

# Landscape influences on dispersal behaviour: a theoretical model and empirical test using the fire salamander, *Salamandra atra*

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**Abstract** When populations reside within a heterogeneous landscape, isolation by distance may not be a good predictor of genetic divergence if dispersal behaviour and therefore gene flow depend on landscape features. Commonly used approaches linking landscape features to gene flow include the least cost path (LCP), random walk (RW), and isolation by resistance (IBR) models. However, none of these models is likely to be the most appropriate for all species and in all environments. We compared the performance of LCP, RW and IBR models of dispersal with the aid of simulations conducted on artificially generated landscapes.

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We also applied each model to empirical data on the landscape genetics of the endangered fire salamander, *Salamandra atra*, in northern Israel, where conservation planning requires an understanding of the dispersal corridors. Our simulations demonstrate that wide dispersal corridors of the low-cost environment facilitate dispersal in the IBR model, but inhibit dispersal in the RW model. In our empirical study, IBR explained the genetic divergence better than the LCP and RW models (partial Mantel correlation 0.413 for IBR, compared to 0.212 for LCP, and 0.340 for RW). Overall dispersal cost in salamanders was also well predicted by landscape feature slope steepness (76 %), and elevation (24 %). We conclude that fire salamander dispersal is well characterised by IBR predictions. Together with our simulation findings, these results indicate that wide dispersal corridors facilitate, rather than hinder, salamander dispersal. Comparison of genetic data to dispersal model outputs can be a useful technique in inferring dispersal behaviour from population genetic data.

**Keywords** Circuit theory · Isolation by distance · Isolation by resistance · Landscape genetics · Least cost path

## Introduction

The genetic similarity between isolated populations in the absence of selection declines with time due to genetic drift, and increases with increasing gene flow (Wright 1949). While the impact of genetic drift on population differentiation can be understood using simple models, gene flow resulting from individual dispersal is likely a highly complex process involving multiple factors. Such factors include small-scale movement behaviour, larger scale life

cycle-related dispersal and migration events, the impact of a heterogeneous environment on individual behaviour, as well as various stochastic effects (Slatkin 1985; Templeton 2006). Isolation by distance (IBD) postulates that the gene flow between populations is a direct function of the Euclidian distance between them (Wright 1943). Assumptions of IBD gave rise to early attempts to model genetic differentiation such as the hierarchical island model (Rousset 1997; Slatkin and Voelm 1991).

However, these analyses were based on the assumption of a homogeneous landscape where the resistance to dispersal is uniform. The correlation between genetic and Euclidean distance predicted by IBD would not, however, be expected when the landscape is heterogeneous in its resistance to dispersal and gene flow. As a result, researchers have made attempts to explain patterns of population genetic divergence using landscape features (Dobzhansky et al. 1979; Manel et al. 2003). Many studies have linked genetic divergence to landscape features (e.g. Munshi-South 2012; Schwartz et al. 2009). Others have indicated that either the landscape effect on genetic divergence is minor, or that our ability to detect these effects has been limited (Jaquiéry et al. 2011; Lee-Yaw et al. 2009), especially when differences in landscape resistance to dispersal are slight, or where dispersal is mostly limited by absolute barriers, such as oceans. However, studies such as that of Richardson (2012) have shown that similar species, occupying similar niches, may show different dispersal strategies, leading to very different patterns of genetic divergence with respect to the same landscape features. Further, Brady (2013) showed that different adaptive and maladaptive dispersal strategies can arise within a single species under strong selective pressures.

In many of the previous analyses in landscape genetics, it has been difficult to validate the biological reality of assumptions made about the small-scale (e.g. daily) and medium-scale (e.g. seasonal) movements of individuals (Galpern et al. 2012). Animals typically disperse according to small-scale environmental cues and behavioural influences, and only a small fraction of taxa disperse long distances according to paths that are predictable from one generation to another (Dingle and Drake 2007). Factors influencing movement decisions include immediate resource availability, knowledge of resource distribution at larger scales, predation risk, and abiotic factors such as temperature and moisture (Nathan et al. 2008; Roitberg and Mangel 2010). For instance, relatively short-lived species might follow only short-range resource abundance cues, whereas longer-lived species might retain or even share knowledge of the suitability of dispersal paths beyond the immediate sensory environment (Southwood and Avens 2010). A spectrum of movement strategies is available including, but not limited to, a continuum between a true

Brownian random walk (RW), and a known optimal path between present location and destination. The interaction of these strategies with those landscape features that influence the fitness cost of dispersal (in practical terms, the probability of mortality during dispersal) is likely to produce a pattern of genetic divergence that could be used to infer proximal mechanisms of dispersal behaviour (such as attraction to or avoidance of certain landscape features). For example, two species with a strategy of following the easiest path between two points may show very different genetic divergence patterns if one species can follow corridors of low energetic cost (e.g. river courses), but the other is constrained from doing so (e.g. must cross bridges).

Many different dispersal strategies have been proposed and analysed using theoretical and empirical tools. The simplest of these, the RW or Brownian motion, can be expressed as a mathematically tractable diffusion process (Okubo and Levin 2002). Since this is biologically unrealistic for all but the simplest of organisms or those incapable of independent motion, variations on the diffusion process have been proposed, such as the correlated RW (Cain 1985). In this model, movement is still essentially random (i.e. independent of the environment), but turning angles are not statistically independent, i.e. the organism tends to move in a straighter line than would be expected in Brownian motion. An alternative variation is the Lévy walk, which also appears empirically to describe movement in a wide variety of taxa as diverse as bumble bees *Bombus terrestris* and deer *Dama dama* (Viswanathan et al. 1999). A Lévy walk includes rare instances of long-distance steps, which generate clusters of RWs, connected by an occasional inter-cluster leap. Both correlated RWs and Lévy walks can be used to explain efficient search patterns in foraging animals (Bartumeus et al. 2005; Zollner and Lima 1999). Theoretical considerations indicate that correlated RWs and Lévy walks may be efficient resource search strategies when mortality risks are high and energy reserves are low (Zollner and Lima 1999), but the relevance of such models in animal dispersal is unclear, especially in animals with long life spans and those able to make use of environmental cues (Edwards et al. 2007). The least cost path (LCP) model of animal dispersal has been widely used to explain empirical findings (e.g. Adriaensen et al. 2003; Bunn et al. 2000). The LCP model finds the single path between two populations for which the cumulative cost of moving along that path is the lowest of all possible paths. This represents an extreme case of an individual possessing global habitat information, and is probably biologically unrealistic for most species, simply from a perspective of memory requirement, and the difficulty to create a reliable cognitive map of the whole landscape.

