Modelling functional landscape connectivity from genetic population structure: a new spatially explicit approach

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Abstract

Functional connectivity between spatially disjoint habitat patches is a key factor for the persistence of species in fragmented landscapes. Modelling landscape connectivity to identify potential dispersal corridors requires information about those landscape features affecting dispersal. Here we present a new approach using spatial and genetic data of a highly fragmented population of capercaillie (*Tetrao urogallus*) in the Black Forest, Germany, to investigate effects of landscape structure on gene flow and to parameterize a spatially explicit corridor model for conservation purposes. Mantel tests and multiple regressions on distance matrices were employed to detect and quantify the effect of different landscape features on relatedness among individuals, while controlling for the effect of geographic distance. We extrapolated the results to an area-wide landscape permeability map and developed a new corridor model that incorporates stochasticity in simulating animal movement. The model was evaluated using both a partition of the data previously set apart and independent observation data of dispersing birds. Most land cover variables (such as coniferous forest, forest edges, agricultural land, roads, settlements) and one topographic variable (topographic exposure) were significantly correlated with gene flow. Although inter-individual relatedness inherently varies greatly and the variance explained by geographic distance and landscape structure was low, the permeability map and the corridor model significantly explained relatedness in the validation data and the spatial distribution of dispersing birds. Thus, landscape structure measurably affected within-population gene flow in the study area. By converting these effects into spatially explicit information our model enables localizing priority areas for the preservation or restoration of metapopulation connectivity.

Keywords: capercaillie, dispersal corridors, habitat connectivity, landscape permeability, *Tetrao urogallus*

Received 26 January 2010; revision received 8 April 2010; accepted 22 April 2010

Introduction

Human-induced landscape fragmentation represents a major threat to biodiversity (Soulé 1987; Fahrig 1997), as small and isolated populations frequently suffer from a

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loss of genetic diversity (Frankham *et al.* 2002) and an increased extinction risk (Lande 1993). In fragmented landscapes, specialist species with extensive area requirements often only persist in a metapopulation pattern (Levins 1969), where dispersal plays a key role for long-term population viability as it sustains demographic and gene flow processes (Brown & Kodric-Brown 1977; Hanski & Gilpin 1997; Wiens 2001).

Maintaining landscape connectivity is therefore a primary objective in species conservation, which is frequently realized by the preservation or restoration of dispersal or migration corridors.

Being defined as the degree to which the landscape facilitates or impedes movement between resource patches (Taylor *et al.* 1993), landscape connectivity is inherently species-specific (Goodwin 2003) and includes two aspects: First, the distance and spatial configuration of landscape features (structural connectivity), and second, their influence on animal movement (functional connectivity; Wiens *et al.* 1997; Chetkiewicz *et al.* 2006). Several methods have been developed to quantify landscape connectivity and predict species movements. Friction analyses (e.g. Ray *et al.* 2002), rule-based step-selection functions (Revilla *et al.* 2004; Graf *et al.* 2007) and graph theory models (Urban & Keitt 2001; Pascual-Hortal & Saura 2008; Urban *et al.* 2009) allow for the detection and spatially explicit visualization of potential dispersal corridors. One of the most popular techniques is least-cost modelling (Schadt *et al.* 2002; Adriaensen *et al.* 2003), which combines geographic distance and landscape permeability. Based on raster map representations of the landscape, each landscape feature is assigned a weight that reflects the 'costs' a traversing individual has to pay, which can be estimates of energy expense, mortality risk or other factors affecting crossing-probability. Least-cost algorithms are then employed to determine the path between any pair of points that minimizes the accumulative costs. As least-cost models are intuitive and readily applicable, they are widely employed in conservation planning but suffer from several limitations. First, as empirical data on dispersal costs are rarely available, cost estimates are often based on expert opinion (e.g. Clevenger *et al.* 2002; Schadt *et al.* 2002). This can be problematic as the resulting paths are highly sensitive to the relative height of the cost values assigned (e.g. Adriaensen *et al.* 2003; Rayfield *et al.* 2010). Second, these models imply the animals' ability to find the one optimal path to the next habitat patch. This may be reasonable for short paths, but unlikely for long-distance movements, particularly for species not strictly confined to particular landscape types. Third, path selection is based on accumulative costs (Adriaensen *et al.* 2003). However, depending on species-specific movement patterns or landscape configuration, the influence of landscape permeability may be uncoupled from distance. Whereas accumulative costs may be the most critical measure for ground dispersing species engaged in long distance movement through a hostile landscape, it may be less critical in highly mobile and less physically restricted species (e.g. birds) undertaking short, stepwise patch-to-patch movements.

To base connectivity models on empirical data, measurements of organism movement through the landscape are required (D'Eon *et al.* 2002; Driezen *et al.* 2007; Spear *et al.* 2010). As dispersal events are rare, this can necessitate the marking or radio-tagging of large numbers of individuals. Moreover, given the potential stress occasioned by capture and handling, these methods may be problematic for endangered species. As an alternative, molecular genetic methods based on non-invasive sampling allow estimating gene flow as a surrogate for dispersal. Assuming a migration-drift equilibrium (Slatkin 1993), systematic patterns of genetic differentiation can be inferred by relating genetic population structure to geographical and environmental structures (e.g. Hardy & Vekemans 1999; Manel *et al.* 2003). Measures of genetic distance have been employed to evaluate cost–distance models (Coulon *et al.* 2004; Stevens *et al.* 2006; Epps *et al.* 2007) or to locate landscape-dependent discontinuities in gene flow (Manel *et al.* 2003). However, most approaches addressed the barrier function of a single landscape feature only (e.g. Vos *et al.* 2001; Keller & Largiader 2003; Epps *et al.* 2005) or identified putative barriers without specifying the particular feature affecting dispersal (Sokal & Thomson 1998; Barbujani 2000; Segelbacher *et al.* 2008). In this study, we present a new approach to assess the relative effect of different landscape features and feature combinations on gene flow in order to parameterize a spatially explicit corridor model.

As a model species we chose the capercaillie (*Tetrao urogallus*), a large forest grouse critically affected by habitat fragmentation in Central Europe. Capercaillie are characterized by extensive area requirements and are highly specialized, requiring well-structured forest habitats situated in cold winter climates (e.g. Klaus *et al.* 1989; Storch 1993, 1995; Braunisch & Suchant 2007). In Central Europe, the small and declining populations are restricted to mountain regions (Storch 2007) and—as natal dispersal distances are comparatively short (median: 5–10 km, see review in Storch & Segelbacher 2000)—isolated at the continental scale (Segelbacher *et al.* 2003a). Moreover, these mountain populations are highly fragmented due to topography and human land use with metapopulation structures assumed in most cases (Segelbacher & Storch 2002; Segelbacher *et al.* 2003b, 2008). Combining high habitat specificity, a limited mobility and a patchy population structure, this bird was considered as an ideal candidate species for connectivity modelling.

