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DESERT TORTOISE CONNECTIVITY MODELING

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THE SHAPE OF THINGS TO COME: A WINDOW INTO DESERT TORTOISE CONNECTIVITY IN AN INCREASINGLY URBAN WORLD

Executive Summary

Fragmentation and habitat loss reduce population sizes, impede connectivity, and are primary threats to biodiversity. Urbanization and large-scale solar development in Southern Nevada mainly occur in Mojave desert tortoise (*Gopherus agassizii*) habitat, a species that has shown rapid population declines associated with habitat loss and degradation. Little work has been done to examine how habitat loss and linear barriers impede tortoise connectivity. This study used individually-based spatially explicit forward-in-time simulations to predict genetic connectivity in no disturbance and disturbance scenarios. We modeled 17 areas in Clark County that were 525 – 625 km^2 in area, at a 1 km^2 resolution. These models used resistance surfaces that represented potential barriers or factors that could impede the connectivity of desert tortoise populations. Simulations were run for 200 non-overlapping generations using 20 variable microsatellite loci. We examined population dynamics, genetic diversity (alleles/locus, heterozygosity), and genetic structure (F_{ST}, sPCA, STRUCTURE) through time in each landscape scenario. We used a corridor success index, based on genetic differentiation, to forecast the maintenance of gene flow over time, and translated this metric into structural landscape patterns. As anthropogenic disturbance increased, so did demographic and genetic effects. Habitat degradation resulted in predicted population declines, with the most pronounced losses predicted to be concomitant with increased disturbance. Genetic diversity was increasingly lost as disturbance intensified. Because corridor success was found to be landscape dependent, outcomes for maintaining genetic connectivity were variable, but predicted gene flow was always reduced with disturbance. Connectivity improved when corridors allowed for movement across linear barriers and with higher tortoise densities. Disturbance landscapes with high levels of genetic connectivity tended towards low levels of fragmentation and landscape complexity, while the amount and dominance (based on largest patch size) of suitable habitat remained high. Our results indicate that adequately protecting tortoise habitat and ensuring sufficient connectivity will benefit species recovery.

Introduction

The degree to which a landscape facilitates movement among species habitat areas is a key metric influencing biodiversity, viable population sizes, the potential for demographic rescue, movements in response to environmental change, gene flow, and genetic resilience across a broad range of taxa (Christie & Knowles 2015; Haddad et al. 2003; Henein & Merriam 1990; Taylor et al. 1993; Tewksbury et al. 2002). Fragmentation and habitat loss have been shown to reduce population sizes, and are primary threats to biodiversity (Fahrig 2003; Haddad et al. 2015). Both can impede connectivity, disrupting species interactions, altering landscape use, and reducing rescue effects (Ewers & Didham 2006; Haddad et al. 2017; Hansen et al. 2007; Hand et al. 2014). Careful consideration of maintaining connectivity is critical for effective conservation planning. Functional corridors allow species to move through habitat embedded in a dissimilar matrix and enhance population viability (Beier et al. 2008; Beier & Noss 1998). Corridors are often designated by land managers in potential connective areas as development reduces and fragments habitat, resulting in a loss of connectivity on the landscape. The evaluation of the effectiveness of these corridors is of critical importance (Gregory & Beier 2014).

Nevada ranks first in the United States in human population growth rate, with increases of 12.4% since 2010 (USCB 2018). The bulk of this growth is within Clark County, which has experienced increases of greater than 40% since 2000 (Pendleton et al. 2013), and Las Vegas and Henderson are among the top 15 fastest growing cities in the nation (USCB 2018). Using aerial imagery from 2017 to detect the total land amount with evidence of disturbance in Clark County, it was estimated that 1,100 km^2 within the county has been developed (Clark County 2017). Additionally, large-scale solar facilities have been developed, or approved for development, on 60 km^2 within the county, chiefly on federal lands (BLM 2018a; 2018b; 2018c). Urbanization does not occur without significant environmental impact, and in southern Nevada, land use related to human population growth, and energy development primarily occurs in lower elevation ecosystems like Mojave Desert scrub (Clark County 2017; Pendleton et al. 2013).

Disturbance poses risks to the long-term persistence of species like the Mojave desert tortoise (*Gopherus agassizii*) which has shown rapid population declines associated with habitat loss and degradation due to urbanization (Allison & McLuckie 2018; Doak et al. 1994, Corn 1994, Tracy et al. 2004, USFWS 2011), resulting in federal listing as a threatened species in 1990 (USFWS 1994). Threats to tortoise populations continue to intensify as land is converted for human uses, elevating the need to protect conservation areas and corridors between them that facilitate connectivity (Averill-Murray et al. 2012). Established tortoise conservation areas are limited by current land ownership and land use designations. Range-wide 16,282 km^2 of habitat lie outside conservation areas and are subject to growing development pressures (Carter et al. *in review*), making the need to maintain connective habitat for tortoise populations through the Mojave Desert critical (Averill-Murray et al. 2013).

