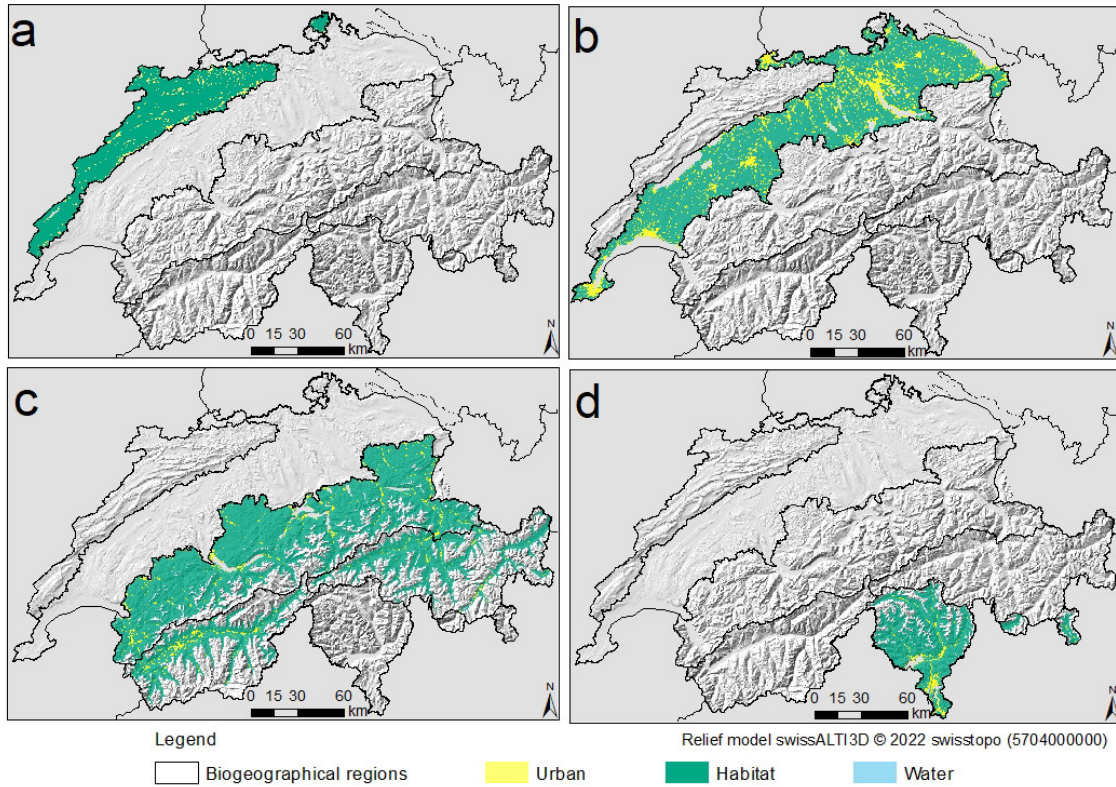
Figure 3. Wild boar potential habitat and artificial surfaces resulting from the reclassified CORINE land cover in different biogeographical regions of Switzerland; (a) Jura, (b) Central Plateau, (c) Northern Alps (including Western Central Alps and Eastern Central Alps), (d) Southern Alps

To test whether closing wildlife passages and blocking corridors is a more effective measure of disease containment in the Central Plateau than in any other biogeographical region (H-3.1), 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 S1). 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 Central Plateau (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 Central Plateau than in any other biogeographical region (cf. equation (6) in Table S1).