The aim of this study was to quantify landscape permeability for capercaillie in the Black Forest (Southwestern Germany) and to localize the 'corridors' crucial to the preservation of connectivity among the inhabited habitat patches. There were several components to the

study: We used genetic differentiation between individuals to identify landscape elements that affect gene flow by measuring systematic deviations from the isolation by distance (IBD) model (Wright 1943). Males and females were examined separately to test for sex-specific differences. We compared two types of landscape effects using an accumulative and a non-accumulative measure of landscape feature abundance between individuals. The measured landscape effects were transferred to a raster map quantifying species-specific landscape permeability. To compute the optimal path between two locations based on this map, we developed an alternative approach to the traditional least-cost-path modelling that was adjustable to the species-specific dispersal pattern and incorporates stochasticity in path selection. The model was evaluated using both data partitioning and observation data of dispersing birds. Finally, we used the model to locate corridors between capercaillie subpopulations providing the best conditions for dispersal and for maintaining and restoring metapopulation connectivity.

Materials and methods

Study area and species

The study area encompasses the Black Forest (7000 km^2, Southwestern Germany) a forested mountain range with an elevation ranging from 120 to 1493 m a.s.l. The capercaillie population, approximately 600 individuals, is distributed over an area of 510 km^2 (Braunisch & Suchant 2006), which is fragmented into more than 100 spatially disjoint patches (Suchant & Braunisch 2004), hereafter referred to as 'capercaillie patches' (Fig. 1). As the current population exceeds only marginally the size of a minimum viable population (500 birds, Grimm & Storch 2000), a disruption to the population connectivity would considerably increase the extinction risk, as each of the resulting parts of the population would fall below the critical size for long term survival.

Capercaillie samples and population genetic structure

Analyses were based on moulting feather samples from 213 individuals (males = 117, females = 96) collected across the study area between 1999 and 2004 and geo-referenced using the Gauss–Krüger grid (Fig. 1). According to census data (Braunisch & Suchant 2006), the sample size corresponded to about one-third of the total population size and the proportion of feathers sampled from each subpopulation roughly represented the respective subpopulation size. A stable population size throughout the sampling period and a long generation time in the species let us assume that spatial and temporal variation of sampling can be neglected. DNA was extracted from individual feather samples using a DNeasy DNA extraction kit (Qiagen) and genotyped at 10 microsatellite loci (TUT1–TUT4, TUT10, BG4–BG6, BG15 and BG18; Segelbacher et al. 2000; Piertney & Höglund 2001) as described in detail in Segelbacher et al. (2008). All samples were genotyped at least twice, the reliability of identifying individuals, potential error rates due to allelic drop out or genotyping errors were estimated using the programmes GIMLET (Valiere 2002) and DROPOUT (Mckelvey & Schwartz 2005) and no evidence for null alleles, allelic drop out or false alleles was found (Segelbacher et al. 2008). We calculated inter-individual relatedness (Lynch & Ritland 1999) as a measure for gene flow within the population using the IDENTIX software (Belkhir et al. 2002).

Landscape variables

We tested landscape variables either related to land cover or topography (Table 1), focusing on variables that had been related to capercaillie habitat selection in previous studies (Sachot 2002; Graf et al. 2005; Braunisch & Suchant 2007). Land cover variables were obtained from Landsat-5 images and the ATKIS road map (Official topographic and cartographic information system of Germany, http://www.atkis.de), distinguishing seven categories, namely 'coniferous and mixed forest', 'purely deciduous forest', 'forest edges', 'roads', 'settlements', 'agricultural land' and 'other'. 'Forest edge' was defined as a 100 m buffer to either side of the actual forest margin. A disturbance buffer of 100 m was added around settlements and roads, which was then treated as part of the settlement or road independent of the actual land cover type. Where the disturbance buffers around roads and settlements overlapped they were attributed to 'settlements.' Land cover types that were too scarce to evaluate separately (<5% of the total area) were pooled and defined as 'other'. The continuous topographic variables (i.e. altitude, topographic exposure and slope) were converted into dichotomous maps, with the thresholds for classification (Table 1) chosen according to the variable's known impact on capercaillie habitat selection (Sachot 2002; Suchant et al. 2003; Graf et al. 2005; Braunisch & Suchant 2007). For each variable, raster maps with a 120 × 120 m cell size were prepared, with cell values of 1 or 0 indicating the presence or absence of the respective feature. Consequently, each cell in the study area was characterized by one unique land cover category and three topographic attributes. The cell size is about 10% of the species' annual homerange size and was chosen so as to maximize resolution within the constraints of the given computing capacity.
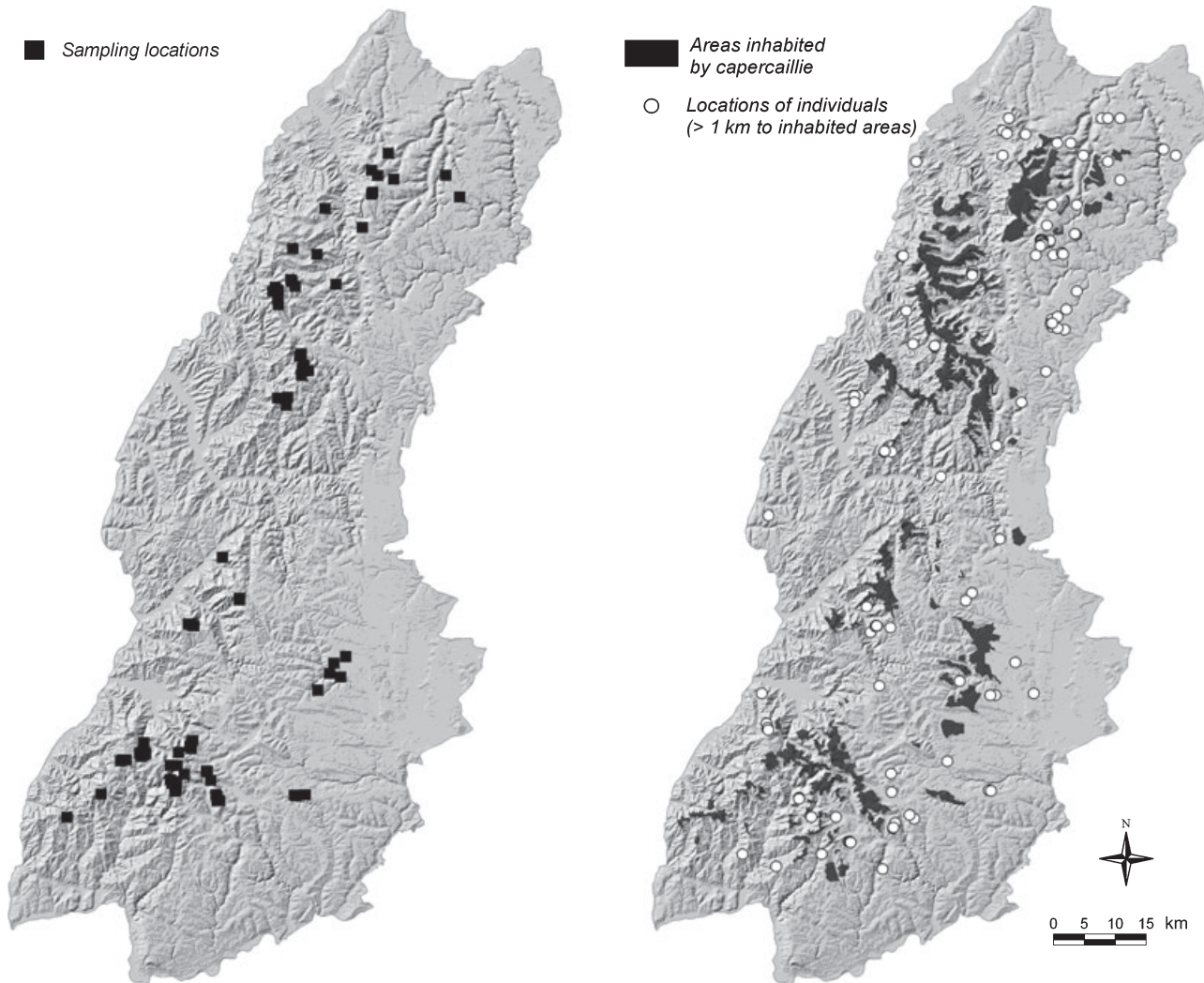
Fig. 1 Black Forest study area. The locations of the capercaillie feather samples (n = 213) are indicated to the left, the areas permanently inhabited by capercaillie and the locations of 'putative dispersers' (birds observed >1 km from inhabited areas, n = 112) are presented to the right.

