



## Evaluating the functionality of expert-assessed wildlife corridors with genetic data from roe deer

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### Abstract

Traffic infrastructure such as fenced motorways may reduce functional connectivity by impeding the movement of wildlife and thus reduce gene flow across landscapes. This may result in increased genetic differentiation, eventually leading to decreasing genetic diversity in wildlife populations owing to genetic drift. Landscape managers and conservation agencies apply a range of measures to mitigate such adverse effects in intensively managed landscapes. Efficient measures to facilitate landscape permeability for wildlife include expert-assessed wildlife corridors. However, whether wildlife corridors are used as such and whether they fulfill their purpose remains largely unknown. Here, we evaluated whether the expert-based categorization of wildlife corridors into functional, impaired and interrupted held true in the Swiss Plateau by testing the landscape's permeability using genetic assessments. We identified the spatial genetic structure of roe deer (*Capreolus capreolus*) and tested, whether the estimated gene flow supported the expert categorization of wildlife corridors. Among the four study regions (ca. 300–2600 km<sup>2</sup>), pairwise genetic differentiation was rather low ( $F_{ST}$  ranging between 0.008 and 0.0264). However, wildlife corridors identified as intact on the basis of expert evaluation showed higher gene flow between populations of roe deer (mean  $F_{ST}$  = 0.008) than corridors classified as impaired or interrupted (mean  $F_{ST}$  = 0.022). Thus, expert judgement on the functionality of wildlife corridors could be generally confirmed by our genetic assessment on the permeability of landscapes for roe deer. This shows that genetic methods may constitute a useful set of tools to identify the state of management measures and to prioritize action plans for maintaining functional wildlife corridors across landscapes.

### Zusammenfassung

Verkehrsinfrastruktur wie eingezäunte Autobahnen können den Verlust funktionaler Vernetzung bewirken, indem sie den Austausch zwischen Wildtierpopulationen unterbinden und so zu einer Reduktion des Genflusses beitragen. Dies erhöht die genetische Differenzierung und kann Inzucht fördern, und genetische Drift kann zu einer reduzierten genetischen Diversität von Wildtierpopulationen führen. Landschaftsschutz- und Naturschutzorganisationen führen eine Reihe von Massnahmen durch, um diese negativen Effekte aufzufangen. Ein Beispiel dafür sind von Experten identifizierte Wildtierkorridore, mit Hilfe derer die Durchlässigkeit der Landschaft für Wildtiere überprüft werden kann. Ob solche Wildtierkorridore tatsächlich genutzt werden und damit ihren Zweck erfüllen ist bisher jedoch kaum bekannt. In der vorliegenden Studie untersuchten wir am Beispiel des Rehs

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(*Capreolus capreolus*) im Schweizer Mittelland, ob die von Experten als “funktional”, “beeinträchtigt”, oder “unterbrochen” eingestuften Wildtierkorridore ihrer Kategorisierung entsprachen. Dazu evaluierten wir quantitativ, ob die genetische Struktur der benachbarten Rehpopulationen die Einteilung der Wildtierkorridore bestätigte. Die genetische Struktur der Rehe in den vier untersuchten Gebieten (ca. 300–2600 km<sup>2</sup>) war generell nur schwach ausgeprägt ( $F_{ST}$  zwischen 0.008–0.0264). Jedoch wiesen Wildtierkorridore, die qualitativ als funktional eingestuft wurden, eine geringere genetische Differenzierung zwischen Rehen auf (im Durchschnitt  $F_{ST} = 0.008$ ), während als unterbrochen eingeordnete Korridore höhere genetische Differenzierung zeigten (im Durchschnitt  $F_{ST} = 0.022$ ). Die Resultate bestätigten grösstenteils die Einschätzung der Experten bezüglich der Durchlässigkeit der Wildtierkorridore für Rehe. Wir konnten somit zeigen, dass Landschaftsgenetik einen für das Landschafts- und Naturschutzmanagement wichtigen Beitrag leisten kann, indem Bedarfsanalysen zur Priorisierung von Massnahmen für die Funktionalität von Wildtierkorridoren durchgeführt werden.

