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Dendritic connectivity shapes spatial patterns of genetic diversity: a simulation-based study.

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Abstract

Landscape features notoriously affect spatial patterns of biodiversity. For instance, in dendritic ecological networks (such as river basins), dendritic connectivity has been proposed to create unique spatial patterns of biodiversity. Here, we compared genetic datasets simulated under a lattice-like, a dendritic and a circular landscape to test the influence of dendritic connectivity on neutral genetic diversity. The circular landscape had a level of connectivity similar to that of the dendritic landscape, so as to isolate the

influence of dendricity on genetic diversity. We found that genetic diversity and differentiation varied strikingly among the three landscapes. For instance, the dendritic landscape generated higher total number of alleles and higher global *Fst* than the lattice-like landscape, and these indices also varied between the dendritic and the circular landscape, suggesting an effect of dendricity. Furthermore, in the dendritic landscape, allelic richness was higher in highly connected demes (e.g. confluences in rivers) than in low connected demes (e.g. upstream and downstream populations), which was not the case in the circular landscape, hence confirming the major role of dendricity. This led to bell-shaped distributions of allelic richness along an upstream-downstream gradient. Conversely, genetic differentiation (*Fst*) was lower in highly than in low connected demes (which was not observed in circular landscape), and significant patterns of isolation-by-distance (IBD) were also observed in the dendritic landscape. We conclude that in dendritic networks, the combined influence of dendricity and connectivity generates unique spatial patterns of neutral genetic diversity, which has implications for population geneticists and conservationists.

Introduction

Describing patterns of biodiversity (i.e. repetitions of definite biodiversity distributions along geographical or environmental gradients; Lawton, 1996) and shedding light on the foremost processes driving biodiversity patterns is a key concern in ecological and evolutionary sciences (Gotelli *et al.*, 2009; Chave, 2013). Understanding how biodiversity is distributed in space and time indeed improve our predictive capacities, for instance by facilitating the forecasting of the distribution of biodiversity in changing environments (Guisan & Thuiller, 2005). In ecosystems

that are strongly structured by complex spatial arrangements, spatial patterns of biodiversity can be influenced by particular landscape features such as topological or environmental constraints (Manel & Holderegger, 2013), and at multiple organizational levels (e.g. genes, species or functional groups; Chave, 2013). This is the case for dendritic ecological networks, such as river basins, hedgerows and caves, a type of ecosystem characterized by a hierarchical spatial structure that mimics the branching pattern of trees (Campbell Grant *et al.*, 2007; Altermatt, 2013; Peterson *et al.*, 2013).

Theoretical studies have explored how landscape organization influences spatial patterns of inter-specific (Muneepeerakul *et al.*, 2008; Carrara *et al.*, 2012; Seymour & Altermatt, 2014) and intra-specific diversity (Labonne *et al.*, 2008; Chaput-Bardy *et al.*, 2009; Morrissey & de Kerckhove, 2009) in dendritic ecological networks. For instance, Carrara and co-authors (2012) demonstrated that connectivity (i.e. the type and the degree of connection between ecosystem portions) in dendritic ecological networks shapes taxonomic diversity at the meta-community level, by comparing patterns of species diversity between two contrasting landscapes (i.e. a dendritic *vs.* a lattice-like landscape). At the intra-specific (or meta-population) level, previous theoretical studies focused on the effects of asymmetric gene flow and overland dispersal on spatial patterns of neutral genetic diversity (Chaput-Bardy *et al.*, 2009; Morrissey & de Kerckhove, 2009), and on the effect of the network structure on population demogenetics (Labonne *et al.*, 2008). The latter study specifically showed that dendritic connectivity may influence genetic diversity and differentiation at the meta-population level depending on the degree of ongoing dispersal between patches (i.e. low or high dispersal; Labonne *et al.*, 2008). Although such study suggests that connectivity can influence the spatial distribution of neutral genetic diversity in dendritic ecological networks, we are not aware of any study testing specifically whether or not dendritic connectivity drive spatial patterns of genetic diversity in dendritic ecological networks.

