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A comparison of regression methods for model selection in individual-based landscape genetic analysis

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Abstract

Anthropogenic migration barriers fragment many populations and limit the ability of species to respond to climate-induced biome shifts. Conservation actions designed to conserve habitat connectivity and mitigate barriers are needed to unite fragmented populations into larger, more viable metapopulations, and to allow species to track their climate envelope over time. Landscape genetic analysis provides an empirical means to infer landscape factors influencing gene flow and thereby inform such conservation actions. However, there are currently many methods available for model selection in landscape genetics, and considerable uncertainty as to which provide the greatest accuracy in identifying the true landscape model influencing gene flow among competing alternative hypotheses. In this study, we used population genetic simulations to evaluate the performance of seven regression-based model selection methods on a broad array of landscapes that varied by the number and type of variables contributing to resistance, the magnitude and cohesion of resistance, as well as the functional relationship between variables and resistance. We also assessed the effect of transformations designed to linearize the relationship between genetic and landscape distances. We found that linear mixed effects models had the highest accuracy in every way we evaluated model performance; however, other methods also performed well in many circumstances, particularly when landscape resistance was high and the correlation among competing hypotheses was limited. Our results provide guidance for which regression-based model selection methods provide the most accurate inferences in landscape genetic analysis and thereby best inform connectivity conservation actions.

KEYWORDS
landscape genetics, linear mixed effects model, Mantel test, model selection, regression on distance matrices, simulation

1 | INTRODUCTION

A primary goal of landscape genetic analysis is to infer how landscapes resist gene flow and thereby create genetic structure between and within populations (Manel & Holderegger, 2013). Such an understanding provides an empirical basis to inform management and conservation of habitat connectivity and to predict the effects of landscape change on population structure (e.g., Wasserman, Cushman, Shirk, Landguth, & Littell, 2012). In an era of widespread conversion of native habitats for human uses, as well as biome shifts driven by climate change, the genetic and demographic viability of many populations is at risk (Banks et al., 2013). For many species, persistence in a rapidly changing environment will require landscapes permeable to movement such that they can track suitable habitat

over time (Rudnick et al., 2012). Permeable landscapes also serve to unite patchily distributed populations into larger aggregates, thereby improving genetic and demographic viability (Banks et al., 2015). Understanding spatial genetic patterns and identifying migration barriers is therefore critical to conservation efforts designed to mitigate current and future threats (e.g., construction of wildlife crossing structures and conservation of habitat in key connectivity corridors).

Landscape genetic analysis begins by formulating hypotheses of how a landscape resists gene flow. A common hypothesis is that of isolation by distance (IBD; Wright, 1943), where the degree of genetic isolation is a function of the Euclidean distance between individuals or populations. In complex landscapes, isolation by resistance (IBR; McRae, 2006) is the predominant mode of genetic isolation. IBR hypotheses are combinations of one or more landscape variables (e.g., roads, landcover type and topography), each of which is characterized by a maximum resistance (R_{max}) and a functional form relating the variable to resistance (P; e.g., linear or a power function). Commonly, hypotheses of landscape resistance to gene flow are used to calculate pairwise distances between genetically sampled individuals (in individual-based analyses) or populations (in population-based analyses). If the mode of genetic isolation for a given hypothesis is IBD, the distances are expressed in Euclidean units. If the mode is IBR, the pairwise distances are expressed in effective units given a raster model of resistance (e.g., circuit theory; McRae, 2006 or based on cost-weighted distances; Spear, Balkenhol, Fortin, McRae, & Scribner, 2010). Collectively, we refer to these pairwise distances (whether Euclidean or effective) as "landscape distances" (LD).

Landscape hypotheses (quantified by pairwise LD) may be empirically evaluated against pairwise genetic distances (GD) given the multilocus genotypes of sampled individuals. In recent years, many statistical approaches have been proposed to select the true model among competing alternative hypotheses based on the strength of this relationship. The simplest of these are regression-based methods relating matrices quantifying landscape and genetic distances. More complex alternatives also exist, including methods based on Bayesian statistics (Guillot, Estoup, Mortier, & Cosson, 2005), maximum likelihood (Clarke, Rothery, & Raybould, 2002) and Moran's eigenvectors (Galpern, Peres-Neto, Polfus, & Manseau, 2014). The goal of any approach is often to identify (i) which variables contribute to resistance, (ii) the magnitude of resistance (R_{max}) for each contributing variable and (iii) the functional form of the relationship between each variable and resistance (P).

Typically, researchers select a range of hypotheses that explore a multidimensional hypothesis space based on various parameterizations of R_{max} and P for a set of variables potentially influencing resistance. Several recent studies have demonstrated the difficulty in selecting the true model among competing alternatives due to several sources of error (Cushman, Wasserman, Landguth, & Shirk, 2013; Kierepka & Latch, 2015; Zeller et al., 2016). Specifically, Zeller et al. (2016) described four major sources of error, including strong correlations among competing hypotheses, the degree of structure in the population, instability in population genetic structure, and violation of the regression assumptions of linearity and independence.

Comparative studies are needed to determine the relative performance of landscape genetic model selection methods so that differences may be attributed to the method rather than the evaluation framework. Population genetic simulations are ideal for this purpose (Landguth, Cushman, & Balkenhol, 2015). A landscape model may be simulated as the true driver of genetic isolation and alternative models may be evaluated against the truth in a model selection framework. Importantly, such a method comparison should assess the ability of each method to deliver on the major goals of landscape genetic analysis noted above (i.e., identify which variables contribute to resistance as well as the R_{max} and P of each variable), in the context of the major challenges to model selection accuracy. For the results to be generalizable, the comparison should be conducted across a variety of realistic landscapes from simple to complex, with a high degree of replication.

To date, three studies have compared the relative performance of three or more model selection methods (Balkenhol, Waits, & Dezzani, 2009; Kierepka & Latch, 2015; Zeller et al., 2016). Collectively, these studies have advanced our understanding of landscape genetic analysis, but there are a number of methods or variations of methods that have not yet been evaluated. In addition, these studies offer only a limited exploration of the types of variables present in real landscapes, with low replication. Thus, despite these recent advances in our understanding of model selection in landscape genetics, there is still a need for more comprehensive comparisons of model selection methods.

