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RESEARCH ARTICLE

Matrix quality and habitat configuration interactively determine functional connectivity in a widespread bush cricket at a small spatial scale

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Abstract Unlike rare or specialised species, widespread abundant species have often been neglected when studying effects of habitat fragmentation. However, recently, it was shown that in the widespread abundant bush cricket *Pholidoptera griseoaptera* gene flow becomes restricted when the share of suitable habitat dropped below a threshold of 20% at the landscape scale. Here, using the same highly fragmented landscape, we studied the impact of habitat configuration and matrix quality on genetic variation and population differentiation of *P. griseoaptera* at a small spatial scale. We investigated four clusters of three populations that were either disconnected or connected and had either low quality (arable land) or high quality (grassland) matrix. The number of alleles was significantly lower in disconnected than in connected clusters, irrespective of matrix quality. Genetic differentiation was equally high in the two disconnected clusters and in the connected cluster with low quality matrix ($G_{ST} \geq 0.030$; $D \geq 0.082$), whereas it was significantly reduced when connected habitats were embedded in a high quality grassland matrix ($G_{ST} = 0.004$; $D = 0.011$). Analyses of least-cost paths showed that grassy landscape elements in fact represent high quality matrix, but that linear grassy margins are costly for dispersal. The effect of habitat configuration on genetic diversity may be explained by lower effective population sizes in disconnected habitats. The fact that only the connected populations in high quality matrix were not differentiated indicates that landscape management should simultaneously consider habitat configuration and matrix quality to effectively promote small and dispersal-limited species, also at small spatial scales.

Keywords Agricultural landscapes · Dispersal · Landscape genetics · Gene flow · *Pholidoptera griseoaptera* · Population genetic structure

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Introduction

Declines in biological diversity are largely driven by anthropogenic land-use activities and the resulting habitat fragmentation (Foley et al. 2005). Particularly, the fragmentation of semi-natural habitats in European agricultural landscapes caused many farmland species to decline (Benton et al. 2003; Billeter et al. 2008). In

contrast to many specialised and rare species, more generalist and widespread species have been considered less susceptible to fragmentation (Marvier et al. 2004; Scott et al. 2006; Devictor et al. 2008). Hence, these widespread species have received rather little attention in species-specific studies on the ecological effects of habitat fragmentation (Tscharntke et al. 2002; Henle et al. 2004). However, in modern agroecosystems it was recently found that critical thresholds of habitat fragmentation exist, below which gene flow was negatively affected also in a widespread species (Lange et al. 2010).

Since many widespread species are often abundant, they are quantitatively important for ecosystem functioning. This is particularly true for insect species that serve as pollinators, herbivores, predators and decomposers as well as food for many vertebrates. Inter-patch dispersal and gene flow are reduced by habitat fragmentation, which can seriously alter ecosystem functioning (e.g. Diekötter et al. 2007a; Haynes et al. 2007; Farwig et al. 2009) or result in reduced fitness (e.g. Reed and Frankham 2003) and increased local extinctions (e.g. Nieminen et al. 2001). Therefore, it is important to elucidate the configuration and spatial scale, at which the landscape affects also widespread species to ensure their persistence and functioning in modern agricultural landscapes.

Populations that are distributed across different habitat patches are impacted by the landscape structure in various ways. For example, populations and the inhabited landscape elements may be more or less spatially isolated or connected, thus, forming either a continuous habitat or spatially isolated patches separated by non-habitat matrix. This matrix, in turn, may again differ with respect to temporal persistence and structural composition and, thus, being either of low or of high quality. Hence, fragmentation effects have been attributed either to inter-patch distance (Neve et al. 2000; Şekercioğlu et al. 2002), the quality of the intervening matrix (Brosi et al. 2008) or a combination of both (Haynes and Cronin 2003; Bender and Fahrig 2005; Diekötter et al. 2010). In a quantitative review, Prevedello and Vieira (2010) showed that patch size and isolation were the main determinants of ecological parameters like movement behaviour or abundance. However, in 44% of the studies reviewed a matrix effect equal or greater than that of patch isolation was found (Prevedello and Vieira 2010). Hence, further investigations are needed to infer the role of landscape matrix relative to patch isolation, which may guide landscape planning and conservation in fragmented landscapes.

Using the flightless bush cricket, *Pholidoptera griseoaptera*, as a model for widespread species in modern agroecosystems, Lange et al. (2010) determined a threshold effect of habitat fragmentation. The authors found that once suitable habitat dropped below an area percentage of 20%, genetic differentiation among very highly fragmented populations significantly increased compared to less fragmented populations. Moreover, the patterns of differentiation indicated that inter-patch distance and matrix quality had interactive effects on dispersal, gene-flow and thus on the persistence of even widespread species in modern agroecosystems.

