Landscape and Urban Planning 160 (2017) 107–114

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan

Research Paper

Prediction of genetic connectivity in urban ecosystems by combining detailed movement data, genetic data and multi-path modelling

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HIGHLIGHTS

- A priori models based on GPS tracking best explain genetic connectivity.
- Distinct genetic clusters of hedgehogs within the city coincide with the rivers and main highways.
- Small scale landscape elements influencing gene flow are identified.
- Circuit theory models outperform least-cost connectivity models in the investigated complex urban habitat.

ARTICLE INFO

Article history:
Received 14 February 2016
Received in revised form
21 September 2016
Accepted 21 December 2016

Keywords:
Habitat connectivity
Landscape genetics
Erinaceus europaeus
Least-cost analysis
CIRCUITSCAPE
GPS tracking
Genetic

ABSTRACT

Urban areas are expanding worldwide, yet little is known how anthropogenic landscape fragmentation affects the connectedness and gene flow in urban wildlife. The European hedgehog (*Erinaceus europaeus*) is a ground dwelling mammal which also inhabits variable urban habitats. We investigated habitat connectivity and the spatial genetic structure of urban hedgehogs in the largest Swiss city. We addressed the following questions: i) At the city-scale, which prominent landscape elements affect the spatial distribution of genetic clusters? ii) Which landscape elements affect gene flow in an urban mammal within the clusters? iii) Does individual movement data improve the prediction of landscape-wide gene flow?

We used two Bayesian methods to examine the influence of water bodies and major traffic routes on genetic hedgehog clusters, using microsatellite data of 147 hedgehogs. Further, we used extensive movement data to parameterise single-path and multi-path connectivity models, which were then used to predict genetic distance between hedgehog individuals.

First, we found that both Bayesian methods consistently showed three distinct genetic clusters, separated by the main rivers and the parallel running transportation axes. Second, the best model indicates that gene flow was facilitated by urban green areas and hampered by all other land cover types. Third, multi-path models based on detailed GPS movement data clearly outperformed models based on a priori assumptions to predict gene flow.

Multi-path connectivity models based on movement data reveal to be a powerful tool to detect gene flow in highly fragmented habitats and could be a crucial step in implementing effective conservation measures.

1. Introduction

Understanding how anthropogenic landscape fragmentation affects habitat connectivity is crucial for wildlife conservation and management (Fischer & Lindenmayer, 2007). Fragmentation is particularly accentuated in urban areas, where the landscape is generally characterized by a complex matrix of habitats, ongoing human disturbances and frequent habitat transformations (Grimm et al., 2008). Urban areas are expanding rapidly across the globe – 70% of the human population is expected to life in urban areas by 2050 (United Nations, 2013), and urbanization is considered a threat to biodiversity worldwide (McKinney, 2006). Despite the recognized importance of urban biodiversity in providing ecosystem services, large knowledge gaps on ecological connectivity in

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http://dx.doi.org/10.1016/j.landurbplan.2016.12.011
0169-2046/

urban areas remain. Particularly little is known how urban landscape elements affect movement and genetic exchange for urban dwelling organisms (de Groot et al., 2015; LaPoint, Balkenhol, Hale, Sadler, & van der Ree, 2015).

Habitat connectivity is a spatio-temporal species-landscape interaction, which is intrinsically difficult to quantify, and little consensus exists on how to measure it (Goodwin, 2003; Tischendorf & Fahring, 2000). Habitat connectivity is closely linked to daily movement and occasional dispersal of individuals across the landscape. Movement and dispersal may result in gene flow, with potential consequences on fitness, adaptability and survival of local populations (Reed, 2004). However, the relationship of individual movement and dispersal leading to gene flow is not always straightforward, as they occur on different temporal and spatial scales (Beier, Majka, & Spencer, 2008).

The field of landscape genetics combines landscape ecology with population genetics and allows thus to assess the relationship between landscape and genetic structure (Manel, Schwartz, Luikart, & Taberlet, 2003). One approach is to detect genetic discontinuities of individuals using clustering algorithms, without assigning individuals to pre-defined populations (Guillot, Leblois, Coulon, & Frantz, 2009; Pearse & Crandall, 2004). The border between the inferred discrete clusters can then be used post-hoc to identify potential barriers to gene flow.

An alternative approach is to compare genetic distances between individuals or populations with effective distances. Effective distances are calculated with GIS-based models based on cost or resistance surfaces, which describe the propensity of individuals to move through different land cover types (Adriaensen et al., 2003). In this context, the most commonly used GIS-model is least-cost analysis, which identifies the path between two focal points with the lowest "cost to movement" (e.g. Ferreras, 2001; Walker & Craighead, 1997). CIRCUITSCAPE is a recently developed alternative to least-cost-path models, and calculates the resistance distance between focal point based on electrical circuit theory (McRae, Dickson, Keitt, & Shah, 2008). Importantly, CIRCUITSCAPE considers not only the "least costly" but all possible paths between points, and thus acknowledges variation in individual movement patterns (McRae, 2006).

