RESEARCH ARTICLE

Open areas in a landscape enhance pollen-mediated gene flow of a tree species: evidence from northern Switzerland

U. Kamm · F. Gugerli · P. Rotach · P. Edwards · R. Holderegger

Abstract Habitat fragmentation often has negative consequences for genetic diversity, and thereby for the viability of populations. However, these negative consequences might be counteracted by gene flow as the latter provides functional connectivity between apparently isolated habitat fragments. Gene flow is itself influenced by landscape structure and composition, and it is therefore important to understand the relationship between gene flow and landscape structure and composition. We used linear LAD regression models to investigate the relationship between contemporary gene flow by pollen in the rare, insect-pollinated forest tree *Sorbus domestica* and several landscape features. None of the landscape components—which included closed forest, deep valleys, open land and settlements—proved to be an impermeable barrier to gene flow by pollen. We found evidence that settlements, large open areas, and a pronounced topography increased long-distance gene flow in the landscape as compared to a random model including all possible gene flow trajectories. These results are encouraging from a conservation view, as gene flow in species pollinated by generalist insects seems to provide functional connectivity and may help to maintain genetic diversity in rare plant species in fragmented landscapes.

Keywords Landscape genetics · LAD regression · Paternity analysis · Functional connectivity · Insect pollination · Pollen dispersal · Switzerland

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Introduction

Ongoing changes of land use in the cultural landscapes of Central Europe, leading to the loss of many remaining natural and semi-natural habitats (Schrott et al. 2005), are increasing the spatial subdivision and fragmentation of populations. From the genetic point of view, the resulting spatial isolation of the remaining habitat fragments threatens the survival of many species in various ways: (1) local populations that have been reduced in size only contain a fraction of the original gene pool, (2) alleles and genetic

diversity is lost due to random genetic drift, and (3) inbreeding might be elevated due to reduced availability of un-related individuals (Young et al. 1996).

For sessile organisms such as plants, the negative effects of landscape change on genetic diversity may be counteracted by gene flow, which can provide functional connectivity even between spatially isolated populations (Hamrick 2004).

Most large-scale investigations of gene flow have been carried out, partly for technical reasons, on tropical tree species that naturally occur at low densities. Such studies have shown high genetic diversity even in fragmented populations, provided evidence for long-distance gene flow by pollen (Nason et al. 1998; White et al. 2002; Lowe et al. 2005) and led to the conclusion that populations of many tropical trees have a high resilience to habitat fragmentation (Hamrick 2004). However, landscape change does not only lead to larger geographical distances among populations, but also to changes in the composition and quality of the intervening habitats. Landscape genetics attempts to understand how gene flow (i.e. functional connectivity) is affected by landscape composition (i.e. structural connectivity; Holderegger and Wagner 2008). To achieve this goal, one must consider not only the distances among populations, as in population genetic studies, but also the quality and spatial arrangement of the various habitat elements (Manel et al. 2003).

Although the importance of landscape composition and structure for gene flow has been recognized for some time (Sork et al. 1999; Gram and Sork 2001), research has been hindered by a lack of suitable tools for relating landscape structure to population genetic processes (McRae 2006). When studying animal species, most landscape genetic studies have relied on estimates of least cost resistance distances (LCD) as a measure of structural connectivity so far. Using partial Mantel tests, these least cost distances can be compared with geographical distances to determine which landscape feature best explains the distribution of genetic distances. One problem with this approach, however, is that estimating least cost distances largely relies on expert knowledge about the resistance of different landscape components to animal movement. A further difficulty is that least cost distances are usually restricted to a single resistance model (McRae 2006), though this can be overcome by testing many different landscape-resistance

models (Cushman et al. 2006). A possible alternative to using least cost distance would be to derive some cumulative measure of the structure of a whole landscape, but such an approach has rarely been used (Storfer et al. 2007).

