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A simulation-based evaluation of methods for inferring linear barriers to gene flow

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Abstract

Different analytical techniques used on the same data set may lead to different conclusions about the existence and strength of genetic structure. Therefore, reliable interpretation of the results from different methods depends on the efficacy and reliability of different statistical methods. In this paper, we evaluated the performance of multiple analytical methods to detect the presence of a linear barrier dividing populations. We were specifically interested in determining if simulation conditions, such as dispersal ability and genetic equilibrium, affect the power of different analytical methods for detecting barriers. We evaluated two boundary detection methods (Monmonier's algorithm and WOMBLING), two spatial Bayesian clustering methods (TESS and GENELAND), an aspatial clustering approach (STRUCTURE), and two recently developed, non-Bayesian clustering methods [PSMIX and discriminant analysis of principal components (DAPC)]. We found that clustering methods had higher success rates than boundary detection methods and also detected the barrier more quickly. All methods detected the barrier more quickly when dispersal was long distance in comparison to short-distance dispersal scenarios. Bayesian clustering methods performed best overall, both in terms of highest success rates and lowest time to barrier detection, with GENELAND showing the highest power. None of the methods suggested a continuous linear barrier when the data were generated under an isolation-by-distance (IBD) model. However, the clustering methods had higher potential for leading to incorrect barrier inferences under IBD unless strict criteria for successful barrier detection were implemented. Based on our findings and those of previous simulation studies, we discuss the utility of different methods for detecting linear barriers to gene flow.

Keywords: Bayesian, boundary detection, CDPOP, fragmentation, genetic clustering, individual-based simulations

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Introduction

Habitat loss and fragmentation can severely affect biodiversity at the genetic, species and ecosystem levels (Fahrig 2003; Dobson *et al.* 2006). In highly fragmented landscapes, many species only persist in small disjunct populations; their long-term viability depends on the degree to which the landscape impedes or facilitates demographic and genetic exchange among remnant populations (e.g., Ricketts 2001; With *et al.* 2006). Landscape connectivity increases the probability of long-term survival, because successful dispersal has positive effects on abundance and fitness (e.g., through demographic and genetic rescue effects; Vila *et al.* 2003; Reed 2004). As the extinction of keystone species can also impact ecosystem functions, maintaining or establishing functional landscape connectivity is a key component of biodiversity conservation (e.g., Beier *et al.* 2006; Kettunen *et al.* 2007).

Genetic data are increasingly used to identify landscape characteristics influencing species-specific connectivity (e.g., Storfer *et al.* 2010). The number of landscape-genetic studies and the number of analytical

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approaches available for such studies are increasing rapidly (Storfer *et al.* 2010). As applying different analytical techniques to the same data set may lead to different conclusions (e.g., Balkenhol *et al.* 2009), it is important to evaluate the efficacy and reliability of different statistical methods. When evaluating the performance of multiple analytical methods, simulations have high utility because they allow researchers to create known landscape-genetic relationships, although they also require simplifications for tractability (Epperson *et al.* 2010). In addition to quantifying the degree of landscape resistance, detection of landscape barriers using population genetic data has been a long-standing goal in landscape genetics (Storfer *et al.* 2007, 2010). However, the relative performance of existing analytical methods remains unclear because simulation studies use only a subset of methods, making it difficult to compare multiple statistical approaches. For example, Safner *et al.* (2011) recently demonstrated that Bayesian clustering approaches outperformed boundary detection methods for inferring barriers to gene flow, while Landguth *et al.* (2010) found that partial Mantel tests based on individual genetic distance can reliably detect genetic barriers after 1–15 generations, outperforming population-based statistics (F_{ST}).

Synthesizing results from multiple simulation studies is challenging because of the differences in analysis methods and simulation approaches. For example, time required to detect a newly established barrier ranged from 1 to 15 generations with partial Mantel tests (Landguth *et al.* 2010) to 100s–1000s of generations with Bayesian clustering methods and boundary detection methods (Safner *et al.* 2011). Although the assumptions and inference techniques for methods differ, these results raise questions about the usefulness of Bayesian clustering and boundary detection methods for detecting recent genetic barriers and suggest that the partial Mantel statistic based on cost-weighted distances may be the superior method for this task. However, it is also possible that the different simulation approaches affected the time to detect the barrier, making it unclear which method should be used to test for a recent barrier to gene flow in empirical studies.

In this study, we use a subset of the Landguth *et al.* (2010) data to re-evaluate the utility of clustering and boundary detection methods to infer recent barriers to gene flow under comparable conditions. We are specifically interested in determining whether simulation conditions, including dispersal ability, affect the power of different analytical methods for detecting barriers. We compare the performance of two boundary detection methods (MONMONIER, WOMBLING), three Bayesian genetic clustering approaches (TESS, GENELAND, STRUCTURE) and two non-Bayesian clustering methods (PSMIX, DAPC) using genetic data simulated with a landscape barrier to gene flow under two dispersal constraints. We compare methods based on (i) the success rate of detecting the simulated barrier; and (ii) the time to successful barrier detection. We combine our findings with previous simulation studies to discuss the advantages and limitations of different approaches for genetically detecting linear landscape barriers to gene flow in empirical studies.

Materials and methods

Simulated data

To evaluate the utility of different methods for genetic barrier detection, we used data sets from Landguth *et al.* (2010), who conducted spatially explicit, individual-based genetic divergence simulations in the program CDPOP (Landguth & Cushman 2010). Landguth *et al.* (2010) used the simulated data sets to assess the time (in generations) to successful barrier detection with the individual-based partial Mantel statistic and the population-based F_{ST}. In CDPOP, mating and dispersal are simulated as probabilistic functions of movement costs across a landscape. Landguth *et al.* (2010) simulated genotypes for 1000 individuals of an animal species within a study landscape of 70 × 100 km. Simulations were initiated with 30 loci and 30 alleles maximum per locus (resulting in 900 total possible alleles and mean H_o = 0.967), a *k*-allele mutation rate of 0.0005 in a two-sex mating structure with sex assigned randomly with equal probability (see Landguth *et al.* 2010 for details). Landscape resistances to movement were homogeneous on either side of a complete (i.e., impermeable) linear barrier that bisected the landscape into a western and eastern half (500 individuals on either side; Fig. S1, Supporting information). A linear barrier was chosen for simplicity and to represent common barriers to gene flow such as roads, rivers and canals.