A major challenge of all these methods constitutes the quantification of the relative costs (resistances) that different land cover types impose on movement (Beier et al., 2008; Spear, Balkenhol, Fortin, McRae, & Scribner, 2010). Using expert knowledge is the most common approach to assign resistance values to land cover types, but this has been frequently criticized to be subjective. Alternatively, costs can be based on empirical movement data, but this approach remains rare (2% of the articles reviewed by Zeller, McGarigal, & Whiteley, 2012) and only few studies combined this approach with genetic data (e.g. Cushman & Lewis, 2010; Reding, Cushman, Gosselink, & Clark, 2013). Although it is not straightforward to identify the relationship between individual movement and gene flow (Beier et al., 2008), we suggest that the combination of movement data with genetic population structure allows an objective parameterization of resistance values for subsequent landscape genetic analysis.

Here, we used the European hedgehog *(Erinaceus europaeus)* as a model species, representing ground dwelling mammals in urban environments. European hedgehogs have non-territorial home-ranges of 10–40 ha (Morris & Reeve, 2008) and show no clear dispersal phase in their life history (Doncaster, Rondinini, & Johnson, 2001). The main activity of this nocturnal generalist insectivore is foraging (60–80%), frequently covering distances of 1000–1500 m per night (but occasionally up to 7 km; Zingg, 1994). Since the 1960ies, European hedgehog populations in the United Kingdom appear to decline (Roos, Johnston, & Noble, 2012), and concerns for a similar decline exist for the native European mainland populations (Huijser & Bergers, 2000). The causes for these declines remain unknown, but previous studies suggest that increased habitat loss and fragmentation, and increased mortality through road traffic and predation may be major drivers (Baker & Harris, 2007). Although habitat fragmentation is particularly pronounced in cities (Grimm et al., 2008), for certain species, functionally connected communal parks and private gardens can form a city-wide habitat network (Goddard, Dougill, & Benton, 2010). Hedgehogs have successfully colonized urban areas, and hedgehog densities have recently been reported to be higher in urban than in rural areas, possibly a result of higher food and shelter availability, milder climatic conditions and reduced predation by badgers in cities (Hof, Snellenberg, & Bright, 2012; Hubert, Julliard, Biagianti, & Poulle, 2011). For efficient conservation management of native European hedgehogs, a better understanding on how habitat fragmentation affects hedgehog movement and genetic population structure is required. Genetic research on hedgehog populations remains scarce (Becher & Griffiths, 1998; Bolfikova & Hulva, 2012), mirroring the large research gap on the genetic structure of urban wildlife (Gardner-Santana et al., 2009; Kajdacsi et al., 2013).

The goal of this study was to investigate the spatial genetic structure of a ground dwelling mammal in a highly fragmented urban habitat, and to investigate the effect of landscape elements on the genetic structure by combining genetic microsatellite data with a unique set of detailed individual movement records. We asked i) whether or not urban hedgehogs show spatial genetic clustering and whether these clusters coincide with large, prominent landscape elements, ii) which landscape elements affect gene flow in an urban mammal within the clusters, and iii) whether gene flow in hedgehogs is better predicted by resistance surfaces based on *a priori* assumptions or detailed individual movement data? In particular, we tested the following hypotheses (i) if prominent landscape elements such as the lake, the two rivers and the main transportation axes determine population structure and gene flow at a large spatial scale, we expect these elements to coincide with the borders of the genetic clusters, (ii) if small-scale landscape elements do influence hedgehog movement at finer spatial scales (i.e. within the genetic clusters), then we expect that genetic distance between individual hedgehogs can be predicted with effective distances considering these landscape elements, and (iii) if using individual movement data improves predictions of gene flow, we expect these models to best predict genetic distances in urban hedgehogs.

2. Materials and methods

2.1. Sample collection and genotyping

We investigated the spatial genetic structure of European hedgehogs in the city of Zurich, Switzerland. Zurich extends on an area of almost 100 km^2, and one million people inhabit the extended metropolitan area. Despite the high concentration of buildings and the dense road network in the urban centre, 20% of the area of the city of Zurich is covered by forest and 30% by other green surfaces (parks, gardens, hedgerows, etc.). Hedgehogs commonly use urban parks and gardens as habitat, and their population can reach higher density in cities than in rural areas (Hubert et al., 2011). In Braaker et al. (2014) the nightly movement of 40 male hedgehogs was GPS tracked at a 10 s interval between May and September 2009 in the city of Zurich (up to 6 consecutive nights per individual). Females were excluded from GPS tracking to avoid interference with their raising of offspring. During the same time-period we collected hair samples from 156 hedgehogs encountered across the whole city, including the 40 GPS tracked males. Individual colour codes on the spines prevented sampling the same animal twice. The license for collecting non-invasive tissue (hair) samples

of hedgehogs was obtained from the Veterinary Office of Canton Zurich (Nr 73/2009 04.05.2009).