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**Keywords:** Classification uncertainty; Fragmentation; Functional connectivity; Genetic structure; Landscape genetics; Landscape permeability; Nuclear microsatellites; *Capreolus capreolus*

## Introduction

Traffic infrastructure and urban sprawl are major factors of habitat fragmentation in densely populated areas, contributing to impermeable landscapes for wildlife movement (Frantz et al. 2012). Impermeable landscapes may lead to a loss of functional connectivity, i.e., an increase in genetic differentiation among populations (Epps et al. 2005), reduced genetic diversity (Kuehn et al. 2007; Holderegger & Di Giulio 2010), and foster inbreeding as a consequence of reduced mate availability in small populations (Corlatti, Hacklander, & Frey-Roos 2009). For some wildlife (e.g., ungulates), it has been shown that traffic infrastructure such as fenced motorways are virtually impossible to pass (Hepenstrick, Thiel, Holderegger, & Gugerli 2012) whereas for other groups such as carnivores, permeability may only become reduced (BUWAL, SGW, & Vogelwarte 2001).

Wildlife corridors are paths of animal movement which are restricted by natural and anthropogenic structures or intensely used areas (BUWAL et al. 2001). Increasing traffic infrastructure and the spread of settlements has impaired or blocked 72% of the regionally important corridors in Switzerland since the 1950s (BUWAL et al. 2001), especially on the Swiss Plateau, where high road densities of six to seven km road per km<sup>2</sup> land are common (Klaus 2012). The Federal Office for Environment (BAFU, formerly named BUWAL) commissioned a report with regionally and internationally important wildlife corridors. This represents the unified knowledge of hunting administration, game keepers and wildlife experts on connectivity of terrestrial wildlife and their corridors in Switzerland (BUWAL et al. 2001). The report categorized wildlife corridors into intact (i.e., fully permeable), impaired (i.e., partly permeable) and interrupted (i.e., fully impermeable). In total, only about a third (85 out of 303) were considered intact (BUWAL et al. 2001).

To date, only a few, spatially restricted studies about the effects of traffic infrastructure on the genetic structure of wild ungulates are available (Coulon et al. 2004, 2006; Epps et al. 2005; Kuehn et al. 2007; Hepenstrick et al. 2012). Also, the spatial genetic structure and the effect of multiple wildlife corridors have not yet been investigated in a landscape context. We considered roe deer (*Capreolus capreolus*), a common and widespread species of relatively large body size, as a suitable model species for studying population genetic structure at the landscape scale. A previous study of Hepenstrick et al. (2012) showed that linear landscape elements, in particular fenced roads, induced genetic differentiation of roe deer in a nationally important wildlife corridor.

The present study identified the genetic structure of roe deer in four regions of Switzerland (300–2600 km<sup>2</sup>). The goal was to assess the permeability of the landscape by evaluating whether the genetic structure found in roe deer reflected the expert-assessed categorization of wildlife corridors into intact, impaired and interrupted. Overall, we expected to find low levels of genetic differentiation of roe deer across the landscape, since roe deer was eradicated from Switzerland or survived as relicts only in the second half of the 19th century. Around 1900, the Swiss Plateau was re-colonized in a broad front from Germany and France, and the species' range has rapidly expanded since then. In turn, we hypothesized that roe deer on either side of interrupted wildlife corridors were genetically differentiated, reflecting barrier effects induced by landscape elements hampering gene flow. Our landscape-scale assessment relating the genetic structure to expert-assessed functionality of wildlife corridors will allow recommendations to prioritize the construction or restoration of wildlife corridors and may serve as a basis for later evaluation of the efficiency of connectivity measures promoting gene flow in roe deer.

## Materials and methods

### Study areas

We considered four regional study areas on the Swiss Plateau and the northern Prealps (Fig. 1; Table 1). The Swiss Plateau extends between the Lake of Geneva in the southwest to the Lake Constance in the northeast with a mean altitude of 580 m a.s.l. The Plateau, bordered by the mountain ranges of the Jura and the Alps (EDA 2013), is the most densely populated and intensely managed area in Switzerland (BAFU 2010; Klaus 2012).