Measuring gene flow at the landscape scale also presents methodological problems. In typical landscape genetic studies, gene flow is usually indirectly inferred from the genetic distances between populations or individuals, but such pairwise estimates of functional connectivity are influenced by historic genetic processes and may not adequately reflect gene flow in the contemporary landscape (Whitlock and McCauley 1999; Storfer et al. 2007). In contrast, gene flow patterns assessed by parentage analysis (mainly in plants) or assignment tests (in both animals and plants) provide a measure of contemporary functional connectivity in the present landscape (Holderegger and Wagner 2008). Despite of the great potential of direct gene flow assessment for estimating contemporary functional connectivity, these methods have rarely been used to relate gene flow to landscape structure or structural connectivity. One reason may be the sampling effort required, since parentage analysis needs all mature individuals within the study area to be considered (Sork et al. 1999). As gene flow frequency by pollen markedly decreases with increasing distance (Austerlitz et al. 2004), the number of long-distance gene flow events identified between individuals may also be too small to assess the influence of landscape structure. Another hindrance to using current gene flow estimates in landscape genetics is the lack of generally accepted statistical methods for correlating functional and structural connectivity (the often used partial Mantel tests cannot be used for this purpose; Holderegger and Wagner 2008). Here, we try to overcome these limitations by making use of a long-term inventory of the rare forest tree, *Sorbus domestica* (L.), using information on all mature trees in an area of over 100 km^2 in northern Switzerland. A parentage analysis provided precise data on current gene flow patterns by pollen over a large spatial scale (Kamm et al. 2009). Instead of quantifying structural connectivity using least cost distances, we assessed the influence of landscape structure on realised gene flow by pollen by comparing the latter with a spatially explicit random model including all possible gene flow events in the study population. First, we

used linear regression models with permutation tests to investigate the relationship between current gene flow distances and landscape composition, and then we compared the realised relationship with that of the random model and landscape composition. This approach does not require a preliminary evaluation of movement costs for insect pollinators in the landscape, but assumes a straight line flight of pollen vectors. We asked the following questions. (1) How do open land areas (i.e. agricultural fields) influence pollen-mediated gene flow? (2) Do settlements decrease gene flow by impeding the movement of pollen-vectors? (3) How does topography influence gene flow patterns?

Materials and methods

Landscape characterisation and study species

The study area (103 km^2; 8.62°E; 47.67°N) in the Canton of Schaffhausen in northern Switzerland ranged between 470 and 730 m a.s.l. and was composed of north–south oriented valleys flanked by steep slopes (>30°) as well as elevated plains on calcareous bedrock. The landscape was a mixture of open agricultural land (35%), mainly meadows and arable fields, in the valley bottoms and on the plains and forests (61%) dominated by deciduous trees on hill slopes. Only a small proportion (4%) was occupied by settlements, mainly small villages surrounded by orchards. The rather dry climate of the study area with warm summers is suitable for viniculture, which has a long tradition in the region (Brütsch and Rotach 1992).

The study species *Sorbus domestica* (Rosaceae) is a light demanding forest tree that is intolerant of lateral crown closure (Brütsch and Rotach 1992) and is regarded as a weak competitor (Franke and Dagenbach 1995). It has a scattered distribution in the study area, occurring either as single trees or in small groups. Most trees in the study area grow in south-facing locations, often at the crests of slopes where the forest structure is rather open. Like related species, the hermaphrodite flowers of this insect pollinated tree attract a large variety of generalist pollinators such as bees, bumblebees and Diptera (Raspé et al. 2000; Oddou-Muratorio et al. 2006). Although the species is usually regarded as outbreeding, it can produce seed through self-pollination (Kamm et al. 2009).

Inventory of trees

Sorbus domestica trees have been monitored in the region for conservation and seed collection purposes over more than 20 years. We supplemented this long-term inventory of *S. domestica* locations with data from regional forest inventories and our own systematic survey of the remaining area. We are thus confident that almost all reproductive individuals are known and that we had precise locations for all trees as determined using a hand-held GPS receiver. The trees in the study area (103 km^2) formed two subpopulations, referred to as Schaffhausen (Fig. 1, density 0.03 trees/ha) and Osterfingen (0.04 trees/ha).