The general objective of this study is to theoretically test whether or not dendritic connectivity shapes spatial patterns of neutral genetic diversity at the meta-population level. Using simulated microsatellite genetic datasets, we first tested the null hypothesis that genetic diversity indices measured at the landscape scale did not vary between meta-populations living in a dendritic landscape and those living (i) in a classical two-dimensional stepping-stone landscape ("lattice landscape") displaying high levels of connectivity among demes, and (ii) in a quasi-circular landscape ("circular landscape") characterized by connectivity levels similar to those of the dendritic landscape, but that was not dendritic. Given that increasing connectivity decreases isolation between demes in meta-populations, we expect to reject this null hypothesis for the comparison between the dendritic *vs.* the lattice landscape, but not for the comparison between the dendritic *vs.* the circular landscape. We rather predict that within-deme diversity should be higher in the lattice (highly connected) landscape than in the dendritic landscape, whereas the reverse is expected for among-deme genetic differentiation. Concerning the dendritic *vs.* the circular landscape comparison, rejecting the null hypothesis would imply that differences in genetic diversity and differentiation between the two landscapes arise from structural differences (i.e. dendricity), and not only from the level of connectivity. Second, we tested the working hypothesis that dendritic connectivity generates a non-random spatial distribution of genetic diversity in dendritic networks, by (i) characterizing spatial patterns of genetic diversity in the dendritic landscape and by (ii) comparing levels of genetic diversity and genetic differentiation between low *vs.* highly connected demes in this landscape. It has been empirically shown that genetic differentiation tends to be higher in upstream demes (low connected) than in confluence demes (highly connected) in river networks (Finn *et al.*, 2011; Pauls *et al.*, 2014); this is a pattern we predict to observe for data simulated under the dendritic landscape, but not for those simulated under the circular landscape, which would suggest a strong role of dendricity. Furthermore, we predict that –in the dendritic but not the circular landscape– the most connected demes should harbor the

highest within-deme genetic diversities, which may explain yet unresolved patterns observed in the field characterized by higher within-deme genetic diversity at the core of the network (e.g. Watanabe *et al.*, 2008; Alp *et al.*, 2012). Our results, combined with those from other authors (Finn *et al.*, 2011; Carrara *et al.*, 2012; Múrria *et al.*, 2013) constitute a new step towards the understanding of how dendritic connectivity *per se* can shape biodiversity in dendritic ecosystems.

Materials and Methods

Simulated genetic data

We used a homemade computational pipeline that allowed handling, generating and analyzing multiple simulated genetic datasets under different population genetics models. Specifically, we used the program ABCsampler (Wegmann *et al.*, 2010) to (i) choose model parameter values from prior distributions (defined below); and to (ii) feed the coalescent-based genetic data simulator Simcoal 2 (Laval & Excoffier, 2004) with these parameter values. We then used the programs ADZE v1.0 (Szpiech *et al.*, 2008) and arlsumstat (Excoffier & Lischer, 2010) to calculate, for each simulated dataset, a set of basic statistics describing genetic diversity at the deme or the whole landscape level (see below). The program PGDSpider v2.0 (Lischer & Excoffier, 2011) was also integrated in the pipeline to convert the output files of Simcoal 2 to the input format required by ADZE, and the R statistical software v3.0.1 was used to analyze the data.

This pipeline was used to simulate microsatellite genetic datasets (i.e. fifteen independent loci considering the Stepwise Mutation Model (SMM) and a unique mutation rate $\mu = 5 \times 10^{-4}$) under three contrasting landscapes: (i) a lattice-like landscape (the "lattice model", Fig. 1A), composed of thirty-six demes connected in a two-dimensional stepping-stone fashion

(Kimura & Weiss, 1964; Fig. 1A); (ii) a quasi-circular landscape, (the "circular model", Fig. 1B), characterized by a circular stepping-stone chain of twenty-seven demes, to which nine single external demes are attached, and (iii) a dendritic network landscape (the "dendritic model") composed of twenty-nine demes connected in a dendritic fashion, to which a seven-demes-long linear stepping-stone chain is attached (Fig. 1C). Although different in terms of spatial structure, the dendritic and circular models display similar levels of connectivity when considering a simple measure of connectivity (i.e. the number of connections between a deme and its nearest neighbours, see Figs. 1B-C). Accordingly, "low" connected demes for both models are those being connected to a single other deme (hereafter, C1 demes; Figs. 1B-C), whereas "highly" connected demes are those being connected to three other demes (hereafter, C3 demes; Figs. 1B-C). In the dendritic model, C1 demes are equivalent to the most upstream and downstream populations of a putative river network, whereas C3 demes correspond to populations situated in confluences. The seven-demes-long linear stepping-stone chain situated in the downstream part of the dendritic model corresponds to the main stem (i.e. the trunk) of a putative river network.