More recently, algorithms from electronic circuit theory that explain the movement of electrons through networks

of resistors have been used to model animal dispersal in heterogeneous landscapes (McRae and Beier 2007; McRae et al. 2008). This isolation by resistance (IBR) model has the advantage of considering multiple dispersal pathways between populations, weighted by their relative dispersal costs. In this sense, it is a compromise between the global information of the LCP model, and the stochasticity of various RW models. For elaboration on the relationships between these different movement models, more detailed mathematical texts exist (e.g. Lovász 1993).

Although a number of studies have made use of the IBR model, few have compared its predictions to the LCP or RW models. While IBR may be intuitively appealing, behavioural differences between species may not make it the most appropriate model in all systems. Munshi-South (2012) compared the LCP and IBR models in predicting the landscape genetics of the white-footed mouse (*Peromyscus leucopus*) on the assumption that canopy cover is required for dispersal, and found that IBR predicted the observed genetic differences better than LCP. On the other hand, Schwartz et al. (2009) also attempted to compare LCP and IBR analyses of the dispersal of wolverines (*Gulo gulo*), but computational limitations prevented them from drawing firm conclusions. Row et al. (2010) found that LCP and IBR methods produced similar results in predicting genetic patterns in eastern foxsnakes (*Mintoinus gloydi*), but suggested that their results did not constitute a rigorous test of these two models because extensive fragmentation in their study area forced dispersal through a small portion of the landscape.

Many models of landscape genetics are based on assumptions about the influence of various landscape features on the dispersal ability of a target species, for instance whether rivers or roads might constitute dispersal barriers, or whether a particular vegetative cover might facilitate dispersal. There may be empirical evidence, or support via habitat suitability models, that a particular feature (for example, terrain slope or lack of vegetative cover) forms a barrier to animal dispersal, or assumptions are made on the basis of physiology, or intuitive reasoning, and this calls into question the validity of the analysis (Sawyer et al. 2011). For example, amphibian species may be suspected to prefer moist landscapes because of their intrinsic physiology, or central place foraging animals may be expected not to wander far from suitable shelter from predators (Kershbaum et al. 2011). However, these assumptions have been rarely tested empirically.

The aim of this study was twofold. First, we examined how the landscape-wide dispersal behaviour differed between the different dispersal models by simulating a variety of artificial environments and calculating the effect of model choice on simulated dispersal. In particular, we tested how different landscape features such

as roughness, and the presence of wide valleys, might affect dispersal. We hypothesised that dispersal through regions with multiple pathways of similar cost would produce markedly different predictions for different dispersal models. Second, we confronted different dispersal models with empirical genetic data. Rather than assuming a particular dispersal model for our target species and then fitting the predictions of one particular model to the empirical data, we employed the three dispersal models described above and tested which of them best explained the observed pattern of genetic differentiation in the empirical data on genetic divergence between breeding sites of the fire salamander, *Salamandra infraimmaculata*, in northern Israel.

*S. infraimmaculata* is a locally endangered species in northern Israel, where it lives at the southern edge of its global distribution (Warburg 2007). This species is found in mountainous regions (Blank and Blaustein 2012), aestivates during the hot dry summer and emerges when the autumn rains begin. Adult females emerge from their summer aestivation site with a full complement of larvae, depositing them into permanent or temporary water bodies, most of which are lentic (Degani 1996). Early evidence suggested that *S. infraimmaculata* demonstrated breeding site fidelity, returning numerous times to the same breeding site (Warburg 1994). However, recent work indicates that it can disperse between breeding sites (Bar-David et al. 2007), and that landscape barriers such as elevation and soil type are predictors of suitable breeding site habitat (Blank and Blaustein 2012). In general, amphibians are particularly well suited for the examination of landscape genetic models because a number of landscape features have been implicated as influencing amphibian dispersal (Richardson 2012; Spear et al. 2005). In addition, their reliance on aquatic habitats for at least part of their life cycle constrains dispersal on time scales greater than a single generation, since dispersing individuals that do not arrive at aquatic breeding sites will not have offspring to continue the dispersal process. Considerable literature exists indicating that various amphibian species use non-random dispersal (e.g. Phillips and Sexton 1989). As *S. infraimmaculata* is locally endangered, there has been much interest in creating corridors between breeding sites as a conservation technique (Israel National Parks Authority, I. Sinai). Planning for effective corridors depends critically upon the mode of dispersal as well as landscape features.

We also took advantage of our multiple dispersal models to provide a simple test for the appropriateness of dispersal cost assumptions. We posit that variation in a landscape feature that causally influences dispersal cost will be positively correlated with genetic divergence separating populations when an appropriate dispersal model is chosen.