The conservation value of a corridor lies in its ability to provide functional connectivity (Beier & Noss 1998). Appropriate corridors are determined by habitat selection and movement (Chetkiewicz et al. 2006), with features of primary importance determined by multiple factors (e.g. length, width, topography, vegetation, adjacency to human activities, and the habitat needs of the species of interest), and not necessarily based on a simple measurement of area (Beier & Loe 1992; Noss 1987). The Mojave desert tortoise is commonly associated with desert scrub, but is known to occupy and move through heterogeneous habitat (Morafka & Berry 2002), and has been recorded in rugged terrain (O'Connor et al. 1994, Dutcher et al. *in review*). The mean home-range for desert tortoises is highly variable (1.3-53 ha; Berish & Medica 2014). For taxa with limited dispersal, such as tortoises, corridors are likely not used for swift movement events or migrations; rather individuals may need days to generations to achieve connectivity (Beier & Loe 1992). Beier et al. (2008) suggest that corridor dwelling species may require corridor widths considerably larger than home-range width to provide most, if not all, ecological needs.

In species with limited dispersal genetic tools can provide a framework to examine hard to observe processes, such as dispersal (Brooks 2003; Cushman et al. 2013; Lowe & Allendorf 2010; Dileo & Wagner 2016; Slatkin 1985). Incorporating landscape structure into analyses of dispersal enhances our understanding of the role heterogeneous habitats play in shaping genetic diversity and population structure (Holderegger & Wagner 2008; Manel et al. 2003; Sork & Waits 2010; Storfer et al. 2007). For desert tortoises a historically well connected landscape with few barriers to movement has resulted in a range-wide pattern of isolation-by-distance (IBD) with gene flow and little genetic differentiation (Britten et al. 1997; Murphy et al. 2007; Hagerty & Tracy 2010; Hagerty et al. 2011; Sanchez-Ramirez et al. 2018; Shaffer et al. 2015).

Landscape genetics are sensitive to temporal scale, often revealing gene flow on a historic landscape even if it no longer occurs (Waples & Gaggiotti 2006). While the effects of fragmentation can be strong and persistent, their timescale is uncertain (Haddad et al. 2017). Landscape genetics studies find the timescale to detect the effects of habitat disturbance and the creation of barriers on the landscape can be decades to millennia (Gauffre et al. 2015; Gonzales et al. 2010; Leblois et al. 2004; McRae et al. 2005; Murphy et al. 2008; Row et al. 2011; Segelbacher et al. 2003). Time is best measured using the generation time for the species of interest and has been predicted to range from 1 – 200 generations (Landguth et al. 2010), often making real time evaluations of corridor effectiveness challenging (Gregory & Beier 2014). Because desert tortoises are estimated to reach reproductive age at 17 years, on average (USFWS 2011), directly evaluating the consequences of recent or planned habitat loss and fragmentation on genetic connectivity requires investigations of potential future patterns of population genetics.

Spatially explicit forward-in-time simulations can merge projections of changing conditions with landscape genetics to predict population persistence and functional connectivity in the future (Epperson et al. 2010; Creech et al. 2017; Rebaudo et al. 2014; Thatte et al. 2018). However, spatially correlated natural and anthropogenic features complicate inference, making interpretation difficult without comparative study design (Beier & Noss 1998). For example, anthropogenic barriers, like roads, can reduce gene flow, but the effects may be confounded by long-standing natural features (Dileo et al. 2013; Vandergast et al. 2007). Evaluation of connectivity with and without habitat disturbance can disentangle these effects (Beier & Noss 1998), and forward-in-time simulations can be used to model multiple landscape scenarios.

Understanding the relationship between gene flow, connectivity corridors, and physical barriers is important for desert tortoise recovery (USFWS 2011) and little work has been done to determine corridor suitability (i.e. size in the context of suitable habitat and disturbance levels) for tortoises, or to examine how habitat loss and linear barriers may impede connectivity in otherwise connected habitat. This study uses forward-in-time simulation modeling to predict tortoise genetic connectivity in Clark County, Nevada using three landscape scenarios: (1) no habitat disturbance, (2) current levels of habitat disturbance, and (3) future projections of habitat disturbance given by development scenarios currently under consideration. In quantifying the genetic effects of current and planned habitat disturbance on populations through time, we sought to uncover what constitutes corridor success by investigating the shared characteristics of corridors projected to maintain genetic connectivity for Mojave desert tortoises into the future.

Materials & Methods

Forward-in-time simulation model

We preformed individually-based spatially explicit genetic simulations of gene flow across 200 generations in our landscape scenarios using the program SIMADAPT v.1.8.0 (Rebaudo 2014). SIMADAPT uses the NETLOGO environment (Wilensky 1999) to model mating and dispersal in non-overlapping generations using a georeferenced area with closed boundaries and three landscape characterization files: habitat type (here used as a proxy for geographic populations), carrying capacity of each grid cell, and landscape resistance. The model simulates landscape genetic processes with user defined simulation parameters, including initial genetic structure, and records the alleles of all individuals from forward-in-time generations (Rebaudo et al. 2013).

Study landscape and digital representation

The cost of movement, reduction in survival, or willingness of an individual to move through its environment can be represented using a landscape resistance model (Zeller et al 2012), and movement depicted as a function of features on a map using resistance values (i.e. high resistance values may be assigned to urban areas or major roads) for each pixel cell in a gridded raster (Cushman et al. 2013). The sampling grain (size of the sampling unit; i.e. raster pixel size) should ideally be smaller than an average home-range size or dispersal distance (Anderson et al. 2010). Landscapes were constructed and mapped using the R packages *ggmap* v.3.0.0.901, *raster* v.2.9-5, and *rgeos* v.0.4-3 (Kahle & Wickman 2013; Hijmans 2019; Bivand & Rundel 2019).