Using these data, we compared the relative performance of our methods under different dispersal scenarios. We used data from 10 independent Monte Carlo simulations and under two dispersal distances. In the first scenario (10 k), the maximum simulated dispersal distance was 10 km, while in the second scenario (60 k), the dispersal distance was set to 60 km. These scenarios use the two most extreme dispersal distances simulated by Landguth *et al.* (2010) and correspond to species exhibiting short- vs. long-range dispersal relative to the spatial extent of the study area. Because we were interested in testing the performance of methods for inferring recent barriers to gene flow, we applied the methods only to the first 20 generations after barrier imposition.

The simulated barrier scenarios allow us to compare methods in terms of their relative sensitivity for detecting a linear barrier to gene flow, provided that such a barrier

actually exists. However, it is possible that some methods will also indicate the presence of a linear barrier when no such barrier is influencing gene flow. Assessing this false-detection rate is important, because methods that are particularly powerful in detecting actual barrier effects could also be prone to high type-1 errors. Ideally, methods should have high power for detecting true barrier effects, but a low probability of incorrectly inferring such effects when a hypothesized barrier is not actually affecting gene flow. False detection of a barrier is particularly likely when genetic structures are not completely panmictic, but instead show some kind of clinical spatial pattern, such as isolation-by-distance (IBD; Schwartz & McKelvey 2008; Frantz *et al.* 2009; Safner *et al.* 2011). Thus, to assess type-1 error rates, we also applied all methods to two IBD scenarios of Landguth *et al.* (2010). These IBD scenarios were simulated in the same way as the barrier scenarios, but without a linear barrier in place. Following Landguth *et al.* (2010), we used five Monte Carlo simulations of these data at generation 400 and again focused on scenarios simulated with 10- and 60-km dispersal distances, respectively.

Description of barrier detection methods

We analysed the simulated data with seven different methods that can be used to infer barriers to gene flow. All of the methods work at the level of individuals, meaning that 'traditional' a priori delineation of populations is not necessary. The methods can be classified into two broad categories: boundary detection methods and clustering methods (Safner *et al.* 2011). Boundary detection methods focus on finding regions of abrupt change in a variable of interest (e.g., in allele frequencies). Clustering methods use multilocus genotypes to define genetic clusters and to assign sampled individuals to their most likely cluster of origin. Clustering methods can further be divided into Bayesian and non-Bayesian methods, depending on the underlying statistical approach, and into spatial and aspatial methods, depending on whether or not the spatial locations of individuals are used in the clustering approach.

Boundary detection methods compared in this study include Monmonier's algorithm (MONMONIERs; Monmonier 1973) and WOMBLING (Womble 1951), consistent with the study of Safner *et al.* (2011). Two of the spatial Bayesian clustering methods compared by Safner *et al.* (2011) were evaluated: TESS (Chen *et al.* 2007) and GENELAND (Guillot *et al.* 2005). We omitted BAPS5 (Corander *et al.* 2008) in our analysis as it did not perform well in the Safner *et al.* (2011) comparison. Instead, we added STRUCTURE (Pritchard *et al.* 2000), one of the most commonly used aspatial Bayesian clustering methods (Kalinowski *et al.* 2010), and one often employed as a benchmark for method comparison (e.g., Jombart *et al.* 2010). Further, we added two recently developed, non-Bayesian clustering methods (PSMIX, Wu *et al.* 2006; DAPC, Jombart *et al.* 2010). Below, we briefly describe each method and parameterization. Note that we refer to some methods by the name of the implementing software. See Table 1 for detailed information on original publications and software manuals.

To identify genetic boundaries, the Monmonier algorithm (Monmonier 1973) first calculates genetic distances between neighbouring sampling points (i.e., individuals) along a graph network (e.g., Delauney triangulation). The algorithm starts the boundary between the two sampling locations associated with the highest genetic distance and then extends the boundary line to neighboring locations associated with the next largest genetic distance. The Monmonier algorithm was implemented using the ADEGENET package in R (R Development Core Team 2006) using a Delaunay triangulation, no boundary to loop, and 2 and 10 stating points, respectively.

The WOMBLING algorithm (Womble 1951) measures the gradient or slope of changes in local allele frequencies, identifies areas with the highest slope and tests whether the highest slope value(s) are significant and constitute a boundary. We implemented WOMBLING through the WOMBSOFT package in R (Crida & Manel 2007), using a fixed window size of 10 km for interpolating local allele frequencies.

Table 1 Overview of analytical methods used to test for a barrier to gene flow.

Name of method	Original reference	Type of method	Software used and software reference
Monmonier's algorithm	Monmonier (1973)	Boundary detection	R–package ADEGENET 1.3–0 (Jombart 2008)
WOMBLING	Womble (1951)	Boundary detection	R–package Wombsoft 2.0 (Crida & Manel 2007)
TESS	Chen *et al.* (2007)	Bayesian clustering (spatial)	Software TESS 2.3 (Durand *et al.* 2009a)
GENELAND	Guillot *et al.* (2005)	Bayesian clustering (spatial)	R–package GENELAND 3.2.1 (Guillot *et al.* 2005)
STRUCTURE	Pritchard *et al.* (2000)	Bayesian clustering (aspatial)	Software STRUCTURE 2.3.3 (Hubisz *et al.* 2009)
PSMIX	Wu *et al.* (2006)	Non-Bayesian clustering	R–package PSMIX 1.1–1 (Wu *et al.* 2006)
DAPC	Jombart *et al.* (2010)	Non-Bayesian clustering	R–package ADEGENET 1.3–0 (Jombart 2008)

DAPC, discriminant analysis of principal components.