## Materials and methods

### Theoretical analysis

We simulated dispersal on fractal landscape raster maps generated using the Diamond square algorithm (Fournier et al. 1982) as implemented in Matlab 7.1 (Mathworks, Nantick, MA). We generated three sets of 100 random landscapes. In the first set, each of extent  $256 \times 256$  pixels, we varied the roughness factor ( $H$ ) from 0 to 1.  $H$  determines the high frequency variation in landscape altitude, i.e. how variable the altitude is within any given region. Low values of  $H$  produce smoothly varying terrain; high values of  $H$  produce rough, craggy landscapes. We generated the second set of 100 landscapes with extent  $256 \times 256$  pixels and with  $H = 0.9$ , but clipping the height map at between zero and 3 SD from the mean height (to produce flat-bottomed valleys and flat-topped peaks). In the third set of 100 random landscapes with no clipping and  $H = 0.9$ , we varied the extents (i.e. landscape size) between  $2^3 \times 2^3$  and  $2^{10} \times 2^{10}$  pixels to give different landscape resolutions. Examples of such landscapes are shown in Fig. 1. We chose to test landscapes with varying roughness and extents, as these represent fundamental properties of any terrain, and we modelled the valley clipping specifically to test our hypothesis of the effect of wide flat valleys on random walkers. Since we chose to approximate dispersal cost by terrain slope, we then converted these three-dimensional maps to two-dimensional rasters of slope, by taking the first-order derivative of Gaussian distribution in both  $x$ - and  $y$ -directions using a two-pixel kernel, and averaging the absolute gradients in the two directions. Having generated slope rasters, we defined the dispersal cost ( $C_{AB}$ ) along a path between pixels  $A$  and  $B$  as the sum of the slope pixel values along that path.

We considered three different types of dispersal models. In the first, the LCP model, the modelled animal takes the lowest cost (i.e. minimum summed terrain slope) route from source to destination. We used Geographic Resources Analysis Support System version 6.4 (Neteler and Mitasova 2008) to calculate the cost of the LCP using the `r.cost` function. In the second, the RW model, we used a Markov model to calculate the expected time to arrive at the destination pixel, and defined this time as the dispersal cost. For an  $N \times N$  landscape, we calculated a  $N^2 \times N^2$  sparse transition matrix ( $T$ ), where the probability of moving from pixel  $a$  to pixel  $b$  is proportional to the cost of pixel  $b$  if  $a$  and  $b$  are adjacent, and zero otherwise. We then standardised the probabilities row-wise so that the total transition probability for each source pixel  $a$  was equal to unity. Defining  $Q$  as the transition matrix having excluded the row and column of the absorbing (destination) pixel  $b$ ,  $Q = T_{[1, N^2] \neq b [1, N^2] \neq b}$

, and the fundamental matrix  $F$  as  $F = (I - Q)^{-1}$ , where  $I$  is the identity matrix, and the expected time to absorption  $t_b$  is given by  $t_b = F_c$  where  $c$  is a column vector whose elements are all unity (Grinstead and Snell 1997). The third IBR model, is implemented in Circuitscape 3.5.7, <http://www.circuitscape.org>, (McRae et al. 2008), and we calculated the equivalent resistance between two pixels  $a$  and  $b$  using the four-pixel connection scheme, and defined this as the dispersal cost.

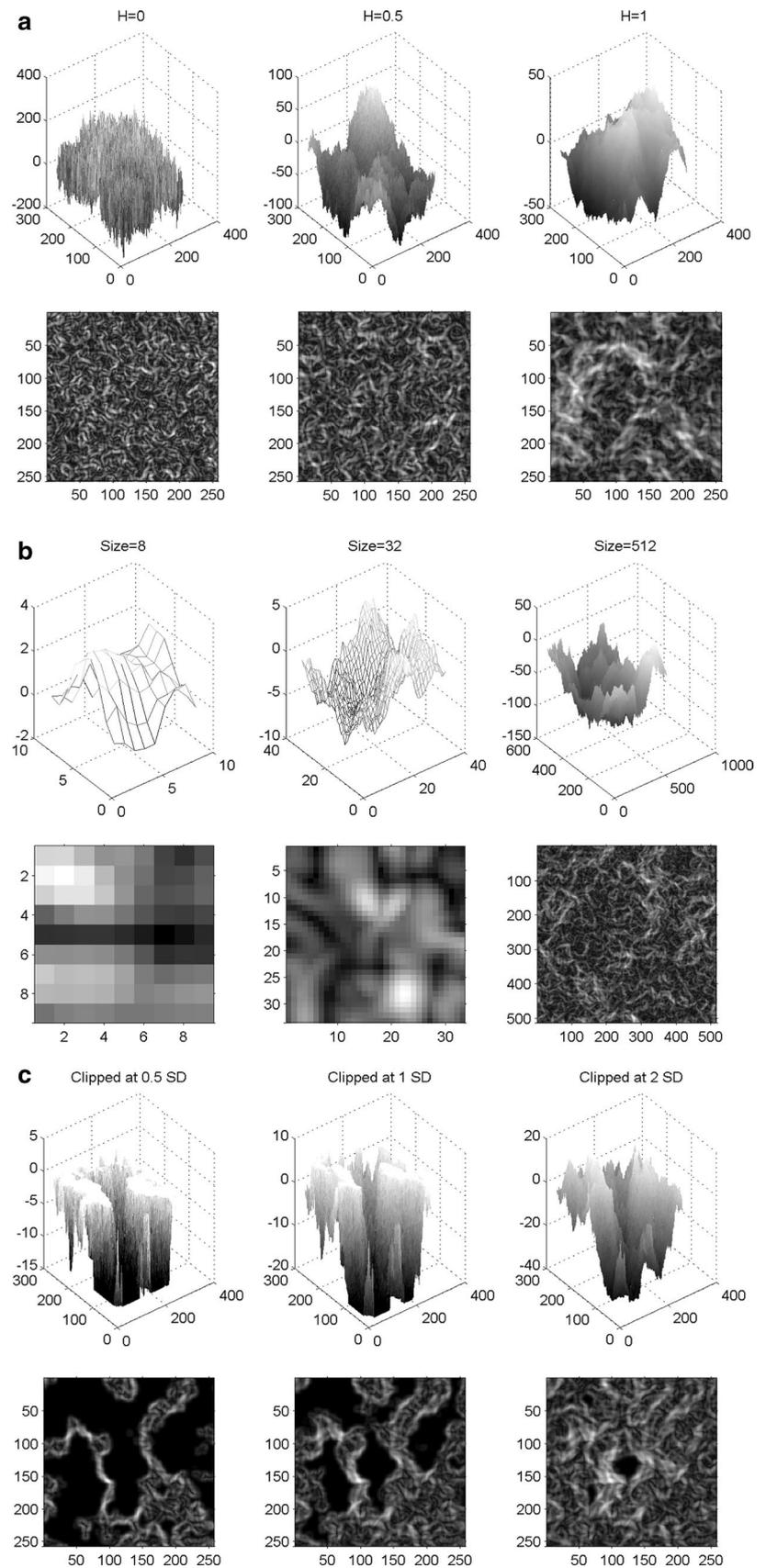
For each landscape, we calculated the dispersal cost from the upper-left to lower-right corners, e.g.  $a = (1, 1)$ ,  $b = (256, 256)$  using each of the three dispersal models. We repeated the corner-to-corner analysis for the 100 landscapes with varying  $H$ , the 100 landscapes with varying clipping, and the 100 landscapes with varying extents. Since we were interested in the responses of dispersal cost to varying parameters, and since each model calculated dispersal cost values in different and arbitrary units, we standardised all dispersal costs by dividing by the maximum value, separately for each varying parameter, which enabled direct comparison between models.