We first created several proof of concept (POC) models to ensure that our initial parameter estimates were functioning as expected. Our POC landscapes were hypothetical areas ≥ 25 x 25 km of 1 km^2 grid cells, constructed as neutral landscapes (without barriers allowing for IBD), with a semi-permeable linear barrier, and an absolute barrier to dispersal, to evaluate differences in genetic diversity and structure in simplified landscape scenarios (see Appendix I for details). We used resistance values of 0 (no resistance), 0-0.6 (variable resistance), 1 (absolute barrier), and 0.7 (permeable areas embedded within an absolute barrier).

The study landscape focused on Clark County, Nevada using a neutral representation without anthropogenic disturbance, current levels of habitat disturbance, and future projections of disturbance based on a 50 year forecast (Fig. 1; forecast data provided by Clark County). Any location bisected by a political boundary was allowed to include areas outside the county. We modeled areas 525 – 625 km^2 with a 1 km^2 resolution at 17 locations within the study landscape, using the three habitat scenarios above, plus a hypothetical neutral landscape with an absolute barrier to dispersal based on existing landscape features/projected disturbance (see Results for Fig. 2 of each landscape). Within the study landscape the inverse of an existing desert tortoise habitat suitability model (illustrating range-wide habitat potential and key areas for connectivity in the absence of anthropogenic disturbance; Nussear et al. 2009) was used for resistance.

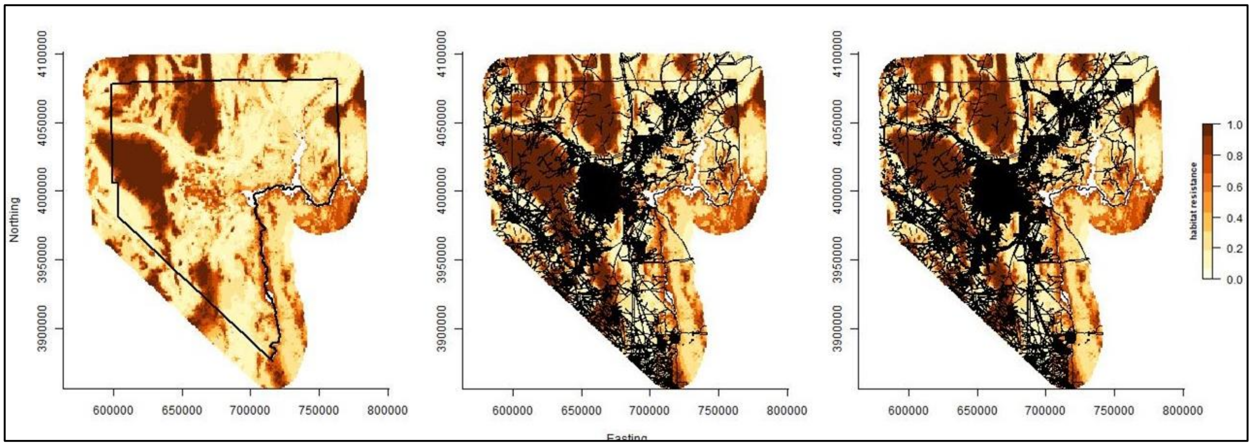


Fig. 1 Resistance surfaces of study landscape (Clark County, Nevada) with a 20 km buffer. Left to right: neutral landscape without disturbance; current disturbance; future projections of disturbance based on a 50 year forecast.

To account for habitat disturbance, we used conversion factors as values of possible degradation to adjust habitat suitability values prior to taking the inverse for resistance. Scale factors were adapted for desert tortoises based on those used by Inman et al. (2013) as:

$$habitat\ suitability - (habitat\ suitability * conversion\ factor)$$

Because habitat disturbance associated with urbanization, human access, and off highway vehicles are considered range-wide threats to desert tortoises (Darst et al. 2013) we categorized habitat disturbance as urban/cleared land, solar, railway, major roads, minor roads (e.g. unpaved), and utility corridor right-of ways (ROWs). Conversion factors were applied to each category to simulate reduced habitat suitability in disturbed areas (Table 1). We assumed that urban/cleared land and fenced solar facilities represent a complete loss of habitat, as tortoises have been extirpated from large areas of their range in and near cities and towns (USFWS 1994) and large-scale solar development typically includes complete removal of vegetation, grading, and fencing (Lovich & Ennen 2011). Formidable linear features (major roads and railways) fragment habitat and tortoise populations are depressed several hundreds of meters from roadways, likely due to extended periods of elevated mortality (Boarman & Sazaki 2006; vonSekendorff Hoff & Marlow 2002); therefore, we expected major roads and railroads to represent substantial, but not complete, loss of habitat (Rautsaw et al. 2018). We applied a relatively low maximum conversion factor to minor roads based on length, so cells with higher road density were associated with higher penalties. We assumed a fairly low conversion factor for ROWs. Both minor roads and ROWs are generally unfenced with greater abundance of tortoise sign than well-traveled paved roads, but still with detectable impacts (Nafus et al. 2013).

Table 1. Conversion factors (CV) used to adjust habitat suitability values (HSV) for models with anthropogenic disturbance. The inverse of habitat suitability was used to calculate landscape resistance.