The four study regions represent the Swiss Plateau and the northern fringe of the Alps (Fig. 1), and range between 300 and 2600 km<sup>2</sup> in size. They were selected to include national motorways as main elements intersecting landscapes that represent characteristic mixtures of various other landscape elements such as forest, agricultural land, streams and waterbodies, transportation infrastructure or settlements. In Switzerland, national motorways are fenced, comprise four or more lanes, are at least 25 m wide and were mainly constructed in the 1960s and 1970s (ASTRA 2001, 2007). The lengths of the motorways within the four study areas ranged between 47 and 146 km (Table 1). Study region I was located in the area of the Y-junction of the motorways A7 (Winterthur–Frauenfeld) and A1 (Winterthur–Wil; Figs. 1A and 2A). Study region II was bordered by the motorway A4 (Schwyz–Sihlbrugg) in the west and the A13 (Sargans–Altstätten) and the river Rhine in the east (Figs. 1B and 2B). Motorway A3 (Sargans–Freienbach) divided the study area into a northeastern and a southwestern part. Study region III contained the national motorway A6, which passed from north (Bern) to south (Thun; Figs. 1C and 2C). Study region IV contained stretches of the national motorways A1 (Aarburg–Aarau) and A2 (Aarburg–Luzern; Figs. 1D and 2D).

### Study species

The roe deer (*Capreolus capreolus*) is the most common native ungulate species in Switzerland. Its home range in the Swiss Plateau varies between 5 and 40 ha (Kurt 1991), within which dominant males defend their territories (Linnell, Wahlström, & Gaillard 1998). Adult females occupy their entire home range, and dispersal occurs mainly through yearlings of both sexes (Linnell et al. 1998). Roe deer occur in various habitats from the lowlands (400 m a.s.l.) to the tree line 1800–2200 m a.s.l.

### Genetic data

The genetic data relied on heart-tissue samples of 1102 individuals of roe deer from regular hunting and traffic casualties, collected between December 2004 and December 2005. The coordinates of the location of each individual

were assessed with a GPS or printed map at a resolution of 1:25,000. The sample comprised 704 males, 389 females, and nine individuals with unknown sex. Less than 10% of the individuals were juvenile, i.e., in their first year of their lives. The number of roe deer individuals ranged between 65 and 561 per study region (Table 1). All samples were genotyped at 12 nuclear microsatellite loci as described in Kuehn et al. (2007).