Hair samples were stored in 70% ethanol. From 147 samples sufficient DNA could be extracted to successfully perform PCR amplification. DNA was extracted from hair shafts by using the DNeasy Blood and Tissue kit (Qiagen), following the manufacturers protocol for animal tissues. We used ten primer pairs developed by Becher and Griffiths (1997) and Henderson, Becher, Doncaster, and Maclean (2000) for *E. europaeus* (EEU1, EEU2, EEU3, EEU4, EEU6, EEU12, EEU36, EEU37, EEU43 and EEU54). All primers were labelled with fluorescent dyes and arranged in four multiplex PCR reactions. Additional details on the genotyping procedure are given in Supplementary Material 1: S1 and Table S1. PCR reactions were performed using a Verity Thermal Cycler (Applied Biosystems), and fragment analyses were run on an ABI Prism 3130 Genetic Analyzer (Applied Biosystems). The data were analyzed using genemapper v. 4.0 (Applied Biosystems).

2.2. Population genetic structure

We used two spatially explicit Bayesian clustering methods to identify genetic clusters and the assignment of individuals to these clusters (GENELAND v. 4.0.4 (Guillot, Santos, & Estoup, 2008) and BAPS v.6 (Corander, Waldmann, & Sillanpaa, 2003)). GENELAND is based on the assumption of Hardy-Weinberg equilibrium and linkage equilibrium within clusters, while BAPS seeks spatially smooth and genetically homogeneous clusters (Francois & Durand, 2010). First, we identified the number of clusters with GENELAND including coordinates of the sampled individuals by running ten independent runs (10^6 MCMC iterations, thinning of 10^3, burn-in of 100, uncorrelated allele frequency, filtering potential null alleles and varying k from 1 to 10). Once the number of clusters was inferred, we repeated the algorithm 100 times with k fixed to the inferred number (25×10^4 MCMC iterations, thinning of 250, all other parameters equal above). We selected the run with the highest posterior probability and post-processed it for graphical display showing the population membership of each individual. Second, we used BAPS to infer the number of clusters, running BAPS 30 times for each k max of 2–10 and another 100 times with k fixed to the inferred number of clusters. An admixture model was run for the inferred number of clusters (100 iterations, minimum individuals per cluster = 5, reference individuals = 200, iterations for reference individuals = 20). Based on these results, we grouped individuals into genetic clusters for the remaining analyses.

To describe genetic diversity of the three clusters, we assessed the number of hedgehogs included, the percentage of missing genotypes, and the absolute and mean number of alleles with the R package PopGenReport (Adamack & Gruber, 2014). The number of private alleles (alleles unique for the cluster) and the allelic richness adjusted for sample size were calculated with HP-RARE (Kalinowski, 2005). Furthermore, we calculated overall and cluster specific estimates of the mean observed and expected heterozygosity, measured F_{IS} indices (Weir & Cockerham, 1984) and checked for Hardy-Weinberg equilibrium and linkage disequilibrium after a Bonferroni correction for multiple testing in ARLEQUIN 3.1 (Excoffier, Laval, & Schneider, 2005). We estimated the degree of genetic differentiation among clusters (Fst; Weir & Cockerham, 1984) in SPAGEDi version 1.4c (Hardy & Vekemans, 2002), and significance was tested with 10^4 permutations of individual genotypes between clusters. Additionally, we used the software FreeNa (Chapuis & Estoup, 2007) to estimate the frequency of null alleles with the algorithm of Dempster, Laird, and Rubin (1977) and computed F_{ST} estimates corrected for the presence of null alleles. We performed an assignment test in GENECLASS (Piry et al., 2004) using the Rannala and Mountain (1997) Bayesian method and applied a migrant detection analysis using the L-home/L-max criterion. For these tests we calculated exclusion probabilities with Monte Carlo resampling of 10^4 individuals (Paetkau, Slade, Burden, & Estoup, 2004) and a threshold of 0.01.

