

METHODOLOGICAL ADVANCES - INFERENCE OF SPATIAL STRUCTURE

Relationships between migration rates and landscape resistance assessed using individual-based simulations

E. L. LANDGUTH,*† S. A. CUSHMAN,† M. A. MURPHY,‡ and G. LUIKART§¶

*University of Montana, Mathematics Building, Missoula, MT 59812, USA, †USDA Forest Service, Rocky Mountain Research Station, 800 E Beckwith, Missoula, MT 59801, USA, ‡Colorado State University, Biology Department, Fort Collins, CO 80523-1878, USA, §Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto (CIBIO-UP), Campus Agrário de Vairão, 4485-661 Vairão, Portugal, ¶University of Montana, Division of Biological Sciences, Missoula, MT 59812, USA

Abstract

Linking landscape effects on gene flow to processes such as dispersal and mating is essential to provide a conceptual foundation for landscape genetics. It is particularly important to determine how classical population genetic models relate to recent individual-based landscape genetic models when assessing individual movement and its influence on population genetic structure. We used classical Wright–Fisher models and spatially explicit, individual-based, landscape genetic models to simulate gene flow via dispersal and mating in a series of landscapes representing two patches of habitat separated by a barrier. We developed a mathematical formula that predicts the relationship between barrier strength (i.e., permeability) and the migration rate (m) across the barrier, thereby linking spatially explicit landscape genetics to classical population genetics theory. We then assessed the reliability of the function by obtaining population genetics parameters (m , F_{ST}) using simulations for both spatially explicit and Wright–Fisher simulation models for a range of gene flow rates. Next, we show that relaxing some of the assumptions of the Wright–Fisher model can substantially change population substructure (i.e., F_{ST}). For example, **isolation by distance among individuals on each side of a barrier maintains an F_{ST} of ~ 0.20 regardless of migration rate across the barrier, whereas panmixia on each side of the barrier results in an F_{ST} that changes with m as predicted by classical population genetics theory.** We suggest that individual-based, spatially explicit modelling provides a general framework to investigate how interactions between movement and landscape resistance drive population genetic patterns and connectivity across complex landscapes.

Keywords: computer simulation, F_{ST} , gene flow, habitat fragmentation, isolation by distance, landscape genetics, partial barriers, population connectivity, spatial statistics

Received 11 January 2010; revision received 27 March 2010; accepted 2 April 2010

Introduction

A primary goal of landscape genetics is to understand how landscape features influence genetic structure and gene flow patterns in natural populations (Manel *et al.* 2003; Holderegger & Wagner 2006; Storfer *et al.* 2007; Balenhol *et al.* 2009a). Much of classical population genetic theory is founded on several simplifying assumptions, including discretely bounded and panmictic populations in a homogeneous environment (Wright 1943). However,

most organisms occupy heterogeneous landscapes in which populations are seldom discretely bounded and internally panmictic. This spatial complexity may fundamentally alter interpretations of spatial population genetic structure and F_{ST} estimates. The mathematics of population genetics in spatially complex environments is difficult, and closed-form solutions akin to those of classical population genetics are generally intractable (Epperson 2003). Spatial modelling with computer simulations is an attractive alternative in which the effects of landscape heterogeneity can be stipulated as spatial processes and the resulting population genetic patterns can be assessed (e.g., Currat *et al.* 2004; Manel *et al.* 2007).

Correspondence: Erin L. Landguth, Fax: (406) 243-2674; E-mail: erin.landguth@umconnect.umt.edu

Extensive investigations using spatial simulations have been conducted addressing the effects of autocorrelation on genetic patterns (see Sokal *et al.* 1989, 1998; Epperson 1993, 2003). For example, effects of spatial autocorrelation in homogeneous landscapes have been explored at fine scales (Epperson 1995, 2007). However, the effect of simple landscape heterogeneity, such as multiple different resistance barriers, is not tested under these models.

Recent empirical studies have detected the effects of landscape features and seascape structure on gene flow patterns (Antolin *et al.* 2006; Cushman *et al.* 2006; Neville *et al.* 2006; Perez-Espona *et al.* 2008; Selkoe *et al.* 2008; Pavlacky *et al.* 2009; Schwartz *et al.* 2009; Murphy *et al.* 2010) and suggest that spatially explicit, individual-based approaches might often be the best means to help establish correlative explanations and provide a foundation for spatial population genetic theory in heterogeneous landscapes. Furthermore, landscape effects on genetic connectivity can potentially provide insights into key biological processes, such as individual movement patterns of mating or dispersal (Storfer *et al.* 2007), and link back to classical population genetics by estimating gene flow (i.e., through m and F_{ST}).

A rapidly growing number of empirical studies use landscape genetic approaches, yet there remains limited understanding of the basic influences of spatial complexity on population genetic processes (but see Ezard & Travis 2006; Murphy *et al.* 2008; Balkenhol *et al.* 2009b; Cushman & Landguth 2010). Simulation studies are needed to verify reliability, develop theory, and link new landscape genetic approaches to the rich theory of classical population genetics (Hedrick 2005). In this study, we use a spatially explicit, individual-based cost distance landscape genetic models to explore how gene flow parameters are related to individual-based landscape genetic processes and classical population genetic theory.