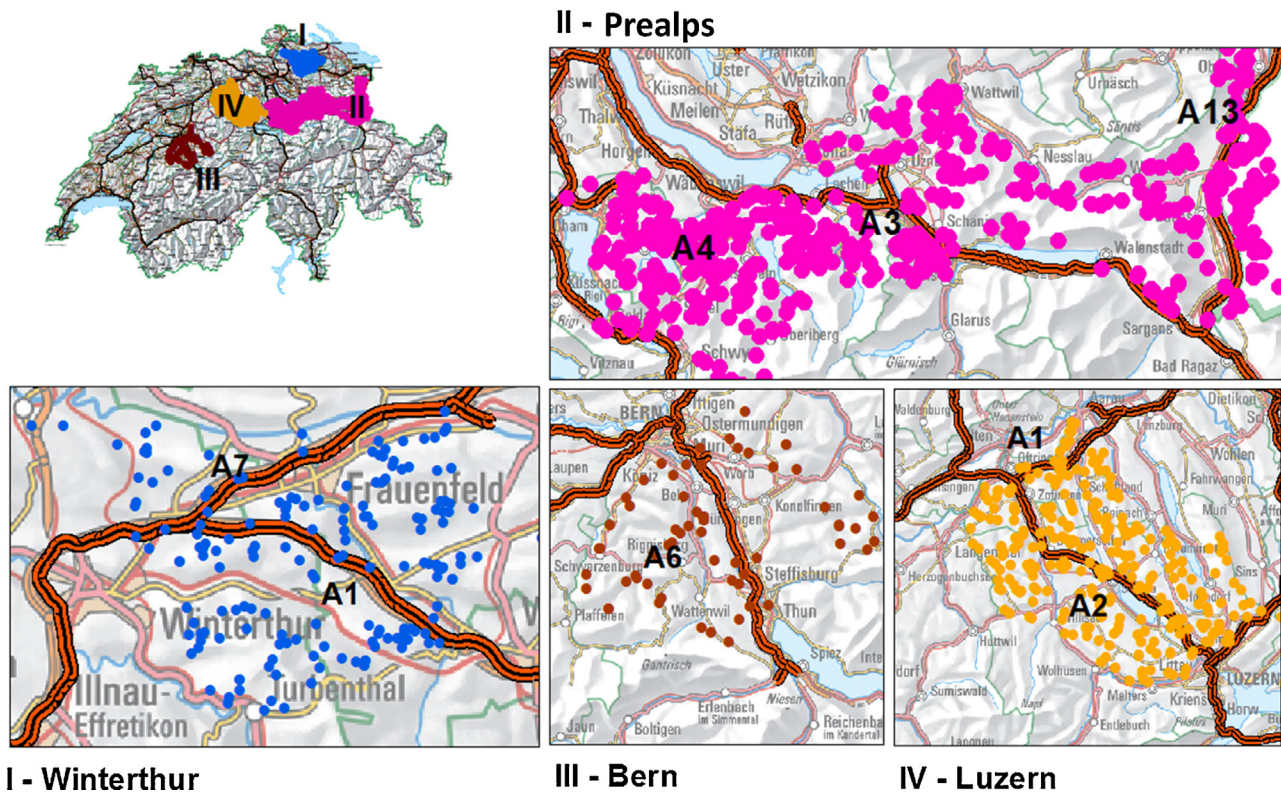
### Wildlife corridors

A wildlife corridor is defined here as an elongated element in a landscape which is bordered by natural and/or artificial obstacles along its sides and therefore represents a likely passage for wildlife (UVEK 2001). Wildlife corridors across Switzerland are expert-assessed: cantonal hunting authorities, hunters and wildlife guards were asked to delineate areas where wildlife predominantly crossed the landscape (BUWAL et al. 2001). The information obtained was mapped, with larger settlements and motorways assumed impassable. Reduced permeability was assigned to rocks, lakes and areas around settlements. Open agricultural land was identified as moderately permeable, whereas forests and conservation areas were considered fully permeable. Based on this scheme, wildlife corridors were identified and categorized into intact, impaired or interrupted according to experience by cantonal hunting authorities and wildlife guards (Table 2).

### Genetic structure

First, we checked for the genetic structure of the four study regions on the basis of empirical genetic data. Second, the spatial genetic structure of roe deer within each of the four pre-defined regions was identified. For this, we used STRUCTURE 2.3.4 (Prichard, Stephens, & Donnelly 2000; see Appendix A: Figs. S1 through S3), and GENELAND 4.0.2 (Guillot, Santos, & Estoup 2008). Next, we tested for genetic differentiation ( $F_{ST}$ ) among the four study regions using ARLEQUIN 3.5 (Excoffier & Lischer 2010). In contrast to the spatially implicit algorithm implemented in STRUCTURE, GENELAND uses spatially explicit information on multilocus genotypes to define genetic clusters and to assign individuals to their most likely cluster (Blair et al. 2012). GENELAND assigns roe deer individuals into clusters of randomly mating individuals with minimized deviation from Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium (LD). Departure from HWE and LD causes the splitting of a population into subpopulations (Guillot 2008).

GENELAND parameterization conformed to standard settings. The number of iterations was set to one million with burnin and thinning set to 1000. The uncertainty on coordinates was zero because individual sampling locations were precisely known. We used the correlated allele frequency model, which best suits the contiguous occurrence of roe deer in the study area; the spatial model and the null allele model were assumed to be true. Pixel size varied between 11 and



**Fig. 1.** The four regional samples I–IV of roe deer (*Capreolus capreolus*), located on the Swiss Plateau and northern Prealps. Respective colored circles in the map of Switzerland (top left) illustrate the location of the sampling areas. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