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 (Fig. 4).
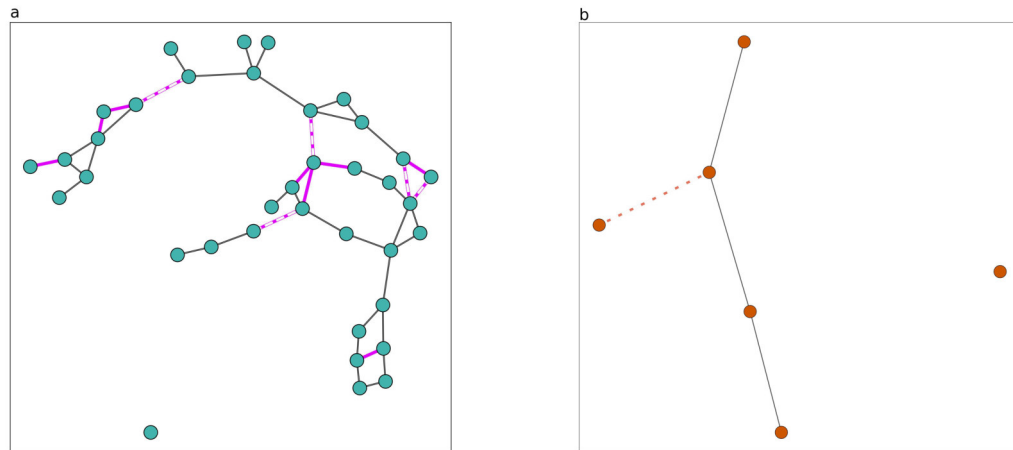
Figure 4. Graph representation of the wild boar networks of (a) the northern population and (b) the southern population. Emphasized links show corridors/passages that can be blocked/closed; dashed links indicate where the networks were decomposed to reduce the potential epidemic size (PES) on a large scale, they correspond to the cutting lines in Fig. 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.