Disturbance Type	**CV**	**Example HSV**	**HSV Scaled by CV**	**Resistance Value**
None	0	0.500	0.500	0.500
Urban/Cleared Land	1.00	0.500	0	1.000
Solar Energy Development	1.00	0.500	0	1.000
Railway	0.75	0.500	0.125	0.875
Major Roads	0.75	0.500	0.125	0.875
Minor Roads (max length)	0.25	0.500	0.375	0.625
Right-of-Ways	0.25	0.500	0.375	0.625

Simulation parameters

Simulations were initiated with Mojave desert tortoise genotypes at landscape carrying capacity (maximum density supported by the habitat) based on the relationship between habitat suitability and population density (Table 2; Nussear et al. in prep). Annual density estimates for desert tortoises are highly variable (0.2-28/km^2; Allison & McLuckie 2018). Based on tortoise densities in 1 km^2 plots in a current study in Ivanpah Valley, along the Nevada/California border, we calculated 24/km^2, and used this value for high density in our models. Medium and low densities were estimated at 14/km^2 and 3/km^2. To account for uncertainty in population growth rates we ran POC models using a low of 0.5% annual growth (Turner 1986) and moderate estimate of 1% (USFWS 1994). Both were multiplied by 48 breeding years, based on average lifespan (USFWS 1994; Medica et al. 2012) minus average age of reproductive maturity (17 years; McCoy et al. 2014; USFWS 2011). As there are no empirical data on an individual's dispersal likelihood, we used telemetry data from Ivanpah Valley to calculate the percentage of animals that left 1 km^2 study plots without returning to approximate probability of dispersal at 50% (Steve Hromada Pers Comm.). Individuals were allowed to move up to ten grid cells per generation (≤14 km).

Table 2. Carrying capacities determined by habitat suitability values (HSV) from a desert tortoise habitat suitability model (Nussear et al. 2009). Landscape resistance values calculated as inverse of the HSV by each grid cell.

HSV	**Resistance**	**Carrying Capacity**
0	1.00	1
0.01 – 0.10	0.90 – 0.99	1
0.11 – 0.20	0.80 – 0.89	1
0.21 – 0.30	0.70 – 0.79	3
0.31 – 0.40	0.60 – 0.69	6
0.41 – 0.50	0.50 – 0.59	9
0.51 – 0.60	0.40 – 0.49	12
0.61 – 0.70	0.30 – 0.39	15
0.71 – 0.80	0.20 – 0.29	18
0.81 – 0.90	0.10 – 0.19	21
0.91 – 1.00	0 – 0.09	24

We simulated gene flow for 200 non-overlapping generations, sampling individuals every five generations. We used neutral loci, not under selection, with a mutation rate of 0.0005 per locus per generation (Dileo et al. 2013; Estoup & Angers 1998; Landguth et al. 2010). This value falls within the range estimated by Edwards et al. (2015) for desert tortoises. Because there is concern in population genetic studies regarding attention to genotyping versus sampling (Meirmans 2015) we ran simulations with increased numbers of loci to determine if changes in genetic diversity or population genetic structure could be detected earlier in time or more clearly with more loci. Simulations were run to generate genotype files, investigate six POC scenarios (model behavior, computational limitations, population density, population growth, increased number of loci, and heterogeneous landscape), and model 17 Clark County, Nevada locations using four landscape scenarios, resulting in 91 simulation models (Table 3).

Table 3. Simulation parameters. Surface: (S) simple resistance surface with no resistance outside barriers; (H) heterogeneous resistance surface (0-0.6) outside barriers; (R) representative resistance surface of landscapes modeled without disturbance, with current disturbance, future projections of disturbance, and without disturbance but with a hypothetical absolute barrier. Cells: number of grid cells per simulation. Density: carrying capacity in each 1 km^2 grid cell; (Variable) varies with resistance surface (range 1 – 24). N: number of tortoises used to seed simulations; (Variable) varies with location modeled (range 11,880 – 7,063). *r*: population growth rate. Data: (IG) initial genotypes from a continuous population; (GP) genetic parameters from initial genotypes; (SG) simulated genotypes. Loci: number of loci. Reps: number of repetitions per simulation. No.: number of models run.

Simulation	**Surface**	**Cells**	**Density**	**N**	***r***	**Data**	**Loci**	**Reps**	**No.**
Genotypes	S	625	24	170	0.48	IG	20	1	1
Behavior	S	625	14	8750	0.48	GP	20	1	3
Limitations	S	1050	14	14700	0.48	GP	20	1	1
Density-low	S	625	3	1875	0.48	SG	20	30	3
Density-med	S	625	14	8750	0.48	SG	20	30	3
Density-high	S	625	24	15000	0.48	SG	20	30	3
Growth	S	625	14	8750	0.24	SG	20	30	3
Loci	S	625	14	8750	0.48	GP	80	30	3
Landscape	H	625	Variable	9366	0.48	SG	20	30	3
Clark County	R	525-625	Variable	Variable	0.48	SG	20	30	68

Genetic data

Neutral genetic markers are not influenced by selective forces, making them ideal for investigations of gene flow (Holderegger et al. 2006). We used a genetic dataset amplified at 20 variable microsatellite loci previously developed for tortoises (Edwards et al. 2003; Hagerty et al. 2008; Schwartz et al. 2003) sampled from a continuous population in the Ivanpah Valley, removing any individuals with missing alleles (Appendix II; Dutcher et al. *in review*). Statistics from these data were used to parameterize genotype simulations in POC models to evaluate model behavior, computational limitations, and increased number of loci.