Model generation

The model generation involved six successive steps (Fig. 2): (i) the analysis of landscape-structure effects on relatedness; (ii) the generation of landscape permeability maps and (iii) the corridor calculation. The model was evaluated using (iv) part of the data previously set apart and (v) independent data from dispersing birds. Finally, the model was applied to localize potential dispersal corridors in the study area (vi).
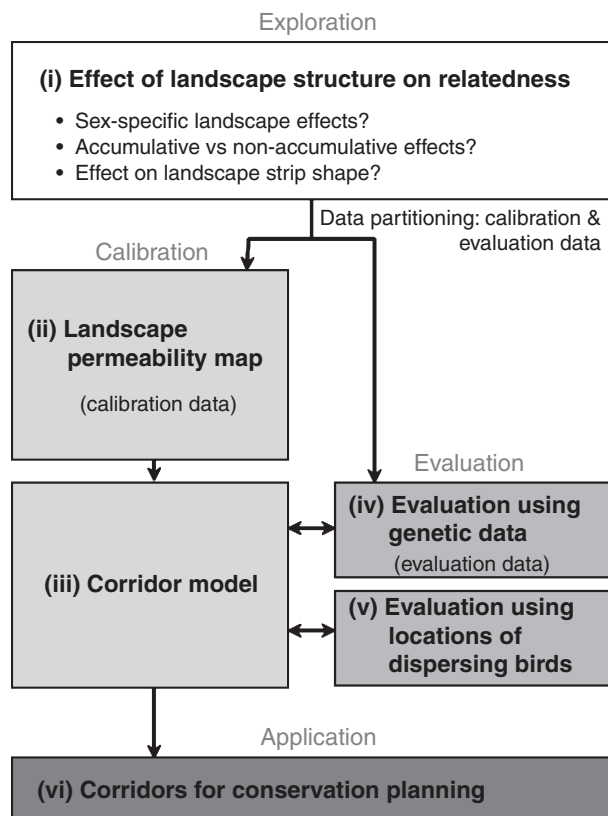
(i) Effect of landscape structure on relatedness

The first aim was to test whether, in addition to geographic distance, landscape structures affected interindividual relatedness, and to identify the variables

that promote or hinder dispersal. As Segelbacher *et al.* (2008) found male-biased IBD, we evaluated males and females separately to test for sex-specific differences in landscape effects and to assess whether a common corridor model for both sexes would be adequate.

First, the pairwise geographic (Euclidean) distance (D_p) between the sampling locations of all p possible pairs of individuals was calculated for both sexes. Then we assessed the abundance of each landscape feature within rectangular landscape strips connecting all pairs, as proposed by Emaresi *et al.* (2009). We compared five different strip-shapes, three with a fixed width of 1, 5 and 11 cells (F1, F5 and F11, corresponding to 120, 600 and 1320 m) and two with a length:width ratio of 5:1 (R5) and 11:1 (R11). For each strip type two measures

Table 1 Land cover and topography variables tested in the model

Variable description	Code	Definition	Data source
Land cover			
Coniferous and mixed forest	FCOMI	Coniferous and mixed forest	Landsat 5
Deciduous forest	FDEC	Purely deciduous forest	Landsat 5
Forest edges	FOEDG	Proportion of border area between forest and open land (100 m to either side of the forest edge)	Landsat 5
Roads	STALL	Areas influenced by roads (all road categories pooled) including 100 m buffer to either side	ATKIS
Settlements	SETTL	Urban areas and settlements including 100 m buffer	Landsat 5
Agricultural used land	AGALL	Intensively and extensively used grassland, pastures, agricultural land	Landsat 5
Other	OTHER	Water, wetland, vegetation-free areas	Landsat 5
Topography			
Topographic exposure	CONC	Depressions, e.g. valley floors (topex values >50)	DEM, topex-to-distance index 2000,
	CONV	Exposed areas, e.g. ridges, hilltops (topex values <50)	modelled according to Mitchell *et al.* (2001)
Slope	SLOPE	Slope >30°	DEM
Altitude	HIGH	High montane areas, defined according to Schlenker & Müller (1978) (Southern Black Forest: >1080 m a.s.l., Northern Black Forest: >900 m a.s.l)	Digitized according to Schlenker & Müller (1978)
	LOW	All lower altitudes	

Fig. 2 Analytical steps used in this study. The numbers in parentheses correspond to the numbers given in the chapter headers of the methods and results section.

were calculated, (a) the absolute number of grid cells in the pth strip ($C_{p,i}$) containing the ith landscape variable (V_i), and (b) the proportion of cells containing a landscape feature; that is, $C_{p,i}$ divided by the total number of cells in the strip (A_p). Whereas $C_{p,i}$ assumes the effect of a landscape feature to be accumulative over all intervening cells, $C_{p,i}/A_p$ tests for non-accumulative effects. Strip statistics were calculated using the FRICTIONNATOR programme (Hirzel & Fontanillas 2007, unpublished; available at: http://www.unil.ch/biomapper/friction nator/frictionnator.html).

To uncouple the effects of landscape and geographic distance, we first quantified IBD by calculating a two-matrix Mantel test (Mantel 1967; Legendre & Fortin 1989) between pairwise relatedness (REL$_p$) and D_p, and then tested for additional landscape effects by using the residuals (R_p) of the IBD model (eqn 1) in mantel tests with each of the landscape variables. Mantel tests were performed in R (R Development Core Team 2006) with the package ECODIST 1.1.2 (Goslee & Urban 2007), significance was assigned on the basis of 1000 randomizations.

$$\text{REL}_p \propto \beta_0 + \beta_1 D_p + R_p, \tag{1}$$

where REL$_p$ is the relatedness coefficient between individuals of the pth pair, D_p is the geographic distance between them, β_0 and β_1 are the intercept and regression coefficient of D_p, respectively, and R_p is the residual value.