2.3. The effect of landscape elements on gene flow

To test whether landscape elements affect genetic structure at a smaller spatial scale, we compared the relationship between genetic distances and isolation by effective distance using CIRCUITSCAPE resistance distances and least-cost distances between the sampling sites of individuals. The calculation of CIRCUITSCAPE resistance and least cost distance is based on resistance maps where a resistance value is attributed to each land cover type. Braaker et al. (2014) investigated how 20 land cover types (Supplementary Material 1: Table S2) influence the daily movement of hedgehogs in Zurich by modelling a spatially explicit connectivity map with CIRCUITSCAPE. To avoid subjective assignment of resistance values, Braaker et al. (2014) derived landscape resistance from a habitat preference analysis based on GPS tracking data of 40 hedgehogs. First a habitat preference analysis was conducted based on a multivariate analysis between the ratio of available and used habitat (Calenge & Dufour, 2006). An inverse relationship of habitat preference to habitat resistance was demonstrated and four alternative transformation functions were used to describe a linear, a logistic, an exponential or a step wise (reclass) relationship between preference and resistance. Four land cover types were excluded from habitat preference analysis as they were either not available or not used by hedgehogs and were set *a priori* to maximal resistance in the final habitat resistance models (for a detailed method description see Braaker et al., 2014). In this study, we used the same four habitat resistance models and additionally created five a-priori hypothesis models for comparison (Table 1). Three a-priori models were based on the hypotheses that the lake and the two main rivers *(r-water)*, forest patches *(r-forest)* or the main transportation axes *(r-transp)* act as strong barriers while all other land cover types are corridors for gene flow. Two models assumed that all urban green areas *(r-green*: except agricultural land, forest and hedges) or all urban green areas which contain structures such as bushes or wood heaps providing shelter *(r-struct)* act as corridors while all other habitat types are strong barriers (Table 1). To compare the 'isolation by effective distance models' with 'isolation by distance models' we created appropriate null models using a uniform resistance surface of value 1 *(r-null)*. All maps had a spatial resolution of 10×10 m cell size. To avoid effects of artificial map boundaries, we added a 2 km buffer of randomized land cover type around the city with the same proportional composition as the landscape map of Zurich (Koen, Garroway, Wilson, & Bowman, 2010).

For all ten resistance maps, we assessed least-cost distances between the sampling location of all individuals using the Landscape Genetics Gis Toolbox (Etherington, 2011) in ArcGis 10 (ESRI, 2009) and calculated the pairwise matrix of CIRCUITSCAPE resistance distance with the software CIRCUITSCAPE 4.0.4 (McRae, Dickson, Keitt, & Shah, 2008). We estimated gene flow as multivariate genetic distance between all pairs of individuals according Smouse and Peakall (1999) with the R package PopGenReport (Adamack & Gruber, 2014). Mantel tests are the most frequently used method to test for the relationship between genetic distances and effective distances, which are described as distance matrices. However, the validity of simple and partial Mantel tests has recently been questioned (Castellano & Balletto, 2002; Graves, Beier, & Royle, 2013; Raufaste & Rousset, 2001), especially their ability to discriminate between similar landscape models is low, and the risk of Type I errors high (Balkenhol, Waits, & Dezzani, 2009). As a promising alternative Bayesian generalized linear mixed models (GLMMs) allow to account for the non-independence of pairwise comparisons involving the same site, by correctly estimating

Table 1
Habitat resistance values of the six landscape models, obtained by transforming habitat preference of hedgehogs for 20 land cover types (description in Supplementary Material 1: Table S2). Resistance models are named after the transformation function: *r-lin*: linear transformation of inverse habitat selection values; *r-log*: natural logarithm of *r-lin*; *r-exp*: *r-lin* raised to the power of five; *r-reclass*: division of *r-lin* in three classes. Additionally 6 models based on a-priori hypotheses were tested: *r-water*: large water as absolute barrier; *r-transp*: main transportation axes as barriers: *r-forest*: forest as barrier; *r-green*: urban green as corridors; *r-struct*: structured urban green (containing single bushes, wood-heaps etc.); and *r-null*: null model with all land cover types set to resistance one.

Land cover	*Resistance value*									
	r-lin	*r-log*	*r-exp*	*r-reclass*	*r-water*	*r-transp*	*r-forest*	*r-green*	*r-struct*	*r-null*
Garden with structures	1	1	1	1	1	1	1	1	1	1
Green area few structures	1	1	1	1	1	1	1	1	100	1
Flower garden	18	71	1	1	1	1	1	1	100	1
Green area with structures	24	76	1	1	1	1	1	1	1	1
Pasture	41	85	1	50	1	1	1	100	100	1
Hedge	50	88	3	50	1	1	1	100	1	1
Lawn	56	90	5	50	1	1	1	1	100	1
Ruderal	57	90	6	50	1	1	1	100	100	1
Small street	60	91	8	100	1	50	1	100	100	1
Impervious	67	93	13	100	1	1	1	100	100	1
Footpath	68	93	14	100	1	1	1	100	100	1
Sidewalk	75	95	23	100	1	1	1	100	100	1
Gravel	83	97	39	100	1	100	1	100	100	1
Forest	100	100	100	100	1	1	100	100	100	1
Marsh	100	100	100	100	1	1	1	100	100	1
Highway	100	100	100	100	1	100	1	100	100	1
Large street	100	100	100	100	1	100	1	100	100	1
Small water	100	100	100	100	1	1	1	100	100	1
Buildings	abs. [a]	abs.	abs.	abs.	abs.	abs.	abs.	abs.	abs.	1
Large water	abs.	abs.	abs.	abs.	abs.	abs.	abs.	abs.	abs.	1

[a] abs: absolute resistance.