In this study, we evaluated seven regression-based model selection methods using landscape genetic simulations on a broad array of landscapes with high replication (Table 1). Some of these methods allowed for independent assessment of each variable's contribution to resistance in a model with multiple predictor variables. However, to facilitate comparison across methods, our statistical analysis was limited to a single predictor based on an additive combination of all landscape variables in the resistance model. Also, all methods we evaluated provided significance tests as well as metrics of model fit. However, in our analysis, model selection was based on model fit alone. We varied the number and type of variables (continuous, categorical or linear feature) contributing to landscape resistance, the magnitude of resistance (R_{max}) for each variable, the functional form of the relationship between each variable and resistance (P), the degree of aggregation of resistance in the landscape (H), the presence or absence of stable genetic structure and the maximum degree to which competing hypotheses were correlated. We also explored the effect of various transformations to linearize the relationship between genetic and landscape distances. In total, we evaluated model selection accuracy using 1,530 unique resistance surfaces. Our primary goal was to compare methods for landscape genetic model selection in terms of accuracy in identifying the correct variables and their parameters R_{max} and P, within the context of the major sources of model selection error noted above.

2 | METHODS

2.1 | Landscapes

We produced an array of continuous, categorical and linear feature landscapes that varied in terms of the degree to which landscape heterogeneity was aggregated or dispersed. All landscapes consisted of a square 1,024 × 1,024 cell raster grid. We produced continuous landscapes (see Figure 1 for an example) using the program QRULE (Gardner, 1999). We specified that 30% of the cells had a value of zero and the remaining cells were assigned values ranging from 1 to 128 in equal proportions. The aggregation of these grids was controlled using the cohesion parameter (*H*), which we specified to be 0.1, 0.5 or 0.9 (the larger the value the greater the aggregation). We produced 10 replicates for each level of *H*, for a total of 30 continuous landscapes.

We produced categorical landscapes using the randomClusterNN function of the NLMPY PYTHON package (Etherington, Holland, & O'Sullivan, 2015). This function produces discrete patches of grid cells with identical values, which we reclassified such that 30% of the landscape had a value of zero and the remainder of the landscape was equally apportioned into patches with values ranging from 1 to 8. Like to the QRULE landscapes, the function includes a cohesion parameter (*H*), which we specified to be 0.1, 0.5 or 0.9. We produced 10 replicates for each level of *H*, for a total of 30 categorical landscapes.

We produced linear feature landscapes by first generating continuous landscapes with QRULE as described above. We then randomly selected a y coordinate ranging from 1 to 1,024 and then connected the left edge grid cell at (0,y) to the right edge grid cell at (1024,1024-y) via the least-cost path given the QRULE landscape as a resistance surface. With the same approach, we created a second least-cost path from the top edge to the bottom edge. This produced two irregular linear features bisecting the landscape horizontally and vertically (see Figure 1 for an example). In general, high cohesion of the resistance surface produced linear features that curved broadly around the large patches of high resistance. Conversely, low cohesion produced linear features that were more direct, but locally circuitous as they weaved around smaller, more fragmented patches of high resistance. Both linear features were assigned a value of 1, and all other grid cells were set equal to zero. We produced a total of 10 replicates for each level of *H*, for a total of 30 linear feature landscapes.

2.2 | Resistance surfaces

We created two sets of parameters for converting the above landscapes into resistance surfaces (Appendix). Parameters included a vector (*V*) of the landscapes to be included (one, two or all three variables could be included), a power function (*P*) to be applied to each landscape relating the landscape values to resistance and a

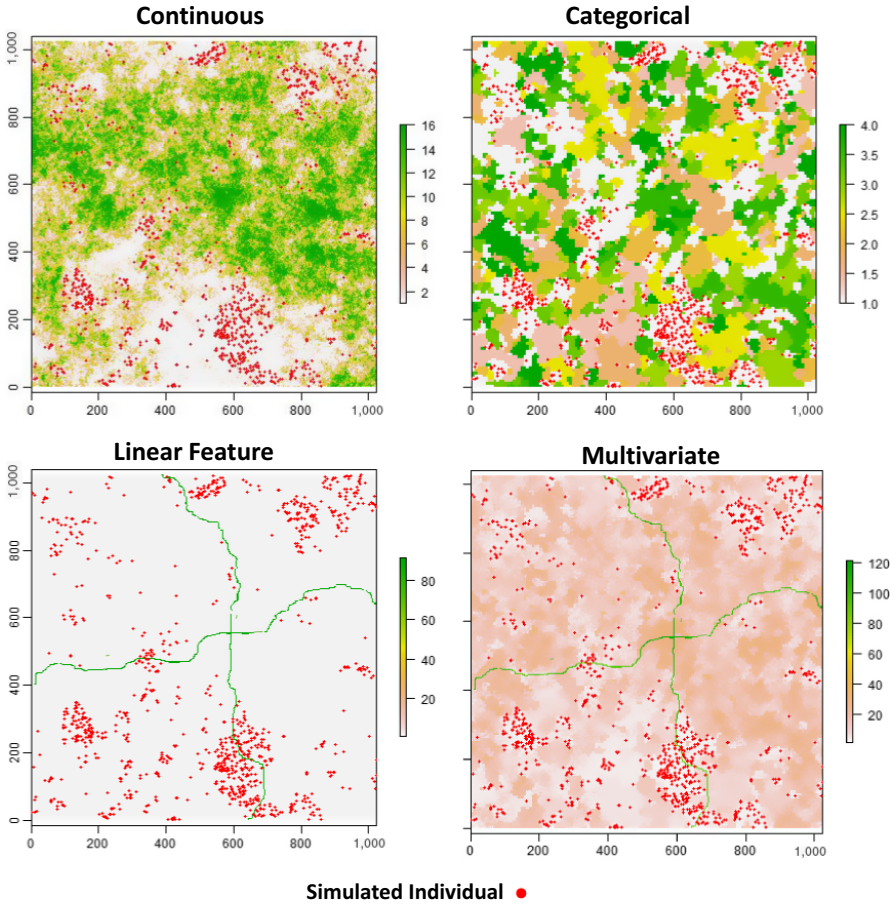

FIGURE 1 Simulated landscapes and populations. Examples of continuous, categorical and linear feature resistance surfaces are shown, as well as a combination of all three variables. Resistance surfaces varied by parameters controlling the number (from one to three) and types of variables contributing to resistance, landscape cohesion, maximum resistance, and the functional relationship between resistance and the landscape variable. In total, we evaluated the model selection methods using a total 1,530 unique resistance surfaces in a total of 60 sets of models. The spatial distribution of the 1,085 individuals in the population (red dots) was constant for each set and was a function of the inverse of resistance in the three-variable model in each set with the highest mean resistance [Colour figure can be viewed at wileyonlinelibrary.com]

maximum resistance (R_{max}) of the resistance surface, which was used to rescale the power function result to range from zero to R_{max}. All three variables could vary independently for each landscape type included in the resistance surface, although not all combinations of parameters were included, as this would have produced an intractable number of models to evaluate.