(ii) Landscape permeability map

In order to create a map quantifying the relative landscape permeability of each grid cell in the study area, we calculated multiple regressions on distance matrices (Manly 1991) between the residuals of the IBD-model and each combination of land cover and topography variables (significant in univariate models) that could co-occur in a cell (eqn 2). For this, the datasets of males and females were randomly and equally partitioned into a calibration and a validation subset, using only the former for model generation (Fig. 2). Models were calculated for both sexes combined and utilized the relative measure of landscape feature abundance ($C_{p,i}/A_p$) within a 5-cell wide landscape strip, as no sex-specific differences, no effect of absolute landscape feature abundance ($C_{p,i}$) and no differences between strip shapes had been recorded in the preceding analyses (*i*, see Fig. 2). Multiple regressions were performed using F_{stat} (Goudet 2001), with significance assigned after 1000 randomizations:

$$R_p \propto \alpha_0 + \sum_{i=1}^{n} \alpha_i \frac{C_{p,i}}{A_p} + \varepsilon_p, \qquad (2)$$

where R_p: residuals of the regression of relatedness and geographic distance, for the *p*th pair of individuals, *n*: number of features considered, α_0: intercept, α_i: regression coefficient of the variable V_i, $C_{p,i}$: the number of cells in the strip between the *p*th pair of individuals with occurrence of the variable V_i, A_p: the total number of cells in the strip between individuals of the *p*th pair and ε_p: error term.

Assuming the effect of each variable or variable combination on relatedness to be a correlate of species specific landscape permeability, and permeability to be an additive function across landscape variables, the permeability value (L) of each cell (x) was then computed by summing up the significant regression coefficients that describe the relationship between the residuals from the IBD model and the landscape variables present in this cell (eqn 3). The non-significant regression coefficients ($P > 0.05$) were set to zero.

$$L(x) = \sum_{i=1}^{n} \alpha_i O_{x,i} \qquad (3)$$

where $L(x)$ is the permeability value of cell x, α_i are the coefficients computed in eqn 2 and $O_{x,i}$ is equal to 1 if the feature i occurs in cell x and is equal to 0 otherwise. O may thus be seen as $C_{p,i}/A_p$ computed for a single cell.

(iii) Maximum permeability path (MLP) and MLP-corridors

We developed an alternative approach to the least-cost-path method to localize the best connection between any pair of points: First, 1000 random paths are calculated between the pair of points in question and the best path (maximum landscape permeability path, MLP) retained. This 'best path' can be selected so as to maximize the mean permeability (μ_L, non-accumulative effects) or the accumulative of permeability (Σ_L), respectively, depending on the observed species-specific gene flow pattern. Repeating this procedure *n*-times (with *n* being user-defined) results in *n* partly overlapping MLP replicates forming a corridor. The path selection routine was implemented in the FRICTIONNATOR software (Hirzel and Fontanillas, 2007, unpublished).

(iv) Model evaluation using genetic data

We evaluated the permeability map for males and females separately. To quantify the effect of modelled permeability on relatedness and to test whether permeability along MLP-corridors explained more variance than permeability along straight strips the results of two models were compared. First, we calculated the effect of Euclidean distance (D_p) on relatedness, then using the residuals of this model to test for an additional effect of mean landscape permeability (μ_L) within straight landscape strips (5-cell width). Second, we generated MLP-corridors consisting of 10 paths between all pairs of individuals, averaging MLP-length and μ_L over the 10 MLP-replicates. We compared 'isolation by Euclidean distance' to 'isolation by MLP-length' and used the residuals of the latter model to determine the additional effect of μ_L along the MLP-corridor. Two-matrix Mantel tests (1000 randomizations) were performed, using the *R*-package ECODIST 1.1.2 (Goslee & Urban 2007).

(v) Model evaluation using locations of dispersing birds

To test whether individuals preferred high-permeability areas during dispersal, we performed a second, independent model evaluation, using data (collected from 1996 to 2005 according to Braunisch & Suchant 2006) pertaining to moving or potentially dispersing birds observed more than 1 km from the capercaillie patches (Fig. 1). The 1 km threshold was chosen because a telemetry study showed that more than 95 % of non-dispersing birds sporadically using areas outside of the permanently inhabited sites remained within this distance (Braunisch & Thiel, unpublished). The locations of these birds ('putative dispersers', $n = 112$) were compared to random locations using bootstraps (100 replicates). The locations of each random replicate were chosen so as to have the same distance distribution to the capercaillie patches to exclude potential influences of distance.

In a first step we tested whether the spatial patterns of 'disperser' observations supported the genetics-based results of landscape features positively or negatively affecting dispersal. Based on the assumption that the bird came from the closest inhabited patch, we compared observations and random locations regarding the landscape feature proportions (C_d/A_d) within the d landscape strips connecting the locations with the closest capercaillie patch.

Subsequently, we assessed whether the modelled permeability contributed to explaining the spatial pattern of the disperser observations. First, landscape permeability at the birds' locations was compared to that of the random locations. Second, the mean permeability (μ_L) within the landscape strips connecting the dispersers' locations with the next capercaillie patch and third, μ_L along the corresponding MLP-corridor (10 MLP-replicates averaged) were calculated and compared to random expectation.

(vi) Corridors for conservation planning

Finally, to locate the areas with the best relative conditions for inter-patch dispersal, we calculated corridors between all capercaillie patches located more than 1 km from the next neighbour. Corridors consisted of 100 MLP-replicates between the patches' centroids in the Delaunay triangulation network (Fig. 6). The centroid-to-centroid approach was chosen as we were only interested in corridor location and not in values of inter-patch connectivity. For the same reason it was preferred over an edge-to-edge calculation (e.g. Fall *et al.* 2007) because it requires no a priori assumptions about the MLPs' start and ending points, which may depend on the permeability pattern within the patches. As the MLP-replicates are calculated independently, the number of paths passing through a grid-cell of the study area can be regarded as an indicator of the cell's relative importance for inter-patch connectivity.

Results

Effect of landscape structure on relatedness

Inter-individual relatedness varied greatly within the Black Forest capercaillie population (min.: −0.46; max.: 0.94; mean: −0.01; SD: 0.17). IBD differed significantly between the sexes and was greater in males (Mantel $R = -0.0945$, $P < 0.001$) than in females (Mantel $R = -0.0388$, $P < 0.01$; Fig. 3). Most of the land cover variables and two of the topographic variables additionally explained relatedness, but only when considering the proportion of landscape features within interconnecting landscape strips ($C_{p,i}/A_p$) (non-accumulative effect, Fig. 3a). Except for altitude, no significant effects were recorded for the absolute number of cells containing a landscape feature ($C_{p,i}$) (accumulative effect, Fig. 3b). Relatedness was positively correlated with the proportion of coniferous and mixed forest and negatively correlated to forest edges, roads, settlements and agricultural land. Topographic exposure and altitude revealed a significant effect in males and females respectively. No sex-specific differences were recorded with regard to landscape feature effects (Fig. 3a,b).