We randomized the samples to remove any potential signal of IBD in order to create seed genotypes. These genotypes were simulated forward-in-time with no landscape resistance, using a burn-in of 100 generations to create a large genotype file from which we subsampled as input for the remaining POC models and modeled landscape simulations. We tested for departures in Hardy-Weinberg equilibrium, applying a Bonferroni correction, and examined genetic diversity and population genetic structure in the original data from Ivanpah Valley and the simulated data. Simulations evaluating parameters (population density, population growth, increased number of loci, and heterogeneous landscape) as well as modeled landscape locations were seeded with genotypes equal to the number of individuals at carrying capacity in neutral landscapes.

Population dynamics and genetic diversity

To account for stochasticity in simulations and ensure understanding of average outcomes we performed 30 repetitions for POC scenarios evaluating parameter values and all modeled landscapes, sampling genotypes every five generations. Geographic populations were assigned based on models with hypothetical absolute barriers to dispersal. We compared population dynamics in neutral landscape models with barrier and disturbance models, by evaluating the total number of individuals through time. In simulated datasets with > 750 individuals we randomly sampled without replacement to create subsamples for analyses. Evolutionary potential was calculated using genetic diversity statistics as the number of alleles/locus (A), and observed heterozygosity (H_o) using the R package *adegenet* v.2.1.1 (Jombart 2008). Simulated data were examined through time, using average outcomes.

Population genetic structure

We investigated population genetic structure in the original genotypes and simulation output using pairwise genetic differentiation (F_{ST}; Nei 1973) in the R package *hierfstat* v.0.04-22 (Goudet 2005), spatial principal components analysis (sPCA; Jombart et al. 2008), and a Bayesian clustering analysis (STRUCTURE v.2.3.4; Pritchard et al. 2000). In simulated data we evaluated F_{ST} in time-series, using average outcomes. We also examined population genetic structure with genotype files best representing the mean F_{ST} at generation 200 to ensure capture of the effects of landscape. STRUCTURE analyses were performed using the admixture model, with correlated allele frequencies, and location as a prior, which improves inference when genetic structure is weak. We estimated the probability of K population clusters = 1-10 using ten replicate runs of 1,000,000 Markov Chain Monte-Carlo iterations following a burn-in of 500,000. We calculated the mean log probability of the data ($Pr(X|K)$ in Pritchard et al. 2000). Because $Pr(X|K)$ may overestimate genetic clusters when there are patterns of IBD we also calculated the second order rate of change (ΔK in Evanno et al. 2005). Results were visualized using *PopHelper* in R (Francis 2017). Because STRUCTURE may misrepresent genetic clustering when spatial autocorrelation is present (Pritchard et al 2010, Schwartz & McKelvey 2008) we used sPCA to evaluate cryptic genetic patterns in the presence of IBD. This multivariate method differs from STRUCTURE by maximizing genetic diversity (variance) in individual allele frequencies while accounting for spatial structure (spatial autocorrelation measured by Moran's I). The genetic patterns were compared to 999 randomized Monte-Carlo permutations to test for differences between observed structure and the distribution of random expectations.

Quantifying corridor success

We used a corridor success index to forecast how well disturbed landscapes maintain gene flow over time. The corridor success index was based on average F_{ST} outcomes from forward-in-time simulations. Genetic differentiation at disturbed landscape locations was compared with differentiation in the neutral (connected) landscape and in the hypothetical absolute barrier (isolated) landscape. The corridor success index for current and disturbed landscapes was adapted from Gregory & Beier (2014) and calculated as:

$$(disturbance - isolated) \; / \; (connected - isolated)$$

Values near 1 indicate gene flow comparable to the neutral landscape, while values near or below 0 indicate failure to maintain genetic connectivity. Because of the lag time for genetic divergence, it is possible to falsely assume gene flow is retained if measured too soon. Therefore, we report values at generation 200 to ensure capture of possible genetic differentiation.

Disturbed landscapes were ranked by ability to maintain genetic connectivity from high to low based on their corridor success index value into one of three categories: high = 1-0.70, intermediate = 0.69-0.35, low/no genetic connectivity = 0.34-negative index values. To assess the influence of landscape spatial patterns on genetic connectivity we quantified landscape metrics in neutral landscapes, with current disturbance, and projections of future disturbance. Habitat suitability values (Nussear et al. 2009) were used to designate binary landscape classes: suitable habitat = 1-0.3; unsuitable habitat = 0.2-0. All metrics assumed queens case for cell connectivity (8 directions) and landscape boundaries were not included in edge counts. We characterized categorical landscape patterns using *landscapemetrics* v.1.2.1 in R (Hesselbarth et al. 2019). Translation of functional connectivity to structural metrics often misses crucial aspects of landscape pattern (Kupfer 2012). To increase ecological relevance, we used a combination of metrics that are considered strong descriptors of landscape pattern and consistent in interpretation (Cushman et al. 2008). We evaluated if/how landscape fragmentation (number of patches by class), configuration (edge density), composition (percent land area and percent core area by class), and dominance (largest patch index) differed by corridor success index rank.