One of the parameter sets included 21 parameter combinations that varied the landscapes included in each model (V) as well as P (0.3, 1 or 3) while holding R_{max} constant at 16. The other set of parameters included 30 parameter combinations that varied the landscapes included in each model (V) as well as R_{max} (4, 16 or 64) while holding P constant at 1 (linear). We applied both sets of parameters to each of the 10 replicate sets of landscapes at each of three levels of H to produce a total of 60 sets of models containing a total of 1,530 resistance surfaces. The resistance surfaces in each of the 60 sets were all derived from the same three landscape models. Each model set also included an IBD model which was represented by a resistance surface with all grid cell values equal to 1.

To produce a resistance surface from a set of landscapes and parameters, we first raised the grid cell values of each of V landscapes to the power (P) specified in the parameters and then linearly rescaled the values of the exponentiated raster to range from 0 to R_{max}. If the parameters specified a univariate resistance surface, we added one to all grid cells such that the minimum value was one rather than zero, thus making it comparable to the IBD model. If the parameters specified a multiple-variable resistance surface, we first summed the surfaces before adding one such that the final resistance surface also had a minimum value of one. Also, the mean pairwise cost distance among all individuals in the continuous and categorical landscapes averaged 5.65 times greater than the linear feature landscapes, because only the linear feature had resistance >1. To make the linear feature landscapes have the same magnitude of effect on dispersal as the other landscape types, we multiplied the resistance of the linear feature by 5.65, resulting in R_{max} values of 23, 91 or 362.

2.3 | Population genetic simulations

We used CDPOP (Landguth & Cushman, 2010) to simulate 100 nonoverlapping generations of mating and dispersal on each model in each of the 60 sets of resistance surfaces described above. For each set of resistance surfaces, we created a unique population of 1,085 diploid individuals probabilistically distributed in grid cells as an inverse squared function of the three-variable resistance model with the highest mean resistance in the model set. Thus, for each of the 60 model sets, the spatial distribution of individuals was fixed and individuals were located in low resistance grid cells.

CDPOP is an individual-based simulator of population genetic processes. It simulates mating and dispersal in a finite population assigned to fixed locations, recording allele usage by all individuals per generation. In each generation, adult individuals mate according to a user-specified mating system and probability function based on proximity in Euclidean or effective distance. Once mated, females give birth to a number of offspring determined by a user-specified probability function which can also control the sex ratio at birth. After birth, adult mortality occurs probabilistically based on user-specified demographic parameters. Finally, vacant locations where adults died are filled by dispersing offspring. Dispersal probabilities follow a user-specified function based on Euclidean or effective distances to the vacant locations. If all locations are occupied, any remaining offspring not yet assigned to a location are eliminated.

We ran one CDPOP simulation for each resistance surface in each of the 60 model sets. Dispersal and mating probabilities were a function of the inverse square of the pairwise landscape distances, with a maximum distance set to the average maximum possible pairwise Euclidean distance between individuals in the landscape (1,309 units). We calculated cost distances (i.e., accumulated cost of the least-cost path between all pairs of individuals, given a symmetrical raster resistance surface) using the costDistance() function from the "GDISTANCE" package (van Etten, 2014) in the R statistical environment (R Core Team 2016).

The CDPOP parameters were the same in all simulations and designed to reflect an ideal population meeting Wright–Fisher assumptions (Wright, 1931). Generations were discrete and nonoverlapping (i.e., all adults died simultaneously at the end of each generation). There was no selection, mutation or immigration from outside the population. Individuals were diploid. Mating was sexual and with replacement for either sex. The number of offspring was based on a Poisson distribution with a mean of 4. This provided ample offspring to fill all vacant locations. The simulation tracked alleles at 30 codominant marker loci, with 30 alleles randomly assigned per locus to the first generation (i.e., the population was initiated in a state of panmixia, and then over time, genetic structure formed as a function of landscape distances). In each generation for 100 generations, CDPOP recorded the genotypes of all individuals in the population. Previous simulations using similar landscapes and populations have shown that landscape genetic patterns emerge and equilibrate within 100 simulated generations (e.g., Landguth et al., 2010). To track the formation of genetic structure over time within the simulations, we calculated the inbreeding coefficient (F_{IS}) from observed (H_o) and expected (H_e) heterozygosity recorded each generation in the CDPOP output file ($F_{IS} = 1 - H_o/H_e$).

2.4 | Landscape genetic analysis framework

For each of the 60 hypothesis sets, we assessed the ability of seven model selection methods to correctly identify the true model among the competing alternatives (22–31, depending on whether we varied R_{max} or P, and including IBD), with pairwise genetic distances as the response variable. Rather than base our analysis on the genotypes of the entire population, we used a stratified random sampling approach that is commonly used in field sampling for population genetic analyses. We divided the square landscape into a large 4×4 grid and randomly subsampled 16 individuals from each quadrant for a total of 256 samples. If there were fewer than 16 individuals in a quadrant, we increased the number of individuals sampled in other quadrants until the total of 256 was met.

To estimate genetic distances, we used the program SPAGeDi (Hardy & Vekemans, 2002) to calculate Rousset's *a* (an individual-based genetic distance metric designed to reflect the genetic structure of continuous populations; Rousset, 2000) from the multilocus genotypes of all 256 sampled individuals. Landscape distances (pairwise cost distances calculated between all sampled individuals given the resistance model) were either untransformed, log-transformed or Box–Cox (Box & Cox, 1964) transformed. We calculated genetic distances at generation 5 and 100, reflecting the population before and after population genetic structure stabilized, respectively. We also evaluated model selection accuracy across three levels of maximum correlation allowed, including 1.0, 0.95 and 0.90. In each model set, all models that had greater correlation with the true resistance surface than the maximum allowed were removed from the candidate model pool.

For each model set, at each level of maximum correlation (0.90, 0.95 and 1.00) and generation corresponding to the two levels of genetic structure stability (5 and 100), we iteratively specified that each of the competing models was the true driver of genetic isolation. Using the GD matrix from the simulation corresponding to the true model as the response variable, at the generation corresponding to stable or unstable genetic structure, we performed a model selection routine for all resistance surfaces in the set. Model selection was based on relating GD to the LD matrices corresponding to the hypothesis in the model set. To potentially increase the linearity of the relationship between GD and LD, we performed model selection three times using untransformed distances, log-transformed LD or Box–Cox transformed GD.