Landscape permeability map

The results of the univariate regression models for both sexes combined corresponded to the sex-specific results (Table 2). Multiple regressions included the combinations of the two significant topographic variables CONV and CONC with each of the significant land cover variables (FCOMI, FOEDG, STALL, SETTL, AGALL; see Table 1 for variable codes). Landscape permeability values (L) ranged between −0.220 and 0.078. They were positive for cells containing variable combinations that were positively correlated with relatedness and negative for variable combinations that hindered gene flow accordingly (Fig. 4).

Model evaluation using genetic data

Mean landscape permeability (μ_L) within the connecting landscape strips was significantly correlated with inter-individual relatedness after removing the effect of Euclidean distance (D_p) (Table 3). In both sexes gene flow tended to be more strongly correlated with MLP-length than with Euclidean distance, but differences were not significant. Although the MLPs maximized mean permeability, μ_L along the MLP corridor still made a significant additional contribution to explaining relatedness. The overall amount of explained variance was very low for all models; nevertheless relatedness was slightly better explained by distance and permeability along the corridor than along the straight connection (Table 3).

Model evaluation using locations of dispersing birds

Evaluation of the variable rating. The observations of moving or dispersing birds were located within a mean distance of 3.44 km (min.: 1.02; max.: 17.68) from the closest capercaillie patch. The results obtained for the variable proportions measured within the connecting landscape strips corresponded to the results obtained from the genetic data. Compared to random expectation, a higher proportion of coniferous and mixed for-
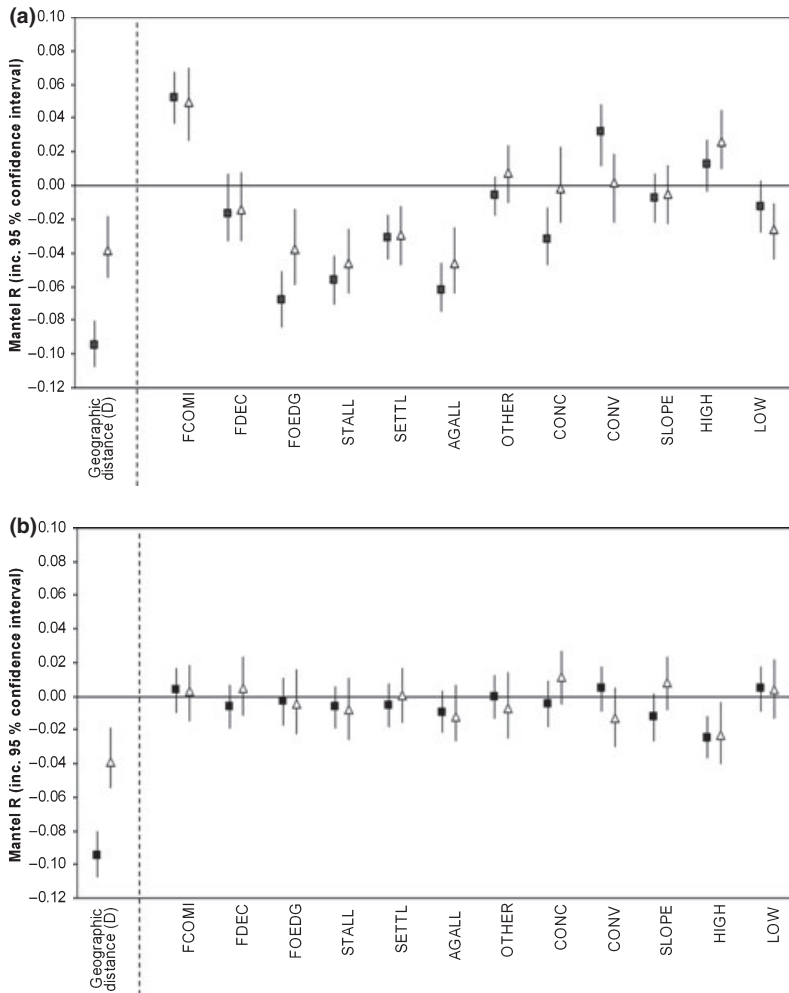
Fig. 3 Results of two-matrices mantel tests calculated between inter-individual relatedness and geographic distance (*D*) and between the residuals of the IBD model and the relative (a) or absolute (b) abundance of each landscape variables, measured within a 5-cell wide landscape strip. We compare males (squares) and females (triangles). The Mantel *R* with 95 % confidence interval (based on 1000 permutations) is indicated. The codes for the landscape variables are explained in Table 1.

est, and a lower proportion of forest edges, agricultural land and roads, was recorded in the disperser's strips. Moreover, though not significant, they tended to contain lower proportions of deciduous forests and settlements, and a higher proportion of exposed sites, compared to depressions and valleys (Table 4).

Evaluation of the permeability map and the MLP-corridor model. The landscape at the dispersers' locations was characterized by significantly higher permeability than at the random locations. Moreover, the mean permeability (μ_L) within the dispersers' landscape strips was higher than expected and the same applied to μ_L over the 10 MLP replicates (Fig. 5). On average, the dispersers' MLPs were 1.8 times longer than the Euclidean distance to the next capercaillie patch. The relative increase in distance was similar for the random points (bootstraps, 95 % CI: 1.76–1.94), so the higher permeability recorded along the disperser's MLPs was not associated with longer detours.

Corridors for conservation planning

MLP-corridors were calculated between 108 pairs of capercaillie patches (Fig. 6). The 100 MLP-replicates between pairs of patches differed considerably in some regions, depending on the spatial pattern of permeability of the intervening landscape. Corridors deviated from the straight connection between centroids and frequently crossed spatially isolated, unoccupied habitat patches previously identified by a habitat model in the study area (Braunisch & Suchant 2007, results not illustrated).

Discussion

Effect of landscape structure on gene flow

We related landscape structure to the genetic structure of a fragmented capercaillie population, characterized by a low but significant overall genetic differentiation

Table 2 Results of (a) univariate and (b) multiple regressions on distance matrices, investigating the correlations of all variables and variable combinations that can occur in any cell within the study area with relatedness (both sexes). The residuals of the 'isolation by distance'-model served as the dependent variable

(a) Single variables

V_1	R_1	α_1	$P(\alpha_1)$	L
FCOMI	0.061	0.083	***	0.083
FDEC	−0.029	−0.086	*	−0.086
FOEDG	−0.072	−0.103	***	−0.103
STALL	−0.072	−0.165	***	−0.165
SETTL	−0.041	−0.195	**	−0.195
AGALL	−0.062	−0.112	***	−0.112
OTHER	0.003	0.002	n.s.	0.000
HIGH	0.024	0.014	n.s.	0.000
LOW	−0.024	−0.014	n.s.	0.000
CONV	0.035	0.037	**	0.037
CONC	−0.035	−0.037	**	−0.037
SLOPE	−0.026	−0.121	n.s.	0.000