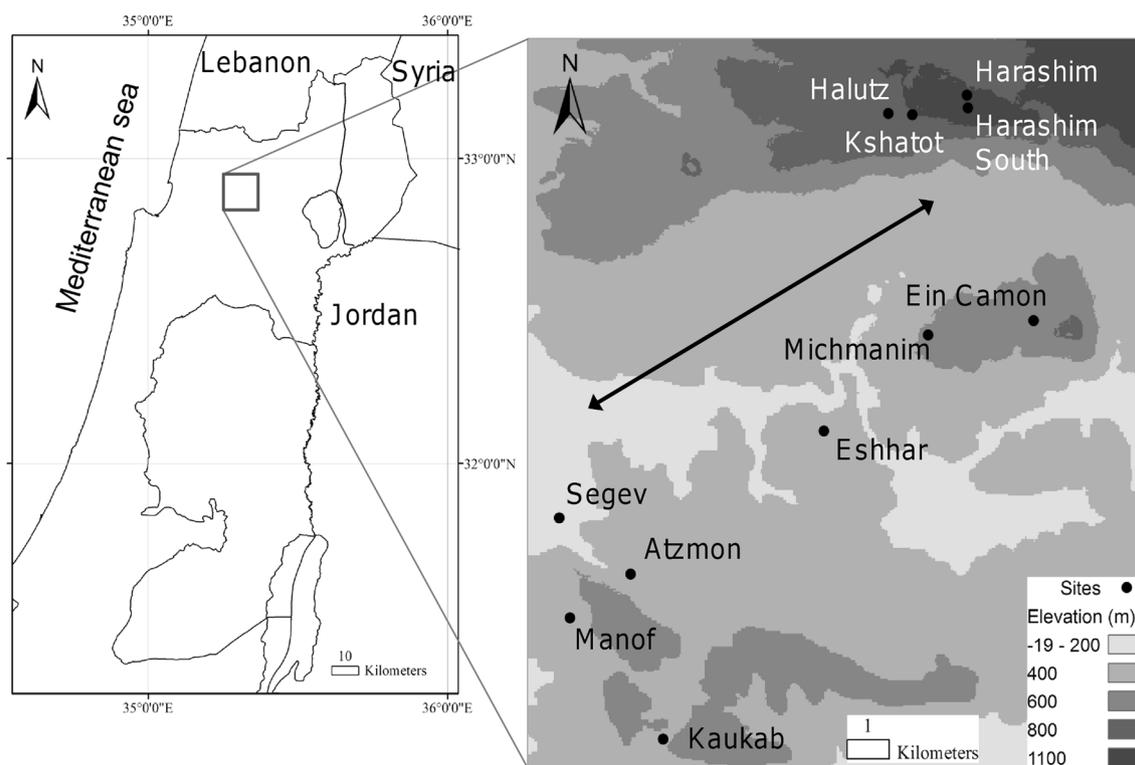
### Empirical data analysis

We examined the relationship between genetic divergence and dispersal behaviour in the fire salamander *S. infraimaculata* by sampling 11 known fire salamander breeding sites across the Galilee region of northern Israel (Fig. 2; Table 1). At each site, we took a tissue sample from the tail tips of adults (mean  $n = 21$ ), preserved them in 95 % ethanol in the field, and kept them subsequently at  $-20^\circ\text{C}$  until further processing.

We used 15 microsatellite loci to estimate the genetic divergence between each pair of populations using DEMEtics (Gerlach et al. 2010). Ten microsatellite loci (Sal E2, Sal E5, Sal E6, Sal E7, Sal E8, Sal E11, Sal E12, Sal E14, Sal 3 and Sal 23) were synthesized following Steinfartz et al. (2004), and five microsatellite loci (SST-A6-I, SST-A6-II, SST-C3, SST-E11 and SST-G6) following Hendrix et al. (2010). We used the Qiagen Multiplex polymerase chain reaction (PCR) kit (Qiagen) and diluted 1:100 the PCR products. The fragments were electrophoresed on a MegaBACE 1000 capillary sequencer (Amersham Biosciences). Product sizes were determined using Et-ROX400 size standard (Amersham Biosciences). Allele size scoring was performed using the Fragment Profiler version 1.2 software (Amersham Biosciences). We tested for statistically significant linkage disequilibrium and Hardy–Weinberg equilibrium (HWE) using FSTAT 2.9.3 (Goudet 2002) and Genepop (Rousset 2008), respectively. We used the sequential Bonferroni correction to adjust significance levels for multiple tests (Rice 1989). Linkage disequilibrium was not detected for any pair of loci in the data. Only locus L6

**Fig. 1** Artificial fractal landscapes showing the height maps (*top row*) and corresponding absolute slope (gradient) calculated using a two-pixel kernel (*bottom row*) for varying parameters: **a** roughness factor ( $H$ ) = 0, 0.5 and 1; **b** landscape size 9, 33, and 513 pixels; **c** clipping of the height map at 0.5, 1, and 2 SDs from the mean





**Fig. 2** Map of the survey area and the *Salamandra inframaculata* breeding sites, showing (left) regional location, and (right) topographic elevation. The double-headed arrow in the topographic map

shows the location of the valley proposed as the cause of the greater than expected similarity between the northern mountain range and the western mountain range

deviated significantly from HWE in the Harashim subpopulation and locus L23 in Halutz and Ein Camon sites. More details on the genetics of the population under study, and the techniques used, can be found in Blank et al. (2013).