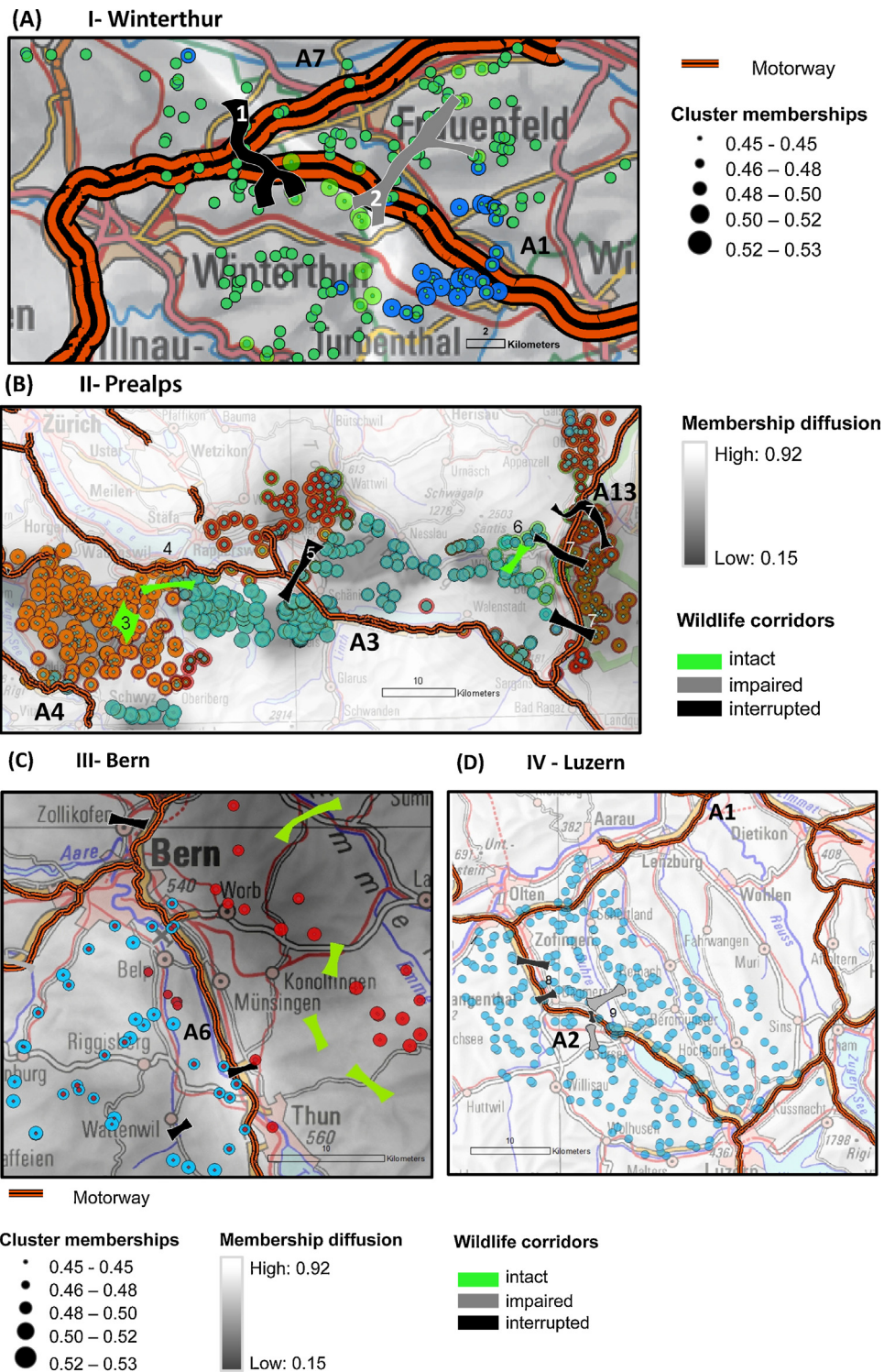
**Table 1.** Characterization of the regional samples I to IV (cf. Fig. 1). The total genetic sample size of roe deer amounted to 1102 individuals.

Region	No. of roe deer	Area [km <sup>2</sup> ]	Motorway (length) [km]	Motorways and time of construction/opening <sup>a</sup>	Corridor Nr
I	175	709.4	47.4	A1 Winterthur–Wil: 1966–1970 A7 Winterthur–Frauenfeld: 1966–1976	2 1
II	561	968.4	146.5	A4 Schwyz–Goldau: 1976–1980 A3 Sargans–Horgen: 1968–1987 A13 Sargans–St. Margrethen: 1964–2002	5 7 3, 4, 6
III	65	337.9	31.6	A6 Bern–Thun: 1966–1973	
IV	301	2629.1	75.1	A1 Olten–Aarau: 1967 A2 Luzern–Zofingen: 1980–1981	8, 9

<sup>a</sup> Source: Astra, Federal Roads Office.