For each model, each deme was characterized by an identical effective population size (hereafter, effective deme size N_e) and a symmetrical pairwise migration rate (MR) with its immediate neighbour(s). We tested the effects of different N_e and MR on genetic diversity by running a total of 35,000 simulations *per* model, considering three alternative effective deme sizes, corresponding to low (i.e. 10), medium (100) and high (1,000) N_e values, and for MR values ranging from 0.01 to 0.5 (proportion of migrants *per* generation).

We assumed for each model the same combinations of N_e and MR values, so as to allow direct comparisons between dendritic, lattice and circular models. We simulated microsatellite markers because of its wide use in empirical surveys describing patterns of genetic diversity (Putman & Carbone, 2014). Simulations were performed on an ALTIX ICE 8200

EX cluster (Silicon Graphics International, Fremont, CA, USA) hosted by the CALMIP group (University Paul Sabatier, Toulouse, France).

Summary statistics

At the landscape scale, we calculated the total number of alleles, the *per* deme allelic richness averaged across all demes and over all loci (mean allelic richness), the variance in allelic richness across all demes and the global *Fst* observed over the whole landscape (*totNA*, *meanAR*, *varAR* and *global Fst* respectively) for each simulation from the lattice, circular and dendritic models. Statistics derived from allelic richness are analogous to measures of α-diversity; *totNA* is analogous to γ-diversity, whereas statistics derived from the *Fst* index can be seen as measures of β-diversity.

At the deme level and for the dendritic and circular models only, we estimated for each simulation the mean allelic richness over all loci *per* deme (*AR*), pairwise genetic differentiation estimates between demes (*pairwise Fst*) and mean pairwise *Fst* values *per* deme (*mean Fst*; i.e. the mean *Fst* value calculated for each deme from each pairwise comparison with other demes).

Comparison between lattice, circular and dendritic landscapes

We tested whether or not dendritic connectivity influenced α-, β- and γ-diversity in the dendritic landscape by comparing, for each combination of N_e *per* deme and MR, *totNA*, *mean AR*, *varAR* and *global Fst* values estimated for the dendritic model with those estimated for the lattice and circular models. As an alternative, we also compared (for each model) the relationships between *totNA*, *mean AR*, *varAR*, *global Fst* and the N_e x MR product. This later

parameter is commonly used in theoretical population genetics to quantify the amount of ongoing gene flow between pairs of populations (here, the number of genes that are transferred between pairs of demes each generation).

Comparison between low and highly connected demes in dendritic and circular landscapes

We tested for each simulation generated under dendritic and circular models whether or not *AR* and *mean Fst* calculated at the deme level varied between low (C1) and highly (C3) connected demes. Specifically, we calculated (for each model and each combination of N_e *per* deme and MR) differences (in percentage) of *AR* and *mean Fst* values between C3 and C1 demes (C3 – C1). Additionally, we expressed these differences as a function of the N_e x MR product.

Spatial patterns of genetic diversity in the dendritic landscape

We characterized for each simulation of the dendritic model spatial patterns of genetic diversity, by representing, for each combination of N_e *per* deme and MR, the relationship between *AR* and the distance of each deme from the putative river mouth (i.e. the most downstream part of the network, see Fig. 1C), given that an increase in *AR* in downstream sections is generally assumed in this type of landscape (Pollux *et al.*, 2009; Paz-Vinas *et al.*, 2013). Finally, we assessed patterns of isolation-by-distance (IBD), i.e. linear relationships between the geographic distance between pairs of demes (in number of demes) and *pairwise Fst* values, as given by the formula *Fst* / (1 – *Fst*) (Rousset, 1997) for each simulated genetic dataset. We specifically assessed the strength of each linear relationship by calculating Pearson's correlation coefficients (*r*).