The three Bayesian clustering methods (TESS, GENELAND and STRUCTURE) identify the most likely number of genetic clusters or 'populations' (denoted by K) and assign individuals to their most likely cluster. The exact algorithms and tools of inferences for these tasks vary among the methods, but they all attempt to group individuals so that Hardy–Weinberg and linkage disequilibria are minimized. TESS and GENELAND also use the spatial locations as prior information and assume that individuals that are close in space have a higher probability of belonging to the same population (see Guillot *et al.* 2009; Francois and Durand 2010 for review).

Bayesian clustering methods are most commonly used to estimate the most likely number of genetic groups (K) without a priori knowledge of population structure. However, clustering methods are also used to test for barrier effects of linear landscape features bisecting a study area (Riley *et al.* 2006; Coulon *et al.* 2008; Gauffre *et al.* 2008). For the latter purpose, it is sufficient to cluster individuals into two groups (i.e., $K = 2$) and assess whether the resulting cluster memberships correspond to the hypothesized landscape barrier. Thus, with all Bayesian clustering methods, we set the number of possible populations (K) to 2 and evaluated the assignment of individuals into the two inferred populations to determine whether the simulated barrier had correctly been detected (see Data analysis below). This use of Bayesian clustering methods enables a fair comparison with the other methods used in this study (see Study reliability in the discussion).

Data analysis

In our analyses, we used the following run parameters. In the mixture model implemented in TESS, the degree to which spatial proximity of samples influences population membership is controlled via a spatial autocorrelation parameter ψ. Following François *et al.* (2006), we set $\psi = 0.6$, using 50 000 sweeps, a burn-in of 10 000 and 10 independent runs per analysis. All TESS analyses were performed using TESS 2.3.1 (François *et al.* 2006; Chen *et al.* 2007; Durand *et al.* 2009a). We parameterized GENELAND 3.2.1 (Guillot *et al.* 2005) without spatial uncertainty in spatial locations and used the correlated allele frequency model. We used 50 000 iterations each with a thinning of 10 and a burn-in of 25% of the samples before observing cluster membership, with 10 independent runs per analysis. In STRUCTURE 2.3.3 (Pritchard *et al.* 2000; Falush *et al.* 2003; Hubisz *et al.* 2009), we chose the admixture model and assumed correlated allele frequencies. We used a burn-in of 20 000, followed by 80 000 MCMC iterations and conducted 10 independent runs per data set.

PSMIX (Wu *et al.* 2006) is similar to the Bayesian clustering methods in that it minimizes Hardy–Weinberg and linkage disequilibrium when clustering individuals into a predefined number of populations. However, it utilizes a maximum-likelihood approach and does not estimate the most likely number of populations K. We implemented the method in the R package PSMIX 1.1.1 (Wu *et al.* 2006), setting $K = 2$, using a maximum number of iterations of 100 000 and a convergence criteria of 10^{-10}.

Finally, DAPC is a multivariate method for identifying genetic clusters through sequential clustering and model selection. The method first transforms the genotype data into principal components and then uses k-means clustering to define groups of individuals so that within-group variation is minimized, while among-group variation is maximized. We implemented the method in R package ADEGENET (Jombart 2008), setting $K = 2$, using 1000 iterations, and chose the number of axes to keep for the principal component analysis so that about 90% of the variation was explained by the axes.

Interpretation of results

The implemented methods produce different types of output data including graphical boundary maps (Monmonier's algorithm), P-values for boundary elements (WOMBLING) and individual admixture proportions or membership coefficients (clustering methods). To compare the performance of the different methods with respect to genetic barrier detection, we developed criteria to determine when a certain method had successfully detected the simulated barrier. We set these criteria to reflect the interpretation of researchers analysing empirical data sets. In other words, we asked whether results obtained with a certain method would lead researchers to conclude that a complete, linear barrier to gene flow existed between the eastern and western halves of the study area.

With Monmonier's algorithm, the criterion for successful detection of the boundary was existence of a contiguous boundary that spatially coincided with the simulated barrier (see Fig. S2, Supporting information). Similarly, with the WOMBLING method, the barrier was successfully detected whether the significant boundary elements ($P < 0.05$) formed a contiguous area zone that spatially coincided with the simulated barrier (Fig. S3, Supporting information). With the clustering methods, we evaluated clustering of individuals into the two inferred populations based on the highest assignment value for each individual. Because we conducted multiple analysis runs with the Bayesian clustering methods, we used the assignment values of the run with the highest likelihood (or lowest DIC for TESS) for final assignments (Coulon *et al.* 2008). The barrier was successfully detected if at least 95% of the individuals were correctly

assigned according to their sampling location with >probability (i.e., east or west of the simulated barrier; Figs S4–S6, Supporting information).

Using these criteria, we compared methods based on (i) the success rate of barrier detection, given by the proportion of data sets where the simulated barrier was detected within the first 20 generations; and (ii) the time-to-barrier detection, given by the earliest generation in which a method detected the simulated barrier. Results are based on data from 10 independent simulated batches for both dispersal distances.

To assess false-detection rates (type 1 error), we analysed the IBD (i.e., nonbarrier) scenarios with all methods and again tested for effects of a linear barrier that bisected the study area from north to south. We used the same 'success' criteria for deciding whether a method had (incorrectly) detected the barrier in these IBD scenarios.

Results

Across scenarios, the simulated barrier was detected in ≥70% of all cases, and within *c.* 16 generations or less (Table 2). Clustering methods had higher success rates than boundary detection methods (0.9 vs. 0.4) and also detected the barrier earlier (13.2 vs. 16.9 generations). All methods detected the barrier more quickly in the 60 k scenarios (mean of 11.5 generations across methods) compared with the 10 k scenarios (mean of 15.8 generations). The Bayesian clustering methods performed best overall, both in terms of highest success rates and lowest time to barrier detection.