(b) Variable combinations

V_1	V_2	R_1	R_2	α_1	α_2	$P(\alpha_1)$	$P(\alpha_2)$	L
FCOMI	&CONV	0.057	0.008	0.078	0.008	***	n.s.	0.078
FDEC	&CONV	−0.009	0.028	−0.027	0.030	n.s.	n.s.	0.000
FOEDG	&CONV	−0.068	0.010	−0.098	0.011	***	n.s.	−0.098
STALL	&CONV	−0.069	0.027	−0.157	0.028	***	*	−0.129
SETTL	&CONV	−0.039	0.032	−0.185	0.035	**	*	−0.150
AGALL	&CONV	−0.058	0.024	−0.103	0.025	***	n.s.	−0.103
FCOMI	&CONC	0.057	−0.008	0.078	−0.008	***	n.s.	0.078
FDEC	&CONC	−0.009	−0.028	−0.028	−0.030	n.s.	n.s.	0.000
FOEDG	&CONC	−0.068	−0.010	−0.098	−0.011	***	n.s.	−0.098
STALL	&CONC	−0.069	−0.026	−0.158	−0.028	***	*	−0.186
SETTL	&CONC	−0.039	−0.032	−0.185	−0.035	**	*	−0.220
AGALL	&CONC	−0.058	−0.024	−0.103	−0.025	***	n.s.	−0.103

V_i: landscape variable (for variable codes refer to Table 1). R_i: (partial) regression coefficient for variable V_i, α_i: non-standardized regression coefficient of V_i, $P(\alpha_i)$: level of significance of α_i-based on 1000 randomizations (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, n.s. = not significant). Landscape permeability (L) is defined as the sum of significant regression coefficients.

(Segelbacher *et al.* 2008). Correlations between inter-individual relatedness and landscape feature abundance were thus low; as was the overall amount of variance explained by the resulting models. Nevertheless, significant landscape-related patterns in gene flow were found, with coefficient values commensurate with those of other studies (e.g. Coulon *et al.* 2004; Elmer *et al.* 2007).

Landscape effects were investigated independent from geographic distance, by applying mantel tests on the residual matrix of the IBD model. This procedure resembles partial mantel testing as proposed by Smouse *et al.* (1986). Partial mantel tests have recently been controversially discussed (Raufaste & Rousset 2001; Castellano & Balletto 2002; Rousset 2002; Goslee & Urban 2007), as they tend to produce higher type-1

errors than expected due to the permutation procedure (Raufaste & Rousset 2001; Rousset 2002). However, as landscape effects and distance effects are often strongly intercorrelated, there is an even higher risk of incorrectly rejecting the null hypothesis when testing for the former without controlling for the latter (Cushman & Landguth 2010). The partial mantel approach, when used for 'causal modelling' (Cushman *et al.* 2006), proved to be a valuable tool to detect and control for spurious correlations and to correctly filter out the driving factors of gene flow (Cushman & Landguth 2010).

The observed landscape effects on capercaillie, dispersal largely corresponded to the birds' habitat selection pattern: Gene flow was positively correlated with preferred landscape features (as coniferous forest or topographically exposed sites) and negatively with
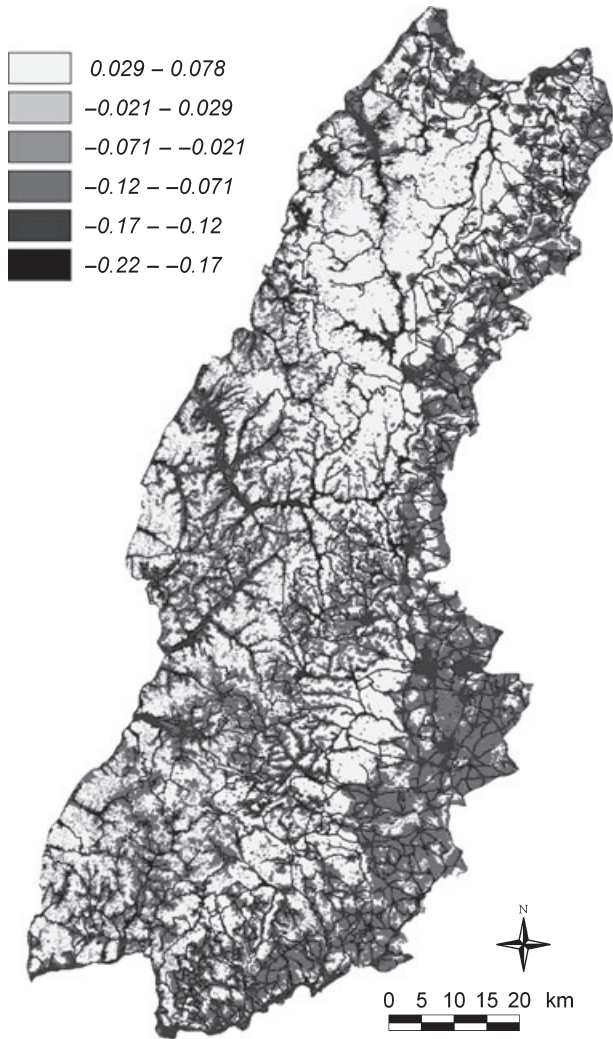
Fig. 4 Landscape permeability for capercaillie. Positive values indicate high and negative values indicate low landscape permeability.

features avoided in habitat selection (e.g. streets, settlements, agricultural land, forest edges). This is reasonable, as suitable habitat is expected to attract moving animals and to involve lower migration costs; e.g. with regard to food availability or predation risk. Based on these considerations, inverse values of resource selection functions have been employed to parameterize corridor models (e.g. Carroll *et al.* 2001). However, the factors driving habitat selection may deviate considerably from those affecting movement (Chetkiewicz *et al.* 2006; Spear *et al.* 2010). In capercaillie, altitude revealed the greatest explanatory value in habitat selection models (Sachot 2002; Suchant & Braunisch 2004), but was not correlated with dispersal. This makes ecological sense as altitude is a surrogate for climate, with cold regions promoting favourable vegetation structures (Braunisch & Suchant 2007)—crucial for inhabitation and reproduction, but not necessarily for movement. The birds' movement pattern along ridges or between hilltops, which is hypothesized as a strategy for saving energy while maintaining altitude, was rather reflected by a positive effect of exposed sites on gene flow. Consequently, although suitable habitat may reveal the best conditions for movement, the decrease in habitat suitability does not necessarily equal the decline in landscape permeability for a species.