Our sample size among the populations varied (Table 1). We thus used Jost's genetic distance ( $D$ ) as a measure of genetic divergence (Jost 2009; Takahata and Nei 1984). However, we also tested models with  $F_{ST}$  that yielded very

similar results. For the landscape analysis, we used a digital elevation model layer at 33-m resolution obtained from Hall et al. (1999) as well as the corresponding slope layers. The breeding sites sampled represent, to the best of our knowledge, all the known breeding sites in the area, as determined by extensive field studies (I. Sinai, unpublished data).

We used a Mantel test to test for a correlation between Euclidean distance and genetic divergence between pairs of sites. We then built dispersal models using landscape features to determine dispersal cost. Although there is no direct indication of which landscape features hinder salamander dispersal, we speculated that both slope and elevation play a role in restricting their dispersal. Slope would seem to be a good candidate for hindering salamander dispersal purely from energetic considerations, and elevation has been shown to be a good predictor for salamander occurrence; breeding sites occurred only above 200 m a.s.l. (Blank and Blaustein 2012, 2014), implying that low elevation might represent a hostile environment also to salamander dispersal. To test these ideas, we generated multiple landscape cost rasters as follows. First, we standardised the slope and elevation maps by dividing pixel values by the maximum pixel value, to bring them both into the range of [0, 1]. Then, we generated a combined cost map ( $C$ ) of the form

**Table 1** Locations of the sampled breeding sites, and the number of samples ( $n$ ) taken at each site

Breeding site	Longitude (°N)	Latitude (°E)	$n$
Halutz	32.953	35.312	23
Harashim	32.956	35.332	26
Harashim South	32.954	35.333	7
Kshatot	32.952	35.318	10
Ein Camon	32.91	35.349	35
Michmanim	32.907	35.322	6
Eshhar	32.887	35.296	30
Segev	32.869	35.229	12
Atzmon	32.857	35.247	17
Manof	32.848	35.231	30
Kaukab	32.823	35.255	31

$C = \alpha S + (1 - \alpha)(1 - E)$ , where  $S$  is the slope map,  $E$  is the elevation map, and  $\alpha$  is a weighting factor which we varied from zero to one, indicating the relative importance of slope vs. elevation in determining dispersal cost. Elevation is expressed as  $1 - E$  because of the purported negative relationship between elevation and cost. For each cost map, we calculated the dispersal cost between each of the sample sites, according to each of the three dispersal models used above (LCP, RW, and IBR). For each cost map and each dispersal model, we calculated the correlation between genetic divergence and dispersal cost using a 10,000 permutation partial Mantel test (Smouse et al. 1986) implemented in Matlab 7.1, which compares two distance matrices (in our case, dispersal cost and genetic divergence), while controlling for a third distance matrix (Euclidean geographic distance). We hypothesised that, if a dispersal model correctly described the interaction of dispersal behaviour with our chosen environmental factors ( $S$  and  $E$ ), then we would expect the correlation  $r$  between dispersal cost and genetic divergence to show a peak for some value of  $\alpha$ , which would represent the most likely relative influence of slope and elevation on dispersal. We then chose the optimum value of  $\alpha$  for each of the three dispersal models and compared them. If a particular dispersal model correctly described the response of gene flow to environmental barriers, we expected a strong correlation between dispersal cost and genetic divergence. If the dispersal model did not describe dispersal behaviour in a realistic way, then we would attribute any correlation between calculated dispersal cost and genetic divergence to geographic distance. Naturally, any correlation between cost and divergence does not conclusively demonstrate that these environmental features are causally linked to animal dispersal, as they may be confounded by unknown environmental attributes. Since the number of populations was small (11) we performed a bootstrap of the Mantel test to ensure that

a significant result was not obtained by chance. We sequentially excluded two of the 11 sites and repeated the partial Mantel test at optimum  $\alpha$  for each of the models, and then compared the resulting populations of  $r$ -values using univariate ANOVA with a post hoc Tukey test (IBM SPSS version 20).