In the present work, we specifically investigate the interaction of habitat isolation and matrix quality on genetic variation in fragmented populations of a widespread species in modern agroecosystems. For doing so, we selected four clusters of three populations of the widespread but flightless bush cricket species *P. griseoaptera* in the same landscape below the fragmentation threshold (cf. Lange et al. 2010) but at a spatial scale roughly seven times smaller ($\leq$1 km). Populations were situated in either structurally connected or disconnected habitat elements and were separated by either low or high matrix quality. This landscape genetic approach allowed for both a categorical analysis in a quasi experimental setup and a whole landscape analysis.

We hypothesized that (i) even at a small spatial scale habitat fragmentation affects gene flow among populations of *P. griseoaptera*, resulting in a greater genetic differentiation and lower genetic diversity for structurally disconnected populations compared to connected ones and (ii) this fragmentation effect is stronger when matrix quality is low, resulting in a greater genetic differentiation and lower genetic diversity for disconnected habitat patches enclosed by low (arable land) than by high (grassland) quality matrix.

Materials and methods

Model species

The dark bush cricket *Pholidoptera griseoaptera* (De Geer, 1773) (Orthoptera: Tettigoniidae) is abundant

and mainly distributed in Central and Eastern Europe (Maas et al. 2002). The species is an omnivorous mesophilic generalist with a biennial life cycle and is strongly associated with woody habitats, where it lays its eggs in crevices in bark or in rotten wood (Ingrisch and Köhler 1998). It is commonly found in woodlands, along woodland edges, hedgerows or in forest clearings, preferably with a grass, tall herb or shrub layer (Guido and Gianelle 2001; Schlumprecht and Waeber 2003; Diekötter et al. 2005). In general, *P. griseoaptera* shows densities between 0.08 and 0.72 individuals per m^2 (Ingrisch and Köhler 1998), but under the presence of a tall grass layer along forest edges or adjacent grassland densities may become as high as two individuals per m^2 (Diekötter et al. 2005). Frequent movement of juvenile and adult *P. griseoaptera* from forest edges into adjacent grassland and back (Diekötter et al. 2005) suggests that managed grasslands provide a complementary resource for this species (cf. Haynes et al. 2007). Thus, managed grasslands are considered high matrix quality. Arable fields, in contrast, are unsuitable for *P. griseoaptera*, which are rapidly left by the species and therefore represent low matrix quality (Schlumprecht and Waeber 2003; Diekötter et al. 2005). Although the bush cricket is completely flightless (brachypterous) and small sized (<20 mm) several studies revealed a high dispersal ability of the species—indicated by low genetic differentiation and widespread occurrence—in agricultural mosaic landscapes (Diekötter et al. 2005, 2010; Lange et al. 2010). However, this high dispersal ability at either small ($\sim$1 km) or regional ($\sim$6.7 km) spatial scales could only be sustained if habitat amount was above 20% (Diekötter et al. 2010; Lange et al. 2010).

Study area and sites

The present study was conducted in the Wetterau in central Hesse, Germany, the agricultural region of very high habitat fragmentation used in Lange et al. (2010) (Fig. 1). This region, with an extent of $\sim$75 km^2, is characterized by an intensive land-use management at which farmland covers more than 50% (cf. Fig. 2 in Lange et al. 2010). The main crop is winter grain and 43% of the arable fields show a size >10,000 m^2; the average field size is 13,380 m^2. The bush cricket's preferred habitat type, woody vegetation, i.e. hedgerow, plane shrub (>50% cover of woody growth) and mixed and deciduous forest, comprised only 16% of the area and showed a proximity index of 1682 (compared to 3261, 3787