Accumulative vs. non-accumulative effects of landscape features

Path-selection models, such as least-cost models, are generally based on the a priori assumption that landscape effects are accumulative over distance. Our analyses show no indication for accumulative landscape effects on capercaillie in the study area. These findings were consistent for single landscape features as well as for the

Table 3 Evaluation of the modelled permeability using the validation datasets

Connectivity measure	Controlling for	Mantel R (95 % CI)	P (Mantel R)	R^2 (%)
Males				
Euclidean distance (D_p)	–	−0.102 (−0.118 to −0.088)	0.001	1.05
MLP-corridor length (C_p)	–	−0.113 (−0.132 to −0.096)	0.001	1.28
μ_L (straight strip)	D_p	0.041 (0.019 to 0.062)	0.01	1.21
μ_L (corridor)	C_p	0.057 (0.038 to 0.077)	0.001	1.61
Females				
Euclidean distance (D_p)	–	−0.039 (−0.062 to −0.017)	0.049	0.15
MLP-corridor length (C_p)	–	−0.052 (−0.073 to −0.029)	0.009	0.26
μ_L (straight strip)	D_p	0.053 (0.022 to 0.077)	0.005	0.43
μ_L (corridor)	C_p	0.067 (0.039 to 0.089)	0.002	0.70

'Isolation by Euclidean distance' and 'isolation by MLP-corridor length' were obtained from two-matrix mantel tests with inter-individual relatedness. The residuals of these models were then used to test for an additional effect of modelled permeability within the straight landscape strip (5-cell width) or along the modelled corridor (10 MLPs averaged) while controlling for the effect of Euclidean distance or MLP length, respectively. *P*-values and 95 % confidence interval are calculated based on 1000 permutations.

Table 4 Mean variable proportions within landscape strips (width: 5 cells) connecting the locations of 'putative dispersers' (Fig. 1) with the closest capercaillie patch.

Variable	Mean	Random expectation (95 % CI)
FCOMI*	0.717	0.589–0.680
FDEC	0.080	0.073–0.119
FOEDG*	0.217	0.274–0.351
STALL*	0.185	0.189–0.250
SETTL	0.084	0.072–0.116
AGALL*	0.153	0.188–0.270
CONC	0.354	0.340–0.451
CONV	0.646	0.549–0.660
SLOPE	0.032	0.015–0.035
HIGH	0.083	0.049–0.114
LOW	0.917	0.886–0.951

*Variables in which the dispersers' paths differ significantly ($P < 0.05$) from random expectation (obtained from bootstraps, 100 replicates, 95 % confidence interval given in parentheses). For variable codes see Table 1.
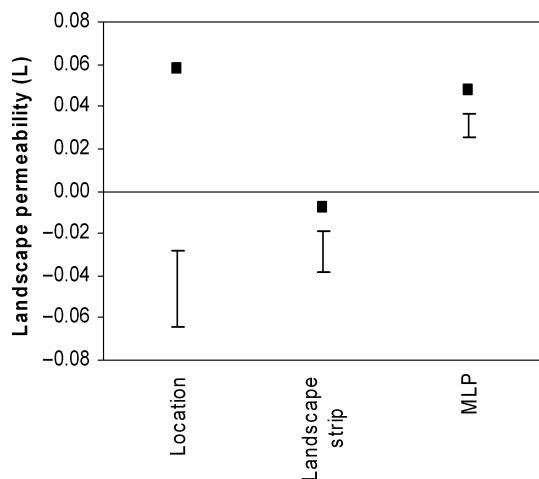

Fig. 5 Spatial distribution of 'putative dispersers' with regard to modelled landscape permeability. The mean permeability values at the dispersers' locations ('location'), within a 5-cell wide landscape strip ('landscape strip') and along the MLP-corridor connecting these locations with the closest capercaillie patch are indicated (squares) and compared to random expectation (bootstraps, 100 replicates, 95 % confidence interval indicated).

modelled landscape permeability, as correlations with relatedness were only found for the mean, not for the accumulative permeability (after transforming L to positive values, results not shown). In contrast to ground-dispersing species, capercaillie is less restricted by physical barriers and a telemetry study in the same area showed that longer distances mostly involved short, stepwise movements between patches of suitable habitat (Brau-

nisch and Thiel, unpublished). Although the landscape permeability in the study area is very heterogeneous, habitat patches and areas of high permeability are quite evenly distributed and there are no large areas that may act as total barriers. Consequently, the probability for movements may more likely be related to the intervening proportion of preferred or avoided landscape features, than to the sum of physically constraining landscape effects that accumulate over critical distances. However, an analysis of capercaillie populations under physically more restricting dispersal conditions (e.g. in the Central Alps) may provide better insight whether this is a general capercaillie pattern or solely related to the landscape conditions specific to the study area.