Results

Wildlife corridors

Forty out of 45 corridors for wild boar in Switzerland are functional (i.e., traversable by wild boar) at present. In the Central Plateau, 7 out of 16 functional corridors (0.438) were qualified as 'easy to block' (Fig. 5), while outside of the Central Plateau, 4 out of 24 functional corridors (0.167) were qualified as 'easy to block'. All over Switzerland, five out of ten 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 (Fig. 6).
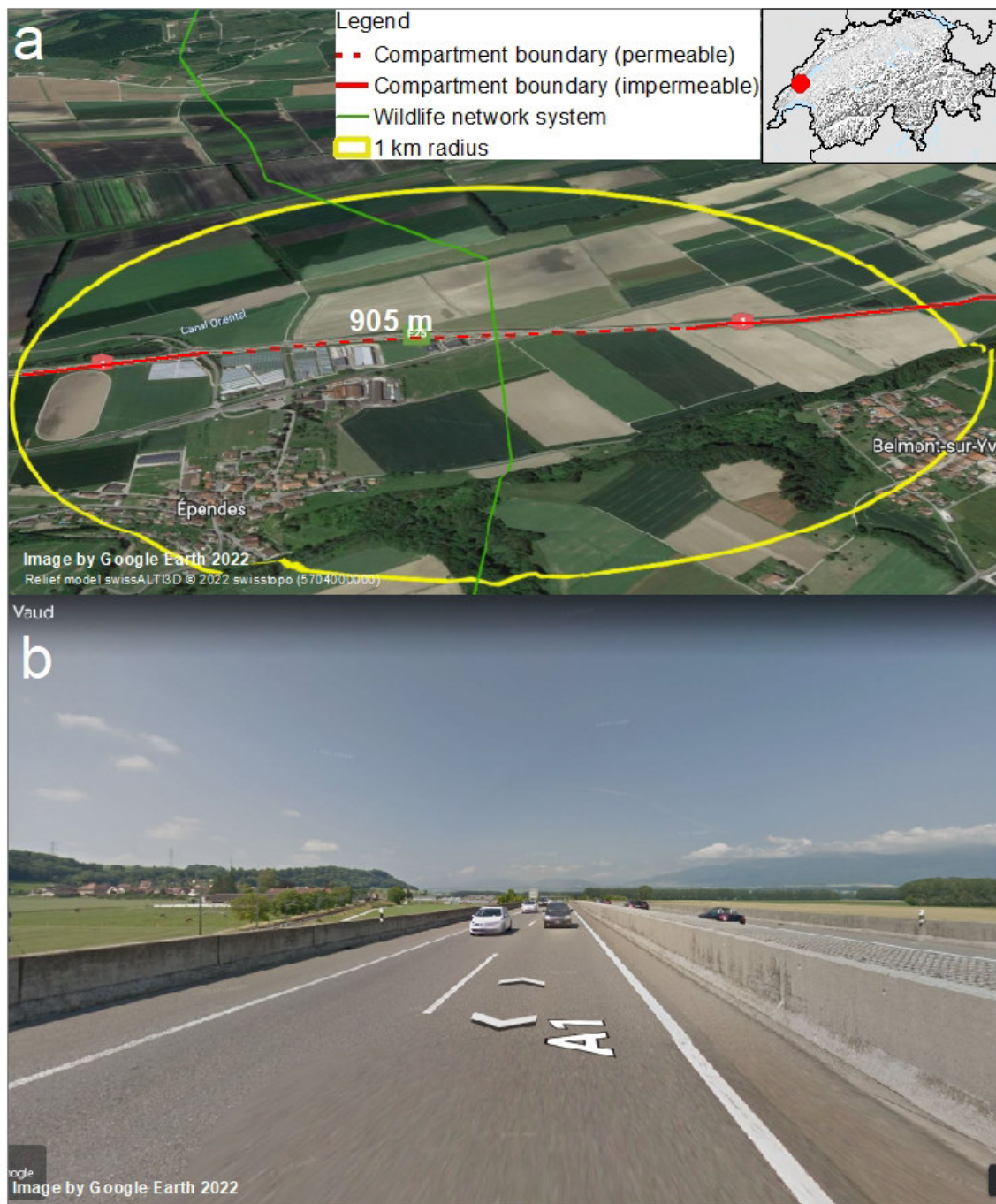
Figure 5. Easy to block wildlife corridor connecting habitat patches underneath a viaduct in the Central Plateau; (a) bird's eye view, (b) close-up view
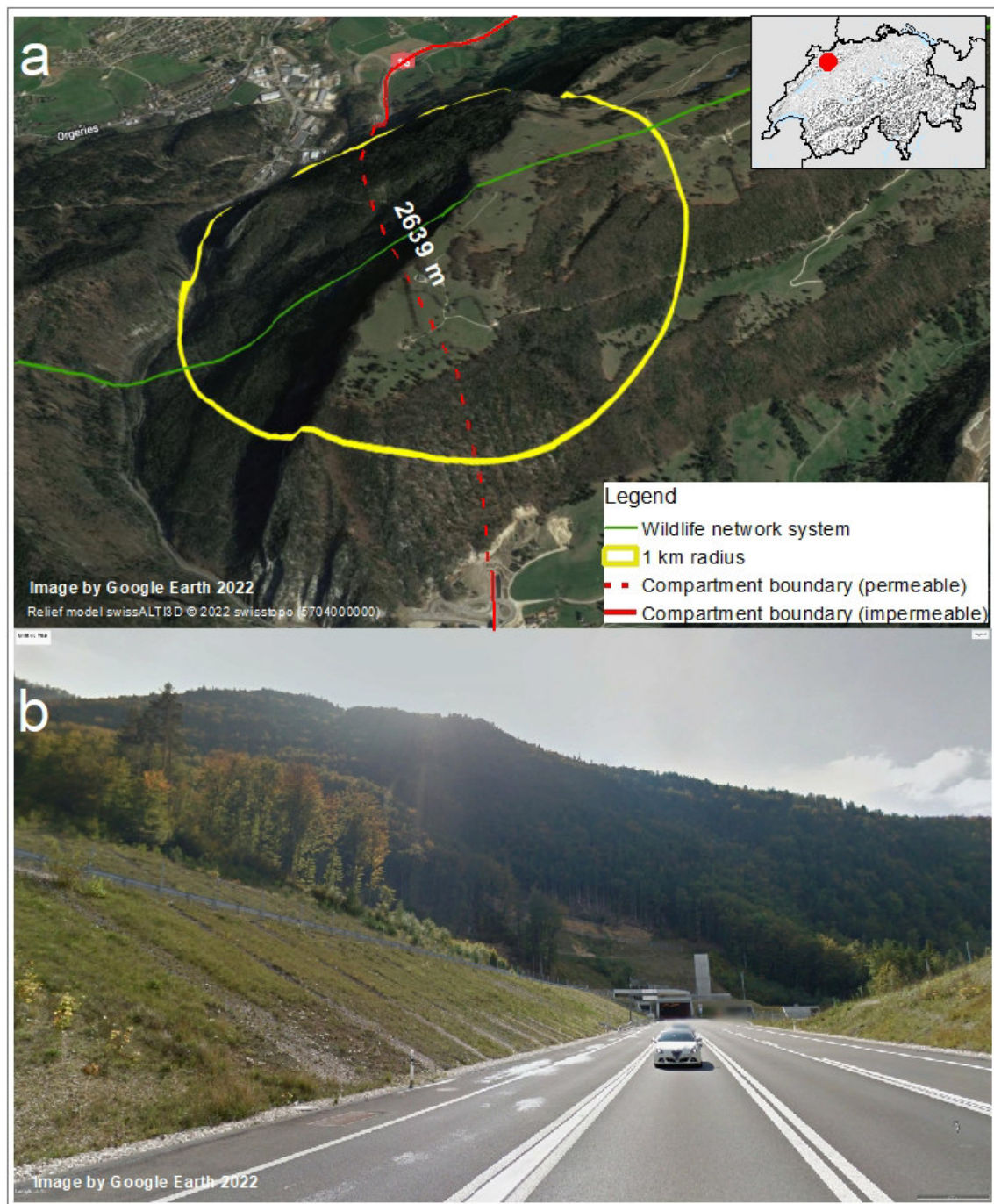
Figure 6. Hard to block wildlife corridor that consists of land covering a tunnel outside of the Central Plateau; (a) bird's eye view, (b) close-up view