Results

Comparison between lattice, circular and dendritic landscapes

Comparisons between dendritic *vs.* lattice models revealed that**,** overall, the total number of alleles (*totNA*) and *global Fst* values were higher in the dendritic than in the lattice model, irrespective of effective deme sizes (N_e) and migration rates (MR; Figs. 1D-F and Figs. 1M-O). Additionally, *varAR* was higher in the dendritic than in the lattice model, especially for low to intermediate MR values (Figs. 1J-L), suggesting that allelic richness differences among demes were higher in the dendritic than in the lattice model. As predicted, *mean AR* over demes was lower in the dendritic than in the lattice model, but only for low to intermediate MR values (irrespective of N_e); for higher MR values, *mean AR* was higher in the dendritic than in the lattice model (Figs. 1G-I).

Comparisons between the circular *vs.* the two other models revealed similarities and differences with both models, depending on the summary statistic being considered. Values of *varAR* were similar between circular *vs.* lattice models, especially for N_e of 100 and 1,000 (Figs. 1J-L), whereas *global Fst* values observed for circular models were close to those observed for dendritic models (except for high MR values; Figs. 1M-O). Additionally, *totNA* and *mean AR* values were similar between circular *vs.* dendritic models for low MR values, but they were higher in the circular model for intermediate and high MR values, especially for N_e values of 100 and 1,000 (Figs. 1D-I).

Comparisons were less straightforward to interpret when *totNA*, *mean AR*, *varAR* and *global Fst* were expressed as a function of the N_e x MR product. Indeed,

values observed for these statistics did not follow single continuous distributions along the N_e x MR gradient at the landscape level, as they strongly depend upon the assumed N_e *per se* (Fig. S1). Consequently, values of *totNA*, *mean AR*, *varAR* (and to a lesser extent, of *global Fst*) strikingly varied for simulations characterized by identical N_e x MR but with different N_e values (Fig. S1A-D).

Overall, these results suggest that (i) dendritic connectivity increases β- and γ-genetic diversities, and to a lesser extent α-diversities in the dendritic landscape, compared to a classical 2D-lattice landscape, (ii) that these effects are not only due to the connectivity level *per se* of the dendritic landscape, but also to its dendricity, and (iii) that the effects of N_e and MR on genetic diversity are difficult to assess by considering the N_e x MR product as a single explanatory variable.

Comparison between low and highly connected demes in dendritic and circular landscapes

Overall, *AR* were higher in highly connected demes (C3) than in low-connected demes (C1) for the dendritic model (Fig. 2A). These differences in *AR* were larger for low N_e (i.e. 10) and decreased as MR increased. Conversely, *mean Fst* values were higher in C1 than in C3 demes (Fig. 2A), with larger differences for low MR (when N_e = 100 or 1,000) to intermediate MR values (when N_e = 10; Fig. 2A). Concerning the circular model, *AR* tended to be higher for C3 demes than for C1 demes, although differences between deme types were lower than those observed in the dendritic model and were close to zero for large MR (Fig. 2B). *Mean Fst* values were marginally larger for C1 than for C3 demes for low MR (Fig. 2B), and differences between deme types became highly stochastic when MR values were higher than 0.15.

As for the comparison between the three landscapes, differences in *AR* and *mean Fst* between C3 and C1 demes did not followed single continuous distributions at the landscape scale when they were expressed as a function of the N_e x MR product (Fig. S2), hence making the interpretation tricky.

These results show that dendricity, and not only connectivity *per se*, favours allelic richness (*AR*) in highly connected demes (e.g. confluences in river networks), while favouring genetic differentiation (*mean Fst*) in low connected demes (e.g. headwaters and river mouths in river networks).

Spatial patterns of genetic diversity in the dendritic landscape

Regarding the relationships between *AR* and distance from the putative river mouth in the dendritic model**,** we detected that for several simulations, *AR* was higher at demes situated at intermediate distances from the putative river mouth (i.e. in the centre of the network), and lower in the most downstream and upstream demes, hence generating bell-shaped relationships (Fig. 3A for N_e = 100; Figs. S3A-B for N_e = 10 and 1,000 respectively). This pattern was particularly strong for low migration rates (i.e. MR between 0.01-0.10) irrespective of N_e, and its strength progressively decreased until reaching a flat relationship as MR increased (Fig. 3A, Fig. S3 and Fig. S4 for snapshot examples).