40 m among regional samples because the number of pixels in the spatial domain should be chosen such that there is only one roe deer individual per pixel. The GENELAND analysis was repeated 10 times per regional data set, allowing  $k$  to vary between 1 and 10. Then, GENELAND was run 100 times at

the optimal  $k$ . From the latter analysis, means of the 10 runs with the highest posterior probability were considered for cluster assignment (Coulon et al. 2006, 2008; Chen, Durand, Forbes, & Francois 2007; Frantz, Cellina, Krier, Schley, & Burke 2009). Based on individual assignment probabilities



**Fig. 2.** Genetic cluster memberships of roe deer (*Capreolus capreolus*; in color) and membership diffusion (gray shades) for the four regional samples I to IV (A–D). The larger the colored symbol, the higher the probability of an individual roe deer is a member of a particular genetic cluster. The darker the gray shades, the stronger the degree of association of a location on the map with the respective genetic clusters. Wildlife corridors were classified into intact, interrupted and impaired. Note that the single genetic cluster found in region IV precluded the calculation of cluster membership and diffusion. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Table 2.** Characterization of the nine selected wildlife corridors in the four regional samples I, II and IV. The table contains information concerning the regional samples and the number of individuals ( $N$ ) per group. Subscripts (N, S, E, W) indicate the position of each group of roe deer relative to the wildlife corridor. Furthermore,  $F_{ST}$  values between groups and the expert condition of the corridor are listed. Wildlife corridors were merged if their permeability was evaluated the same and if they were located within 8 km distance of each other (e.g., three wildlife corridors categorized as interrupted are labeled 3 × interrupted).

Study region	Corridor Nr	Individuals/group	$F_{ST}$	Corridor condition
I-Winterthur	1	$N_N = 37, N_S = 8$	0.0506*	Interrupted
	2	$N_N = 14, N_S = 13$	0.0135	Impaired
II-Prealps	3	$N_W = 35, N_E = 32$	0.0111	Intact
	4	$N_E = 11, N_W = 30$	0.0081	Intact
	5	$N_N = 32, N_S = 36$	0.0220*	Interrupted
	6	$N_N = 16, N_S = 25$	0.0056	Intact
	7	$N_E = 77, N_W = 29$	0.0236*	3 × Interrupted
IV-Luzern	8	$N_N = 20, N_S = 14$	−0.0014	2 × Interrupted
	9	$N_E = 25, N_W = 31$	0.0223*	Interrupted

\*  $P \leq 0.05$ .

to particular clusters, we generated membership maps with 100 m resolution to reduce data complexity for visualization. We spatially overlaid the genetic cluster memberships with available topographic maps (pixmaps<sup>©</sup> 2013 Swisstopo).

### Assessing uncertainties in the spatial genetic structure

GENELAND outputs spatially explicit cluster memberships for each roe deer individual, which allowed us to identify the spatial genetic structure. Aggregating spatial information into clusters introduced a variety of uncertainties whose degree and extent may differ spatially. Therefore, the degree of association of each pixel with the overall clusters was assessed. This resulted in areas of high or low agreement with respect to the overall clusters. We applied membership diffusion (Zhu 1997; Bolliger & Mladenoff 2005) as an overall indicator for the degree of association of a particular pixel on the map with the set of genetic clusters as assessed by GENELAND. Membership diffusion is a spatial extrapolation of the degree of association of each pixel with the highest membership of the genetic clusters as identified by GENELAND. Membership diffusion varied between zero and one, with zero indicating no association and one indicating a high association with the respective genetic clusters.

### Evaluating the functionality of wildlife corridors using genetic data

We evaluated those wildlife corridors for which at least 10 roe deer were sampled within a radius of 5 km at each end of the corridor. Each roe deer individual was assigned to one wildlife corridor only. An individual was not included if sampled in an area that was clearly separated from the respective wildlife corridor (e.g., lake) to avoid confounding effects of landscape elements on gene flow other than the respective corridor. Roe deer individuals on one side of a corridor were

defined as a group. Each corridor therefore contained two groups (e.g., east and west, Table 2). We calculated pair-wise genetic differentiation ( $F_{ST}$ ) for the two groups of roe deer per wildlife corridor with ARLEQUIN 3.5 (Excoffier & Lischer 2010). Nine wildlife corridors were available in the four study regions for which the functionality was evaluated using genetic data. Three of these corridors were considered intact and six were rated as impaired or interrupted (Table 2, Fig. 2A–D). Wildlife corridors located nearby (within 8 km) were merged into one corridor as they likely complemented each other (Table 2). This affected corridors 7 and 8, where three nearby corridors were merged each.