Habitat connectivity

For 16 out of 20 open wildlife passages in the wild boar network of the northern population were the adjacent patches within a distance of 20,000 m. 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 out 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 (Fig. 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 7 wildlife passages are planned for the far future (i.e., after 2026) and were not considered here.
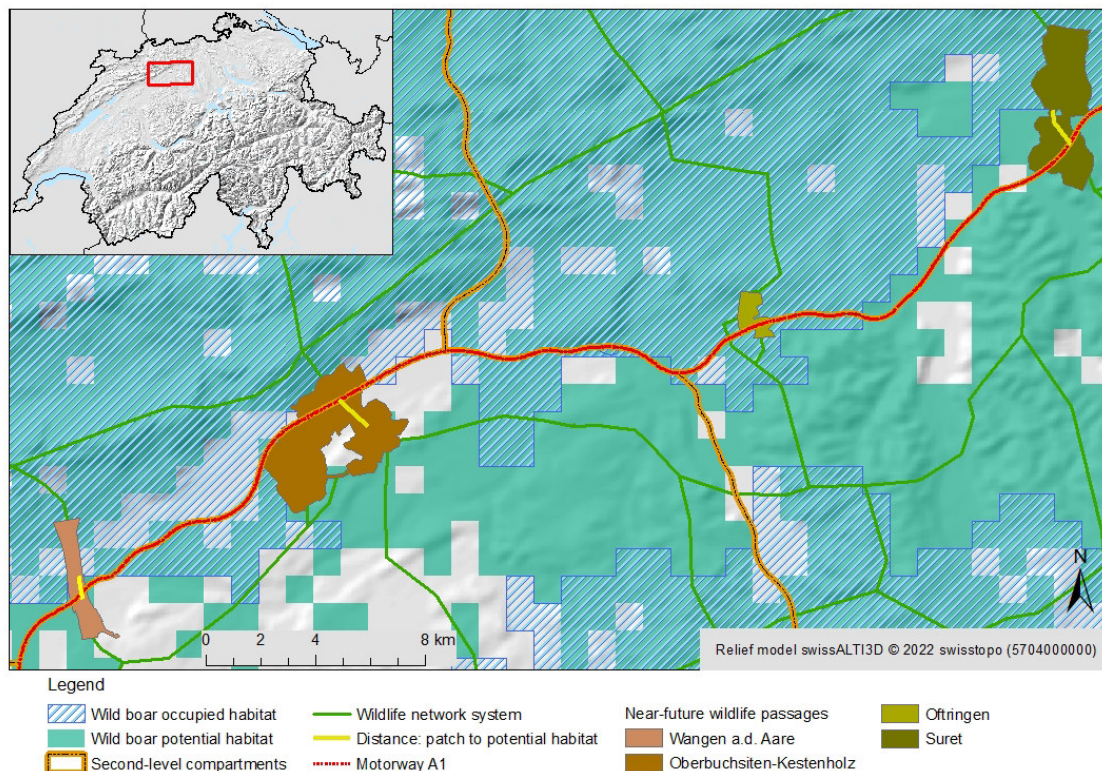
Figure 7. Near-future wildlife passages connecting habitat occupied by wild boar northwest of motorway A1 with potential habitat southeast of A1