2.5 | Model selection methods

Three of the model selection methods we evaluated were based on the Mantel test (Mantel, 1967) for correlation between distance matrices. The first was based on identifying the candidate model with the maximum simple Mantel correlation between GD and LD. The second was based on a causal modelling framework (Cushman, McKelvey, Hayden, & Schwartz, 2006) where the initial goal was to determine whether the mode of genetic isolation was IBD or IBR. We calculated a partial Mantel correlation (Smouse, Long, & Sokal, 1986) relating GD to the IBD distance matrix in the resistance model set while partialling out the effect of each alternative candidate resistance model distance matrix in turn. We then calculated the partial Mantel correlation relating GD to each IBR hypotheses while partialling out the effect of the IBD distance matrix. If the partial Mantel correlation was higher for the IBD model than any of the IBR model, IBD was declared the most supported. If not, the IBR model with the largest partial Mantel correlation after controlling for the effect of the IBD distance matrix was declared the most supported model. The third Mantel-based method was reciprocal causal modelling with relative support as the model selection criterion (Cushman, Wasserman et al., 2013). This method involved creating an $N \times N$ matrix of partial Mantel correlations where N was the number of competing resistance models. Each value in the matrix reflected the partial Mantel correlation between GD and LD corresponding to the column hypothesis, after controlling for the effect of the row hypothesis. Relative support for each candidate was calculated as the mean value of each row. The candidate model with the highest row mean (i.e., the largest average relationship to GD after partialling out the effect of other candidate models) was declared the most supported. All Mantel-based methods were performed using the *mantel*() function in the R package "ECODIST" (Goslee & Urban, 2007).

In addition to the three Mantel-based methods, we also included two forms of regression on distance matrices (RDM; Legendre, Lapointe, & Casgrain, 1994) as model selection criteria. For each candidate resistance surface, we fit a linear regression model relating GD to LD after converting both matrices to vectors. We then performed model selection among the candidates based on either the highest R^2 or the lowest Akaiki information criterion (AIC; Akaike, 1973) score.

We also evaluated a form of linear mixed effects modelling as a model selection criterion. We used the MLPE.*lmm*() function of the R package "RESISTANCEGA" (Peterman, 2014) to fit maximum-likelihood population effects (MLPE; Clarke et al., 2002) models relating GD to LD for each candidate model in a set. The MLPE mixed effects model is used to account for the nonindependence (by specifying the covariance structure of the matrices) among the pairwise data (Clarke et al., 2002). We compared candidate models based on the lowest AIC score. AIC scores calculated from mixed models fit with restricted maximum likelihood have been shown to be unreliable (Clarke et al., 2002). However, we set REML=FALSE in the *MLPE.lmm*() function parameters, which results in a valid AIC score fit with maximum likelihood.

We also evaluated the Procrustes rotation test (Gower, 1975) as a model selection criterion using the *protest*() function in the R package "VEGAN" (Oksanen et al., 2013). This is a correlation test performed after rotating the dependent variable (the LD matrix) in Euclidean space to minimize the sum of squares difference with the response variable (the GD matrix). It has been explored as an alternative method to Mantel tests and as a means of model selection in landscape genetics (Peres-Neto & Jackson, 2001). We identified the most supported model in each hypothesis set based on the resistance model with the maximum Procrustes correlation between GD and LD.

2.6 | Model selection assessment

We assessed the accuracy of the above model selection methods in the context of several factors known to affect model selection accuracy. We calculated model selection accuracy as the proportion of the time the true model was correctly identified among all competing alternatives (including an IBD model) in the hypothesis set, for both stable (generation 100) and unstable (generation 5) genetic structure and at three levels of maximum correlation allowed among hypotheses (0.90, 0.95 and 1.0). The probability of identifying the correct hypothesis by chance was calculated as the reciprocal of the

number of hypotheses in the model set. We also assessed accuracy in identifying the correct R_{max} and P (only for the corresponding hypothesis sets where we varied R_{max} and P, respectively) for each variable in the true model. The probability of identifying the correct R_{max} or P (with three possible levels of each) was calculated as $1/3^N$, where N equalled the number of variables correctly identified in the hypothesis set. We assessed accuracy in identifying the correct variables as the proportion of the true variables identified in the most supported model minus the proportion of variables not in the true model that were part of the most supported model.

We also assessed the effect of the magnitude and aggregation of resistance in the landscape on model selection accuracy. We calculated the mean resistance for each resistance surface in all hypothesis sets. For each of the seven model selection metrics, we calculated mean accuracy in model selection (the proportion of time the most supported model was the true model) as a function of the mean resistance of the true model, binned into six classes (1–2, 2–4, 4–8, 8–16, 16–24 and 24–48). We also calculated the mean accuracy in model selection as a function of landscape cohesion (H). Furthermore, we assessed model selection accuracy for each of the seven methods as a function of the number of variables in the true resistance model, as well as the type of variable (continuous, categorical or linear feature; only assessed for the single-variable models).

3 | RESULTS

Population structure (measured by F_{IS} calculated over the entire simulated population) arose quickly within the first 25 generations of the simulations and then began to plateau after 100 generations at $F_{IS} \sim 0.10$ (Fig. S1). At generation 5 (the generation used to reflect unstable genetic structure), mean F_{IS} was approximately 0.05.

Linear mixed effect models was the best performing model selection method among those we evaluated in every way we evaluated accuracy, including overall (Figure 2), as well as identifying the correct variables (Fig. S2) and their parameters R_{max} (Fig. S3) and P (Fig. S4). Linear mixed effect models (LME) also exhibited higher accuracy compared to other methods as a function of the magnitude and cohesion of resistance in the landscape as well as the number and types of variables in the resistance model (Figure 3). Mantel-based methods and RDM using R^2 performed nearly as well in many cases. RDM using AIC and the Procrustes rotation performed poorly in most aspects of our assessment.

The biggest factor affecting model selection accuracy was the degree of correlation among competing hypotheses (Table 2). Across all methods, model selection accuracy was reduced by an average of about 45% when the maximum correlation among hypotheses was reduced from 1.0 to 0.90 (Figure 2). Accuracy in selecting the correct variables (Fig. S2), as well as the parameters R_{max} (Fig. S3) and P (Fig. S4), was similarly affected. The degree of correlation generally did not change the relative performance among the metrics.