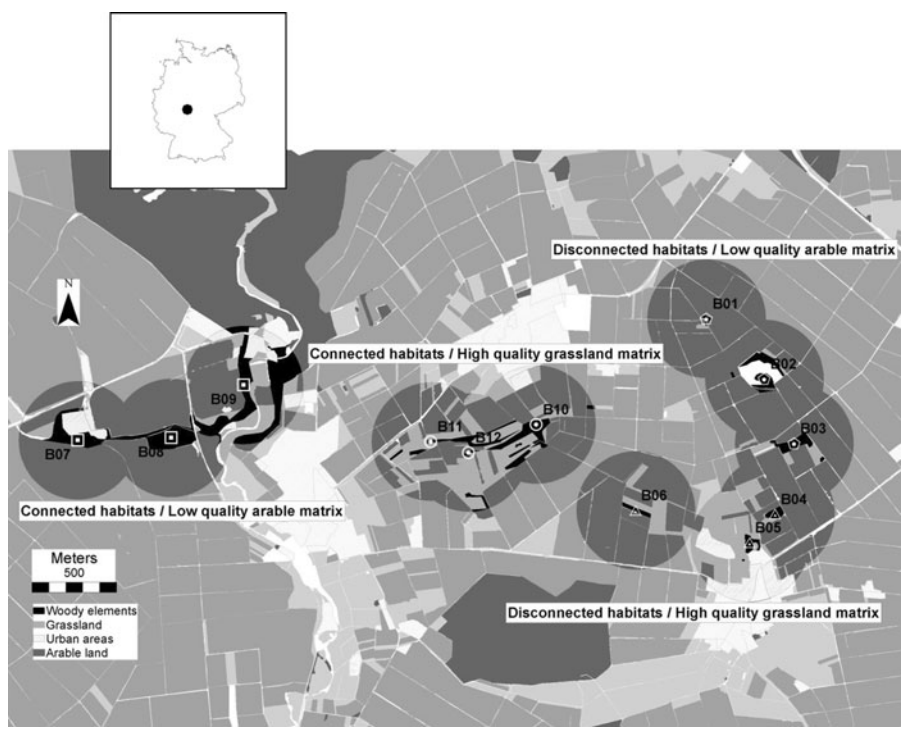

Fig. 1 Location of the 12 study sites, in which individuals of *P. griseoaptera* were collected for genetic sampling. Three sites were located within one of four different clusters, defined by a combination of matrix quality (low: arable land vs. high: grassland) and the structural connectivity of habitats (connected vs. disconnected)

Table 1 Descriptive landscape parameters of the four clusters. Habitat connectivity (Proximity woodland) and share of main habitat types (Grassland, Arable land, Woodland)

Cluster	Proximity woodland	Grassland (%)	Arable land (%)	Woodland (%)	mEED (m)	mPopDist (m)
Disconnected/arable land (DL)	169	4.3	87.0	3.7	358	606
Disconnected/grassland (DH)	6	22.5	62.7	1.7	356	584
Connected/arable land (CL)	9,653	10.6	62.3	16.2	10	706
Connected/grassland (CH)	7,685	30.5	58.7	6.4	17	433

Woodland represents suitable habitat. *mEED* mean edge-to-edge distance between inhabited patches, *mPopDist* mean geographical distance between pairs of populations, *L* low quality matrix, *H* high quality matrix

and 5161 in the three less fragmented classes; cf. Lange et al. 2010).

Within this landscape and based on a digital vector-based land-use map (EFTAS Fernerkundung Technologietransfer GmbH 2007), we selected twelve focal habitat patches, three of which formed one of four clusters that accorded to either of two levels of small-scale habitat configuration (structurally connected vs. disconnected) and matrix quality (high vs. low). Hence, focal habitat patches belonged to either of four clusters of landscape features: connected/high quality grassland matrix (CH), connected/low quality arable matrix (CL), disconnected/high quality grassland matrix (DH) and disconnected/low quality arable matrix (DL) (Table 1; Fig. 1). Spatial distances between populations within clusters ranged from 233 to 1,034 m and did not differ significantly among clusters (ANOVA: $F_{3,8} = 0.530$, $P = 0.674$). The small-scale configuration of suitable woody habitat was quantified using the proximity index as defined by McGarigal et al. (2002) within the GIS extension V-LATE (Lang and Tiede 2003). Proximity was calculated for each cluster by merging circular sectors with a radius of 350 m (this radius ensured the merging) around the focal habitat patches. Comparatively higher proximity values indicate higher connectivity of the habitat type of interest. Structurally connected woody habitat elements showed proximity values of 7,685 and 9,653 and edge-to-edge distances ranged from 9 to 31 m. Proximity values of the disconnected woody habitats were 6 and 169 and edge-to-edge distances ranged from 148 to 779 m (Table 1).

Matrix quality was defined as high quality when focal patches within a cluster were cross-linked by grassland (meadows, pastures, meadows with scattered fruit trees and grassy margins). When focal patches within a cluster were cross-linked by arable land (winter grain, summer grain, rape, root crops and other field crops), in contrast, matrix quality was defined as low. The area percentage of grassland within the chosen clusters was 22.5 and 30.5% for high matrix quality clusters and 4.3 and 10.6% for low matrix quality clusters. All clusters encompassed comparatively large amounts of arable land (Table 1). Landscape analyses were conducted in ArcGIS 9.2.

Sampling, microsatellite genotyping and null alleles

Tissue samples for DNA extraction were collected by removing one hind leg of individuals in a total of 12 focal patches in June/July 2009. Within each focal patch, between 30 and 36 individuals (termed population hereafter) were sampled (Table 2). Individual legs were immediately put in 95% ethanol and stored until processing. Altogether 381 individuals of *P. griseoaptera* were genotyped at eight microsatellite loci that were shown to behave neutral: WPG1-28, WPG2-15, WPG2-16, WPG2-39, WPG7-11, WPG8-2, WPG9-1, WPG10-1 (Arens et al. 2005) following the same protocol as Lange et al. (2010).