Landscape fragmentation

The potential habitat of wild boar was almost twice as fragmented in the Central Plateau (CP) than in the other regions occupied by the northern population (referred to as 'North w/o CP' in Table 2) (Table 1). The fragmentation seems to be driven by artificial surfaces, the percentage of which in the Central Plateau 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 Central Plateau, 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.

Table 1. 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

After closing all wildlife passages and blocking all 'easy to block' corridors the change in the three connectivity metrics was consistently larger in the Central Plateau than in the other regions occupied by the northern population and in the Southern Alps (Table 2). In contrast, the change in the potential epidemic size (PES) was smaller in the LCC of the Central Plateau 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 Central Plateau the size of the patches was also a driver.

Table 2. 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

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 (Fig. 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 out 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 3 and 1 compartments both bordering Italy. None of the four compartments in the southern network could be isolated by closing wildlife passages and blocking corridors.
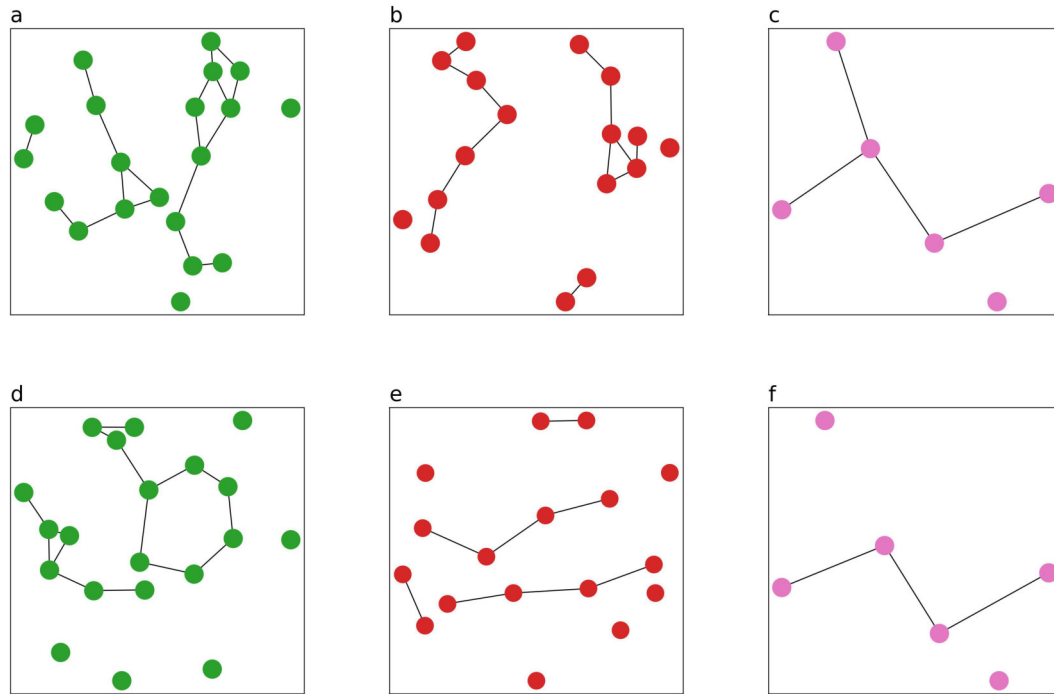
Figure 8. Graph representation of the wild boar networks in the Central Plateau (b, e), the other regions occupied by the northern population (a, d), and the Southern Alps (c, f) before (a–c) and after (d–f) closing all wildlife passages and blocking all 'easy to block' corridors