## Results

### Genetic structure and membership diffusion

The 12 nuclear microsatellite loci showed 3–19 alleles (mean 9.58) per locus in the total sample. In study region I, one locus (MM12) was monomorphic. No deviation from Hardy–Weinberg equilibrium and no linkage disequilibrium were observed among the chosen loci at various geographical scales (Kuehn et al. 2007; Hepenstrick et al. 2012).

STRUCTURE analyses of the entire sample showed a genetic structure that was not compatible with the a priori distinguished four regions even when using LocPrior, i.e., assigning each individual to its regional sample (optimal  $K=10$ ; see Appendix: Figs. S1 and S2). This result conforms to the outcome of ARLEQUIN. Pairwise values of  $F_{ST}$  between the study regions were low (0.008–0.0264), indicating weak overall genetic structure. On the basis of this shallow genetic structure, we retained the four study regions as delineated in the original study design, particularly as the genetic clusters served as visualization only.

Within the study regions, STRUCTURE results appeared as inconclusive, with optimal numbers of clusters  $K$  being one in region III, three in regions I and IV, and eight in

region II (see Appendix: Fig. S3). The number of genetic clusters identified by GENELAND further differed from those obtained by using STRUCTURE. Whereas in study region IV (Fig. 2D), all roe deer individuals belonged to the same cluster, regions I and III exhibited two genetic clusters each (Fig. 2A and C), and region II showed seven clusters (Fig. 2B). When qualitatively overlaying the genetic structure with the landscape, motorways appeared to influence the genetic structure in study region I (Fig. 2A) and partly in region III (Fig. 2C). The inconsistencies of cluster numbers between the two assignment approaches were likely due to the very shallow regional genetic structure and no isolation-by-distance pattern (Appendix: Figs. S4 through S8). As our focus was the spatially explicit visualization of genetic structure, we chose to retain the outcome of GENELAND for further analyses, i.e., emphasizing the incorporation of spatial information in the Bayesian clustering as implemented in GENELAND.

Membership diffusion on the basis of GENELAND results indicated the degree of association of each pixel on the map with a given set of clusters. Overall, membership diffusion visualized the breaks between clusters (Fig. 2A through C), particularly for study regions I and II (Fig. 2A and B). Study region IV did not exhibit membership diffusion, as there was only one cluster (Fig. 2D).

### Functionality of wildlife corridors

The evaluation of expert-assessed wildlife corridors based on genetic data of roe deer showed that corridors identified as intact were generally confirmed by low  $F_{ST}$  values (mean  $F_{ST} = 0.008$ ), indicating high gene flow (Table 2). Contrarily, wildlife corridors classified as impaired or interrupted exhibited higher genetic differentiation (mean  $F_{ST} = 0.022$ ,  $P \leq 0.05$ ), indicating that these corridors had likely more restricted gene flow (Table 2). However, the overall rate of gene flow was high and the genetic comparisons of groups of individuals on either end of a wildlife corridor were not in all cases statistically significant (Table 2).

For study region I, one corridor classified as interrupted (1) and one identified as impaired (2) were confirmed by relatively high mean  $F_{ST}$  values of 0.03 (Table 2, Fig. 2A). In study region II, the wildlife corridors classified as interrupted (5, 7) were confirmed by higher mean  $F_{ST}$  values of 0.02 in comparison to corridors classified as intact (3, 4, 6; mean  $F_{ST}$  values of 0.007; Table 2, Fig. 2B). Study region IV exhibited two interrupted corridors (8, 9; Fig. 2D). Mean  $F_{ST}$  values of the two corridors were 0.012, and are thus in a similar range as observed for impaired or interrupted corridors in the other study regions (Table 2).