Blind and independent marker amplification was repeated twice for a random 10% of samples to account for genotyping errors and high proportions of null alleles in Orthoptera (Chapuis and Estoup 2007). We included one negative and six positive controls in each run of 96 PCRs to allow for detection of stochastic allelic dropouts and to enable standardization across genotyping plates. Averaged over all loci the mean error rate per locus was 0.006 (cf. Pompanon et al. 2005). Homozygous null alleles at a locus were assumed if repeated PCRs for a sample did not yield any product. Null allele frequencies were estimated

Table 2 Size of inhabited patch and genetic diversity within populations of the bush cricket species *P. griseoaptera*

Cluster / Population ID	Patch size (m^2)	*N*	H_E	*A*
Disconnected/arable land (DL)				
B01	1,545	30	0.658	6.88
B02	8,016	30	0.635	6.13
B03	12,694	36	0.635	6.75
			0.644	*6.58*
Disconnected/grassland (DH)				
B04	5,354	32	0.664	6.50
B05	5,792	33	0.621	6.38
B06	4,278	33	0.614	6.38
			0.633	*6.42*
Connected/arable land (CL)				
B07	33,333	30	0.568	6.38
B08	33,031	31	0.659	8.25
B09	32,343	31	0.667	7.50
			0.632	*7.38*
Connected/grassland (CH)				
B10	20,307	32	0.643	7.25
B11	13,712	33	0.685	8.38
B12	1,494	30	0.682	6.88
			0.670	*7.50*

Number of individuals (*N*), expected heterozygosity (H_E) and number of alleles (*A*). Averages were calculated over all loci and populations within each cluster. For significance of differences among clusters, see Fig. 2. *L* low quality matrix, *H* high quality matrix

with the software MICROCHECKER 2.2.3; high proportions were detected in WPG8-2 and WPG2-39 (averaged over populations: 0.13 and 0.32). Both loci were adjusted by introducing a new allele using the estimator of Van Oosterhout et al. (2004). Deviation from Hardy–Weinberg equilibrium (HWE) per locus and population was tested before and after null allele correction using an exact test as described in Guo and Thompson (1992) to check the correction of null alleles (Table S1 in Supplementary material). HWE tests were carried out with 1,000,000 steps in the Markov chain and 10,000 dememorization steps in ARLEQUIN v.3.5.1.2 (Excoffier and Lischer 2010). Six of the 96 tests showed significant deviation from expected genotype frequencies after correction for null alleles; however, only two cases included one of the two adjusted loci, WPG8-2.

Genetic data analysis

The program FSTAT 2.9.3 (Goudet 2001) was used to calculate the inbreeding coefficient (F_{IS}) and the number of alleles (*A*) for each locus per population. The program Arlequin v.3.5.1.2 (Excoffier and Lischer 2010) was used to calculate the observed heterozygosity (H_O) and the unbiased expected heterozygosity (H_E), again for each locus per population. Owing to the similar sample sizes (30–36; Table 2) we did not use a rarefaction method to standardize the allele number (cf. El Mousadik and Petit 1996). Given that the loci were corrected for null alleles, the calculation of H_O and F_{IS} is inappropriate (Van Oosterhout et al. 2004) and was only performed prior to correction (Table S1 in Supplementary material).

Genetic differentiation was first analyzed at the cluster level. We estimated genetic differentiation among the three populations within each cluster as (i) G_{ST} (Nei 1987), (ii) θ, using the algorithm developed by Yang (1998) in the R-package HIERFSTAT (Goudet 2005), (iii) standardized G_{ST} (G'_{ST}) following Hedrick (2005) and (iv) *D* as described in Jost (2008) (D_{est}, Eq. 12). The traditional measures G_{ST} and θ and the newly introduced measures G'_{ST} and *D* were used in parallel to allow for comparisons to other studies using either of these measures (e.g. Gerlach et al. 2010; Lange et al. 2010; Meirmans and Hedrick 2011). The statistical significance of population differentiation was tested for θ with a generalized likelihood-ratio test (Goudet et al. 1996) implemented in HIERFSTAT and for G_{ST}, G'_{ST} and *D* by following a similar procedure of

permuting individual genotypes among populations within clusters, recalculating differentiation and determining if the observed differentiation value was significantly greater than the randomized data set. In both tests we used 1,000 permutation trials at $\alpha = 0.05$ for assigning the proportion of significant results.

Statistical differences in A, H_E, G_{ST}, θ, or D among clusters were assessed by constructing approximate 95% confidence intervals (CI) using the range of the percentile values (2.5–97.5%) of 1,000 estimates based on bootstrapping alleles within populations (Chao et al. 2008). 95% CI were corrected according to the percentile method (Chao and Shen 2003) as described in Lange et al. (2010).