Interestingly, the success rates for barrier detection and the time-to-barrier detection varied considerably among methods and simulated dispersal distance (Table 3). Overall, simulated dispersal distances did not substantially impact Bayesian clustering methods, while Monmonier's algorithm and DAPC were particularly sensitive to dispersal parameters. With short (10 k) dispersal, success rates were highest for Bayesian clustering methods and Monmonier's algorithm, while WOMBLING and DAPC had the lowest success rates in these scenarios (0.2 and 0.1 for WOMBLING and DAPC, respectively). However, with 60 k dispersal, DAPC had a perfect success rate of 1.0 and detected the barrier quite quickly (7.3 generations on average). In contrast, Monmonier's algorithm never detected the simulated barrier in the 60 k scenario.

In the 10 k dispersal scenarios, Monmonier's algorithm required the shortest time to barrier detection (average of 12.4 generations), while WOMBLING and DAPC took longest to detect the barrier (20 generations). With 60 k dispersal, time to detection was lower for all methods, except for MONMONIERs, which never detected the barrier within the first 20 generations. GENELAND had shortest detection times for the 60 k scenario (average time to detection of 4.3 generations), as well as overall (9.7 generations).

Based on our criteria for successful barrier detection, none of the methods incorrectly detected a barrier in the two IBD scenarios. Specifically, the barrier elements suggested by the edge-detection methods did not coincide with the hypothesized barrier bisecting the study area (Fig. 1e,f). Similarly, clustering methods correctly assigned <95% of individuals according to their sampling locations on the two sides of the hypothesized barrier (Fig. 1b,c). Thus, while methods were influenced by the simulated IBD and detected some spatial structure, results did not lead us to incorrectly accept our barrier hypothesis based on the strict criteria for successful barrier detection. However, results from clustering methods had greater potential for leading to incorrect inferences about barrier effects under IBD than edge-detection methods, particularly when dispersal distances were short (see Discussion).

Discussion

Habitat loss and fragmentation can have detrimental effects on all levels of biodiversity (Fahrig 2003; Krauss

Table 2 (a) Success rates and (b) time-to-barrier detection (generations) across different types of methods for each of the two simulated scenarios (10 k and 60 k), and across scenarios. 'Boundary detection' includes Monmonier's algorithm and WOMBLING; 'All clustering' includes the other five methods; 'Bayesian clustering' includes TESS, STRUCTURE and GENELAND; 'Non-Bayesian clustering' includes PSMIX and DAPC. Values represent averages obtained from 10 independent simulations for each scenario.

	Boundary detection	All clustering	Bayesian clustering	Non-Bayesian clustering	Across methods
(a) Success rates					
10 k dispersal	0.60	0.80	0.97	0.55	0.73
60 k dispersal	0.20	1.00	1.00	1.00	0.70
Across scenarios	0.40	0.90	0.98	0.78	0.71
(b) Time to detection					
10 k dispersal	14.80	16.34	14.83	18.60	15.76
60 k dispersal	19.00	9.98	9.80	10.25	11.48
Across scenarios	16.90	13.16	12.32	14.43	13.62

Table 3 Number of generations required by each method evaluated in this study (7) to detect a simulated barrier in 10 simulated scenarios (a) with 10 km dispersal distances, (b) with 60 km dispersal distances, and (c) across both simulated scenarios. ND means that the barrier was not successfully detected within the first 20 generations after barrier imposition. Bold values summarize the success rates (proportion of times the barrier was successfully detected) and time to detection (earliest generation that a barrier was correctly identified) across the 10 simulation runs of each scenario. Values in parentheses show standard deviations.

	Monmonier two barrier approach	Monmonier 10 starting points approach	WOMBLING	TESS	STRUCTURE	GENELAND	PSMIX	DAPC
(a) 10 k dispersal								
Simulation 1	14	ND	ND	16	13	13	16	ND
Simulation 2	9	9	ND	19	10	20	17	ND
Simulation 3	16	12	20	20	13	13	18	ND
Simulation 4	ND	ND	20	18	15	19	18	ND
Simulation 5	10	15	ND	18	12	12	18	ND
Simulation 6	10	10	ND	12	12	12	17	20
Simulation 7	15	ND	ND	ND	16	16	16	ND
Simulation 8	11	14	ND	18	14	18	15	ND
Simulation 9	10	15	ND	14	12	13	19	ND
Simulation 10	13	12	ND	13	14	14	18	ND
Success rate	**0.9**	**0.7**	**0.2**	**0.9**	**1.0**	**1.0**	**1.0**	**0.1**
Time to detection	**12 (2.6)**	**12.4 (2.4)**	**20 (0)**	**16.4 (2.8)**	**13.1 (1.7)**	**15 (3.0)**	**17.2 (1.2)**	**20 (0)**
(b) 60 k dispersal								
Simulation 1	ND	ND	19	13	11	3	12	11
Simulation 2	ND	ND	17	14	10	4	15	6
Simulation 3	ND	ND	ND	13	9	4	13	7
Simulation 4	ND	ND	ND	15	10	4	11	8
Simulation 5	ND	ND	19	15	11	4	14	6
Simulation 6	ND	ND	ND	15	10	6	13	8
Simulation 7	ND	ND	19	15	12	4	14	6
Simulation 8	ND	ND	ND	15	12	4	13	6
Simulation 9	ND	ND	20	15	12	3	15	6
Simulation 10	ND	ND	20	13	11	7	12	9
Success rate	**0.0**	**0.0**	**0.6**	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**
Time to detection	**ND**	**ND**	**19 (1.1)**	**14.3 (0.9)**	**10.8 (1.0)**	**4.3 (1.3)**	**13.2 (1.3)**	**7.3 (1.7)**
(c) Across scenarios								
Success rate	**0.45**	**0.35**	**0.40**	**0.95**	**1.0**	**1.0**	**1.0**	**0.55**
Time to detection	**12.0 (2.6)**	**12.4 (2.4)**	**19.3 (1.0)**	**15.3 (2.3)**	**12.0 (1.8)**	**9.7 (5.9)**	**15.2 (2.4)**	**13.7 (4.2)**