The next most important determinant of model selection accuracy was the magnitude of landscape resistance (Table 2). Across all methods, when the mean resistance was <4, accuracy was 35% lower, on average, compared to when the mean resistance was >16 (Figure 3). The spatial pattern of resistance (i.e., the cohesion) in the landscape was far less influential than the magnitude of resistance (Figure 3), with <1% difference in accuracy between low (H = 0.1) and high (H = 0.9) cohesion landscapes (Table 2).

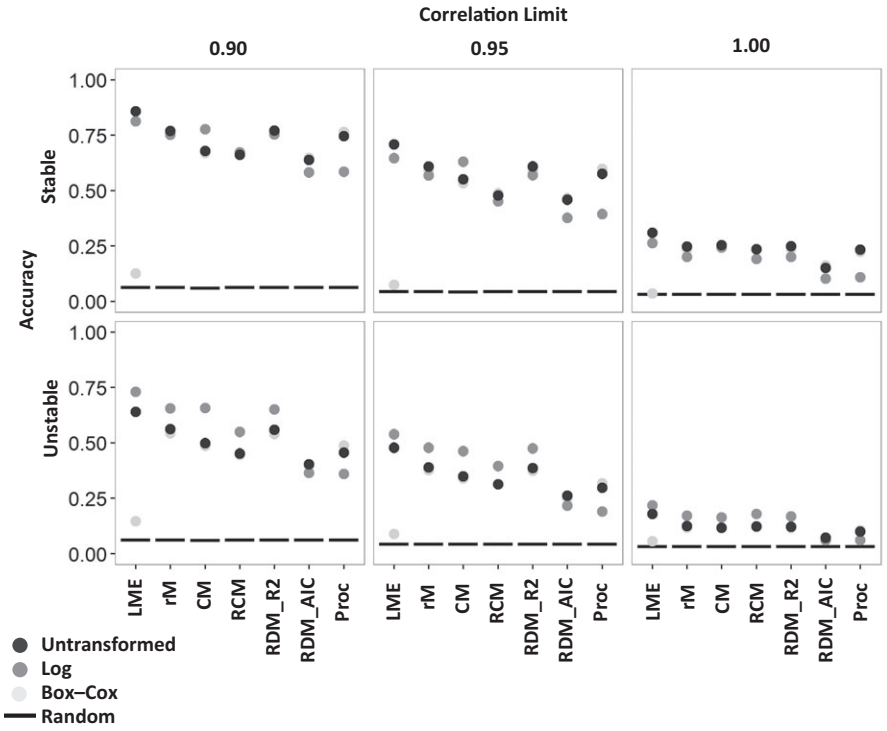

FIGURE 2 Overall model selection accuracy. The proportion of resistance models that were correctly identified as the true model among competing alternatives (varied from 22 to 31) are shown for each of the seven model selection methods. We assessed model selection accuracy when population genetic structure was stable (top row) and unstable (bottom row) across a range of maximum correlations allowed among competing alternative models (varied from 0.90 to 1.0 from left to right columns). We also assessed the accuracy of each method with distances that were either untransformed (black circles), log-transformed (medium grey circles) or Box–Cox transformed (light grey circles). In most cases, accuracy using the Box–Cox transformed distances was identical to untransformed distances. The horizontal black bars represent the proportion of correctly identified models expected by chance

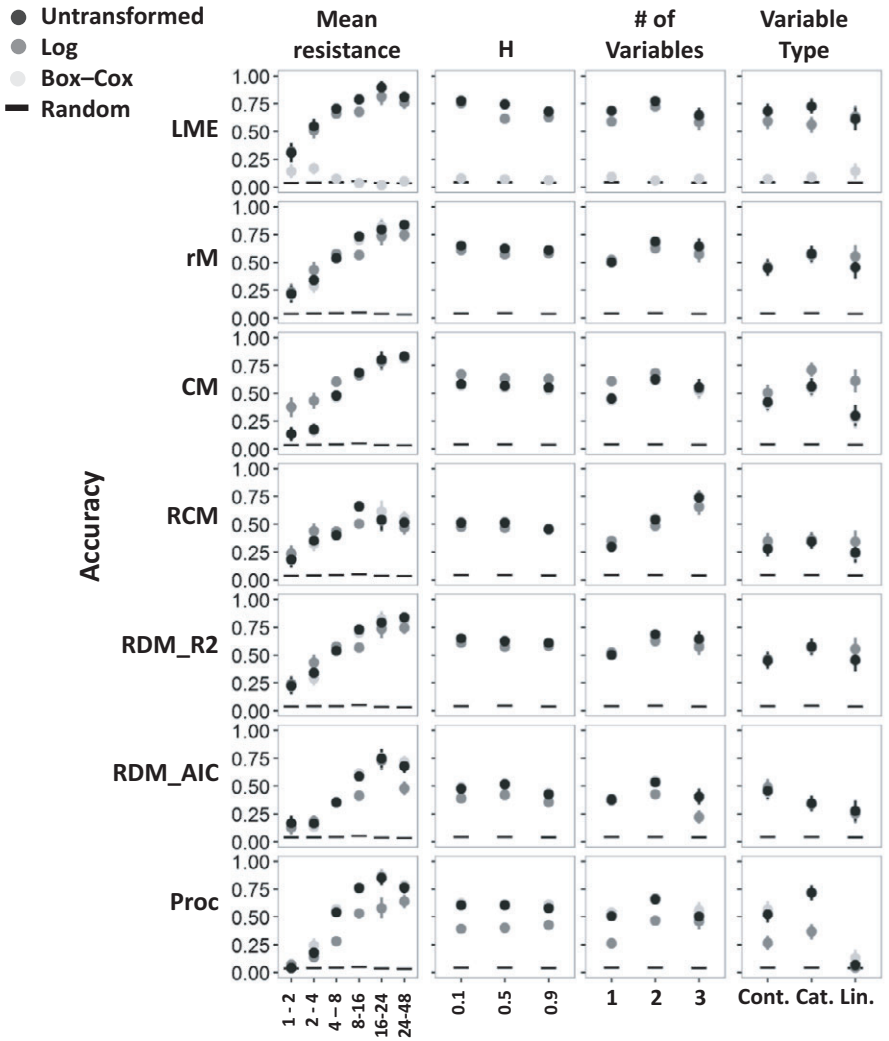

FIGURE 3 Model selection accuracy as a function of mean resistance, resistance cohesion, the number of variables contributing to resistance, and the type of variable. The proportion of resistance models that were correctly identified as the true model among competing alternatives (varied from 21 to 30) is shown for each of the seven model selection methods as a function of the mean resistance of the true landscape model (first column), the cohesion parameter (*H*) controlling the aggregation of resistance in the landscape (second column), the number of variables in the true resistance model (third column), and the type of variable (fourth column), including continuous (cont.) categorical (cat.) and linear feature (lin.). We assessed the accuracy of each method with distances that were either untransformed (black circles), log-transformed (medium grey circles), or Box-Cox transformed (light grey circles). In most cases, accuracy using the Box-Cox transformed distances was identical to untransformed distances. The horizontal black bars represent the proportion of correctly identified models expected by chance