We had four specific objectives. Our **first** objective was to **derive a mathematical function to predict the relationship between barrier strength and the migration rate across the barrier**, linking population genetic theory to landscape genetics. **Second**, we sought to **verify the reliability of the function by simulating migration rates associated with a range of barrier strengths**. **Third**, we **compared simulation results** from a recently published individual-based, spatially explicit population genetics model with a frequently used population-based genetics program under ideal Wright–Fisher assumptions to **show the equivalence of the simulation approaches under ideal conditions**. **Fourth**, we explored how relaxing some of the assumptions of the Wright–Fisher model to use more **biologically realistic parameters substantially changes population substructure**. The mathematical function we derive explicitly predicts the interpopulation migration

rate as a function of individual-based movement and barrier permeability. Our study demonstrates how individual-based, cost distance modelling of population genetics can provide a framework to understand relationships between biological processes and population genetic patterns across landscapes.

Models and methods

Objective 1: functional relationship between migration rate and landscape resistance

Our analysis is based on simulating gene flow via mating and dispersal in a simple landscape (Fig. 1). **Mating is defined as movement of a gamete** (e.g., males migrating to mate or pollen flow across a barrier), whereas **dispersal refers to offspring movement across the landscape**. The landscape is populated by 1000 individuals, with 500 on either side of a barrier. We stipulate a range of resistance values for this barrier, relative to a maximum organism dispersal distance (e.g., how far an individual could possibly move on the landscape). The conceptual framework for this analysis considers the probability of dispersal to any given location or mating with any given potential mate to be a function of the cost of traversing the resistant landscape from the original location occupied by the individual, defined as a movement cost (Landguth & Cushman 2010). In this context, we define a **partial barrier as a landscape feature whose resistance attenuates but does not completely eliminate gene flow between the two ‘populations’ separated by the landscape feature**.

Given the strength of the partial barrier and the stipulated maximum organism dispersal distance, it is straightforward to derive a mathematical function predicting classical interpopulation **migration (m)** as a function of partial barrier strength and maximum organism dispersal distance. We define m as the **proportion of individuals in a population (or area) that are immigrants as in classical population genetics**. We define a **movement threshold (T)**, as the **maximum distance in cost units that any one individual can disperse or mate on the landscape**. For example, if T equals 100, then a movement across a barrier with resistance of 100 would not be possible. Similarly, a movement across 10 grid spaces (pixels), each with a resistance of 10, would be the maximum dispersal distance.

We define **partial barrier strength (B)** with units of movement cost as the **resistance of the partial barrier relative to T** . Thus, for all $B < T$, B is a partial barrier that would allow for some migration across the barrier, with a complete barrier blocking all migration at $B \geq T$ (i.e., two isolated populations). Likewise, when there is no barrier present ($B = 0$), we obtain a maximum migration rate of

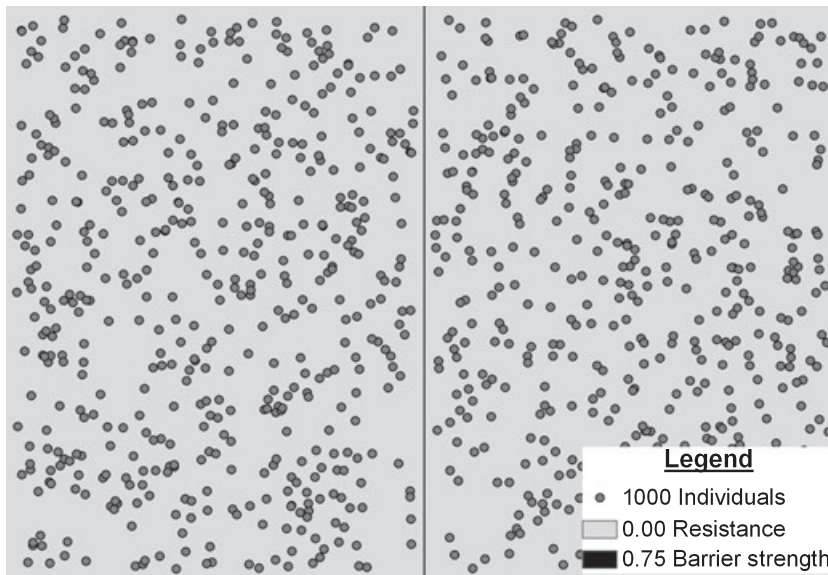


Fig. 1 Simulated landscape. An example of 1000 randomly located individuals on a resistance surface of zeros and a partial barrier resistance, $B = 0.7500$. The vertical line in the middle is the partial barrier.

$m = 0.5$ indicating equal probability of any individual dispersing to either side of the putative barrier (i.e., one large panmictic population). We restrict partial barrier strengths to be between 0 and T , as negative barrier strengths are undefined and all barrier strengths larger than T are equivalent. Given two equally sized panmictic population groups separated by a barrier of strength B and for an organism with maximum dispersal ability T , we suggest that

$$m = \frac{T - B}{2T - B}. \quad (1)$$

In other words, proportion of migrants (m) is a function of individual movement ability relative to the strength of the partial barrier.