et al. 2010), but these effects can be partially mitigated if functional landscape connectivity among remaining habitat can be restored or maintained (Damschen *et al*. 2006; Haddad & Tewksbury 2006). Thus, the ability to reliably and rapidly detect landscape characteristics that impede dispersal and gene flow is vital for effective conservation management and landscape planning (Bennett 2003; Kettunen *et al*. 2007). While genetic data are increasingly used for this task, it is not clear whether genetic approaches can detect landscape impediments to gene flow at the temporal resolution relevant for applied conservation and management (Safner *et al*. 2011). Therefore, in this study, we specifically evaluated the performance of seven different methods for detecting recent barriers to gene flow using multilocus genetic data. Our results demonstrate that a wide variety of the compared methods are effective for detecting barriers to gene flow, as all methods were capable of detecting simulated barriers within 20 generations. However, our results also show that some methods outperform others and that relative method performance can depend on the simulation parameters (e.g., dispersal distances).

Across simulated scenarios, our results suggest that clustering methods detect barriers to gene flow more rapidly and more reliably than boundary detection methods. We identified GENELAND (Guillot *et al*. 2005) as the overall best approach for detecting barriers under our simulated conditions, based on its somewhat faster barrier detection at high dispersal abilities compared with other tested methods. The better performance of clustering methods compared with boundary detection methods is likely due to the fact that edge-detection methods are better suited to detect local patterns of genetic differentiation, whereas clustering methods work particularly well at broader geographic scales (Murphy *et al*. 2008).

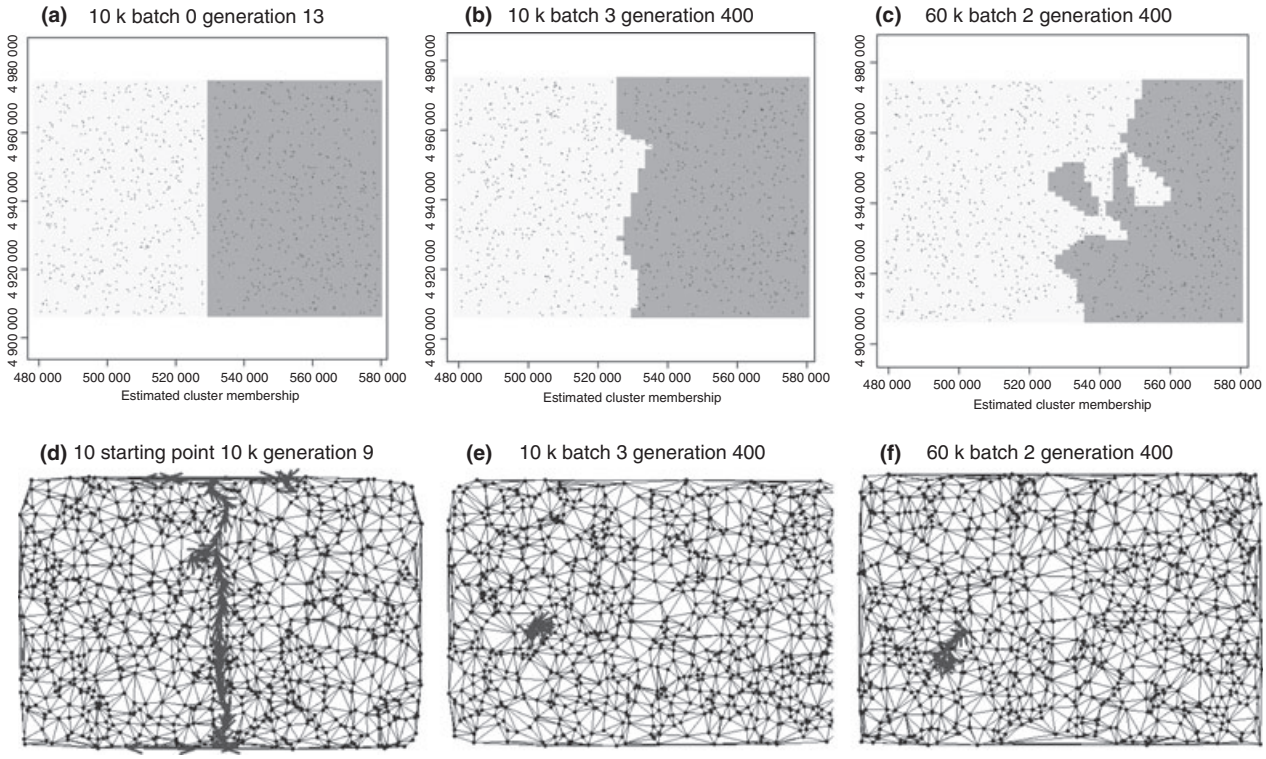

Fig. 1 Comparison of GENELAND and Monmonier's algorithm when data are generated under both a barrier (a, d) and pure isolation-by-distance model (b, c, e, f).