We compared metrics of landscape disturbance (number of suitable habitat patches, largest suitable habitat patch, percent suitable habitat area) with population dynamics and genetic statistics. We used Akaike's information criterion (AIC) to rank the strength of relationships. Differences between disturbance and neutral landscape values were used to determine losses in individuals, alleles/locus, and heterozygosity, and increases in genetic differentiation.

Results

Proof of concept models – dynamics, genetic diversity, and structure

We examined the total number of individuals, genetic diversity (A, H_o), and genetic differentiation for six proof of concept models: behavior, computational limitations, population density (low, moderate, high), population growth rate (low), increased number of loci (80), and heterogeneous landscape. We compared neutral landscapes with barrier models for each of the six categories. We found that the number of individuals was highest in neutral landscapes and lowest with an absolute barrier in all models. Genetic diversity followed the same pattern. Genetic differentiation was always lowest in neutral landscapes. Semi-permeable barriers allowed for low levels of admixture. Absolute barriers created isolated populations. Of the modeled categories, two proof of concept models we were able to detect population genetic structure earlier in time: low population density and increased number of loci. Detailed discussion of results can be found in Appendix I.

Modeled habitat – dynamics, diversity, and structure

We modeled 17 landscape locations in Clark County, Nevada using a neutral landscape scenario, current disturbance levels, and future projections of disturbance (see specific sections below for Figs. 2.1 – 2.17 of all landscapes). We examined each landscape scenario for total number of individuals, genetic diversity, and genetic differentiation in time-series. The number of individuals was highest in neutral landscapes, and decreased as habitat was lost to disturbance. Genetic diversity statistics (A, H_o) exhibited a similar pattern. Genetic differentiation and population genetic structure was lowest in neutral landscapes, with a tendency to increase with disturbance. Significant differences (p-values) are based on two-sided t-tests between disturbance scenarios and the neutral landscape, and reported with 19 degrees of freedom. We also examined population genetic structure with genotype files best representing the mean F_{ST} value at generation 200 for STRUCTURE and sPCA (Table 4; see specific sections below for Figs. 3.1 – 3.17 of each landscape result).

Table 4. Results for each landscape scenario: neutral; current disturbance; future disturbance based on a 50 year forecast. Reported values use average outcomes ± standard deviation. Results for: (*N*) number of individuals; (*A*) mean number of alleles/locus; (H_o) observed heterozygosity; (F_{ST}) genetic differentiation; (*K*) number of genetic clusters. Because *Pr(X|K)* may overestimate clusters with IBD we report *ΔK*, except where *Pr(X|K)* = 1.

		N	***A***	H_o	F_{ST}	***K***
Boulder City	Neutral	9889.8 ± 34.7	23.7 ± 0.5	0.797 ± 0.007	0.001 ± < 0.001	1
	Current	7644.6 ± 26.5	22.5 ± 0.5	0.774 ± 0.008	0.004 ± < 0.001	2
	Future	5847.0 ± 16.2	21.5 ± 0.5	0.734 ± 0.009	0.008 ± 0.001	2
Coyote Springs	Neutral	7973.8 ± 23.7	22.8 ± 0.4	0.781 ± 0.006	0.003 ± <0.001	2
	Current	6892.6 ± 29.9	22.2 ± 0.4	0.765 ± 0.010	0.006 ± 0.001	2
	Future	6612.1 ± 20.3	22.1 ± 0.4	0.761 ± 0.009	0.008 ± 0.001	2
Dry Lake	Neutral	11348.1 ± 20.5	24.3 ± 0.4	0.804 ± 0.006	0.001 ± < 0.001	1
	Current	8604.9 ± 19.6	23.1 ± 0.4	0.778 ± 0.009	0.005 ± 0.001	2
	Future	7923.7 ± 27.8	22.8 ± 0.5	0.771 ± 0.006	0.006 ± 0.001	3
Eldorado Valley	Neutral	7919.5 ± 23.3	22.7 ± 0.5	0.788 ± 0.006	0.002 ± < 0.001	2
	Current	7298.1 ± 25.7	22.3 ± 0.4	0.782 ± 0.007	0.003 ± < 0.001	2
	Future	6992.5 ± 26.4	21.9 ± 0.5	0.771 ± 0.010	0.004 ± < 0.001	2
Indian Springs	Neutral	6370.7 ± 18.7	21.9 ± 0.4	0.774 ± 0.007	0.002 ± < 0.001	2
	Current	4955.9 ± 25.3	21.0 ± 0.4	0.743 ± 0.010	0.005 ± 0.001	2
	Future	4860.5 ± 29.7	20.7 ± 0.5	0.740 ± 0.009	0.005 ± 0.001	2
Ivanpah Valley	Neutral	7847.4 ± 25.5	22.8 ± 0.5	0.778 ± 0.007	0.003 ± < 0.001	2
	Current	5984.4 ± 22.2	21.4 ± 0.5	0.746 ± 0.010	0.010 ± 0.001	5
	Future	5523.5 ± 20.9	21.3 ± 0.5	0.741 ± 0.008	0.016 ± 0.002	2
Jean/Roach	Neutral	8723.0 ± 25.4	23.2 ± 0.5	0.791 ± 0.006	0.002 ± < 0.001	2
	Current	6869.8 ± 24.8	22.2 ± 0.5	0.764 ± 0.007	0.010 ± 0.001	2
	Future	5320.7 ± 19.4	21.2 ± 0.6	0.710 ± 0.011	0.023 ± 0.003	3
Las Vegas East	Neutral	6924.5 ± 29.5	22.1 ± 0.5	0.759 ± 0.010	0.010 ± 0.001	2
	Current	4924.0 ± 25.0	20.3 ± 0.5	0.717 ± 0.010	0.024 ± 0.003	2
	Future	4338.3 ± 26.7	20.2 ± 0.4	0.704 ± 0.008	0.027 ± 0.003	2