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 Central Plateau, whereas outside of the Central Plateau only 17% were easy to block, which supports hypothesis H-1.1. 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 20,000 m was 0.800 in the network of the northern population and 1.000 in the southern network. These results support hypothesis H-2.1: 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 out 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 hypothesis H-2.2. More wildlife passages are to be constructed after 2026 (Hirschi, 2021). These may open additional areas to potentially colonizing wild boar.

Closing wildlife passages and blocking corridors was found a more effective measure of disease containment in the Central Plateau than in any other biogeographical region of Switzerland which supports hypothesis H-3.1. This was related to the potential habitat of wild boar, which is more fragmented in the Central Plateau than in the other regions occupied by the northern population (Table 2). 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 (Fig. 3 (d)), 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 potential epidemic size (PES) of the second largest connected component (SLCC) was larger than that of the largest connected component (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. This suggests that connectivity management should be complemented by raising gamekeepers' awareness of possibly escaping animals. 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 BLV, 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, Carmo, Berezowski, Fischer, Santos, & Grütter, 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 modeling (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, and can have further side effects, such as shifting human-wildlife conflicts to other areas (Osipova, et al., 2018). Considering epidemic modeling 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. The analyses carried out have implications also outside of the context of this study:

– 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. This adds to existing work where fragmentation and connectivity are often considered two opposing poles of the same concept (Mühlner, Kormann, Schmidt-Entling, Herzog, & Bailey, 2010).
– Limiting the analysis to corridors and passages that connect habitat patches across compartment boundaries, which cannot be bypassed easily by dispersing animals, proved to be specific enough to find out where wildlife networks can be decomposed on a large scale in case of a disease outbreak.
– Complementing the permeability model (Holzgang, et al., 2001) with a species distribution model (Vargas-Amado, Grütter, Fischer, Suter, & Bernstein, 2020) turned out to be essential to identify connected habitat patches for the species of concern.
– The features established to qualify corridors on compartment boundaries as 'easy to block' or 'hard to block' were found adequate. Being familiar with the local landscape was helpful for qualification.
– The division of landscape after reclassifying some CORINE land cover classes (Fattebert, Baubet, Slotow, & Fischer, 2017) to obtain a new 'potential habitat' class proved to be fine-grained enough to distinguish regions that differ in their general character quantitatively (Lin, et al., 2021).
– Redefining PES such as to consider also the surface area of occupied habitat patches and relative abundance of the species of concern turned out to be a better metric than counting the number of patches in a connected component (Dubé, Ribble, Kelton, & McNab, 2011; Kao, Danon, Green, & Kiss, 2006).

Author contributions

Author contributions were as follows:

– Conception and design (MEVA, RG),
– acquisition and analysis of data (MEVA),
– interpretation of data (MEVA, BV, CF, SRRP, RG),
– drafting the article (MEVA, BV, CF, SRRP, RG).

All authors gave final approval of the manuscript to be published.

Conflict of interest

The authors declare no competing interests.

Data availability statement

The occurrence probabilities and the relative abundance of wild boar are available from the corresponding author on reasonable request. All other data used in this study are openly accessible from the sources indicated in Section 'Material and methods'.

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