the error structure and the posterior mean (Clarke, Rothery, & Raybould, 2002; Hadfield, 2010). As random correlation structure with multiple memberships, we added two vectors containing the identifier of the compared individuals (random effects) to each model (Roberts, Angermeier, & Hallerman, 2013). We used a Gaussian distribution and uninformative priors (mean = 0.002, variance = 1) and ran all models for 10^5 MCMC iterations with a burn-in of 10^4 and a thinning interval of 100. We fitted competing GLMMs with genetic distance as response using the MCMCglmm function (R package MCMCglmm; Hadfield 2010). We created GLMMs using each of the CIRCUITSCAPE resistance model and least-cost distance model as univariate predictor for genetic distance. Additionally, we recalculated each GLMM including the null models for isolation by distance for CIRCUITSCAPE and least-cost models, respectively. We converted the predictors to z-scores to be able to compare the coefficients and calculated the variance inflation factor for models with two predictors (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). To check for convergence, proper mixing and low autocorrelation of the chains, we examined plots of the sampled outputs. To infer the relative support for competing models, we used the relative deviance information criterion (DIC), a Bayesian analogue to the frequentist Akaike information criterion (AIC, Spiegelhalter, Best, Carlin, & van der Linde, 2002). As for AIC, the model with the lowest DIC value is considered as being the best model, and models with DIC differences (delta DIC) of 1–2 "deserve consideration", while models with delta DIC of 3–7 have "considerably less support" (Spiegelhalter et al., 2002). All R packages were run in R version 3.0.2 (R Core Team, 2013).

3. Results

The 147 successfully genotyped hair samples represented 70 males, 75 females and 2 individuals of unknown sex. Overall, ca. 20% of the genotyped individuals were identified as juveniles born in the study year (28 individuals). All ten microsatellite loci were polymorphic, having 2–15 alleles (average 8) per locus (Supplementary Material 1: Table S1). Both clustering methods (GENELAND and BAPS) inferred three genetic clusters (Supplementary Material 1: Fig. S1). The geographic distribution of these clusters was coherent across both clustering methods (Supplementary Material 1: Fig. S2a–b): Clusters according to GENELAND were geographically corresponding to a northern (N), a south-western (SW) and south-eastern (SE) group (Fig. 1c–e). Borders between clusters spatially coincided with the two main rivers and the main transportation axes, with the exception of two individuals that were grouped to the N cluster although located south of the river Limmat (individuals surrounded by a triangle in Fig. 1c–e). BAPS showed very similar clustering results as GENELAND and largely confirmed the separation by the two rivers and the major transportation axes (Supplementary Material 1: Fig. S2b).

Only one locus EEU1 in a single cluster showed a significant departure from Hardy-Weinberg equilibrium, and a total of 6 allele pairs out of 135 comparisons were not in linkage equilibrium. However, no consistent pattern across clusters was observed. Null allele frequencies were low (<0.05) for nine loci and moderate for locus EEU1 (average: 0.08, range: 0.04–0.13). Null alleles have been shown to only slightly decrease the correct assignment of individuals to genetic clusters but that the number of loci has a greater effect on the accuracy of assignment tests (Carlsson, 2008). We therefore kept all loci in further analyses. Genetic diversity measures were similar for all three clusters (Table 2). F_{IS} inbreeding coefficients were low and not significant, while all pairwise F_{ST} values among clusters were highly significant (overall F_{ST}: 0.064; p-value:<0.0001; Table 2). Correction for null alleles only resulted in minimal changes of F_{ST} (Table 2). The GENECLASS assignment test assigned 87.8% of the individuals back to their sampled cluster (quality index = 70.59%), and only one individual (1 female) was cross-assigned to another cluster with a probability >75% and a <70% probability to the resident cluster. Six individuals (including the female above) were identified as migrants by GENECLASS (Supplementary Material 1: Fig. S3). Sexes of the migrants were equally distributed (4 males, 2 females, no juveniles).

To identify the connectivity model which best explained genetic distances between individuals, we ranked the Bayesian GLMM models according to delta DIC. The null models (isolation by distance) as single predictors ranked poorly (Supplementary Material 1: Table S3). Also adding the null models to the effective distance models did not change the ranking of the effective distance mod-