Las Vegas North	Neutral	7029.6 ± 20.2	22.3 ± 0.4	0.783 ± 0.006	0.006 ± 0.001	2
	Current	5390.3 ± 25.7	21.0 ± 0.4	0.762 ± 0.008	0.007 ± 0.001	2
	Future	3987.8 ± 16.5	19.9 ± 0.5	0.718 ± 0.010	0.012 ± 0.001	8
Las Vegas West	Neutral	6653.6 ± 22.2	22.1 ± 0.5	0.759 ± 0.009	0.009 ± 0.001	2
	Current	3929.4 ± 18.9	21.3 ± 0.5	0.677 ± 0.008	0.020 ± 0.002	2
	Future	2951.7 ± 14.3	21.9 ± 0.4	0.531 ± 0.012	0.037 ± 0.006	2
Laughlin	Neutral	8992.1 ± 30.0	23.2 ± 0.2	0.788 ± 0.006	0.002 ± < 0.001	2
	Current	8603.4 ± 25.6	22.9 ± 0.4	0.785 ± 0.006	0.003 ± < 0.001	3
	Future	8180.8 ± 20.5	22.9 ± 0.5	0.781 ± 0.007	0.003 ± < 0.001	3
Mesquite	Neutral	9928.4 ± 20.8	23.6 ± 0.6	0.790 ± 0.007	0.005 ± 0.001	2
	Current	8746.8 ± 22.5	23.1 ± 0.5	0.782 ± 0.007	0.008 ± 0.001	2
	Future	8365.3 ± 22.6	23.0 ± 0.5	0.782 ± 0.005	0.008 ± 0.001	2
Moapa Valley	Neutral	10951.7 ± 20.8	24.1 ± 0.4	0.801 ± 0.005	0.002 ± < 0.001	1
	Current	7959.9 ± 23.5	22.8 ± 0.5	0.777 ± 0.008	0.004 ± 0.001	2
	Future	6139.5 ± 23.9	21.8 ± 0.5	0.746 ± 0.008	0.009 ± 0.001	2
Red Rock	Neutral	7295.1 ± 23.2	22.4 ± 0.3	0.777 ± 0.008	0.002 ± < 0.001	2
	Current	2653.0 ± 15.1	19.3 ± 0.5	0.648 ± 0.014	0.026 ± 0.004	2
	Future	2468.0 ± 17.4	21.2 ± 0.4	0.594 ± 0.011	0.028 ± 0.003	2
Sandy Valley	Neutral	6574.8 ± 26.8	21.9 ± 0.6	0.771 ± 0.010	0.004 ± < 0.001	2
	Current	6298.1 ± 29.4	21.7 ± 0.4	0.766 ± 0.008	0.006 ± 0.001	2
	Future	5703.0 ± 21.8	21.2 ± 0.5	0.746 ± 0.010	0.011 ± 0.002	2
Searchlight	Neutral	10144.9 ± 17.2	23.8 ± 0.4	0.797 ± 0.008	0.002 ± < 0.001	1
	Current	9137.6 ± 22.3	23.1 ± 0.5	0.783 ± 0.008	0.004 ± 0.001	3
	Future	8775.4 ± 23.0	23.0 ± 0.5	0.779 ± 0.007	0.004 ± 0.001	3
Trout Canyon	Neutral	10158.2 ± 20.3	23.7 ± 0.6	0.795 ± 0.006	0.001 ± < 0.001	1
	Current	8516.9 ± 23.4	22.8 ± 0.5	0.781 ± 0.007	0.003 ± < 0.001	3
	Future	8314.7 ± 20.7	22.6 ± 0.5	0.777 ± 0.007	0.004 ± 0.001	3

BOULDER CITY CONSERVATION EASEMENT NORTH (Fig. 2.1): Current disturbance simulations predicted a 22.7% loss in individuals, decreasing by 40.9% with future disturbance. Based on the 17 locations modeled. this location ranked 8^{TH} (current disturbance) and 5^{TH} (future disturbance) in loss of population. Compared with the neutral landscape this location lost an average of 4.9% ($p = 0.002$) and 9.0% ($p = 1*10^{-12}$) alleles/locus in current and future disturbance scenarios. This location was predicted to lose 2.8% ($p = 0.023$) and 7.8% ($p = 6*10^{-7}$) H_o in current and future disturbance scenarios. Genetic differentiation in the neutral landscape was stable, and the current disturbance scenario showed indications of reaching stability. Genetic structure analyses supported one cluster in the neutral landscape with evidence of a cline. Spatial autocorrelation was predicted to increase with disturbance, with gene flow largely absent in future projections (Fig. 3.1).