Gene flow trajectories

Based on nine polymorphic nuclear microsatellite loci with a total of 62 alleles, we successfully genotyped 189 single stems and finally identified 167 genetically distinct adult individuals (Kamm et al. 2009). We investigated current gene flow by pollen that resulted in successful fertilisation using paternity analysis. To do this, we genotyped 1183 embryos (open pollinated offspring) from 49 mother trees distributed over the study landscape (Kamm et al. 2009). We determined the most likely pollen donor of each embryo based on a maximum-likelihood approach (Meagher 1986) implemented in CERVUS (Marshall et al. 1998). From all genotyped embryos ($N = 1183$), 744 could be assigned with a high significance ($\geq 95\%$) to a single pollen donor. Finally we obtained 495 distinct gene flow events (from inferred father to known mother). The other assigned seeds were selfed ($N = 249$, over all selfing rate: 33.5%). A total of 108 reproductive trees took part in these reproductive events. For all analyses, the data for the two subpopulations were lumped, but realised gene flow events between the subpopulations were too rare and thus omitted from analysis.

To represent gene flow by pollen trajectories (i.e. pollinator movement), we used a geographical information system (ARCGIS 9.2) to connect the father and mother trees for every mating event by a straight line (Janzen 1971). Realised gene flow events (for an example see; Fig. 1a) had a predominance of near-neighbour gene exchange (30% within the first 250 m), but showed also a surprisingly high proportion
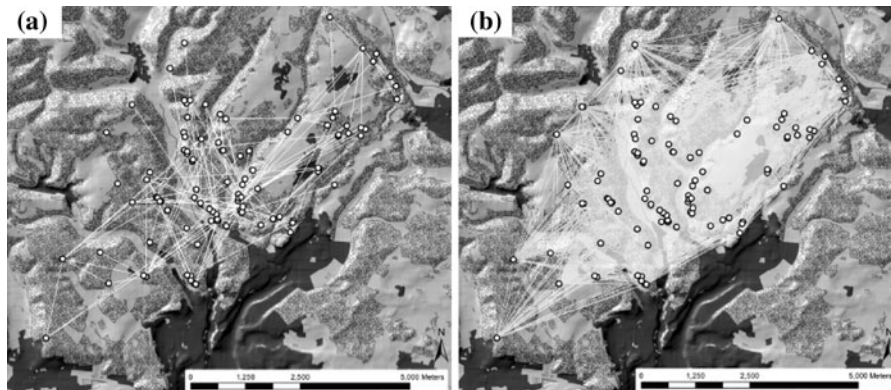
Fig. 1 Example of (**a**) realised current gene flow by pollen events and (**b**) all potential possible gene flow by pollen events (random model) in one of the two studied subpopulations (Schaffhausen) of *S. domestica* in Northern Switzerland. White dots indicate reproductive trees, whereas gene flow by pollen is symbolised by straight white lines. Structured grey areas represent forest, light grey areas indicate open land and dark grey areas are settlements. Exposition shading is added to the map to illustrate the heterogeneous topography of the study landscape

of long-distance pollen flow events (33% > 1 km, 10% > 2 km, 8% > 3 km; Kamm et al. 2009).

To evaluate which landscape characteristics affected gene flow distances, we constructed a random model of mating events, in which all reproductive trees were connected to each other by mating events and thus by straight lines (Spider Diagram in ARCGIS 9.2; 4768 straight lines in total). This random model thus included all possible pollination trajectories within the study landscape (Fig. 1b).

Landscape structure and composition

To assess different land cover types, we used a digital landscape model of Switzerland (VECTOR25 © Swisstopo; accuracy 3–8 m). In this model, objects were displayed in vector format and were georeferenced. By merging objects other than "forest" and "settled area" (i.e. meadows, crop fields, orchards, marshes, rivers, lakes, quarries, gravel pits) to the compound object "open land", the original data set was simplified to three categories.

The two data layers containing the realised and the random model gene flow events as line themes were intersected with the vector map (Spatial Analyst Tools in ARCGIS 9.2). We then calculated the distances (m) of each single gene flow events going over open land, forest or settled area, and computed the proportions (%) of each landscape element per single gene flow event.