Overall, correlations between *pairwise Fst* and distance between demes were strong for all parameter combinations (r > 0.55; Fig. 3B). Patterns of IBD were however stronger for intermediate effective deme sizes (N_e = 100) than for low and high N_e values (10 and 1,000; Fig. 3B). For intermediate and high N_e (100 and 1,000), the

strength of the IBD was strong for low MR values, and gradually decreased in strength for intermediate to high migration rates, whereas for low N_e (10), the strongest IBD patterns were found at intermediate MR values (Fig. 3B). This shows complex interactions between N_e and MR in shaping IBD in dendritic networks.

Discussion

We showed that dendritic connectivity strongly controlled the level and the distribution of genetic diversity at the meta-population level. We notably demonstrated that, overall, the mean allelic richness over demes was lower in the dendritic than in the lattice landscape (only for low migration rates), whereas the total number of alleles observed at the landscape scale, the global *Fst* and variance in allelic richness was higher in the dendritic landscape under most situations. This latter result was probably because in the dendritic landscape, allelic richness was lower in low connected demes than in highly connected demes, hence generating a strong spatial heterogeneity in allelic richness (which was more reduced in the circular landscape, and absent in the lattice landscape due to its high connectivity level). The difference in allelic richness between low and highly connected demes we highlight here may also explain why, when migration rates were low to intermediate, we observed bell-shaped relationships between allelic richness measured at the deme level and the distance of each deme from the river mouth (i.e. increase in allelic richness in the centre of the network). This shows that dendritic connectivity may explain empirical patterns that have been previously observed empirically but remained poorly (or not) explained (Watanabe *et al.*, 2008; Alp *et al.*, 2012).

The increase in allelic richness in highly connected demes (i.e. the nodes situated at the core of the network) in the dendritic landscape may be due to the fact that these demes receive alleles from several demes that are highly genetically differentiated from each other. Accordingly, we demonstrated that mean *Fst* measured at the deme level were strikingly lower in highly connected demes than in low connected demes in the dendritic landscape for most realistic combinations of effective deme sizes and migration rates. Interestingly, the effect of deme connectivity on the spatial distribution of genetic diversity was exacerbated in the dendritic landscape, since differences (both in terms of allelic richness and genetic differentiation) between highly and low connected demes were much more pronounced in the dendritic and in the circular landscape. To sum up, these results show that dendritic connectivity affects neutral genetic differentiation in dendritic networks, by notably promoting differentiation in the less connected (and hence more isolated) demes (e.g. headwaters). A direct consequence of this dendritic connectivity-driven effect on genetic differentiation is the generation of strong IBD for all combination of effective deme sizes and migration rates (which was not the case for the lattice landscape, where the mean Pearson's coefficient calculated across simulations was of 0.451, *vs*. 0.778 for the dendritic landscape).

The strength of the IBD was however strongly dependent upon the interaction between effective deme sizes and migration rates: IBD were strong for low migration rates when N_e values were intermediate to high, whereas for intermediate migration rates, IBD were stronger when N_e was low. These results show that dendritic connectivity, by modulating the degree of intra-demic gene flow that is exchanged between demes (i.e. the N_e x MR product), may deeply influence patterns of IBD in

realistic landscapes, hence complementing previous findings from an individual-based theoretical approach (Labonne *et al.*, 2008).

Although it was not a primary goal of the study, our results also show that assessing how genetic diversity evolves as a function of the ongoing level of gene flow occurring between populations can be tricky. Indeed, genetic diversity indices followed continuous distributions when they were expressed in function of MR for given N_e values, but this was not true when they were only expressed as a function of the N_e x MR product. This was because, contrarily to migration rates, there is a direct correlation between effective population sizes and genetic diversity (Frankham, 1996). We therefore recommend the use of multi-factorial designs that consider N_e and MR independently in future studies aiming at assessing the effects of effective population sizes and migration on genetic diversity, rather than using the amount of gene flow occurring between populations as a unique explanatory variable.