Objective 2: testing the relationship between migration rate and landscape resistance

The biological processes that influence migration rate (m) are dispersal or gamete movement (e.g. pollen flow or male mating migrations). Importantly, by simulating individual mating and dispersal, we can explicitly link interpopulation migration rate (m) and the behaviour of individual organisms. This link is critical, as it provides a mechanistic underpinning for classical population-based analyses of genetic substructure among populations in terms of individual behaviour.

We sought to confirm that eqn (1) correctly expressed the relationship between migration rate and barrier strength using an individual-based, spatially explicit model (CDPOP; Landguth & Cushman 2010) that simulates movement and mating as functions of cost distances across a resistant landscape. Cost distance modelling

allows patterns of genetic distance between individuals to be correlated with landscape features by building resistance surfaces that assign different resistance-to-movement values to different landscape features (e.g., a high resistance to movement might be assigned to a known barrier). Landscapes created through this approach are based typically on raster data that divide landscapes into many cells (pixels) with unique values that depict different habitat or vegetation types, elevation, slope, or other landscape features (see Cushman *et al.* 2006; Epps *et al.* 2007; Perez-Espona *et al.* 2008). Cells are given weights or 'resistance values' reflecting the presumed influence of each variable on movement of the species in question. A matrix of movement costs can then be computed based on shortest cost paths algorithms between all pairs of individuals. Common approaches to calculating cost distance matrices in landscape genetics include Dijkstra's algorithm (Dijkstra 1959), CIRCUITSCAPE (McRae & Beier 2007), PATHMATRIX (Ray 2005), and COSTDISTANCE in ArcGIS (ESRI Corp., Redlands, CA, USA).

We used CDPOP to simulate genetic exchange in a single Wright–Fisher population with no substructure for 30 varying levels of a given barrier strength, B (see Table 1). All scenarios were run for 1500 generations with 10 repetitions of 1000 spatially random located individuals separated by a barrier of the given strength B to create two populations (see Fig. 1 for an example of one scenario and one repetition). Within each population on either side of the barrier, there is no cost to movement (i.e., each pixel value that is not a barrier pixel has a resistance of 0). The following CDPOP parameter conditions were selected to simulate a Wright–Fisher population process: (i) random mating with replacement (CDOPOP

Table 1 Partial barriers and barrier strength (B) with the corresponding migration rates estimated using eqn (1) and from simulations using CDPOP with $T = 1$. The Kendall tau rank correlation coefficient was used to measure the strength of association between the migration rates from eqn (1) and the CDPOP simulations giving $\tau = 1$ and $P\text{-value} < 0.0001$, a perfect ranking. * indicates the m used for the EASYPOP simulations.

B , Barrier strength	m , Eqn (1)	m , CDPOP	CI , CDPOP
0.0000	0.5000*	0.5000	(0.49659, 0.50237)
0.0500	0.4872	0.4870	(0.47713, 0.49510)
0.1000	0.4737	0.4736	(0.47154, 0.47643)
0.1500	0.4595	0.4601	(0.45584, 0.46880)
0.2000	0.4444	0.4441	(0.44256, 0.45033)
0.2500	0.4286	0.4299	(0.42448, 0.43159)
0.3000	0.4118	0.4115	(0.41049, 0.41623)
0.3500	0.3939	0.3934	(0.38542, 0.40219)
0.4000	0.3750	0.3755	(0.36757, 0.37744)
0.4500	0.3548	0.3554	(0.35219, 0.36401)
0.5000	0.3333	0.3340	(0.33320, 0.33487)
0.5500	0.3103	0.3110	(0.30968, 0.31388)
0.6000	0.2857	0.2858	(0.28064, 0.29499)
0.6500	0.2593	0.2593	(0.25062, 0.26917)
0.7000	0.2308	0.2303	(0.22423, 0.23759)
0.7500	0.2000*	0.2001	(0.19849, 0.20307)
0.8000	0.1667	0.1664	(0.16639, 0.17085)
0.8235	0.1500*	0.1508	(0.14916, 0.15325)
0.8500	0.1304	0.1304	(0.12694, 0.13056)
0.8888	0.1000*	0.1019	(0.09978, 0.10319)
0.9000	0.0909	0.0907	(0.09025, 0.09423)
0.9473	0.0500*	0.0549	(0.05347, 0.05619)
0.9500	0.0476	0.0480	(0.04445, 0.04890)
0.9898	0.0100*	0.0107	(0.01028, 0.01148)
0.9949	0.0050*	0.0055	(0.00507, 0.00596)
0.9989	0.0010*	0.0011	(0.00092, 0.00131)
1.0000	0.0000*	0.0000	(0.00000, 0.00000)

parameters 'Freplace' and 'Mreplace'); (ii) two populations in the landscape (CDPOP parameter 'twopopans'); (iii) no mating across the barrier [CDPOP parameter 'matemovethresh' set to the partial barrier strength (B) and dispersal movement threshold ('dispmovethresh') was set to the movement threshold strength (T)]; (iv) offspring number (CDPOP parameter 'offno') was set to 3 and 1 offspring per mating ('lmbda' = 1) (i.e., this in combination with (ii) will not produce immigrants and offspring will disperse to fill both populations); and (v) non-overlapping generations (CDPOP parameter 'oldmortpercent').