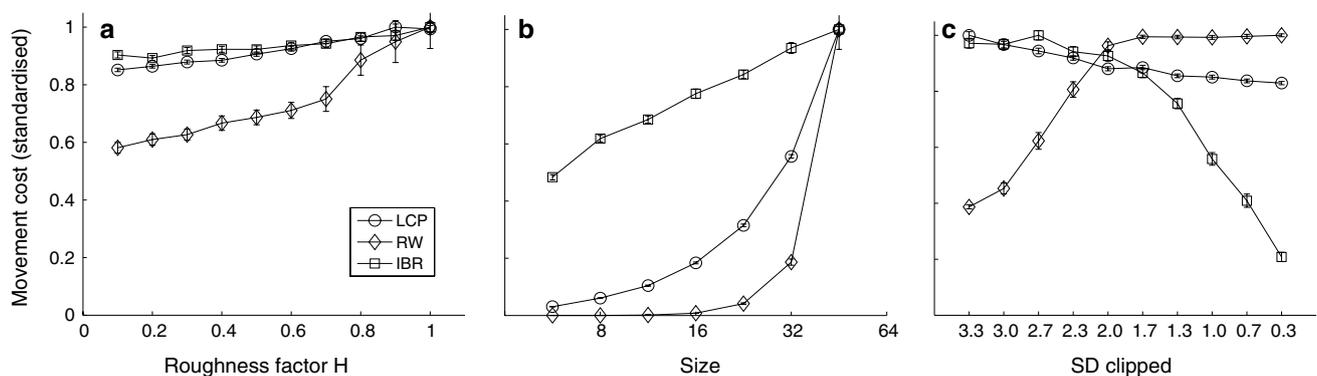
## Results

### Theoretical analyses

The dispersal cost from one corner of the landscape to the other varied much less with the roughness factor (Fig. 3a) for the LCP model (0.85–1.0 = 15 %) and the IBR model (0.89–1.0 = 11 %) than for the RW model (0.58–1.0 = 42 %), but for all models, the cost increased with increasing  $H$  (decreasing roughness). As the size of the landscape was increased, and thus the resolution of height variation (Fig. 3b), the dispersal cost varied less in the IBR model (0.48–1.0 = 52 %) than in the LCP model (0.03–1.0 = 97 %) or the RW model (0.0–1.0 = 100 %); in this case too, dispersal cost increased monotonically with landscape resolution for all models. However, as height clipping increased (Fig. 3c), the different models showed substantially different behaviour. While the LCP dispersal cost varied little (1.0–0.83 = 17 %), the cost of the RW model increased (0.39–1.0 = 61 %), but that of the IBR model fell (1.0–0.21 = 79 %), showing a qualitatively different response of the RW and IBR models.

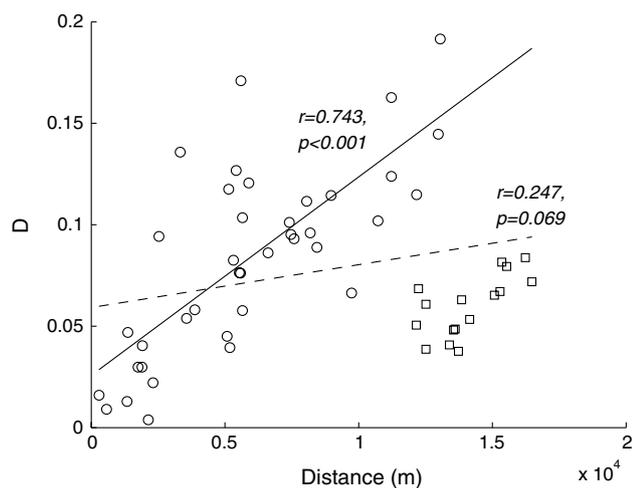
### Empirical analyses

Although a clear Mantel correlation existed between Euclidean distance and genetic divergence among  $S$ .



**Fig. 3** Mean dispersal cost from one corner of the landscape to the other, averaged over  $n = 100$  random landscapes for the three dispersal models: least cost path (LCP), random walk (RW), and isolation by resistance (IBR). Dispersal cost values are standardised by dividing by the maximum value for each model. Error bars indicate

SEM. **a** Scaling of dispersal cost with increasing  $H$ , **b** dispersal cost with increasing landscape extent, and **c** increasing height clipping (note reversal of the  $x$ -axis indicating at which SD from the mean that height is clipped)



**Fig. 4** Correlations between Jost's genetic distance ( $D$ ) and Euclidean distance between sites. Some pairs of sites (shown as *squares*) have a much lower  $D$  than would be expected given the large distance between them. The overall Mantel test correlation of  $D$  to distance (*dashed line*) is much stronger when these sites are excluded (*solid line*)

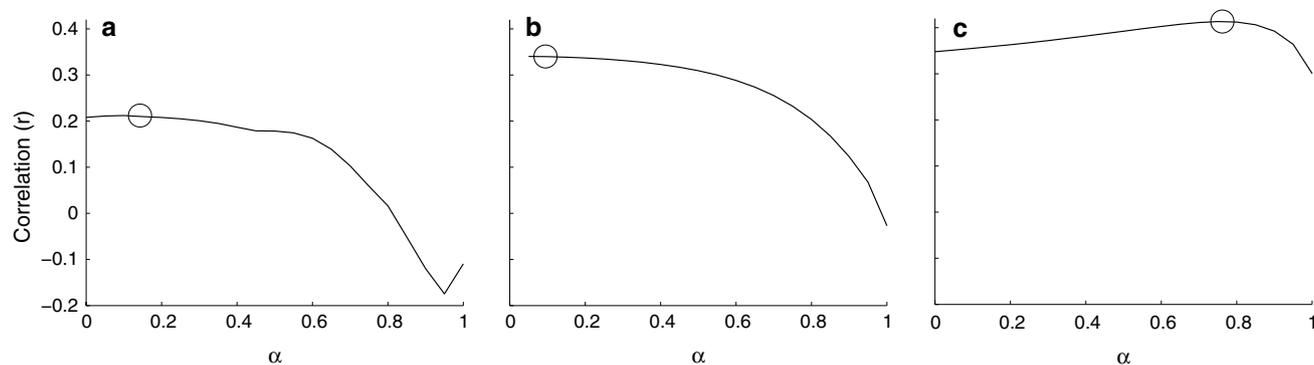
*inframaculata* populations, as measured by Jost's  $D$ , some comparisons between sites did not fall into the overall pattern (Fig. 4). These pairs of sites appeared to be genetically more similar than would be expected from their geographic separation. Examination of these pairs showed that they corresponded to two discrete geographic clusters: Halutz, Harashim, Harashim South and Kshatot (northern mountain range) vs. Segev, Atzmon, and Manof (western range; Fig. 2). This justified analysing the data with these pairs excluded. The correlation between Euclidean distance and  $D$  was much stronger when these pairs of sites were excluded (included,  $r = 0.247$ ,  $p = 0.069$ ; excluded,  $r = 0.743$ ,  $p < 0.001$ ; Fig. 4).