TABLE 1 Model selection methods. For each model selection method we evaluated, the abbreviation used throughout the manuscript, the test statistic and the reference are provided

Method	Abbreviations	Statistic	References
Linear mixed effects model	LME	AIC	Clarke et al. (2002)
Mantel correlation	rM	Mantel *r*	Mantel (1967)
Causal modelling	CM	Partial Mantel *r*	Smouse et al. (1986)
Reciprocal causal modelling	RCM	Partial Mantel *r*	Cushman, Wasserman et al. (2013)
Regression on distance matrices	RDM_R^2	R^2	Legendre et al. (1994)
Regression on distance matrices	RDM_AIC	AIC	Legendre et al. (1994)
Procrustes	Proc	Procrustes correlation	Gower (1975)

The linearity assumption of regression-based methods also affected model selection accuracy, but to a lesser degree compared to the sources of error discussed above. The mean difference between the best and worst performing transformation was 25.8%, but this was heavily influenced by the high sensitivity of the LME method to Box–Cox transformations (Table 2). Log transformation of landscape distances yielded the greatest accuracy for most model selection criteria when the population genetic structure was unstable (Figure 2 and Figs S2–S4). However, after population genetic structure stabilized, untransformed distances performed nearly as well or in some cases better than log transformation. The Box–Cox function generally selected a power of 1, indicating that transformation with a power function did not often improve linearity between landscape and genetic distances. Thus, it had very little effect on model selection accuracy and was almost always very similar or identical to the performance of untransformed distances. A notable exception was

TABLE 2 Effect size of factors influencing model selection accuracy. For each of the seven model selection methods (LME, linear mixed effect models; rM, Mantel correlation; CM, causal modelling; RCM, reciprocal causal modelling; RDM_R2, regression on distance matrices using R2; RDM_AIC, regression on distance matrices with Akaike information criterion and Proc, Procrustes test), the effect size for the four major factors influencing model selection accuracy is shown. We further distinguish between two components of landscape structure, including the mean resistance and cohesion of the true landscape resistance model. The effect size of correlation among competing hypotheses, mean resistance and cohesion were calculated as the difference in model selection accuracy between the highest and lowest values of each factor. The effect size for linearity was calculated as the difference in model selection accuracy between the best performing and worst performing transformation. The effect size of genetic stability was calculated as the difference in model selection accuracy when population genetic structure was stable (generation 100) compared to when it was unstable (generation 5)

		Landscape structure			
Criterion	Correlation	Resistance	Cohesion	Linearity	Genetic stability
LME	0.464	0.266	0.050	0.621	0.101
rM	0.470	0.405	0.000	0.171	0.132
CM	0.458	0.330	0.002	0.215	0.146
RCM	0.382	0.286	0.001	0.186	0.137
RDM_R^2	0.470	0.410	0.003	0.171	0.136
RDM_AIC	0.421	0.326	−0.004	0.171	0.187
Proc	0.455	0.425	−0.003	0.273	0.211
Average	0.446	0.350	0.007	0.258	0.150

with LME as the model selection criterion. The combination of LME and Box–Cox transformation was little to no better than random in every way we evaluated model selection accuracy.

Of the four sources of model selection error we explored, the effect of instability in population genetic structure had the smallest effect on model selection accuracy (Figures 2 and 3 and Figs S2–S4). Unstable structure decreased accuracy by about 15% on average (Table 2). The relative differences in accuracy between model selection criteria were the same, regardless of genetic structure stability.

4 | DISCUSSION

Population genetic simulations are an ideal means to systematically compare model selection methods across a range of factors affecting landscape genetic inferences (Epperson et al., 2010). We simulated mating and dispersal on landscapes varying in the number and types of variables affecting gene flow, parameters affecting the magnitude (R_{max}) and functional form of resistance (P), as well as landscape fragmentation (controlled by the cohesion parameter H). The level of correlation among competing models, the magnitude and pattern of resistance in the landscape, violation of the regression assumptions of independence and linearity, and instability in population genetic structure all affected model selection accuracy to varying degrees. In nearly every way, we evaluated model performance, across the four major sources of model selection error noted in Zeller et al. (2016), linear mixed effects models fit with MPLE outperformed the other regression methods we evaluated. However, Mantel-based methods and RDM using R^2 performed nearly as well in many cases. RDM using AIC and the Procrustes rotation performed poorly in most aspects of our assessment.

Our analysis represents an extension of three previous studies that have used simulations to compare the performance of multiple landscape genetic model selection criteria in a consistent framework (Balkenhol et al., 2009; Kierepka & Latch, 2015; Zeller et al., 2016). We based our analysis in part on the framework of Zeller et al. (2016) which explored four primary sources of error affecting landscape genetic model selection, including the degree and stability of genetic structure in the population, assumptions of linearity and independence, and the degree of correlation among competing hypotheses. However, there are important differences between our study and the analysis of *Zeller* et al. (2016), as well as the other two studies. Unlike Balkenhol et al. (2009), our analysis was individual-based which is more appropriate than population-based analysis for most wild populations that are more continuously distributed (Landguth & Schwartz, 2014). None of the three studies evaluated model selection performance in the context of multiple landscape variables contributing to resistance. Our models were comprised of various combinations of continuous, categorical and linear feature variables that are more representative of landscapes modelled in empirical analyses (e.g., Shirk, Wallin, Cushman, Rice, & Warheit, 2010). Also, the degree of replication was low in these studies, which evaluated between five and 20 unique landscapes. In this analysis, we assessed model selection accuracy across 1531 unique landscapes that differed in terms of the parameters H, R_{max}, and P, as well as the number and types of variables included (continuous, categorical or linear feature). In addition, we assessed performance not only in terms of model selection accuracy, but also in terms of accuracy in identifying the correct parameters (R_{max} and P for each variable contributing to resistance), which are critical components in landscape genetics analyses. Among the three studies, only Zeller et al. (2016) evaluated alternative parameterizations of R_{max} and P, but only four unique parameter sets were assessed, compared to 51 in our analysis. Our study and Zeller et al. (2016) are the only studies to explore the effect of all four sources of error on model selection accuracy. Finally, in our study, we subsampled individuals (256 of 1,024 = 25%) using a stratified random sampling design as is commonly employed in field data collection. The other comparative studies were based on all simulated individuals, which may give an unrealistic expectation of model selection accuracy (though see Landguth et al., 2012).