In order to further assess the effect of matrix quality and geographical distance, we second analysed pairwise population differentiation θ as calculated with the program FSTAT. We tested for an isolation by distance pattern of genetic differentiation with (i) geographical distance (IBD) and (ii) cost distance defined by the resistance of land use types to the species' movement, also named isolation by landscape resistance (IBR) hereafter. Cost distances were determined as the cumulative cost distance of least cost paths between population pairs (cf. Adriaensen et al. 2003). Least-cost paths were determined by assigning resistance values to all land-use types defining their dispersal potential for individuals of *P. griseoaptera*. To systematically explore the effect of matrix quality we generated six models with resistance values for woody/grassy/arable habitat types as follows: A: 1/1,000/1,000, B: 1/10/1,000, C: 1/1/1,000, D: 1/100/100, E: 1/10/100, F: 1/1/100. All other land use types, e.g. roads, were set the respective maximum resistance value (1,000 for A–C, 100 for D–F). Models A–C in contrast to D–F assume a higher resistance of the arable matrix (1,000 vs. 100). In models A and D grassland and arable land represent similar unsuitable matrix (cf. Diekötter et al. 2010), while C and F assume low resistance for both grassland matrix and woody habitat. Models B and E are intermediate and assume medium resistance for the grassland matrix. As linear landscape elements may have a strong influence on least cost analyses (Adriaensen et al. 2003) and grassy field margins are common structures within the studied agricultural landscape we additionally ran models B1, C1, E1 and F1. Here, we differentiated between plain and linear grassy structures by setting the resistance value of linear grassy margins to the respective value of arable land (1,000 for B1 and C1, 100 for E1 and F1), thus, excluding grassy margins as a suitable dispersing habitat. In a prior sensitivity analysis four sets of resistance values ranging from 0 to 1, 1 to 2, 1 to 100 and 1 to 1,000 were used for the generation of the models A–F in order to assess the effect of relative costs on the explanatory power of the resulting least-cost paths (Rayfield et al. 2010). Consistent and biologically meaningful results were obtained for the first and the two last sets, so only the results for the two latter are reported (see above). All distance calculations were performed with the extension PATHMATRIX 1.1 (Ray 2005) in ArcView GIS 3.2.

Isolation by distance patterns were analysed using multiple regression on distance matrices (MRM, cf. Lichstein 2007) with a Pearson correlation. We fitted three different MRMs, using geographical distance alone (MRM 1), cost distance alone (MRM 2) and geographical and cost distance together (MRM 3) as predictors of genetic differentiation. This approach allowed us to assess the pure and shared amount of variation (R^2) explained by geographical distance and landscape resistance, respectively, assuming that variation components are additive. The pure amount of variation explained by geographical distance and landscape resistance and the shared amount was calculated as $R^2_{MRM3} - R^2_{MRM2}$, $R^2_{MRM3} - R^2_{MRM1}$ and $R^2_{MRM1} + R^2_{MRM2} - R^2_{MRM3}$, respectively (Legendre and Legendre 1998; Zuur et al. 2007). To explore the relationship between both predictors, we also estimated R^2 by regressing geographical distance on cost distance. In contrast to an ordinary multiple regression the significance of R^2 from regressions on distance matrices was determined by permutation testing (cf. Legendre et al. 1994) with 10,000 permutations as implemented in ecodist (Goslee and Urban 2007).

Unless otherwise noted, all calculations were performed in R 2.11.1 (R Development Core Team 2008).

Results

Genetic diversity

The mean number of alleles per locus (A) ranged from a minimum of 6.13 to a maximum of 8.38 per population (Table 2). The two connected clusters (CL, CH) harboured significantly more alleles—about 15%

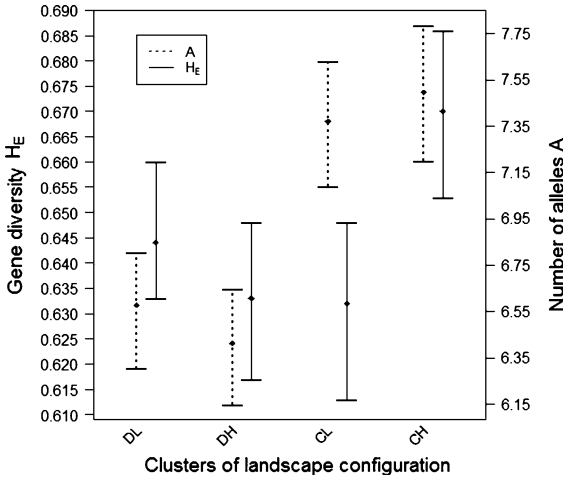

Fig. 2 Average values over loci and populations for the number of alleles (A) and expected heterozygosity (H_E) within each combination of matrix quality (low: arable land (L) vs. high: grassland (H)) and the structural connectivity of habitats (connected (C) vs. disconnected (D)) of the bush cricket *P. griseoaptera*. Error bars show the 95% confidence intervals (CI), i.e. 2.5th and 97.5th percentile of 1,000 simulation trials based on bootstrapping alleles within populations. Non overlapping CIs indicate significant difference