Next, we compared genetic distance to dispersal costs from the three dispersal models, rather than to Euclidean

geographic distance. We identified the optimal mixture of slope and elevation factors as hindering gene flow ( $\alpha$ ) (i.e. best empirical fit to genetic data). All three dispersal models showed variation in the partial Mantel correlation as  $\alpha$  was varied between zero and one. However, only the IBR model shows an intermediate maximum, i.e. a mixture of slope and elevation values that produced an optimal match between genetic divergence and landscape features (Fig. 5). The LCP and RW models both provided better matches for almost pure elevation-based costs than for elevation-slope mixtures, but this match worsened as slope features were given more importance. For the remaining analyses, we consider only the landscape feature mixtures that gave the best correlations, i.e.  $\alpha_{\text{LCP}} = 0.14$ ,  $\alpha_{\text{RW}} = 0.10$ ,  $\alpha_{\text{IBR}} = 0.76$ .

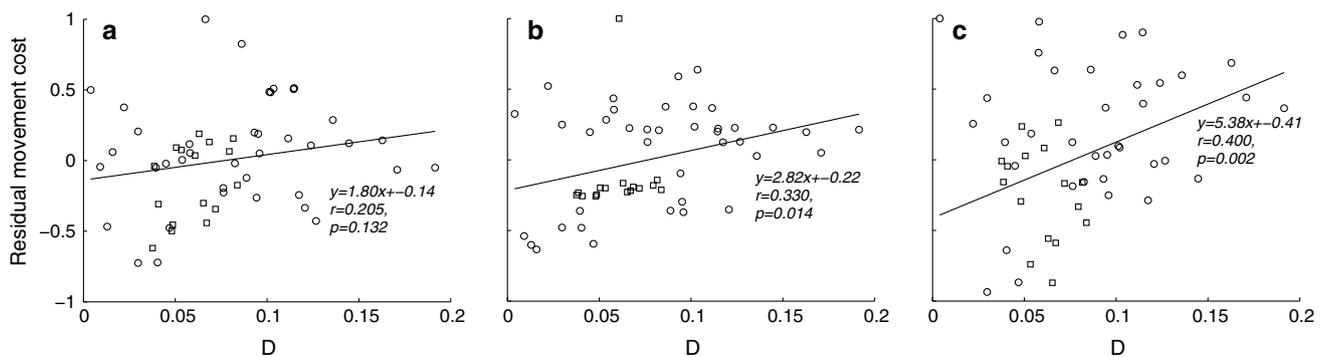
The three dispersal models varied greatly in the extent to which their dispersal costs differed from Euclidean geographic distance. The dispersal cost as calculated by the LCP model remained very strongly correlated with geographic distance ( $r = 0.995$ ), whereas the IBR model was less strongly correlated ( $r = 0.722$ ), and the RW model showed no significant correlation ( $r = 0.169$ ; Online Resource 1). The maximum partial Mantel correlations also differed across the three models at their optimal  $\alpha$  values: 0.212 (LCP), 0.340 (RW), and 0.413 (IBR). Examination of these differences using ANOVA on the bootstrapped data showed that the correlation of the IBR model was significantly higher than that of the LCP or RW models ( $p = 0.042$ ).

Using the results from the dispersal model, we re-analysed the relationship between genetic distance to dispersal cost, including those anomalous sites identified in Fig. 4. We subtracted the linear regression of dispersal cost to Euclidean distance for each of the three models, and Fig. 6 shows the residual dispersal cost plotted against genetic distance for each of the models. Both the RW and IBR



**Fig. 5** Partial Mantel correlation ( $r$ ) of genetic divergence to dispersal cost, when controlling for geographic distance as the relationship between slope and elevation ( $\alpha$ ) in calculating landscape resistance was varied. **a** LCP dispersal model, **b** RW dispersal model, and **c** IBR

dispersal model. For  $\alpha = 0$ , dispersal cost was calculated based only on elevation, and for  $\alpha = 1$ , based only on slope. The *circle* indicates the mixture giving maximum correlation. For other abbreviations, see Fig. 3



**Fig. 6** Detrended correlation of dispersal cost to Jost's  $D$  for **a** LCP model, **b**, RW model, and **c** IBR model. Linear equations and correlation coefficients are for the residual dispersal costs, after subtract-

ing the fit of dispersal cost to Euclidean geographic distance. *Squares* indicate those sites that showed lower than expected  $D$  in Fig. 4. For abbreviations, see Figs. 3 and 4

models show a significant residual correlation, indicating that these models explain more of the genetic isolation than Euclidean geographic distance alone. The LCP model does not provide an additional explanation of genetic isolation, beyond its correlation with geographic distance. For those anomalous pairs of sites that showed lower than expected  $D$  when compared to geographic distance, the residual movement costs are evenly distributed in the IBR and LCP movement models, but are highly asymmetric in the RW model.

## Discussion

All three dispersal models that we studied scale differently with landscape features. All models increased dispersal cost with increasing landscape roughness and increasing landscape extent, but the IBR model was more similar to the LCP model, compared to the wholly stochastic RW model. However, IBR dispersal costs were less sensitive to landscape extent than either LCP or RW. The accuracy of the landscape modelling of genetic divergence decreases with decreasing resolution (Jaqu ery et al. 2011), and our results imply that the IBR model is less prone to these errors than LCP or RW models. This result is not surprising, since the IBR model makes use of multiple dispersal pathways, which makes it less sensitive to the disappearance of LCPs because of low resolution sampling.