Another unique aspect of this study was that our analysis was based on measures of model fit rather than significance testing. The above studies based their method comparisons, at least in part, on significance tests. Significance tests have been shown to be poor model selection criteria in individual-based landscape genetic

analyses (Cushman & Landguth, 2010). We contend that this arises due to the extraordinarily high power inherent in pairwise data. With typical sample sizes, the number of pairwise distances often numbers in the tens of thousands. Moreover, effective or Euclidean distances are likely to show at least a weak association with genetic distances (because all IBD or IBR models predict increased differentiation with increasing landscape distance). Often, even a weak model can be shown to be significant if there is sufficient power (Cushman & Landguth, 2010; Cushman, Wasserman et al., 2013). Indeed, in our experience, under typical sample sizes, most landscape resistance hypotheses being evaluated can be shown to be significantly related to genetic distances in populations exhibiting IBD or IBR. Thus, model selection based on significance testing is often equivocal. For this reason, we used metrics of model fit, rather than significance, for model selection in this individual-based analysis.

Mantel-based model selection criteria in landscape genetics applications have been particularly controversial, with several studies finding them to suffer from high type I error rates (Balkenhol et al., 2009; Guillot & Rousset, 2013; Legendre, Fortin, & Borcard, 2015; Meirmans, 2012), and others propose they have low power (Legendre & Fortin, 2010). However, these criticisms were of inferences based on significance tests. Because we used model fit (the Mantel and partial Mantel correlation) rather than significance tests, our evaluation of Mantel-based methods was not sensitive to these critiques. In this context, although the Mantel-based criteria did not perform as well as LME, they performed nearly as well in most cases. Thus, our results affirm recent studies (Cushman & Landguth, 2010; Cushman, Wasserman et al., 2013; Zeller et al., 2016) that validate the use of Mantel and partial Mantel methods as a criterion for model selection in landscape genetics, so long as they are not based on significance tests. More specifically, our results suggest simple Mantel correlations and causal modelling are more reliable than reciprocal causal modelling, with the exception that the latter performed better on the most complex models with multiple variables contributing to resistance.

Among the four sources of model selection error noted in Zeller et al. (2016), the degree of correlation among competing hypotheses was by far the most important influence on accuracy in our analysis. Strong correlations among competing hypotheses negatively affect all model selection approaches, including those used in landscape genetics. Our analysis and others (Cushman, Wasserman et al., 2013; Zeller et al., 2016) support the notion that correlations >0.90 (and particularly > 0.95) greatly increase the probability of spuriously identifying an alternative model as the true driver of spatial genetic patterns. This precludes fine-tuning of resistance parameters, which necessarily involves highly correlated models. As such, model selection with these methods should be focused on determining the main variables affecting model selection accuracy and a coarse examination of their parameters. Graves, Beier, and Royle (2013) and Zeller et al. (2016) reached similar conclusions about the difficulty of fine-tuning the optimal resistance parameters in landscape genetics.

The degree of structure in the landscape was the second most influential component of model selection error. The marked increase in model selection accuracy with increasing landscape resistance for all methods in our comparison has been a consistent observation in landscape genetic simulation studies (Cushman, Shirk, & Landguth, 2013; Kierepka & Latch, 2015; Zeller et al., 2016). Model selection based on RDM with AIC and Procrustes correlation was particularly inaccurate at mean resistance values <4 (Figure 3), indicating these methods have very low sensitivity. Ordination techniques similar to Procrustes as well as RDM with AIC have been shown to perform poorly in low resistance landscapes in other studies as well (Kierepka & Latch, 2015; Van Strien, Keller, & Holderegger, 2012). Indeed, Van Strien et al. (2012) concluded that AIC and similar model selection criteria should not be applied to RDM models. Consistent with the predictions of Cushman, Shirk, and Landguth (2012), no method performed well in landscapes with low resistance approaching IBD, suggesting that inferences from regression-based landscape genetic analyses in highly permeable landscapes are unreliable (though there is likely to be less need for landscape genetic analysis in such landscapes). Interestingly, the pattern of resistance (as measured by cohesion) was far less important compared to the magnitude of resistance. This has been observed in other recent landscape genetic simulation studies (Cushman et al., 2012; Kierepka & Latch, 2015). Kierepka and Latch (2015) also found that other landscape metrics, including correlation length and clumpiness, were more strongly associated with partial Mantel test correlation coefficients, suggesting these alternative metrics may be better predictors of model selection accuracy than cohesion.

Another aspect of landscape structure was the number and type of variables influencing gene flow. These resistance model attributes did not appear to strongly influence model selection accuracy for the methods we evaluated, with two exceptions. First, reciprocal causal modelling performed poorly compared to other methods in single-variable landscapes, but as the number of variables increased to 3, it became among the top performers. This suggests RCM is better suited than other Mantel-based methods when applied to complex landscapes with multiple variables contributing to resistance. The second exception was the effect of the type of variable on the performance of the Procrustes method. This method was no better than random in evaluating linear feature landscapes. This is a major weakness of the method, as linear features like roads and rivers are common sources of resistance for many species. The binary nature of resistance for linear landscape features appears ill suited for the Procrustes rotation, which was designed for continuous variables.

The third-most influential source of model selection error was the assumptions of independence and linearity. The assumption of independence is often violated because of the pairwise dependencies inherent in distance matrices used to quantify genetic and landscape distances. The LME method was the only one among those we evaluated that accounts for the dependencies inherent in genetic and landscape distance matrices (via use of MLPE to model the covariance structure), and likely for this reason, it was the top performing method among those we evaluated. On the other hand, the worst performing method, RDM with AIC, is known to be

particularly sensitive to violations of the independence assumption (Van Strien et al., 2012). Transformations to improve the linearity of landscape genetic relationship in general had a relatively small effect on model selection accuracy. The main exception was when Box–Cox transformation was used with LME, which resulted in model selection accuracy equivalent to random. We suspect that this had to do with the fact that the MLPE.lmm() function of the R package "ResistanceGA" (used to fit the LME model) scales and centres landscape distances, yet the Box–Cox transformation used was based on landscape distances that were not scaled or centred. That the best transformation varied by method, and the stability of population genetic structure underscores the need to carefully assess linearity in regression-based landscape genetic analyses, and not assume that the commonly used log transformation is always the best approach.