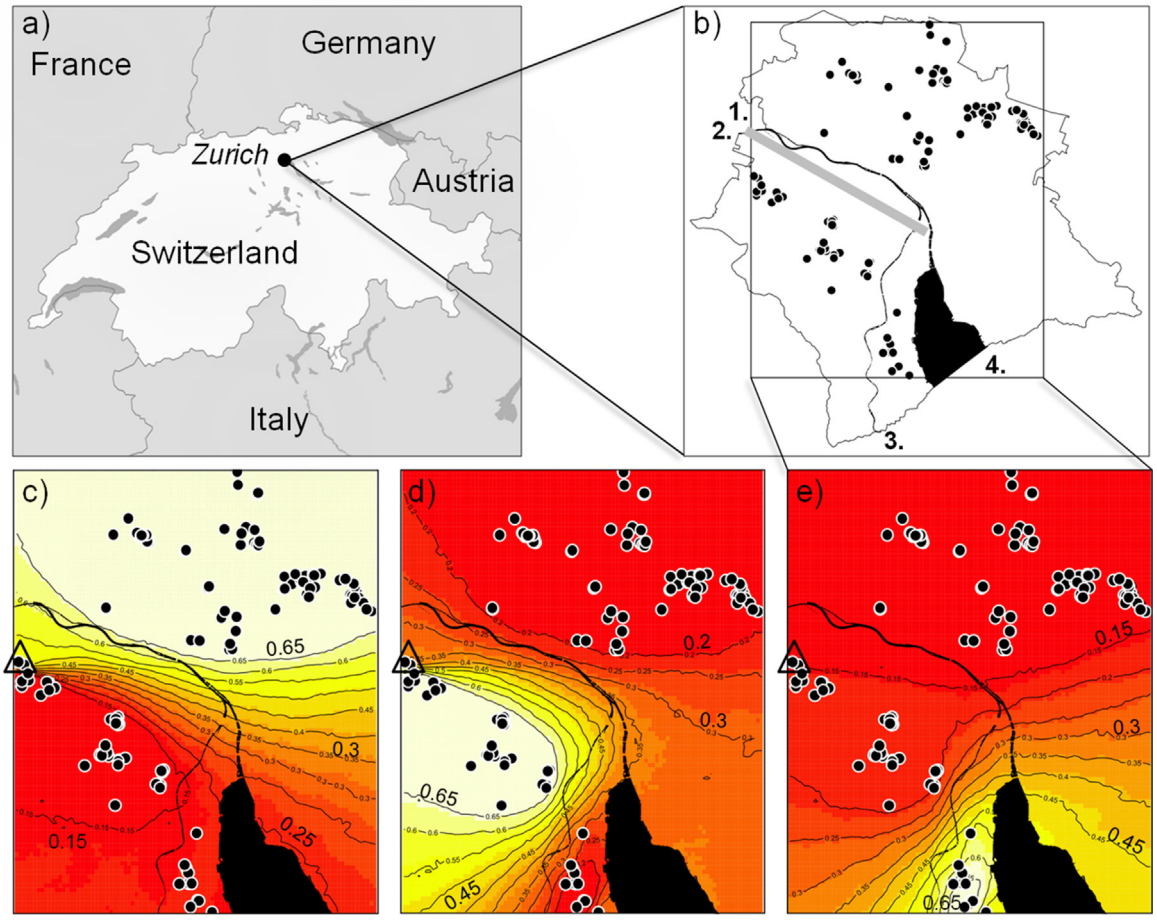

Fig. 1. Map of sampling sites and graphical output of GENELAND. Map (a) shows the geographic location of the city of Zurich in Switzerland. Map (b) shows details of the geography of Zurich with the two major rivers Limmat (1.) and Sihl (3.) as black lines, the main transportation axis (2.) as bold grey line and the lake Zurich (4.) as black shape. The locations of sampled individuals are depicted as black points. The lower row shows the graphical output of GENELAND. Black circles indicate the position of the sampled individuals. Contour lines indicate the posterior probabilities of membership to clusters (yellow for highest, red for lowest values). Map (c) shows the northern (N), (d) the south-western (SW) and (e) the south-eastern (SE) cluster. Two individuals clustering to the northern cluster, although located south of the river Limmat are surrounded by a black triangle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Genetic diversity of 147 individuals belonging to three clusters (for clusters see Fig. 1c–e) as inferred by GENELAND. *N*: sample size; *% missing*: percentage of missing genotypes; *Al*: total number of alleles; *Ar*: mean allelic richness corrected for sample size; *Ap*: average number of private alleles; H_o: mean observed and H_e: mean expected heterozygosity; F_{IS}: inbreeding coefficient (p-value). F_{ST} (upper diagonal): pairwise F_{ST} between all pairs of clusters (all significant at $p < 0.01$); F_{ST} (lower diagonal): pairwise F_{ST} after correction for null alleles (no significance is calculated).

Cluster	*N*	% missing	*Al*	*Ar*	*Ap (average)*	H_o	H_e	F_{IS} (p-value)	F_{ST}		
									N	S-E	S-W
N	100	0.4	73	4.91	14 (0.85)	0.6	0.605	0.003 (0.43)	–	0.071	0.060
S-E	11	0.9	46	4.52	2 (0.61)	0.523	0.569	0.070 (0.17	0.069	–	0.082
S-W	36	0	60	4.71	5 (0.67)	0.631	0.627	−0.006 (0.58)	0.059	0.080	–

Clusters: N: Northern, S-E: South-eastern, S-W: South-Western.

els. Therefore we focus here on the univariate predictor models (Table 3). The two best models were both based on CIRCUITSCAPE resistance, using log- transformed habitat preference values ("c-log") or untransformed habitat preference ("c-lin"), respectively. The model with untransformed resistance values had, however, considerably less support than the best model (delta DIC: 3.9). Further, the five best models (up to delta DIC: 54) included all four CIRCUITSCAPE resistance models derived from habitat preference and only one, weakly supported hypothesis based model (c-water, delta DIC = 22.8).