The response of the models to height clipping (i.e. larger expanses of flat valley bottoms and flat mountain ridges) was substantial. In an RW dispersal model, an animal dispersing through a region of low and uniform resistance will face increased expected crossing time, since it is likely to 'wander' in this cost plateau, rather than exiting the plateau into the surrounding higher cost environment. Conversely, an animal dispersing according to the IBR model will show stronger dispersal across such a plateau (greater

gene flow), since multiple parallel paths exist along which to travel. Dispersal corridors are known to be important for gene flow, (e.g. Schwartz et al. 2009), but we are not aware of any studies that assessed the effect of multiple dispersal paths. Using the circuit theory analogy, parallel resistances always reduce overall resistance. In the LCP model, clipping had no clear effect, since only a single shortest path existed. Pinto and Keitt (2009) studied the effect of multiple paths of similar resistance, and combined them into an adjusted LCP measure. In contrast to our results, they found an increase in resistance in very homogeneous environments due to the creation of numerous long, tortuous paths. However, Pinto and Keitt (2009) used average resistance, whereas our use of the parallel resistance of the circuit theory analogy would be expected to lead to different results.

Our use of slope and elevation as proxies for salamander dispersal cost was based on studies showing these factors as being predictors of suitable breeding site habitats (Blank and Blaustein 2012, 2014) and these have been shown to be factors influencing dispersal of other salamander species as well (Lowe et al. 2006; Giordano et al. 2007). Using the IBR model, we achieved an optimal fit of empirical data to predictions, by varying the relative contribution of slope and elevation to dispersal cost, which implies a genuine optimal mixture of landscape features (Khalil and Grizzle 1992), although other landscape factors such as soil moisture may also influence dispersal cost. Schwartz et al. (2009) also examined goodness of fit as dispersal cost assumptions were varied, but found only an asymptotic response in a LCP model, as we did with the LCP and RW models. Our results indicated a poor match between both LCP and RW dispersal models and cost assumptions, with real salamander gene flow in the study landscape.

Other studies have used different dispersal models to predict landscape effects on dispersal and gene flow. Richardson (2012) demonstrated that different amphibian

species make use of different landscape features (e.g. roads vs. rivers) for dispersal corridors. Lee-Yaw et al. (2009) and Richardson (2012) examined the wood frog, *Rana sylvatica*, using an IBR model, and concluded that landscape variables did not explain genetic variation at large scales. However, they did not compare the results of their IBR analysis with a traditional LCP model. In contrast, Munshi-South (2012) did find support for his hypothesis that canopy cover is a critical landscape feature for the dispersal of the white-footed mouse, *Peromyscus leucopus*. He found the IBR model to be superior to the LCP model, stating that isolation by resistance is more biologically realistic than IBD. While this appears to be the case both with *P. leucopus* and *S. infraculata*, our *S. infraculata* results indicated that these models do not fully explain genetic divergence, and it is probable that no particular dispersal model is superior to another for all scenarios. For example, Schwartz et al. (2009) examined gene flow in the wolverine *Gulo gulo* in an extreme environment, where one landscape feature (spring snow cover) appears to restrict potential dispersal paths and found the LCP model to be superior. LCP models are likely to be superior in cases where environmental constraints are more distinct and severe, mortality is high, and energy reserves are low (Zollner and Lima 1999), as the dispersing animal pays a high fitness cost for choosing a sub-optimal path. However, when severe constraints on dispersal exist, it may be difficult to obtain a rigorous test of the LCP and IBR models since dispersal might occur only along a small number of open corridors (Row et al. 2010). Local adaptation can also contribute to genetic differentiation, but it usually affects very few loci or regions in the genome. For this explanation to contribute to our results would require that one or more of the microsatellites we used are involved or closely linked to genes contributing to local adaptation, and it is somewhat implausible that our small set of markers represents the extreme outliers over the whole genome.

The results reviewed above indicate that the choice of dispersal model can strongly influence both the qualitative and quantitative predictions of animal dispersal responses to landscape characteristics. Thus, the accuracy of model predictions depends on the suitability of a particular model to the actual dispersal behaviour of the target species. This is particularly relevant if animals disperse via low-cost paths, for example river valleys. Dispersal corridors have long been proposed as conservation tools, but caution is required since they may also have negative effects on biodiversity and metapopulation survival (Simberloff et al. 1992). Although it may seem that wide corridors would facilitate dispersal, our simulations show that a very wide corridor might increase gene flow (IBR model), have little effect (LCP model), or even reduce gene flow (RW model; Fig. 3). Soule and Gilpin (1991) suggested that individuals

might ‘wander’ in wide corridors, and McRae et al. (2008) noted that reduced resistance can result in increased commuting times, if multiple pathways exist. Our study quantified these phenomena in the context of realistic simulated landscapes, and showed both theoretical and empirical support for the phenomenon of wandering dispersal.

Our empirical data give a possible example of this effect. The IBR model fits genetic divergence better than LCP or RW models: population pairs that were strikingly anomalous in the LCP analysis were well explained by the IBR analysis. This can occur when geographically distant but genetically similar populations are connected by wide corridors with multiple low-cost paths, reducing the overall dispersal resistance in the IBR model, but having no effect in the LCP model. In our case, this could be explained by the presence of the wide shallow valley between the upper and lower Galilee (Fig. 2), or by other processes such as larval drift (Thiesmeier and Schuhmacher 1990; Segev and Blaustein, in press), in which larvae are transported downstream along seasonal watercourses. We are not aware of similar results from studies using a combination of empirical and simulation analyses, although Pinto and Keitt (2009) showed that varying homogeneity could cause diversion of the LCP. Specifically, for the endangered fire salamander populations in Israel, ecological niche modelling (e.g. Blank and Blaustein 2012) must be supplemented with consideration of low-cost corridors when planning conservation and restitution efforts at key habitat sites. Breeding pools situated along favourable dispersal routes could be important in linking isolated populations. However, the effect of dispersal ‘corridors’ on population connectivity must be understood in the context of the response of the focal species to the corridor type: wide corridors may actually inhibit dispersal if the species tends to disperse according to a RW. Moreover, a dispersal corridor could be used by species other than the focal species, and our results indicate that the impact of a single corridor could have diverse—even opposite—effects on population connectivity across species. Such diversity in response should also be considered in conservation planning.

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