For all CDPOP simulation scenarios, we tracked the number of individuals (converted to proportions) that dispersed across the barrier and plotted the barrier strength (B) and proportion of migrants (m) as reported in Table 1 along with eqn (1). If eqn (1) correctly specifies the relationship between migration rate and landscape

resistance, then the numbers of simulated migrants will fall along the same curve as migrants predicted with eqn (1).

Objective 3: comparability of individual-based simulation and Wright–Fisher population simulation under ideal conditions

EASYPOP (Balloux 2001) is widely used to simulate Wright–Fisher population genetic processes for individuals divided among populations. Importantly, it allows the specification of the probability of migrants (m) among these populations. By specifying a certain proportion of migrants among populations, EASYPOP allows simulation of a wide range of spatially structured populations with internal panmixia and probabilistic migration among demes.

We compared simulations from CDPOP with those of EASYPOP to confirm that the two models produce equivalent results under ideal Wright–Fisher population processes. Specifically, we conducted a series of simulations in each program to verify the equivalence of results produced by a spatially explicit, individual-based cost distance genetic model with those of a model simulating demes linked by migration when the cost distance model is parameterized to reflect Wright–Fisher conditions. This enabled us to verify that the relationship between migration rate and barrier strength in terms of proportion of individuals that disperse across a semi-permeable barrier (in CDPOP) is equivalent to migration rates in terms of proportion of alleles that transfer from one population to another (in EASYPOP).

To accomplish this, we simulated nine migration rates in EASYPOP and the nine corresponding partial barrier strengths in CDPOP predicted by eqn (1). See * in Table 1 for the specific values used for the simulation comparisons. All simulations were run for 1500 generations, with 30 loci, initiated with a maximal alleles possible per locus of 30 (starting with 900 total possible alleles and mean $H_o = 0.967$) and a k -allele mutation rate of 0.0005 in a two-sex, equal sex-ratio, random-mating structure. We compared rates of loss of heterozygosity between the CDPOP and EASYPOP simulations to verify that CDPOP correctly expressed the expectation of the Wright–Fisher system. For each time step of each simulation, we averaged the 10 replicates, calculated the migration rate (m), and plotted F_{ST} between the two populations and number of alleles per locus over the 1500 generations.

Objective 4: effects of relaxing assumptions of Wright–Fisher on spatial genetic structure

The final component of our analysis involved simulating two simple deviations away from Wright–Fisher popula-

tion processes with CDPOP. First, we examined mating across a barrier (i.e., gamete movement), in addition to dispersal (i.e., permanent one-time movement of an individual offspring). We define mating across a barrier as breeding migrations, as in Hogg (2000). We allowed individuals to mate across the partial barriers (independent of dispersal) by changing the 'matemovethresh' from the partial barrier strength (B) to the movement threshold strength (T) for the CDPOP simulation scenario (c). Second, we added a uniform cost across the grid to simulate isolation by Euclidean distance on either side of partial barriers. Specifically, we changed the input resistance surface to stipulate the range of partial barrier strengths, but with isolation by Euclidean distance rather than panmixia on either side of the barrier (i.e., each pixel value that is not a barrier pixel now has a resistance value of 1 rather than 0). We then compared changes in F_{ST} for these partial barriers plus isolation by distance (IBD) scenarios to those ideal Wright–Fisher scenarios described earlier to determine the effects of increasing spatial complexity on population genetic structure.

Results

Objective 1 and 2: relationship between migration rate and landscape resistance

Equation (1) accurately predicts interpopulation migration rate (m) as a curve-linear function of individual-based dispersal across barriers of different strength (Fig. 2). The Kendall tau rank correlation coefficient was used to measure the strength of association between the migration rates from eqn (1) and the CDPOP simulations, giving $\tau = 1$ and $P\text{-value} < 0.0001$ (Table 1).

Objective 3: comparability of individual-based simulation and Wright–Fisher population simulation under ideal conditions

Spatially explicit, individual-based simulations in CDPOP were equivalent to EASYPOP when simulating Wright–Fisher populations separated by complete and partial barriers (Fig. 3). The simulations show that the two programs produced the same increase in F_{ST} , as functions of generation time under Wright–Fisher population processes. Comparison between EASYPOP and CDPOP scenarios of increasing partial barrier strength shows identical genetic substructure and increasing F_{ST} with increasing barrier strength until a complete barrier is in place.