For study regions III, no genetic assessment on wildlife corridors could be performed as there was not enough data of roe deer on either side of the corridor (Fig. 2C). The corridor classified as interrupted, however, could be qualitatively

confirmed as the two genetic clusters separated by motorway A6 did not appear to mix strongly (Fig. 2C).

## Discussion

Wildlife corridors connect wildlife populations on the landscape, but need to be tested for their effectiveness. We evaluated such corridors, as identified by experts of hunting administrations, game keepers and wildlife biologists, regarding their functionality by relying on the genetic data of 1102 roe deer individuals in the four study regions of the Swiss Plateau. Results show that corridors identified as intact were confirmed by a higher degree of gene flow than corridors classified as impaired or interrupted which exhibited higher genetic differentiation (Table 2). Out of the five wildlife corridors classified as interrupted, four showed statistically significant  $F_{ST}$  values between groups at each corridor end (Table 2). Two corridors categorized as impaired (2) or interrupted (8) did not exhibit statistically significant genetic differentiation between groups. Corridor 2 was located between Winterthur ZH and Rickenbach ZH, crossing motorways A1 (Fig. 2A); corridor 8 was located in the vicinity of Zofingen (AG), crossing motorway A2 (Fig. 2D). Potential reasons for this outcome may be found in the local landscape context. Both corridors were located within quite densely populated areas with likely more options to cross the motorway if a regular road with limited traffic may be viewed as likely underpass or bridge. Such a landscape context may make the presumed barriers more permeable to gene flow in roe deer. This demonstrated the importance of landscape-scale assessments to understand the local permeability of a landscape for a particular organism instead of solely focusing on the assumed obstacle (e.g., motorway).

To date, 40 wildlife corridors chosen by experts which were classified as interrupted by motorways or main roads are already or will soon be restored through measures such as green bridges or underpasses (ASTRA 2012; Klaus 2012). Whereas corridor 3, intact from a roe deer perspective, was officially identified as one of the 40 regionally important wildlife corridors (ASTRA 2012; Klaus 2012), corridor 9 showed restricted permeability in our study, yet was not identified requiring restoration. The fact that wildlife corridors were not only expert-evaluated for permeability for roe deer, but also other wildlife species, might partly explain such discrepancies (BUWAL et al. 2001). In turn, this outcome also demonstrated the practical need for rigorous methods to test the functionality of wildlife corridors (Luell et al. 2003).

Overall, we found no pronounced genetic structure when considering all 1102 roe deer individuals sampled in the four study areas. This indicated low genetic differentiation with low effects of landscape elements on the pattern of genetic variation. This was in line with the results of Wang and Schreiber (2001), who also found low levels of genetic differentiation in roe deer across Central Europe. We assumed that the large-scale patterns of genetic differentiation in

Switzerland were primarily driven by the historical recolonization of roe deer. About 100 years ago, roe deer were virtually extinct in Switzerland due to widespread hunting and poaching. After the implementation of hunting regulations at the end of the 19th century, roe deer originating from Germany and France recolonized Switzerland (Breitenmoser 1998), which may explain the low genetic structure across the entire study range. In turn, significant genetic differentiation as detected at the regional scale ( $F_{ST} \geq 0.018$ ), could be due to motorway construction which had its prime time in the early 1960s, 1970s and ended in the 1980s – with one exception (A13) for which construction ended only in 2002 (ASTRA 2001). So, most involved motorways are thus older than 10 roe deer generations (ASTRA 2001). Blair et al. (2012) emphasized that GENELAND is considered very powerful in reliably detecting linear barriers to gene flow within 20 generations or less. Nevertheless, there is a presumed time lag of several generations until a changing landscape becomes apparent in a (changing) genetic structure (Anderson, Epperson, & Fortin 2010; Hepenstrick et al. 2012). This needs to be considered when testing connectivity measures for their effectiveness.

To conclude, our study demonstrated that there is a need for rigorously evaluating wildlife corridors in a landscape context. Genetic approaches may be useful to identify the need for setting priorities for reactivating dysfunctional wildlife corridors in intensely managed landscapes. Moreover, our study may later serve for monitoring the performance of mitigation measures to restore gene flow within wildlife at the landscape scale (Epps et al. 2005).

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2015.09.001>.

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