Topographic characteristics of the study landscape were described based on a digital elevation model (DHM25 © Swisstopo; vertical precision 1.5–10 m) with a cell size of 25 m. Surface Tools (Jenness 2006) allowed us to calculate the cumulative elevation change (i.e. all vertical distances crossed by the straight line of a gene flow event) per gene flow event (ARCView 3.x).

Data analysis

Least absolute deviations (LAD) is a mathematical optimization technique similar to the ordinary least squares technique, but it is more robust to outliers in the data set. As our data showed several outliers and an asymmetric error distribution, we used linear regression models with least absolute deviation estimates of conditional medians (LAD) instead of ordinary least squares regressions (Cade and Richards 1996). In addition, we performed permutation tests for significance testing, because our gene flow distances did not represent fully independent data points (because each mother tree could mate with several father trees).

First and by using a multiple LAD regression model, we evaluated whether particular landscape characteristics—forest, open land, settled area and topography—had a significant impact on realised and random gene flow distances. Since the factors in a multiple regression models should not be strongly correlated, we only used those landscape characteristics that were

correlated with others landscape features with $r < 0.5$. This was done by performing linear correlations with 10000 permutation tests among the four landscape characteristics with CORR_PERMUTE (Legendre and Legendre 1998). Realised gene flow distance served as the response variable, and we tested whether single landscape characteristics had a significant impact on the model. Second and for those landscape characteristics having a significant impact, we additionally performed simple LAD regression analysis with 10000 permutations for simple interpretation. Third and following the investigation of realised gene flow distances, we performed the same multiple and single LAD regressions on the random gene flow events. Fourth, we then tested whether realised gene flow interacted differently with landscape characteristics than random gene flow. We assumed a different interaction, if the simple regression lines of the two single linear models differed significantly in slope and/or intercept. Correlations between random and realised gene flow distances and landscape components were again calculated with CORR_PERMUTE (Legendre and Legendre 1998).

When using standard statistical methods, unequal variation in data is often seen as undesirable noise. But unequal variation in data may reflect a complex ecological relationship blurred when exclusively focusing on mean values (Cade and Noon 2003). In such cases, quantile regressions may provide a more complete picture of underlying relationships as they allow us to focus on the lower (e.g. 10th regression quantiles) and/or upper bound (e.g. 90th regression quantiles) of the relationship. Fifth, we therefore estimated the 10th and 90th regression quantiles as well as the normal LAD regression, which represents the 50th regression quantile.

All the above mentioned regressions, the comparison of regression lines and the permutations tests were performed using BLOSSOM (Cade and Richards 2005).

Results

The proportion of open land was negatively correlated with the proportion of forest crossed by gene flow by pollen ($r = -0.98$; $P \leq 0.001$). There were strong positive correlations between the proportion and absolute distance of both open land and settled area

(open land $r = 0.82$, settled area $r = 0.92$; $P \leq 0.001$ in both cases), whereas the proportion and the distance over forest showed a weaker but significant negative correlation ($r = -0.35$; $P \leq 0.001$). Additionally, distance through forest correlated closely with cumulative elevation change ($r = 0.91$; $P \leq 0.001$). Based on these results, we chose three landscape characteristics that were largely independent of each other: proportion of open land (POL, in percent), distance crossing settled area (DS, in metres) and cumulative elevation change (CEC, in metres). Each of these landscape features had a significant influence on realised gene flow distance (linear LAD multiple regression analysis; $P \leq 0.01$).

In all LAD and quantile regressions between landscape variables and realised and random gene flow, the intercept for random gene flow was always significantly higher than for the realised gene flow (Table 1; Fig. 2). For all landscape variables investigated, quantile regressions showed that differences in slopes and intersects between realised and random gene flow were more pronounced the higher the bound of the quantile was set (Table 1).