The differences in heterozygosity reflected through F_{ST} for all barrier strength scenarios are displayed in Fig. 3, with the exceptions of simulation scenarios for $B = 0.7500$, $B = 0.8235$, and $B = 0.8888$, as they are

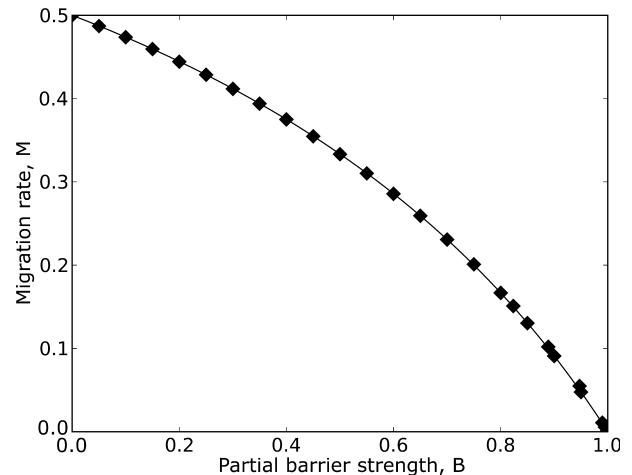


Fig. 2 Migration rate as a function of landscape resistance. The line is the predicted relationship between migration rate and partial barrier strength from eqn (1), while the diamond markers are the results of CDPOP simulation of (B, m) pairs. Note that the confidence intervals for the migration rates in CDPOP are too small to be viewed on this scale. The Kendall tau rank correlation coefficient was used to measure the strength of association between the migration rates from eqn (1) and the CDPOP simulations giving $\tau = 1$ and $P\text{-value} < 0.0001$, a perfect association.

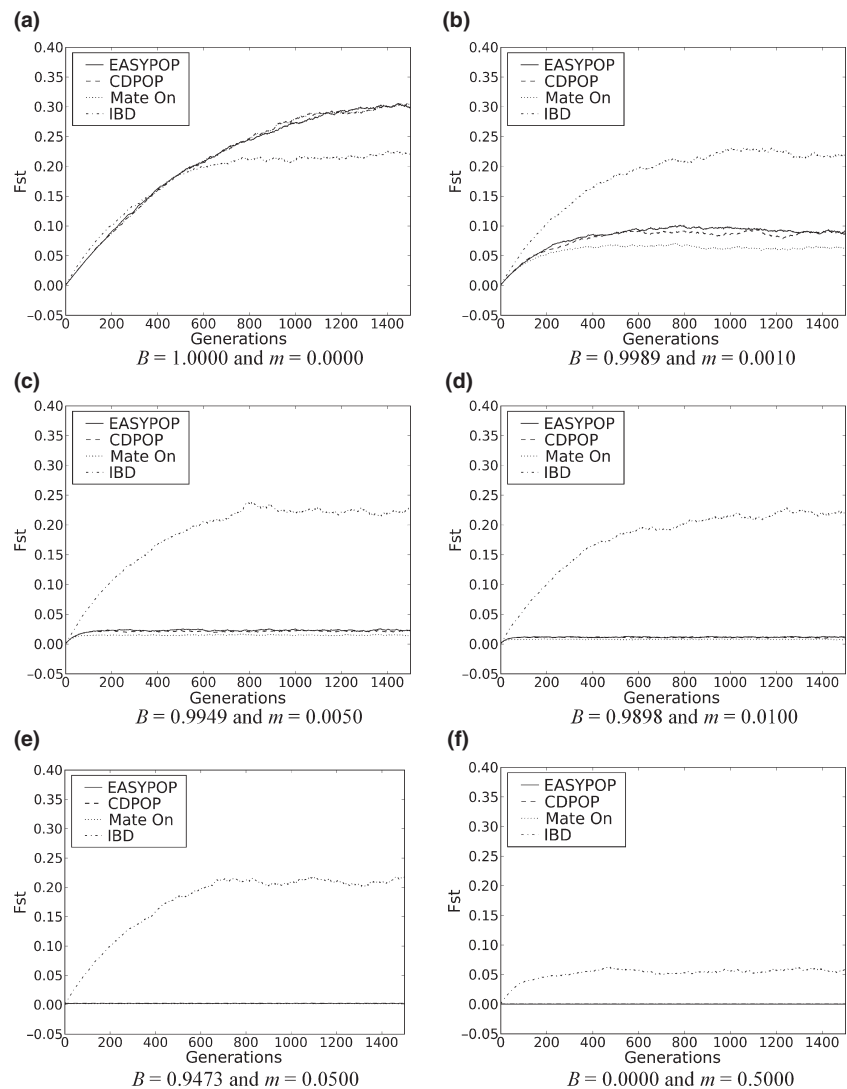
identical to the scenario with $B = 0.9473$. In all cases, EASYPOP and CDPOP produce identical predictions when CDPOP is set to Wright–Fisher parameters.

Objective 4: effects of relaxing assumptions of Wright–Fisher on spatial genetic structure

Notable differences were observed when individuals were allowed to mate and disperse following an isolation by Euclidean distance process on either side of the barriers. Departure between EASYPOP and CDPOP simulations is apparent when CDPOP allowed movement through dispersal and mating (breeding migration) across barriers, effectively increasing m and producing a lower F_{ST} (Fig. 3b,c). When a complete barrier is in place (Fig. 3a), mating cannot occur across the barrier, and the genetic structure predicted by CDPOP becomes equivalent to the EASYPOP results.