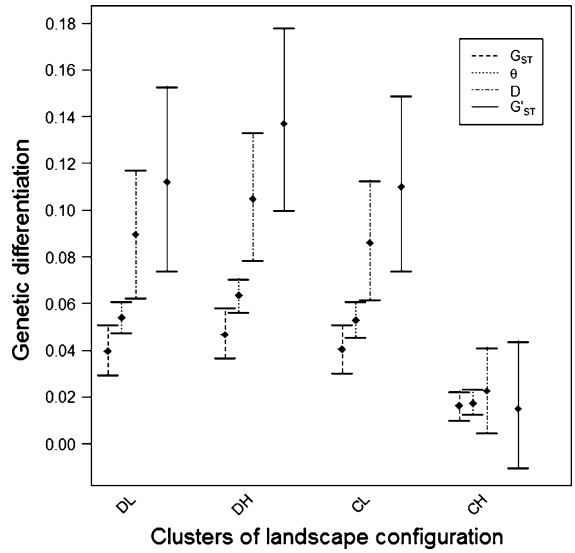

Fig. 3 Genetic differentiation within each combination of matrix quality (low: arable land (L) vs. high: grassland (H)) and the structural connectivity of habitats (connected (C) vs. disconnected (D)) of the bush cricket *P. griseoaptera* measured by the traditional measure θ and the newly developed measure D. The 95% confidence intervals are the 2.5th and 97.5th percentile of 1,000 simulation trials based on bootstrapping alleles within populations. Non overlapping CIs indicate significant difference

higher—than both clusters of disconnected populations (Fig. 2). Matrix quality did not seem to have affected the numbers of alleles as neither the pairs CL and CH nor DL and DH significantly differed in their number of alleles (Fig. 2).

Mean expected heterozygosity (H_E) per population ranged from 0.568 to 0.685 (Table 2). In contrast to the number of alleles, habitat connectivity and matrix type seemed to have interacted in affecting H_E. Connected populations surrounded by a grassland matrix (CH) showed a slightly increased H_E (6% increase; Table 2) compared to clusters CL and DH, though it was not significantly different from DL (Fig. 2).

Genetic population differentiation

Genetic differentiation was significantly smaller among connected populations embedded in a grassland matrix (CH) than among the three populations within the remaining clusters (Fig. 3). Differentiation within CH was low with 0.004 for G_{ST}, 0.005 for θ, 0.015 for G'_{ST} and 0.011 for D. The three remaining clusters did not significantly differ in genetic differentiation among their three populations. Values obtained by the traditional measures were lower with 0.030 (DL), 0.038 (DH) and 0.031 (CL) for G_{ST} and 0.046 (DL), 0.057 (DH) and 0.045 (CL) for θ than those estimated by the newly introduced measures with 0.112 (DL), 0.137 (DH) and 0.110 (CL) for G'_{ST} and 0.086 (DL), 0.103 (DH) and 0.082 (CL) for D, respectively. Genetic differentiation within these clusters was roughly ten times higher than among populations in CH (Fig. 3). Measures of genetic differentiation estimated with θ were significant for all types of landscape features ($P \leq 0.021$). For G_{ST}, G'_{ST} and D genetic differentiation was significant for all clusters ($P < 0.001$) except CH ($P = 0.055$).

Isolation by geographical distance (IBD) and by landscape resistance (IBR)

Significant pairwise population differentiation was found for all pairwise combinations except for population pairs within cluster CH. Genetic differentiation was significantly correlated to geographical distances ($R^2 = 0.159$, $P = 0.013$; Fig. 4), indicating an isolation by geographical distance pattern at a scale less

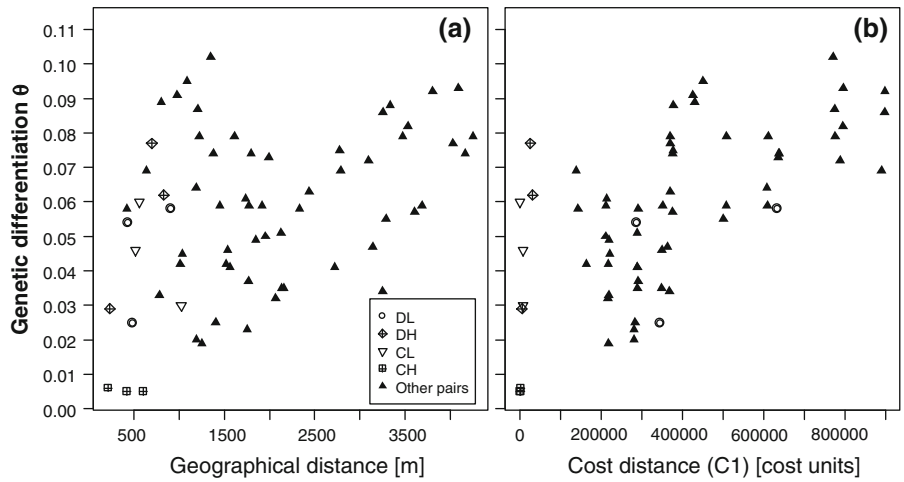

Fig. 4 Isolation by (**a**) geographical distance (IBD) and (**b**) landscape resistance (IBR) for *P. griseoaptera* highlighting pairwise distances within each cluster of matrix quality (low: arable land (L) vs. high: grassland (H)) and structural connectivity of habitats (connected (C) vs. disconnected (D)). The cost distance is defined by landscape resistance values of set C1. Correlation to genetic distance was $R^2 = 0.159$, $P = 0.013$ for geographical and $R^2 = 0.432$, $P < 0.001$ for landscape resistance