Linear LAD regression showed that an increasing proportion of open land (POL) was associated with increasing gene flow distances, both for the realised and random gene flow events (Table 1; Fig. 2a). Quantile regressions tracking the lower bound of the relationship (10th quantile) showed that differences in gene flow distance between realised and random gene flow events were much smaller when POL was high, though the differences in slope and intercepts remained significant. When looking at the intercept (i.e. 0% of open land or 100% forested area, respectively), it was obvious that realised gene flow distances were much shorter than random gene flow distances (Fig. 2a). Increasing distance across settled area (DS) was associated with increasing gene flow distances (Table 1; Fig. 2b). Regression lines for the 10th quantile differed significantly in intercept but not in slope, while quantile regressions describing the upper bound of the relationship (90th quantile) showed the strongest differences between realised and random gene flow events, with the slope of the realised gene flow events being steeper and having a lower intercept than the 90th quantile regression quantile of the random model.

LAD regression showed that increasing cumulative elevation change (CEC) was associated with

Table 1 LAD linear regression equations (general and 10th, 90th quantile) describing the relationship between gene flow distance and landscape components for realised gene flow events and for all possible gene flow events (random model) in *S. domestica*

Landscape component	Regression model	Realised gene flow	Random gene flow	Difference in	
				Slope	Intercept
POL	10th quantile	$y = 6.2 + 10.28x$	$y = 428.5 + 15.18x$	4.9^{ns}	422.3^{**}
	LAD	$y = 110.9 + 37.18x$	$y = 1404.3 + 30.91x$	6.27^{*}	1293.4^{**}
	90th quantile	$y = 863.2 + 76.03x$	$y = 3113.7 + 28.26x$	47.77^{**}	2250.5^{**}
DS	10th quantile	$y = 13.9 + 3.75x$	$y = 706.6 + 2.88x$	0.87^{ns}	692.7^{**}
	LAD	$y = 215.3 + 5.49x$	$y = 1957.5 + 2.87x$	2.62^{**}	1742.2^{**}
	90th quantile	$y = 1881.7 + 8.03x$	$y = 3954.3 + 1.45x$	6.58^{**}	2072.6^{**}
CEC	10th quantile	$y = -6.6 + 4.33x$	$y = 33.3 + 4.42x$	0.09^{ns}	26.7^{**}
	LAD	$y = 55.1 + 5.61x$	$y = 637.3 + 5.00x$	0.61^{*}	582.2^{**}
	90th quantile	$y = 53.1 + 13.52x$	$y = 2501.3 + 3.97x$	9.55^{**}	2448.2^{**}

Landscape component: *POL* proportion of open land (%); *DS* distance across settled area (metres); *CEC* cumulative elevation change (metres)

Significance test for differences for slopes and intercepts between realised and random gene flow events were based on 10000 permutation tests: ** $P < 0.01$, * $P < 0.05$, ^{ns} not significant
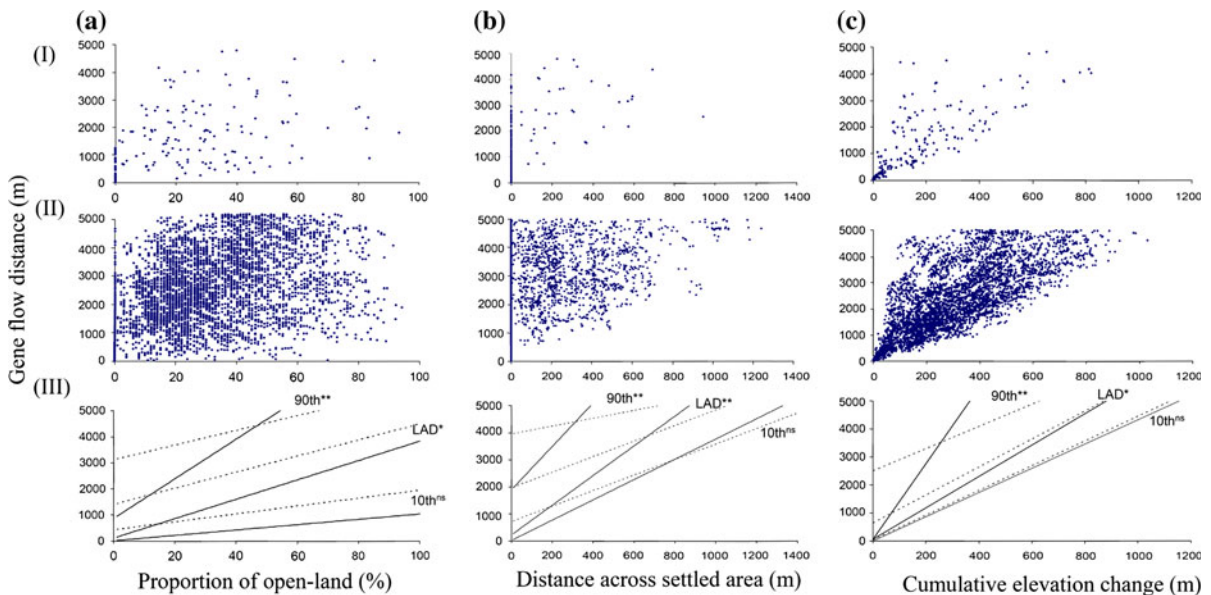