Barrier detection in relation to dispersal

Differences in method performance are at least partially caused by differences in simulated dispersal distances. With short-range dispersal, IBD will be more pronounced than with long-range dispersal (Landguth & Cushman 2010; Landguth *et al.* 2010). At the same time, fewer dispersers will be affected by the barrier in each generation when dispersal distances are shorter, because the barrier can only be reached by dispersing individuals if they are located close to the barrier. Thus, short-distance dispersal will lead to a relatively strong global (i.e., population-wide) IBD pattern, while the barrier effect will be more local and evolve more slowly. In contrast, the barrier will affect the entire population more rapidly with long-range dispersal, while population-wide IBD will be comparably weak. This is why the barrier was detected more reliably in the 60 k dispersal scenarios across methods. Furthermore, the high variability in results obtained with MONMONIERs can be attributed to IBD vs. barrier effects. MONMONIERs is a highly local method because it is based on genetic distances among nearest neighbors. With short dispersal distances, this approach works well because the highest genetic distances will be found between nearest neighbors separated by the barrier. This local barrier effect can rapidly and reliably be detected with MONMONIERs. In contrast, with greater dispersal distances, the barrier effect is no longer just local (i.e., it quickly affects many dispersing individuals, regardless of their spatial proximity to the barrier), so that Monmonier's algorithm has difficulties in finding the true location of the barrier. More generally, the stochastic nature of both dispersal and drift will likely result in outlier individuals, which produce a boundary that is not spatially coincident with the a priori proposed barrier.

Strong IBD can also influence results of clustering methods, as described in several empirical and simulation studies (Schwartz & McKelvey 2008; Frantz *et al.* 2009; Safner *et al.* 2011). Specifically, Bayesian clustering methods will often create artificial population clusters when IBD is present. Here, we circumvented this problem by setting the number of clusters (K) to two for all clustering methods. This approach is adequate when explicitly testing for a linear barrier to gene flow that is defined a priori. Clustering methods are useful in detecting the uppermost level of population genetic structure (Evanno *et al.* 2005; Coulon *et al.* 2008), and while additional levels of genetic structure may exist on both sides of a barrier, setting $K = 2$ should detect the strong barrier effect before detecting the weaker IBD effects. Thus, researchers can test whether a landscape feature really acts as a genetic barrier by comparing the resulting clus-

tering of individuals with the population structure expected under the proposed barrier. While this use of clustering methods is unusual, our results suggest that it improves their power for detecting linear barriers to gene flow.

The only method where setting $K = 2$ a priori did not improve success rates under short dispersal was DAPC. The method worked very well with long-range dispersal, but had a very low success rate with short-range dispersal. In the short-range dispersal scenarios, the method did not cluster individuals according to the two sides of the barrier, but instead created clusters that included individuals from both sides. Thus, the method appears highly sensitive to IBD. For inferring linear barriers to gene flow, this high sensitivity is problematic, but it suggests that the method has high power for quantifying genetic structure in general.

Incorrect barrier inferences under IBD

Setting $K = 2$ is also relevant with respect to the type-1 error rates. Based on our criteria for barrier detection, none of the methods led us to incorrectly conclude that a barrier existed in the IBD scenarios. While edge-detection methods suggested spurious barriers under IBD (e.g., Fig. 1e,f), the barrier elements clearly did not follow the hypothesized linear barrier, and therefore did not provide the opportunity for incorrect barrier inferences. These results are again caused by the fact that edge-detection methods focus on local patterns and are therefore more likely to detect small-sale genetic discontinuities under IBD.

In contrast, clustering methods are more prone to incorrect barrier inferences under IBD. For example, most empirical studies would have concluded a barrier from Fig. 1b, even though the genetic pattern was generated under IBD. In our analysis, this scenario did not lead to a formal type-1 error, because the proportion of cross-barrier assignments exceeded 5% (i.e., more than 5% of the individuals were sampled on one side of the hypothesized barrier, but genetically assigned to the other side of it). Thus, we avoided a formal type-1 error in the clustering methods by setting $K = 2$ a priori and using stringent criteria to determine whether the hypothesized barrier was supported (i.e., no more than 5% of cross-barrier assignment). However, this lack of a formal type-1 error does not mean that incorrect inferences about barrier effects under pure IBD will be avoided in empirical studies. Setting $K = 2$ may reduce the risk of detecting multiple, spurious genetic clusters, which has been shown to be a problem under IBD and under certain sampling schemes (Schwartz & McKelvey 2008; Frantz *et al.* 2009). However, as our results show, setting $K = 2$ does not completely avoid the risk of incorrectly inferring a linear barrier to gene flow under IBD, particularly when dispersal distances are short. Deciding whether researchers not following our strict criteria could have incorrectly concluded a barrier from the clustering results would have involved a great deal of subjectivity, so that an actual quantification of this 'potential' type-1 error would not be meaningful. Nevertheless, it is important to note that the high power of clustering methods for detecting linear barriers to gene flow is accompanied by a certain risk of inferring a barrier when no such barrier is actually present.

We also acknowledge that we sampled all individuals in the study area and that less comprehensive sampling schemes will likely increase the potential for type-1 errors. For example, a spatially clustered sampling of individuals on both sides of a hypothesized barrier is likely going to produce a barrier-line (in the case of edge-detection methods) or population-assignments (in case of clustering methods) that match the presence of the hypothesized barrier, even if genetic structures are actually only influenced by IBD. However, this is a matter of finding an adequate sampling scheme for a certain research question and beyond the scope of this study. Overall, when the sampling design is exhaustive and not biased with respect to the hypothesized barrier, setting $K = 2$ a priori seems to improve the utility of clustering methods for detecting linear barriers to gene flow, but still has the potential for false barrier detection. Thus, researchers should clearly identify the criteria used for inferring barriers from clustering methods and should also not rely solely on clustering methods when genetically testing for barriers.