The source of model selection error with the least impact on accuracy was the stability of population genetic structure. Changes in the landscape that affect resistance take time to manifest in the population genetic structure. If genetic distances in a population do not fully reflect recent changes in effective distances, landscape genetic relationships may be obscured and difficult to detect. However, previous studies have shown that the time to detect barriers after a period of landscape change may be as little as 15 generations (Landguth et al., 2010). In our simulations, the population began in a state of panmixia, but rapidly became genetically structured according to the resistance model used. However, even after only five generations, the effect on model selection accuracy was relatively low (~15% decrease). All methods were similarly affected, suggesting that none are particularly robust to this effect. Zeller et al. (2016) observed an even smaller effect, although they measured accuracy after 25 generations, by which time more of the spatial genetic structure in the population may have been manifest.

Our results suggest several practices that would maximize model selection accuracy in landscape genetic analyses based on regression methods. Use of LME with MLPE as the model selection method provides the greatest probability of identifying the true model from competing alternatives. Use of the poorest performing metrics should be avoided, particularly RDM with AIC, and the Procrustes rotation test when applied to linear features. If population genetic structure is unlikely to be stable, our results indicate log-transformed distances generally provide a modest improvement in model selection accuracy. Otherwise, untransformed distances generally provide a slight increase in accuracy. The correlation among competing models should ideally be 0.90 or less to minimize the likelihood of spurious associations. Our results also suggest no regression-based method is likely to identify the correct model in landscapes with low resistance that approaches IBD. However, understanding the nature of subtle resistance patterns in highly permeable landscapes is not likely to be of high conservation concern. We note that the high accuracy of the best performing methods under ideal conditions to detect landscape genetic relationships (i.e., limited correlation among competing hypotheses, limited dispersal and high resistance) may not be achievable in empirical analyses. We also note that departures from the ideal population we simulated (e.g., nonoverlapping generations, unequal sex ratios, mutation, immigration and age structure) may also affect the accuracy of model selection.

This study provides a broad array of landscapes and resistance surfaces that could serve as a resource for evaluating additional model selection methods, or variations of the methods included in this study. For example, it would be valuable to compare methods not based on regression to our results. Spatial eigenvector mapping (Dray, 2011; Dray, Legendre, & Peres-Neto, 2006), Bayesian methods (Botta, Eriksen, Fontaine, & Guillot, 2015; Bradburd, Ralph, & Coop, 2013), Gaussian Markov random field models (Hanks & Hooten, 2013) and distance-based redundancy analysis (McArdle & Anderson, 2001) have shown promise for use in landscape genetic model selection, for example. In our experience, many of these methods are computationally intensive and were therefore impractical to include in this broad analysis across many landscapes.

To facilitate comparison across methods that differed in their ability to evaluate multiple variables, we calculated landscape distances based on a single raster that summed all variables contributing to resistance. However, some model selection methods can evaluate the contribution of multiple variables concurrently (e.g., RDM), or parse out the independent effects of distance alone relative to resistance (e.g., Bradburd et al., 2013). It would be valuable to compare the performance of such methods using the same framework and resistance models from this study.

The focus of this study was on comparing model selection methods. Therefore, all methods were evaluated against the same sets of models representing a consistent hypothesis space, so that the method criterion was the only influence on accuracy. However, the approach used to define and explore a multidimensional hypothesis space is also a critical aspect of model selection in landscape genetics. Some studies have explored a limited number of plausible models with an information theoretic approach (e.g., Goldberg & Waits, 2010). Others have attempted a limited optimization of resistance models in a constrained search of the hypothesis space (e.g., Graves et al., 2013; Shirk et al., 2010). More recently, genetic algorithms have been used to optimize resistance models (Peterman, 2014). A comparison of these and other approaches to defining and searching hypothesis space, in conjunction with comparisons of model selection metrics such as this study, will help to define the best practices for landscape genetic analysis.

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DATA ACCESSIBILITY

Simulated landscapes, distance matrices, R code and CDPOP simulation outputs are available on DRYAD (https://doi.org/10.5061/dryad.p7m1v). CDPOP software and user manual are available at http://cel.dbs.umt.edu/cms/CDPOP.

AUTHOR CONTRIBUTIONS

A.S. designed the study, produced the simulation inputs, performed the analyses, and wrote the paper. E.L. ran the simulations and provided guidance on the study design and analysis. S.C. provided guidance on the study design and analysis.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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APPENDIX

		R_{max}			P		
Set	Model no.	Continuous	Categorical	Linear	Continuous	Categorical	Linear
R_{max}	1	4			1		
R_{max}	2	16			1		
R_{max}	3	64			1		
R_{max}	4		4			1	
R_{max}	5		16			1	
R_{max}	6		64			1	
R_{max}	7			4			1
R_{max}	8			16			1
R_{max}	9			64			1
R_{max}	10	4	16		1	1	
R_{max}	11	16	4		1	1	
R_{max}	12	4	64		1	1	
R_{max}	13	64	4		1	1	
R_{max}	14	16	64		1	1	
R_{max}	15	64	16		1	1	
R_{max}	16		4	16		1	1
R_{max}	17		16	4		1	1
R_{max}	18		4	64		1	1
R_{max}	19		64	4		1	1

(Continues)

APPENDIX (Continued)

		R_{max}			P		
Set	**Model no.**	**Continuous**	**Categorical**	**Linear**	**Continuous**	**Categorical**	**Linear**
R_{max}	20		16	64		1	1
R_{max}	21		64	16		1	1
R_{max}	22	4		16	1		1
R_{max}	23	16		4	1		1
R_{max}	24	4		64	1		1
R_{max}	25	64		4	1		1
R_{max}	26	16		64	1		1
R_{max}	27	64		16	1		1
R_{max}	28	4	4	4	1	1	1
R_{max}	29	16	16	16	1	1	1
R_{max}	30	64	64	64	1	1	1
P	1	16			0.3		
P	2	16			1		
P	3	16			3		
P	4		16			0.3	
P	5		16			1	
P	6		16			3	
P	7	16	16		0.3	1	
P	8	16	16		1	0.3	
P	9	16	16		0.3	3	
P	10	16	16		3	0.3	
P	11	16	16		1	3	
P	12	16	16		3	1	
P	13	16		16	0.3		1
P	14	16		16	1		1
P	15	16		16	3		1
P	16		16	16		0.3	1
P	17		16	16		1	1
P	18		16	16		3	1
P	19	16	16	16	0.3	0.3	1
P	20	16	16	16	1	1	1
P	21	16	16	16	3	3	1