Fig. 2 Relationship between gene flow distances and landscape components in *S. domestica* (**a**) proportion of open land (POL), (**b**) distance across settled area (DS) and (**c**) cumulative elevation change for (I) realised current gene flow events, (II) all possible gene flow events (random model) and (III) as predicted by linear LAD regression models (general, 10th and 90th regression quantiles). In the latter, black lines represent model predictions for realized gene flow events, and dotted lines give those for the random model. Significant differences in slopes between realised gene flow events and random model were based on 10000 permutation tests (Table 1); ^{ns} non significant, * $P < 0.05$, ** $P < 0.01$. CORR_Permute correlations between realised gene flow and POL ($r = 0.64$), DS ($r = 0.54$) and CES ($r = 0.83$) and between random gene flow and POL ($r = 0.38$), DS ($r = 0.39$) and CES ($r = 0.69$)

increasing gene flow distances, both for realised and potential gene flow (Table 1; Fig. 2c). The regression line for the realised gene flow events had a lower intercept and a steeper slope than in the random model. Quantile regressions showed that at the lower bound (10th quantile) realised and potential gene flow events

differed slightly but significantly ($P \leq 0.01$) in intersect but not in slope, while at the upper bound (90th quantile) these differences were more pronounced. The regression line describing the relationship for realised gene flow events was distinctly steeper than that for random gene flow events (Fig. 2c).

Discussion

The present data on current gene flow by pollen in *S. domestica*, assessed over a relatively large area of 103 km^2 (Kamm et al. 2009), proved to be suitable for investigating interactions of realised gene flow with landscape composition. The results show that landscape composition and topography had a significant influence on realised gene flow by the pollen in this insect pollinated tree. As has been found for certain tropical trees with specialist pollinators (Nason et al. 1998), the generalist pollinators of *S. domestica* were not completely impeded by any landscape feature, and some pollen was even transferred among distant individuals (up to 16 km; Kamm et al. 2009).

The influence of open land

The LAD regression analysis showed that realised gene flow distances were mainly smaller than expected from the random model (Fig 2a). This is partly because the maximum realised gene flow distance over open land (1265 m) was much shorter than the maximum possible gene flow distances across areas with open land (maximum 4490 m). Since the proportion of open land in our landscape model represents approximately the alternative condition to forest cover, forest cover did not favour gene flow over large distances, but that open-land enforced longer gene flow distances (Fig. 2a).

The spatial distribution of the trees and landscape elements (forests mainly on hill sides and partly on plains) in our study area determined that increasing gene flow distance was associated with increasing proportion of open land (open land being mainly found on valley bottoms and partly on plains). However, the regression line for realised gene flow events had a significantly steeper slope than that for random gene flow, and this difference was particularly pronounced for the upper bound of the data (90th quantile; Fig. 2a), reflecting that realised gene flow interacted differently

with the landscape than expected under random gene low, namely that a higher proportion of open land enforced disproportionally longer gene flow distances in the realised gene flow model.