Comparison with Safner et al. (2011)

Several of our findings corroborate results of Safner *et al.* (2011), who concluded that the Bayesian clustering methods outperformed the boundary detection methods and also found GENELAND to be the best clustering approach for barrier detection. Thus, the high power of Bayesian clustering methods in general and of GENELAND in particular, for detecting barriers to gene flow has now been demonstrated by two independent simulation studies. However, Safner *et al.* (2011) did not formally address type-1 error rates and thus, their conclusion that GENELAND is the best method does not consider the potential for false barrier detection with this method. Further, unlike Safner *et al.* (2011), we demonstrated that none of the tested methods require hundreds of generations or more to detect simulated barriers to gene flow. In the study by Safner *et al.* (2011), all methods but GENELAND required at least 500 generations to detect the simulated barrier. This difference in temporal resolution for genetically detecting barriers is

likely caused by the different simulation approaches used to create data sets in Safner *et al.* (2011) vs. Landguth *et al.* (2010) used in this study. Safner *et al.* (2011) focused on simulating data sets where the spatial-genetic structure was at quasi-equilibrium, and based their inferences on a population that existed for 500 generations before the barrier was imposed. This scenario mimics species or populations that have existed in stable environments for a very long time and are then exposed to rapid landscape changes (i.e., rapid emergence of a barrier). However, natural and anthropogenic changes have impacted many landscapes across the globe for extensive periods of time (Kates *et al.* 1990; Meyer & Turner 1994; Antrop 2000; Bicík *et al.* 2001). For plant and animal species living in such dynamic landscapes, traditional population genetic theory and equilibrium assumptions may not adequately represent population genetic structures (Cushman *et al.* 2006; Balkenhol *et al.* 2009). The CDPOP package (Landguth & Cushman 2010) is suitable for simulating such scenarios, as it is not based on equilibrium assumptions, and instead focuses on individual movement and mating across a user-defined landscape. Furthermore, Safner *et al.* (2011) simulated a very large population of 10 000 individuals, while we used data simulated for a 10-fold smaller population (1000 individuals). The combination of equilibrium conditions along with a very large population size is often unrealistic in natural populations and may have substantially increased the time-to-barrier detection in the study of Safner *et al.* (2011). Thus, while the scenarios simulated by Safner *et al.* (2011) are realistic for certain study species and landscapes (e.g., Gauffre *et al.* 2008), we believe that other species and landscapes are better approximated by the simulation approach of Landguth *et al.* (2010). To substantiate this claim, we highlight that many empirical studies have demonstrated the capability of genetic methods for detecting linear barriers to gene flow (i.e., transportation infrastructures) within several generations (see Balkenhol & Waits 2009; Holderegger & Di Giulio 2010). Thus, both empirical and simulation studies support the efficacy of applying genetic methods to detect gene flow impediments at temporal scales that are meaningful for conservation and management.

Comparison with Landguth et al. (2010)

Landguth *et al.* (2010) found that partial Mantel tests were able to reliably detect the simulated barrier more rapidly than the methods tested here. However, it is difficult to statistically compare the relative performance of Bayesian clustering and edge-detection methods with Mantel approaches as they are based on entirely different inference methods. Partial Mantel tests are used to test the statistical significance of a hypothesized barrier to gene flow through permutation (Landguth *et al.* 2010). Conversely, the methods used in this study can be considered 'unsupervised' methods that use the genetic data (with or without spatial information) to test whether resulting clusters coincide with a hypothesized barrier. Thus, the partial Mantel test and other analytical methods are not exactly comparable.

Nevertheless, considering the partial Mantel approach for barrier detection has some advantages over the other methods tested here. Using partial Mantel tests can help to statistically account for confounding IBD or landscape effects when testing for barrier effects, and thus help to avoid incorrect conclusions about barrier effects under gradient variation (Cushman & Landguth 2010). This is particularly important in complex landscapes, where linear landscape features represent only one of many possible landscape effects on gene flow. When gradient landscape structures are hypothesized to also influence gene flow, causal modeling based on partial Mantel tests can help to evaluate the relative importance of linear barriers and landscape gradient in shaping genetic structures (Cushman *et al.* 2006; Cushman & Landguth 2010). Assessing multivariate landscape influences on gene flow in such a model-selection framework will often be necessary to gain a more complete understanding of gene flow in complex environments, which is a prerequisite for practical conservation and management (e.g., corridor design; Epps *et al.* 2007; Cushman *et al.* 2008). The fact that partial Mantel tests do not require any user-defined input parameters, and the ease of interpreting results (i.e., based on *P*–values and correlation coefficients) are additional factors that make the method highly suitable for testing barrier effects in heterogeneous environments. Thus, our results combined with those of Safner *et al.* (2011) and Landguth *et al.* (2010) suggest that the combination of Bayesian clustering methods (in particular GENELAND) with partial Mantel tests can be particularly powerful in detecting recent, linear barriers to gene flow. It should also be noted that Mantel approaches have been substantially criticized in the genetics literature, and that their use requires careful consideration of data types and permutation procedures (Raufaste & Rousset 2001; Balkenhol *et al.* 2009; Legendre & Fortin 2010).

Study reliability

Our study involved several simplifications that are typical of any study using simulated data. Simplifications are not a shortcoming of simulations; rather they are used to control specific factors of interest, which helps clarify complex pattern–process relationships (Epperson *et al.* 2010; Balkenhol & Landguth 2011). First, we focused on strictly linear barriers centrally located in the study area

that impede gene flow completely. Clearly, not all landscape features that influence gene flow will be linear and many will be partially permeable (e.g., Landguth *et al.* 2010). However, there are many landscape features that are highly linear in nature and can hinder movement and gene flow completely. For example, transportation infrastructures (e.g., roads or canals) are often fenced and can thus represent a movement barrier for many species (Jaeger & Fahrig 2004; Epps *et al.* 2005; Riley *et al.* 2006). Furthermore, a method that does not reliably detect a complete, linear barrier to gene flow will be even less likely to detect more complex (i.e., nonlinear and/or partially permeable) barriers. Thus, the scenarios we tested are both ecologically relevant and serve as good starting point for method comparison.