The effects of isolation by Euclidean distance are much more persistent and stable than effects of isolation by partial barriers across a broad range of partial barrier strengths. Interestingly, all partial barrier strengths produced similar levels of F_{ST} , with equilibration at approximately 0.20 at about 700 generations (Fig. 3a–e) with the exception of no barrier (Fig. 3f). This suggests that IBD processes produce a consistent effect on genetic structure across all levels of partial barrier strength, which is quite strong in comparison to the effects of the partial barrier itself.

Fig. 3 F_{ST} for simulations of different B . The average F_{ST} over the 10 replicates through 1500 generations for six of the nine comparison simulations: (a) complete barrier with barrier strength $B = 1.0000$ and $m = 0.0000$; (b) partial barrier with $B = 0.9989$ and $m = 0.0010$; (c) partial barrier with $B = 0.9949$ and $m = 0.0050$; (d) partial barrier with $B = 0.9989$ and $m = 0.0100$; (e) partial barrier with $B = 0.9473$ and $m = 0.0500$; (f) no barrier with $B = 0.0000$ and $m = 0.5000$. Comparison simulations for $B = 0.7500$, $B = 0.8235$, and $B = 0.8888$ are not shown as they are identical to the scenario (f). Output from EASYPOP and the separate CDPOP runs are shown in each subfigure: EASYPOP simulations (solid line – EASYPOP), CDPOP simulations compared to EASYPOP (dashed line – CDPOP), in which individuals were not allowed to mate across the barriers, CDPOP simulations, in which individuals were allowed to mate across the barriers (dotted line – Mate On), and CDPOP simulations, in which individuals were allowed to mate across the barriers in combination with an isolation by Euclidean distance structure on either side (dashed-dotted line – IBD).



Discussion

One of the major challenges that landscape genetics is facing is translating parameters such as migration rates (m) from classical population genetics models (e.g., discretely bounded panmictic populations) into expectations for spatially structured populations (e.g., isolation by landscape resistance) in complex environments. A component of this challenge is re-expressing classical population-based population genetic formulae in an individual-based, spatially explicit context within a heterogeneous landscape. This would improve our ability to understand effects of violating various simplifying assumptions of classical Wright–Fisher and metapopulation models. Specifically, including more realism in mating systems, population dynamics, movement behaviour, and the effects of landscape features on these spatial

population processes is essential to understand landscape genetic approaches and how they relate to population genetic theory.

We have taken three initial steps in this process. First, we showed that the interpopulation migration rate (m) can be expressed as a property of individual-based, spatially explicit, stochastic simulation modelling on resistant landscapes. This is important because individual movements are the mechanisms through which population genetics patterns and processes are affected. This provides a cross-walk between ideal population genetics, where the biotic processes (e.g. actual movement patterns) are often hidden or simplified, and individual-based approaches that explicitly stipulate biotic processes (e.g. individual movement). Knowing the relationship between m and B could potentially help quantify and rank landscape discontinuities, such as barriers; the

relationship could also be applied more broadly to think about gradients of landscape resistance in addition to localized barriers. However, we note the potential limitations in eqn (1) in that it has been tested with two populations governed by panmixia and separated by a single barrier. Future research includes testing these relationships between m and B under more complex landscapes that include isolation by distance and multiple barriers for an arbitrary number of populations.

Second, confirming that spatially explicit simulations with simple biotic processes give the same F_{ST} as ideal population genetic patterns provides a key foundation for studies of the landscape genetics in heterogeneous environments. Extensive verification of m vs. B confirmed the functional relationship and the reliability of the individual-based landscape genetics approach used in CDPOP. For spatially explicit, individual-based models to be used with confidence to explore interactions between complex landscape structure, population processes, and spatial genetic structure, it is first necessary to demonstrate that they produce correct results that are strictly comparable to deme-based population genetic models under ideal Wright–Fisher simulations. This work demonstrates this; individual-based, spatially explicit simulation reproduces the genetic patterns expected under ideal conditions and also provides virtually unlimited flexibility to explore how increased complexity and realism in landscape structures, and movement and mating processes affect spatial population genetic substructure.

Third, we showed that replacing some of the assumptions of the Wright–Fisher model with more biologically realistic parameters, including mating across a barrier (in addition to dispersal), and then isolation by distance on either side of the barrier, can substantially change population substructure assessments. As partial barriers are specified, genetic substructure measured by F_{ST} increases as partial barrier strength increases for both the EASYPOP and CDPOP simulation comparisons. However, when mating is allowed across this barrier (e.g., gamete movement) in addition to dispersal, F_{ST} declines as expected owing to more genetic exchange through mating (in addition to offspring dispersal). However, this is only the case when the barrier strength is strong enough (e.g., $F_{ST} > 0.05$) to show genetic substructure. This shows how even small changes in rules governing movement among populations can have large effects on resulting population genetic substructure and highlights the importance of adopting a flexible, generalized framework in which a large range of movement and mating systems can be evaluated and compared. It also suggests that it might be possible to infer the rates of dispersal or ‘mating migrations’ on population structure; For example, if we know one rate (e.g. dispersal) along with F_{ST} , we could estimate

the other (mating migration rate) essentially dividing the genetic m into two components of variation leading to wider ecological interpretation.