Sorbus domestica relies on pollination by insects (Kutzelnigg 1995), and the foraging and flight behaviour of insect pollinators therefore strongly affects patterns of gene flow. Many papers have been published on this topic, and their results support our main conclusion—that long distance gene flow is more likely to occur over open land than over closed forest. For example, Kreyer et al. (2004) found that bumblebees (*Bombus terrestris*) and honey bees (*Apis mellifera*) preferred open habitats, though forested areas (<600 m in width) were not a significant landscape barrier. Winfree et al. (2007) also found that bees are more abundant in open land (agricultural fields, suburban area) than in temperate forest, with their abundance in forest decreasing as the forest cover in surrounding areas increased. From this result, we would expect pollination success to be greater for trees growing close to open areas where bees should be more abundant. Hymenoptera are likely to be particularly important pollen vectors for long distance dispersal of pollen in agricultural landscapes (Steffan-Dewenter et al. 2002). Greenleaf et al. (2007) showed that larger bee species cover much larger foraging distances than smaller bee species. In particular, honey bees fly long distances (mean $\geq$1500 m), especially when foraging for high reward resources such as flowering trees (Winston 1987), and maximum values of >10 km have been recorded (Steffan-Dewenter and Kuhn 2003). Furthermore, bees and bumblebees are flower-constant over longer time periods, so that even widely spaced foraging plants may be successfully pollinated (Kwak et al. 1998). Finally, a study conducted in an experimental landscape indicated that open land corridors facilitate pollen transfer in a matrix of forest (Townsend and Levey 2005).

Influence of settled area

The regression analysis suggests that settled areas also enforced the movement of insect pollen vectors of *S. domestica*. This was indicated by the steeper slopes of regression lines for realised gene flow events than in the random model (Fig. 2b). However, fewer than 10% of all realised gene flow events, and

only 2.4% of all possible gene flow events shorter than one kilometre crossed settled area (Fig. 2b). Such a data distribution is problematic when using linear regression models. When the analysis was restricted to gene flow events that crossed at least some settled area, the differences between realised and modelled gene flow were no longer significant (data not shown). As this discrepancy could be due to the small number of data points, we cannot reach a firm conclusion about the effect of settled areas on gene flow distances.

Influence of topography

There was a clear relationship between gene flow distances and cumulative elevation change (CEC) for both realised and random gene flow (Fig. 2c) meaning that increasing cumulative elevation change was associated with increasing gene flow distances. At first glance, this finding appears trivial because elongating a straight horizontal line passing through a hilly landscape necessarily increases cumulative elevation change. Yet, the CEC linear regression line of the realised gene flow events had a significantly steeper slope than that for the random model, which implies, especially for the longest gene flow events (90th quantile), that an increasing cumulative elevation change had a different interaction with realised gene flow than with random gene flow. To our knowledge, no solid information on the influence of topography on insect pollinator flights are available at the landscape scale. However, here we showed that substantial altitudinal differences in topography were not impermeable barriers to current gene flow by pollen. In our study landscape, larger cumulative elevation differences (maximum of 823 m) were caused by crossing deep valleys, with the latter obviously enforcing longer pollinator flights than expected from the random model.

Conclusions

This study presents a way to test for the influence of landscape features on realised contemporary patterns of gene flow by pollen. However, this alternative approach also has difficulties in separating the effects of geographical distance and landscape variables on realised gene flow by pollen. We did so by comparing the relationship of realised gene flow distances with landscape features to the relationship of a random model of gene flow in the same landscape. In general, realised gene flow events (i.e. pollinator flights) in *S. domestica* were shorter than expected under the random model (as evidenced by the smaller intercept of the realised model as compared to the random model). Our analysis nevertheless also provided evidence that large areas of open land, a marked topography and, partly, settlements enforce particularly long pollinator flights (as evidenced by the different regression slopes in the realised and random models).

Most palaeoecologists and ecologists consider that the natural vegetation in the lowlands of Central Europe was closed forest (Bradshaw et al. 2003). However human activities—particularly forest clearance for agriculture—began thousands of years ago and drastically reduced the originally closed forest cover. For *Sorbus domestica*, these changes in the structure of the landscape seem to have partly enforced pollen flow over long distances. Thus, from a conservation perspective, it seems that even widely scattered trees are functionally connected in such human-dominated landscape.

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