Parameterizing connectivity models based on population genetic data

Whereas the focus of past studies was on the effect of landscape structure on gene flow (e.g. Coulon *et al.* 2004; Stevens *et al.* 2006; Epps *et al.* 2007; Clark *et al.* 2008), we aimed to translate these effects into spatially explicit information by parameterizinig a landscape permeability map directly applicable for analytical and conservation purposes. However, several potential sources of error have to be considered when deriving permeability-values from genetic data (Epps *et al.* 2007; Spear *et al.* 2010). First, estimates of genetic differentiation reflect dispersal patterns with a temporal delay of usually unknown dimension (e.g. Anderson *et al.* 2010). They can reflect recent habitat fragmentation but also historical events such as population bottlenecks (Whitlock & McCauley 1999). In our case, the genetic structuring can be attributed to the last three decades, as genetic analyses of historic specimens (from 1852 to 1970), revealed no pattern of spatial differentiation (Segelbacher *et al.* 2008). Second, measures of gene flow reveal only effective dispersal; that is, the movement of animals that have reproduced successfully. Dispersal events by non-reproducing animals can only be detected when the individual is sampled directly. As our dataset comprised approximately one-third of the total population, we assume that recent dispersers of this kind have been included to a large extent, but a bias may remain. Third, sex-biased dispersal can cause different patterns in genetic structure (e.g. Coulon *et al.* 2004). These may not only be caused by sex-specific differences in dispersal distance or frequency, but also by different tolerance levels towards particular landscape features. Although in capercaillie IBD was stronger in the philopatric males, we found no sex-specific differences in landscape structure effects. Nevertheless, to exclude potential errors, we recommend that males and females be addressed separately first.
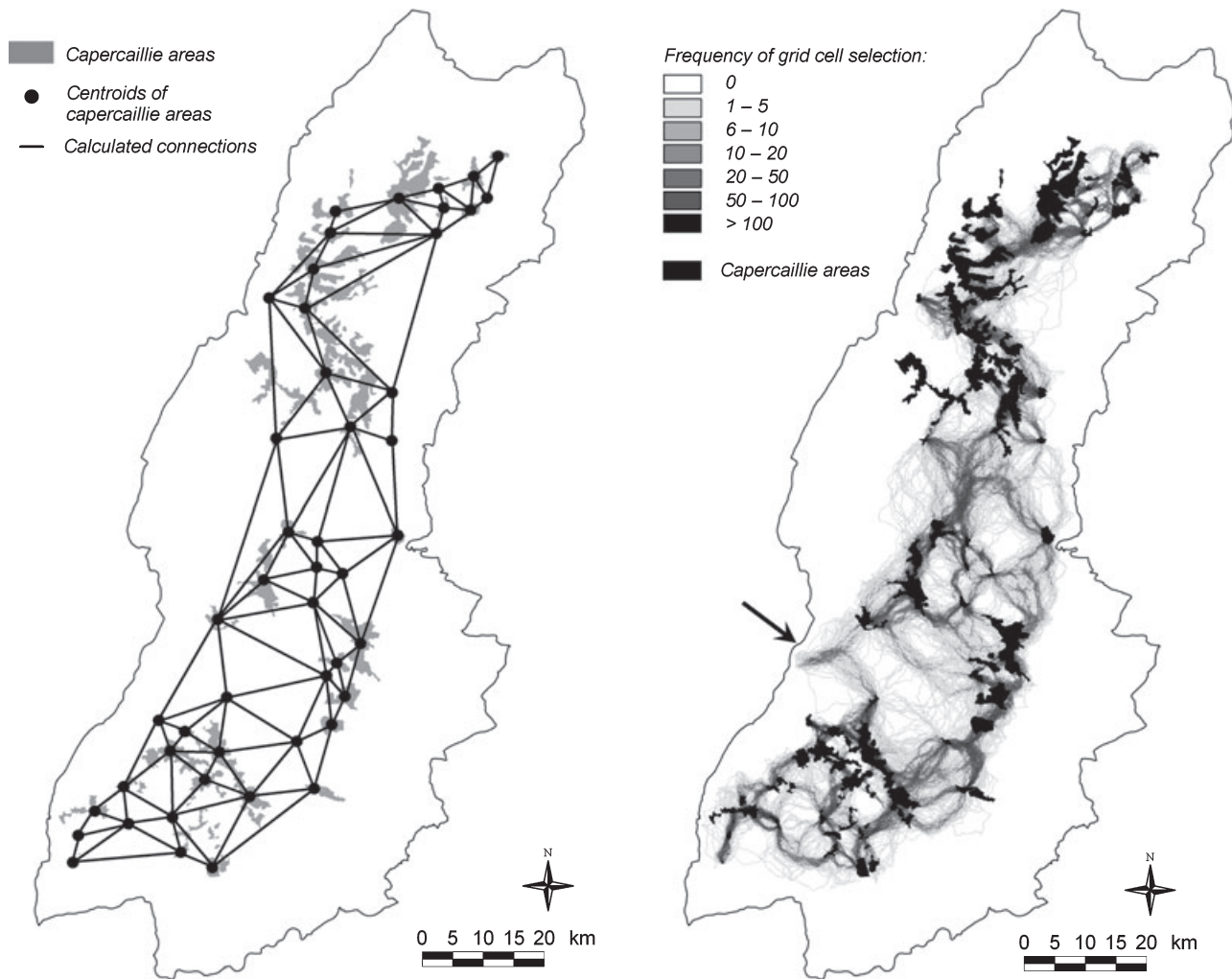
Fig. 6 Connections between the centroids of capercaillie patches (>100 ha, >1 km distance to next neighbour) for which corridors were calculated (left), and the resulting corridors (right). The detour associated with the corridor in the very eastern part of the study area (indicated by an arrow) is remarkable as it leads to an uninhabited habitat patch identified by a habitat suitability model (Suchant & Braunisch 2007).

MLP-corridor model

Dispersal is rarely restricted to one single, optimal pathway and models that included multiple path options have been shown to outperform single-path models in predicting gene-flow (McRae & Beier 2007). We present a new approach to corridor modelling, defining corridors as areas where 'favourable paths' are concentrated. This method is related to the 'multiple shortest path' approach proposed by Pinto & Keitt (2009) and offers several advantages over related techniques such as traditional least-cost-path modelling. First, as the path-selection procedure is repeated several times with random replicates being generated independently, the model simulates stochasticity in animal path selection. There is no absolute 'best path,' but rather a cloud of probability that widens as distance increases. Conse-

quently, the optimal route is shown together with secondary routes that might be upgraded by management efforts (Hargrove *et al.* 2005). Second, the heterogeneity of matrix permeability is visualized, as homogeneous landscapes lead to a larger spread of the paths whereas in heterogeneous landscapes the routes are often concentrated along narrow corridors. This helps to identify bottlenecks of particular importance for functional connectivity—and conservation. Finally, the path-selection routine allows for a flexible adaptation of the path-selection criteria to the observed species-specific pattern of gene flow, e.g. the selection of the path with the lowest accumulative or mean costs, or the most homogeneous path.

Although there were trends, length and mean permeability (μ_L) of the corridor did not explain capercaillie relatedness better than length and μ_L of a straight

landscape strip. Two factors may have contributed to this. First, as the landscape strip covered a broad band, it is likely that it contained the MLP-corridor in some cases, particularly when the distances were short. Second, as capercaillie is not totally restricted with regard to movement, it sometimes may prefer the straight path over the MLP; for example, when the destination is within sight. However, two aspects support the use of corridors. First, although μ_L was maximized along the MLP, and thus covered a much narrower range of values than in the straight landscape strip, it still contributed significantly to explaining relatedness, and this contribution tended to be even stronger than the correlation of μ_L within the strip. Second, μ_L measured along the MLPs of the 'putative dispersers' corresponded more closely with the permeability values prevailing at the locations where the birds were actually observed. Even if dispersing capercaillies may not be strictly confined to the calculated corridors, these corridors reveal information valuable from a conservation perspective, as they indicate where the conditions for inter-patch movements are best and can be either maintained or restored with the least effort.

Conservation implications

The aim of our study was to localize priority areas for dispersal between the capercaillie patches, primarily without addressing absolute measures of inter-patch connectivity in the metapopulation network. In accordance with this focus no thresholds (such as maximum dispersal distances or a minimum threshold for permeability) were included. As a consequence, some of the delineated corridors may be more limited with regard to their actual usability by capercaillie than others. In view of the habitat configuration in the study area with all patches within dispersal distance, and given our model species' ability to fly, we consider this approach to be sufficient for our purposes. However, in other cases, e.g. where species are totally limited in their movement by particular landscape features, or where inter-patch distances exceed the species-specific dispersal limit, such thresholds are indispensable for excluding unusable corridors from management considerations.

In the Black Forest, a broad non-forested valley with roads and settlements separating the northern and southern parts of the population was identified as the most critical barrier to dispersal. We therefore recommend to preserve and restore intervening stepping stone habitat patches and to avoid potentially detrimental impacts along corridors, such as the erection of wind farms. However, as corridors alone do not guarantee dispersal success, corridor improvement must be paralleled by measures to improve habitat quality in order to enhance reproductive success (i.e. the number of potential dispersers) in the source patches.

Conclusions

We present a novel approach of correlating inter-individual genetic distances with landscape features to develop a spatially explicit corridor model. The method presented can also be applied to measures of genetic distance between populations (e.g. F_{ST}-values) instead of individuals. The model provides measures of structural and functional connectivity in terms of corridor length and landscape permeability that can also be used to quantify relative inter-patch connectivity. This information can be included when using the permeability map for other corridor detection approaches; e.g. for specifying movement rules for individual-based random-walk models. Integrating the results in models addressing metapopulation dynamics and viability will be an important issue in future studies and the design of most appropriate conservation plans.

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