Finally, ranking only the *a-priori* models, the best model was the CIRCUITSCAPE model c-water followed by the least-cost models lc-green, lc-struct and lc-transp (min. delta DIC to c-water: 130). Overall, the five best-supported models (delta DIC up to 54) were all based on multiple pathways (i.e. CIRCUITSCAPE resistance distance), while least-cost distance models were clearly not supported (minimal delta DIC: 137).

4. Discussion

Our study investigated the spatial genetic structure of a medium sized, ground-dwelling urban mammal, the European hedgehog, in a highly fragmented habitat in the city of Zurich, Switzerland, with an extensive set of individual movement data. Two different Bayesian methods show that the hedgehog population of Zurich is separated into three well defined clusters within an urban area

Table 3
Results of the GLMM, correlating CIRCUITSCAPE resistance distance (**c-** followed by the model name as in Table 1) and **l**east-**c**ost distance (**lc-** model name as in Table 1) with genetic distance between individuals. The best supported model (DeltaDIC = 0) is CIRCUITSCAPE resistance distance model calculated with the logarithmic resistance surface.

	Model	L-95% CI	U-95% CI	DIC	DeltaDIC
CIRCUITSCAPE resistance	c-log*	0.80	0.93	50521	0
	c-lin*	0.79	0.91	50525	3.9
	c-exp*	0.79	0.91	50539	18.7
	c-water	0.73	0.85	50543	22.7
	c-reclass*	0.79	0.92	50575	54.1
	c-forest	0.55	0.65	50721	200.4
	c-green	0.69	0.82	50743	222.5
	c-struct	0.69	0.83	50787	266.7
	c-transp	0.26	0.42	51154	633.6
	c-null	0.57	0.67	50688	167.6
Least cost distance	lc-log*	0.64	0.75	50670	149.2
	lc-lin*	0.63	0.74	50662	141.7
	lc-exp*	0.60	0.71	50693	172.6
	lc-water	0.57	0.68	50751	229.9
	lc-reclass*	0.62	0.73	50658	137.3
	lc-forest	0.55	0.66	50779	258.2
	lc-green	0.61	0.72	50674	152.9
	lc-struct	0.58	0.69	50712	191.6
	lc-transp	0.59	0.70	50700	179.0
	lc-null	0.54	0.65	50781	259.9

Model: Resistance models see Table 1; L-and U-95%CI: Lower and upper 95% credible interval; DIC: deviance information criterion; DeltaDIC: difference to lowest DIC. Models derived from habitat preference are indicated by an asterisk *, all other models are based on *a-priori* hypotheses.

of 100 km^2. The clusters show moderate but significant genetic differentiation (F_{ST}). Only few comparable studies exist which investigated the genetic structure of nocturnal urban mammals in Europe, in particular for European hedgehogs, and none of them focused exclusively on an urban landscape. A study in the United Kingdom detected significant hedgehog population differentiation in an area of 15 km radius (Becher & Griffiths, 1998). Several genetic clusters, although with a high proportion of admixed individuals, were identified in a study carried out in New Zealand, where hedgehogs were introduced in the 19th century (Bolfíkova, Konecny, Pfäffle, Skuballa, & Hulva, 2013). A study in the Czech Republic performed at larger, country-wide scale (500km × 280 km) did not detect any population structure based on nuclear DNA, while showing a mosaic structure for mtDNA (Bolfikova & Hulva, 2012). The nuclear genetic diversity for urban hedgehogs detected in our study (mean Ar: 4.71, range He: 0.57–0.63) is comparable to other studies, which were carried out on much larger spatial scales in the Czech Republic (mean Ar: 9.81, He 0.68; Bolfikova & Hulva, 2012) and New Zealand (mean Ar: 3.6, range He: 0.47–0.57; Bolfíkova et al., 2013). The relative high genetic diversity of hedgehogs in Zurich is likely the consequence of post-glacial movement and expansion of populations from a glacial refugium which was probably located close to the Alps (Seddon, Santucci, Reeve, & Hewitt, 2001). Genetic diversity of Swiss urban hedgehogs was also comparable to other small urban mammals such as Norway rats in the city of Salvador, Brazil (mean Ar: 3, range He: 0.57–0.72; Kajdacsi et al., 2013), but was lower than the genetic diversity of white footed mice in New York City, which had been considered unusually high for the small geographic scale by the authors (mean Ar: no value, range He: 0.75–0.85; Munshi-South & Kharchenko, 2010). Our results are also in line with the hypothesis of Munshi-South and Kharchenko (2010), who suggested that the combination of high genetic diversity with moderate genetic differentiation is a general characteristic of urban adapters with limited dispersal capabilities. Further, promiscuity and multiple paternity are common in the European hedgehog (Moran, Turner, & O'Reilly, 2009), which can be a reason for the high observed genetic variance (Gardner-Santana et al., 2009; Pearse & Anderson, 2009).