Our analysis shows that replacement of assumptions of inner-population panmixia with isolation by distance has large effects on F_{ST} , also seen with hierarchical structuring (Murphy *et al.* 2008). As expected, no genetic structure is seen in the global panmictic scenarios simulated through EASYPOP or CDPOP through a F_{ST} of zero. As isolation by distance with partial barriers is specified in CDPOP, F_{ST} increases relative to scenarios specifying partial barriers between otherwise panmictic demes. Interestingly, F_{ST} equilibrates at essentially the same value (0.20) in every IBD simulation scenario with a barrier. This suggests that partial barrier effects are highly sensitive to the relative strength of the barrier, but IBD effects are not. However, it is also necessary to discuss the ecological implications for what was found. If organisms mostly disperse and mate within a small radius, then only few individuals will actually encounter the barrier, influencing a smaller fraction of the entire population and thus leading to a stronger IBD effect. Future research involves how isolation by distance of individuals interacts with migration rates, relative strengths of the barriers, and individual dispersal distances through comparisons of correlative landscape features (e.g., through Mantel r). Specifically, research is needed that allows understanding of a barrier as a local effect and landscape gradients as global effects and especially in species with limited dispersal abilities (Landguth EL, Cushman SA, Schwartz MK, McKelvey KS, Murphy M, Luikart G, unpublished data).

Our simulation results suggest that partial barrier effects on F_{ST} are influenced by co-occurring isolation by Euclidean distance effects and that IBD effects are persistent and stable across all levels of partial barrier strength, including the no barrier scenario. This emphasizes the importance of casting landscape genetic processes in terms of isolation by differential resistance across continuous space, rather than focusing on identifying discrete barrier features (e.g. Cushman *et al.* 2006; Cushman & Landguth 2010). Researchers should also test for isolation by distance among individuals (e.g. within population samples) before computing F_{ST} between sampling areas or populations to avoid potential bias (e.g. inflation) of F_{ST} values.

Individual-based, cost distance modelling of population genetics provides a powerful framework to understand relationships between biological processes and population genetics patterns across complex landscapes. Specifically, spatially explicit, individual-based models will be valuable tools for the study of landscape genetics by increasing our understanding about the effects of life history, vagility, and differential models of landscape

resistance on the genetic structure of populations in complex landscapes. By enabling simulation of complex relationships between landscape structure, and individual-based mating and dispersal, these approaches enable exploration of how spatial complexity in the environment interacts with organism ecology and behaviour to influence the spatial genetic structure of populations.

This is the frontier that separates landscape ecology and population genetics. This frontier will be closed over time as more simulation studies are conducted evaluating the effects of different kinds of spatial pattern–process relationships and different variations in organism movement and mating behaviour (Cushman 2006; Epps *et al.* 2007; Murphy *et al.* 2010). Simultaneously, these simulation efforts will enable fruitful integration of empirical analyses with the expectations under known pattern–process relationships (Murphy *et al.* 2008). This will provide a valuable support for empirical analyses. Spatial analysis of empirical data can be used to infer pattern–process relationships governing population genetic substructure (e.g. Cushman *et al.* 2006); spatial simulation of the inferred process can then be used to evaluate the ability of that inferred process to correctly re-create the observed genetic pattern. This combination of empirical induction and simulation deduction provides a strong framework for improved rigour in landscape genetic inference (Cushman & Landguth 2010).

This study shows how classical population genetics models based on ideal Fisher–Wright populations can be connected to spatially explicit, individual-based models to better understand movement ecology and improve our ability to interpret F_{ST} in terms of dispersal and mating across barriers. By moving away from simplistic ideal models towards more complex spatial processes at the individual level, we have produced a glimpse of how sensitive spatial genetic structure may be to the details of how organism behaviour and ecology interact with landscape complexity.

Acknowledgements

This work was supported in part by funds provided by the Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture, and by the National Science Foundation grant #DGE-0504628. G. Luikart was partially supported by the Portuguese American Foundation for Development, CIBIO-UP, and grants from the Portuguese Science Foundation (PTDC/BIA-BDE/65625/2006; PTDC/CVT/69438/2006).

References

Antolin MF, Savage LT, Eisen RJ (2006) Landscape features influence genetic structure of Black-Tailed Prairie Dogs (*Cynomys ludovicianus*). *Landscape Ecology*, **21**, 867–875.