than 4 km. Yet, more variation in genetic differentiation was explained by landscape resistance for all models ($R^2 \geq 0.221$, $P \leq 0.033$) but C ($R^2 = 0.158$, $P = 0.101$) (Fig. 5; Table S2 in Supplementary material). Genetic differentiation, however, was best explained by those models that excluded grassy margins (B1, C1, E1, F1; $R^2 \geq 0.406$, $P < 0.001$, Fig. 5). Lower resistance of arable matrix of 100 (D–F, D–F1) instead of 1,000 (A–C, A–C1) did not explain substantially more variance in genetic differentiation except for model E that explained almost twice as much variance as B. Partitioning the total variation into pure components (Fig. 5), geographical distances explained as low as 0.01% (E) and up to 10.9% (C), but only significantly for model C. Pure effects of landscape resistances ranged from 10.9% (C) to 27.9% (C1) and again showed largest effects in the models that excluded grassy margins. Except for models B and C, cost distances were significantly correlated to geographical distances ($R^2 \geq 0.128$, $P \leq 0.028$).

Discussion

Our results revealed that for the dispersal of small and flightless animals the matrix matters even at a small spatial scale. Using microsatellites we found genetic diversity and population differentiation of the flightless bush cricket *P. griseoaptera* to be affected by both the structural habitat configuration and matrix quality. Populations of more connected habitat elements showed a significantly lower genetic population differentiation only when embedded in high quality grassland matrix. Thus, in the more connected situation individuals seemed to have crossed edge-to-edge distances of 9–31 m more successfully through a grassland matrix than through arable matrix keeping genetic differentiation (D) among populations at a very low and non-significant 1% as compared to a significant differentiation of 8% among populations embedded in an arable matrix.

Previously, much emphasis was put on habitat isolation affecting biodiversity in fragmented landscapes like agricultural ones by following the traditional view of a binary landscape that is considered to consist of suitable habitat surrounded by an inhospitable matrix (Gilpin and Hanski 1991). Since then, a strong influence of the matrix type on dispersal has been revealed (e.g. Ricketts 2001; Haynes and Cronin 2003). In a recent review, Prevedello and Vieira (2010) showed that in 95% of the studies addressing the ecological effects of both, matrix quality and habitat isolation in combination, the matrix surrounding habitat patches had a significant influence on the studied parameters. Though the matrix was shown to

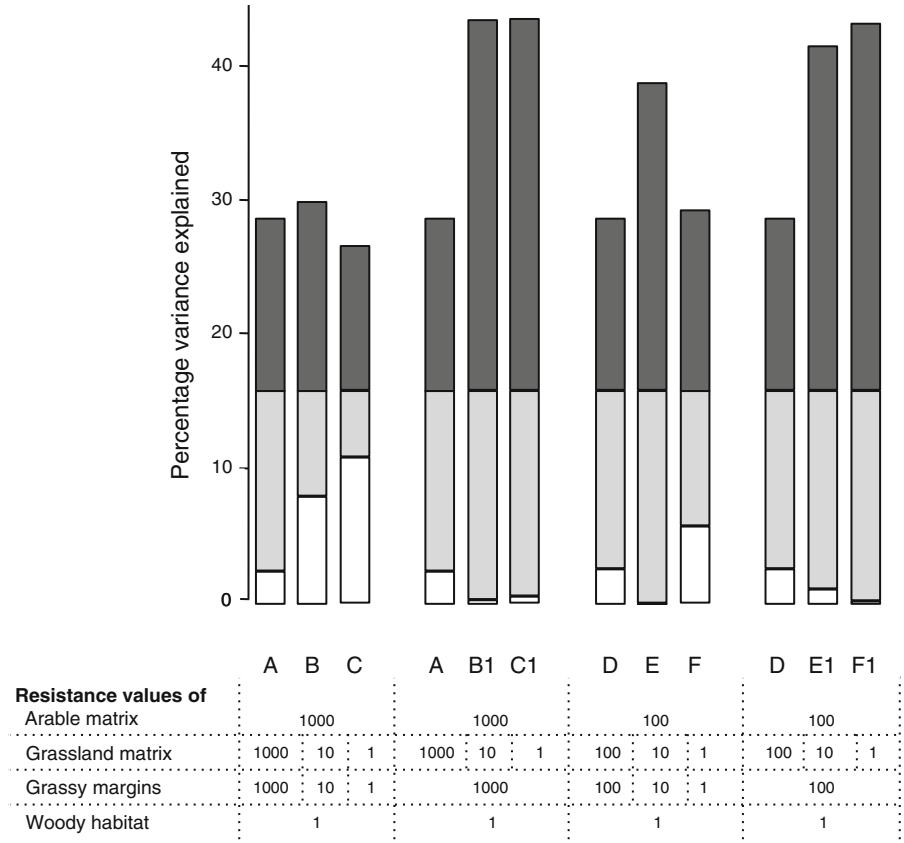

Fig. 5 Least cost analysis of ten models of landscape resistance. Percentage variation explained in genetic differentiation by multiple regression partitioned into effects of pure geographical distance (*white bar*), pure landscape resistance (*dark grey bar*) and shared effects (*light grey bar*) (see also Table S2 in Supplementary material). The total variation explained by geographical distance equals the sum of pure geographical and shared components and is the same across all models (15.9%, see Fig. 4)