In accordance with our first hypothesis, the borders of the three GENELAND clusters spatially coincided well with the two main rivers in the area (Limmat and Sihl) and the main transportation axes (4 lane highway and multiple railway lines) across Zurich. Hedgehogs are able swimmers (Reeve, 1994), but large rivers seem to limit their dispersal, as well as main transportation axes (Huijser & Bergers, 2000). The few migrants and admixed individuals identified and the significant genetic differentiation demonstrate a surprising low gene flow between clusters, indicating that the main rivers and the transportation axes function as barriers. Nevertheless, at the western part of the city, the cluster division according to GENELAND does not strictly follow the course of the main river Limmat. Two individuals, which are geographically located south of the Limmat were grouped with the northern cluster. None of these individuals was identified as migrant by GENECLASS, signifying that they belonged unambiguously to the northern cluster. In the city of Zurich, the rivers and highways are crossed by many bridges, while Bontadina (1991) has shown that hedgehogs have the capacity to cross such large roads and bridges. However, our study demonstrates that this is rarely the case. Possibly, these admixed or migrant individuals either autonomously crossed the river and transportation axes or might have been translocated by humans (which is occasionally documented by the local rescue centre).

While clustering analysis suggested that major rivers and transportation axes hinder gene flow at a large spatial scale, other landscape elements may also impact gene flow at finer spatial resolution, i.e. within the genetic clusters. Our study showed that isolation by distance (null model) alone poorly predicts genetic distance and only marginally improves the prediction when added as additional variable to isolation by effective distance models. This result indicates that effective distance is modulated by the complex urban environment and emphasizes that landscape composition plays an important role in shaping genetic structure of urban small mammals, even within a relative small geographic area of 100 km^2. Our comparison of various spatial connectivity models showed that multi-path models (CIRCUITSCAPE) based on logarithmic or linear transformation of inverse habitat preference performed best. However, while the inverse of habitat preference was best linked to daily movement through an exponential transformation, a logarithmic transformation performed best for the genetic distance. This underlines the close relationship between movement and genetic structure. However, the interpretation of the different transformation functions is not straightforward, and

only few studies exist which compared different habitat preference – resistance relationships (Trainor, Walters, Morris, Sexton, & Moody, 2013). One potential explanation is that movement through low preference habitat does not lead to gene flow. Alternatively, measures of genetic distance and movement may differ in their inherent temporal and spatial scaling properties (Beier et al., 2008).

In this study multipath models predicted gene flow better than single-path models, which is in accordance with other studies on gene flow of small forest rodents (Garrido-Garduño, Téllez-Valdés, Manel, & Vázquez-Domínguez, 2016) and on home-range movement of a species with a broad movement habitat spectrum (e.g. fishers; LaPoint, Gallery, Wikelski, & Kays, 2013). However, there are some examples where single-path models outperformed multi-path models specifically for species that are highly dependent on linear habitat elements (e.g. amphibians dependent on streams; Trumbo, Spear, Baumsteiger, & Storfer, 2013) or that perform directed movements (e.g. migration of ungulates; McClure, Hansen, & Inman, 2016; Poor, Loucks, Jakes, & Urban, 2012). Thus, model performance likely depends on species movement pattern, landscape structure and the evaluated type of connectivity, but based on the respective model assumptions we hypothesize that multi-path models may outperform single-path models for a broad range of different study systems. We predict this occurs particularly in complex habitats; an interesting topic which deserves further investigations.

Connectivity models are a crucial tool to foster the development of effective management strategies, which aim to conserve and increase habitat connectivity (e.g. many conservation programmes) or reduce connectivity (e.g. spread of disease or invasive species). In the present study, we demonstrate that by combining precise movement data, genetic data and state of the art modelling, it is possible to identify critical landscape elements which impact gene flow, even in a highly fragmented urban environment. Conservation measures are, however, seldom implemented for single species. Therefore, theoretical connectivity models should be combined and/or evaluated for multiple species. This would be a further important step, to reduce the gap between scientists and practitioners and increase the chances of a successful implementation of connectivity enhancing conservation measures.

Acknowledgments

We thank the Association Pro Igel and StadtWildTiere.ch, who kindly supported the development and funding of this study. S. Jafarzadeh helped collecting field data. R. Holderegger substantially helped to improve a previous version of the manuscript. GIS layers were provided by the Swiss Federal Office of Topography (Vector25 Swisstopo, 2011, DV03594), and the land cover maps were kindly provided by the city administration “Gruen Stadt Zurich” (Biotoptypenkartierung, 2010). This study was part of the project ENHANCE financed by CCES of the ETH Zurich and we kindly thank the module leader M. Moretti for his support.

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.landurbplan.2016.12.011.

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