The comparison of methods involved some subjectivity, because inferences about barrier effects are based on very different types of output data in the different methods and programs. For example, we used a correct assignment rate of at least 95% to conclude that a clustering method had successfully detected the barrier. In empirical studies, researchers may use lower thresholds to infer barrier effects. Implementation of a lower threshold in our study (e.g., 90%, 85%) could have improved both success rates and time-to-barrier detection for the clustering methods. Similarly, success rates for boundary detection methods could have improved if we had accepted a barrier as successfully detected that at least partially coincided with the simulated barrier. In empirical studies, researchers may conclude a barrier effect with such a result. On the other hand, using less strict criteria for barrier detection also would have led to formal type-1 errors in the IBD scenarios. It should be noted that we simulated an absolute barrier to movement and gene flow, and we sampled all individuals present in the study area. Under such conditions, we can expect a method to be able to clearly and unambiguously identify the barrier, without any need for researcher subjectivity or speculation. Thus, our criteria for success are feasible for the simulated scenarios and the purpose of the study. Implementing different method success criteria did not influence their *relative* performance. Thus, conclusions regarding the relative suitability of tested methods for detecting linear barriers to gene flow would not change based on differing success criteria.

Program input parameters need to be set a priori. We generally followed recommendations given in original software papers and manuals, or implemented settings similar to those found in published studies. Because using different analysis parameters could theoretically change results, we also explored the sensitivity of methods to varying parameters. For example, we used different search radii (1–50 km) with the WOMBLING method, but this did not markedly change results. Similarly, we used varying numbers of MCMC runs (up to 500 000), but results did not change as long as run-times were long enough for results to stabilize. To ensure that analysis distribution stabilized, we examined log-likelihood plots vs. generation in the Bayesian clustering methods for convergence before making inferences about barrier effects. Based on these assessments, we are confident that altering analysis parameters would not have changed final comparisons among methods or recommendations. Further, there has been recent discussion regarding spatial inference using TESS, in particular with the choice of ψ (Durand *et al.* 2009b; Guillot 2009a,b). We acknowledge these criticisms and chose the value of 0.6 as recommended by the program authors as this value generally provides the most reliable results (see Guillot 2009a for additional justification). Lastly, although the choice of mixture vs. admixture models may influence the results (Francois & Durand 2010), our goal was to specify as many of the same parameter settings among programs as possible, keeping with the recommendations of the program authors. Therefore, we focused predominantly on the less computationally intensive mixture models to infer the simulated barrier.

Conclusions and recommendations

Overall, our study illustrates that many of the methods we tested can rapidly and reliably detect a recently created genetic barrier dividing a landscape. Bayesian clustering approaches are among the most powerful methods for this task, as they are capable of reliably detecting linear barriers to gene flow within 20 generations or less. To avoid artificial clustering owing to IBD, we recommend setting the number of clusters in Bayesian clustering methods to the number expected under the proposed barrier (e.g., $K = 2$). Our results and results of Safner *et al.* (2011) suggest GENELAND is the best method available for detecting linear genetic barriers. However, we recommend that researchers testing for genetic barriers use more than one method, as the power and false-detection rate of a method will depend on species-specific dispersal characteristics, sample size (Murphy *et al.* 2008), barrier permeability (Murphy *et al.* 2008; Landguth *et al.* 2010) and spatial distribution of sampling (Schwartz & McKelvey 2008). In particular, combining GENELAND with Monmonier's algorithm and assessing concordance may serve as a powerful approach to maximizing power and minimizing type-1 error.

Furthermore, linear barriers are only one possible effect that landscapes can have on gene flow and population genetic structure. In many instances, landscape heterogeneity will be better described by spatial gradients that interact with linear landscape features to create

complex genetic structures (McGarigal & Cushman 2005; Murphy *et al.* 2008). Quantifying these landscape-genetic relationships will require analytical approaches that go beyond simple barrier testing and evaluate multiple alternative hypotheses or landscape models (e.g., Cushman *et al.* 2006; Shirk *et al.* 2010; Wasserman *et al.* 2010). Cushman & Landguth (2010) found that a causal modelling framework based on partial Mantel tests is effective for such multivariate landscape-genetic analyses. Even though Mantel approaches have been criticized in the literature, they are still the most widely used statistics in landscape genetics (Storfer *et al.* 2010). Developing additional statistical tools for linking landscape and genetic data should be a major objective in future research, and simulations will likely play a key role (Balkenhol *et al.* 2009; Epperson *et al.* 2010; Spear *et al.* 2010; Balkenhol & Landguth 2011). Thus, we encourage others to conduct similar simulation studies exploring factors that could potentially influence the performance of existing and novel landscape-genetic methods, for example, sampling design, sample intensity, effective population size or number of markers used. Combining results from multiple empirical and simulation studies will ultimately help to match the most appropriate statistical technique to a specific research question, thereby leading to more accurate inferences and more meaningful conclusions about landscape effects on gene flow.

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C.B., D.E.W., E.L., S.C., M.M., L.W., and N.B. designed the study. E.L. performed the simulations. C.B., D.E.W., M.B., A.T.H.K., F.M.W., and N.B. performed the statistical analyses. All authors contributed to interpreting the results and writing the manuscript. All authors read and approved the final manuscript.

Data accessibility

Microsatellite data: DRYAD entry doi:10.5061/dryad.3271mn17. These data were also used in the simulation study of Landguth *et al*. (2010).

Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 Graph depicting simulation conditions used in this study.

Fig. S2 Monmonier plots showing complete and incomplete barriers: (a) two barrier approach 10 km run at generation 9, (b) two barrier approach 60 km run at generation 20, (c) 10-starting-point 10 km run at generation 9, (d) 10-starting-point 60 km run at generation 20.

Fig. S3 WOMBSOFT maps showing complete (a) and partial (b) barriers.

Fig. S4 Bar plot from STRUCTURE showing 100% proper population assignment at generation nine (a) and bar plot showing 74% proper assignment at generation four (b) for 60 km dispersal distance.

Fig. S5 Clustering output for GENELAND showing full (a) and partial (b) barrier detection at $K = 2$.

Fig. S6 Plots from TESS showing initial membership (a) and the posterior probabilities at $K = 2$ (b).

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