be important, however, its effects were smaller than those of patch size and isolation (Prevedello and Vieira 2010). These findings are in concordance to our results, where similar values of genetic differentiation of disconnected populations surrounded by either arable or grassland matrix were found suggesting that matrix quality alone was not able to attenuate the negative effects of habitat fragmentation. In contrast, high matrix quality apparently promoted inter-patch dispersal in the CH cluster, where populations were connected as indicated by reduced levels of differentiation. Although on average this cluster with high matrix quality showed the shortest geographical distances between populations, much higher genetic differentiation at similarly short distances but of low matrix quality in the CL cluster, underlines the importance of matrix quality for inter-patch dispersal.

A similar pattern to genetic differentiation was found for expected heterozygosity. Populations surrounded by a high quality grassland matrix in the more connected situation showed the highest value of expected heterozygosity compared to the three remaining clusters. Unlike heterozygosity, the number of alleles was solely affected by habitat connectivity. It was significantly higher in connected populations than in disconnected ones, irrespective of matrix quality. The number of alleles, estimated with neutral markers like microsatellites, is primarily affected by gene flow and random genetic drift (Evanno et al. 2006). Gene flow homogenises allele frequencies between populations and thus is a potent force in reducing the level of differentiation (Hartl and Clark 2007). Since genetic population differentiation, and thus gene flow, differed significantly between high and

low matrix quality clusters in the more connected situation (CH, CL), gene flow seems an unlikely cause for the significantly greater and similar number of alleles in these clusters compared to clusters DH and DL. Alternatively, the smaller effective population sizes that often go along with habitat fragmentation may be held responsible for the lower allelic richness in the disconnected situation by fostering random loss of alleles through genetic drift (Nei et al. 1975; Keller and Largiadèr 2003). Indeed, mean patch area of both disconnected clusters was much smaller (6,280 m^2 vs. 22,420 m^2) than for the connected clusters.

In addition to the mutual effect of matrix quality and habitat configuration on genetic diversity within clusters, gene flow was also negatively affected by geographical distances between populations. However, geographical distance was less important than landscape resistance in explaining the pattern of pairwise population differentiation. Particularly, we revealed that both, assigning only a high instead of a very high resistance of arable matrix (B vs. E in Fig. 5) to dispersal or discriminating between plain and linear grassland elements with low and high resistance values (B–F vs. B1–F1 in Fig. 5), resulted in greater percentage of variance explanation in pairwise genetic differentiation, respectively. Whereas low rates of gene flow through the agricultural matrix that may be inferred from these findings seem congruent with movement patterns previously observed for *P. griseoaptera* (Diekötter et al. 2005) or *Platycleis albopunctata* (Hein et al. 2003), considering results on *M. roeselii* (Lange et al. 2010) or Orthopterans in general (Marshall et al. 2006) the high resistance of linear grasslands to the species' movement was unexpected. In contrast to the seemingly promoting effect of linear woody structures on the dispersal of *P. griseoaptera* (Diekötter et al. 2007b), the resistance of linear grassy structures may be caused by specific microclimatic requirements of *P. griseoaptera* for more moist conditions (Ingrisch and Köhler 1998), a preference for more vertical structures (Guido and Gianelle 2001) or a higher level of predation (MacDonald et al. 2007). The great impact and differences in the suitability of different matrix types for the dispersal of *P. griseoaptera* at a small spatial scale corroborate previous findings by Lange et al. (2010) and Diekötter et al. (2010) at larger scales. Also in these studies gene flow between populations of *P. griseoaptera* was not limited by geographical distance per se, but strongly dependent on the type and share of suitable and unsuitable habitat.

We conclude that for the flightless bush cricket *P. griseoaptera*, gene flow is restricted in a highly fragmented landscape not only at a large but also at a small spatial scale. Our results indicate that even for widely distributed and abundant yet small and dispersal limited species, landscape management needs to consider habitat configuration and matrix quality in order to be effective. Thereby, matrix quality should not only be judged by its amount but also by its geometry, as we revealed a greater suitability of plain over linear elements of the grassland matrix. Thus, suitable habitat patches cross-linked with high quality and plain matrix does seem most promising in promoting gene flow in *P. griseoaptera* and many other arthropod species, for which this bush cricket may be a model.

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