- Balkenhol N, Gugerli F, Cushman SA *et al.* (2009a) Identifying future research needs in landscape genetics: where to from here? *Landscape Ecology*, **24**, 455–463.
- Balkenhol N, Waits LP, Dezzani RJ (2009b) Statistical approaches in landscape genetics: an evaluation of methods for linking landscape and genetic data. *Ecography*, **32**, 818–830.
- Balloux F (2001) EASYPOP (Version 1.7): a computer program for population genetics simulations. *Journal of Heredity*, **92**, 301–302.
- Curat M, Ray N, Excoffier L (2004) SPLATCHE: a program to simulate genetic diversity taking into account environmental heterogeneity. *Molecular Ecology Notes*, **4**, 139–142.
- Cushman SA (2006) Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation*, **128**, 231–240.
- Cushman SA, Landguth EL (2010) Spurious correlations and inferences in landscape genetics. *Molecular Ecology*, doi:10.1111/j.1365-294X.2010.04656.x
- Cushman SA, McKelvey KS, Hayden J, Schwarz MK (2006) Gene flow in complex landscapes: testing multiple hypotheses with casual modeling. *The American Naturalist*, **168**, 486–499.
- Dijkstra EW (1959) A note on two problems in connection with graphs. *Numerische Mathematik*, **1**, 269–271.
- Epperson BK (1993) Spatial and space-time correlations in systems of subpopulations with genetic drift and migration. *Genetics*, **133**, 711–727.
- Epperson BK (1995) Spatial structure of two-locus genotypes under isolation by distance. *Genetics*, **140**, 365–375.
- Epperson BK (2003) *Geographical Genetics*. Princeton University Press, Princeton, NJ.
- Epperson BK (2007) Plant dispersal, neighborhood size and isolation by distance. *Molecular Ecology*, **16**, 3854–3865.
- Epps CW, Wehausen JD, Bleich VC, Torres SG, Brashares JS (2007) Optimizing dispersal and corridor models using landscape genetics. *Journal of Applied Ecology*, **44**, 714–724.
- Ezard THP, Travis JMJ (2006) The impact of habitat loss and fragmentation on genetic drift and fixation time. *Oikos*, **114**, 367–375.
- Hedrick PW (2005) *Genetics of Populations*, 3rd edn. Jones and Bartlett, Boston, MA.
- Hogg JT (2000) Mating systems and conservation at large scales. In: *Invertebrate Mating Systems* (eds Appolonio M *et al.*), pp. 213–252. World Scientific Press, Singapore.
- Holderegger R, Wagner HH (2006) A brief guide to landscape genetics. *Landscape Ecology*, **21**, 793–796.
- Landguth EL, Cushman SA (2010) CDPOP: a spatially explicit cost distance population genetics program. *Molecular Ecology Resources*, **10**, 156–161.
- Manel S, Schwartz M, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. *TRENDS in Ecology and Evolution*, **18**, 189–197.
- Manel S, Berthoud F, Bellemain E *et al.* (2007) A new individual-based spatial approach for identifying genetic discontinuities in natural populations: example application in brown bears. *Molecular Ecology*, **16**, 2031–2043.
- McRae BH, Beier P (2007) Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Science of the United States of America*, **104**, 19885–19890.
- Murphy M, Evans J, Cushman S, Storfer A (2008) Representing genetic variation as continuous surfaces: an approach for

- identifying spatial dependency in landscape genetic studies. *Ecography*, **31**, 685–697.
- Murphy M, Evans J, Stofer A (2010) Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology*, **91**, 252–261.
- Neville HM, Dunham JB, Peacock MM (2006) Landscape attributes and life history variability shape genetic structure of trout population in a stream network. *Landscape Ecology*, **21**, 901–916.
- Pavlacky DC Jr, Goldizen AW, Prentis PJ, Nicholls JA, Lowe AJ (2009) A landscape genetics approach for quantifying the relative influence of historic and contemporary habitat heterogeneity of the genetic connectivity of a rainforest bird. *Molecular Ecology*, **18**, 2945–2960.
- Perez-Espona S, Perez-Barberia FJ, McLeod JE *et al.* (2008) Landscape features affect gene flow of Scottish highland red deer (*Cervus elaphus*). *Molecular Ecology*, **17**, 981–996.
- Ray N (2005) PATHMATRIX: a GIS tool to compute effective distances among samples. *Molecular Ecology Notes*, **5**, 177–180.
- Schwartz MK, Copeland JP, Anderson NJ, Squires JR, Inman RM, McKelvey KS, Pilgrim KL, Waits LP, Cushman SA (2009) Wolverine gene flow across a narrow climatic niche. *Ecology*, **90**, 3222–3232.
- Selkoe KA, Henzler CM, Gaines SD (2008) Seascape genetics and the spatial ecology of marine populations. *Fish and Fisheries*, **9**, 363–377.
- Sokal RR, Jacquez GM, Wooten MC (1989) Spatial autocorrelation analysis of migration and selection. *Genetics*, **121**, 845–855.
- Sokal RR, Oden NL, Thomson BA (1998) Local spatial autocorrelation in biological variables. *Biological Journal of the Linnean Society*, **65**, 41–62.
- Storfer A, Murphy M, Evans J *et al.* (2007) Putting the landscape in landscape genetics. *Heredity*, **98**, 128–142.
- Wright S (1943) Isolation by distance. *Genetics*, **28**, 114–138.