By adopting a design similar to that of Carrara *et al.* (2012), our results further suggest that dendritic connectivity similarly shapes biodiversity patterns from meta-community (Carrara *et al.*, 2012) to meta-population levels (this study). Most of the patterns of genetic diversity we highlighted at the meta-population level (e.g. higher variance in allelic richness and *Fst* in the dendritic landscape; lower allelic richness in "headwater" than in "confluence" demes) are indeed very comparable to those found by Carrara *et al.* (2012) at the meta-community level. Indeed, Carrara *et al.* (2012) demonstrated that dispersal along dendritic corridors increased species differentiation among local communities (β-diversity) and variance in local species richness (α-diversity; Carrara *et al.*, 2012). In addition, α-diversity was lower in "headwater communities" (communities situated on the most extreme branches of the

network) than in "confluence communities" (communities situated at the nodes of the network), whereas the opposite pattern was observed for β-diversity (Carrara *et al.*, 2012). This may indicate a general congruency between neutral genetic and species diversity patterns in dendritic networks, which may have both theoretical and conservation implications. For instance, if both genetic and taxonomic diversities are distributed congruently, conservation actions aiming at preserving diversity at one level will benefit the other level. Local characteristics such as habitat availability or heterogeneity have been advocated as major factors underlying co-variation between genetic and species diversity (Vellend & Geber, 2005). Here, we argue that landscape structure *per se* may also generate spatial co-variation in biodiversity metrics. Future empirical studies should be developed to test this hypothesis.

Understanding the overall functioning of dendritic networks is a pre-requisite for sustaining biodiversity in these habitats. Here, we focused specifically on connectivity and dendricity, but additional processes such as asymmetric gene flow, colonisations and/or difference in effective deme sizes along environmental and/or geophysical gradients (e.g. the upstream-downstream gradient) have to be conjointly considered for ranking their independent and joint effects on empirically observed biodiversity patterns. Additionally, we focused here on a single specific type of dendritic network assimilated to a river network characterized by high dendricity in the upper/central parts of the network (due to the presence of many tributaries and confluences), and by a linear main stem situated in the downstream part. However, other alternative types of river networks exist (e.g. rectangular or trellis-like networks; see Mejía & Niemann, 2008), and spatial patterns of genetic diversity observed in these networks remain to be explored. We hope that our work will motivate future researches to take into account alternative spatial structures and/or the combined effects of multiple processes, and will hence contribute to the development of a general theory on ecological and evolutionary patterns and processes in dendritic habitats.

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Figures captions:

Figure 1: (A) two-dimensional stepping-stone landscape (lattice model), (B) quasi-circular landscape (circular model) and (C) river network-like dendritic landscape (dendritic model)

used to simulate genetic data. Each model was composed of multiple demes (circles) that exchange migrants with their immediate neighbour(s) using dispersal corridors (blue lines). In the circular and dendritic models, we differentiated "low connected" demes (C1 demes; black circles) and "highly connected" demes (C3 demes; grey circles). (D-F) total number of alleles calculated at the landscape level (*totNA*), (G-I) mean allelic richness (*mean AR*) across demes, (J-L) mean variance in allelic richness (*varAR*) across demes, and (M-O) global *Fst* at the landscape level, calculated for each model (blue, red and black dots for the lattice, circular and dendritic models respectively) in function of the effective deme size (N_e = 10, 100 or 1,000) and the migration rate (MR = 0.01 to 0.5).

Figure 2: Differences (expressed as percentages) between C3 demes (i.e. highly connected demes) and C1 demes (i.e. low-connected demes) for allelic richness (*AR*, red symbols) and for mean genetic differentiation (*mean Fst*, blue symbols) calculated at the deme level for (A) the dendritic model and (B) the circular model. Positive values indicate that C3 demes display higher values than C1 demes, and *vice versa*. Results are displayed for three values of effective deme size (N_e = 10, 100 and 1,000) and increasing values of migration rate (0.01 to 0.5 with 0.01 increments). Several replicates were simulated for each N_e-MR combinations; here, only the average values are shown.

Figure 3: (A) perspective plot representing the mean allelic richness calculated over loci *per* deme (*AR*, coloured scale) in function of (i) the distance to the putative river mouth of each deme (in number of demes) and (ii) the migration rate (MR) for simulations generated under the dendritic model considering an effective deme size N_e = 100 have been considered here. (B) perspective plot representing the strength of the isolation by distance pattern (measured as the Pearson's correlation coefficient *r* between the distance between pairs of demes (in number of demes) and *Fst* / (1 – *Fst*) values, coloured scale) in function of (i) the effective

deme size (N_e = 10, 100 or 1,000) and (ii) the migration rate MR. The coloured surfaces at the square bases are surface projections of the 3D-perspective plots.