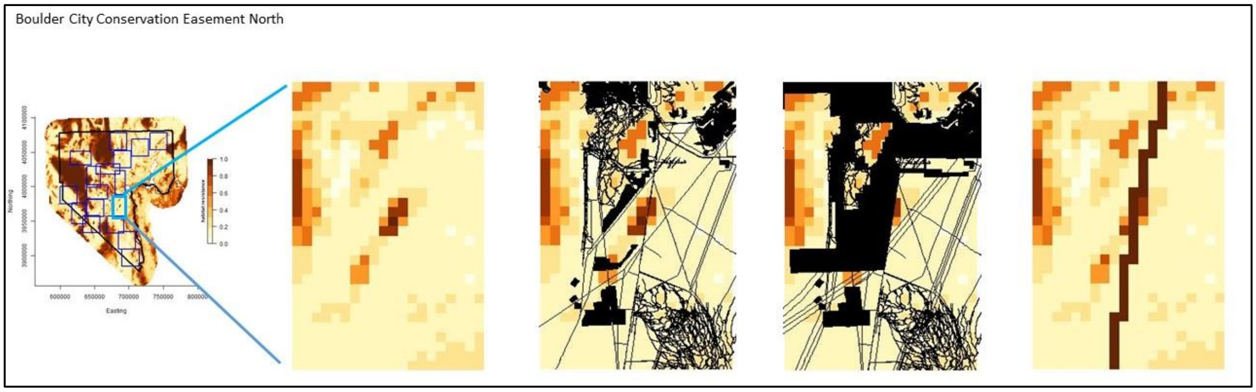


Fig. 2.1 Boulder City Conservation Easement North depicted as a resistance surface (600 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

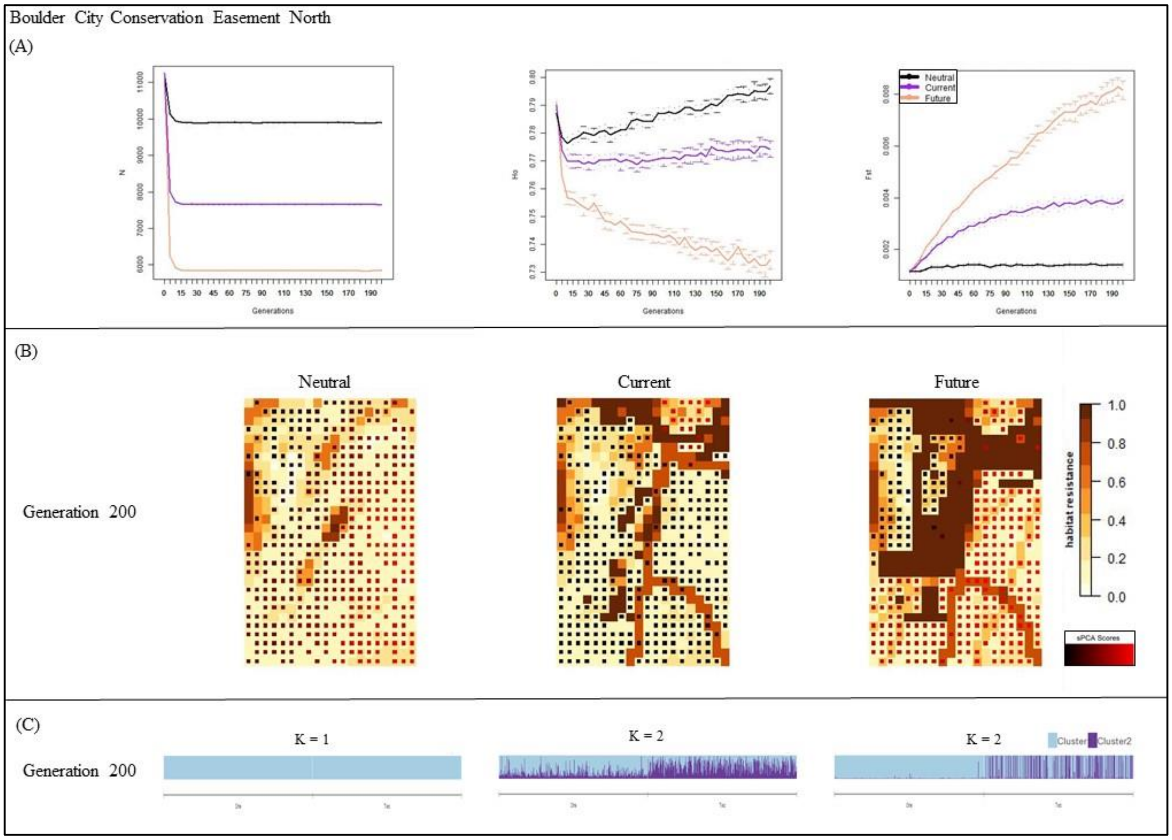


Fig. 3.1 Boulder City Conservation Easement North simulation results. Number of individuals (N) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) N, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because $Pr(X|K)$ may overestimate clusters with IBD we report ΔK, except where $Pr(X|K) = 1$.

COYOTE SPRINGS (Fig. 2.2): Current disturbance simulations predicted a 13.6% loss in population at Coyote Springs, decreasing 17.1% with future disturbance. Based on the 17 locations modeled, this location ranked 12TH in loss of population in both current and future disturbance scenarios. Compared with the neutral landscape this location lost 2.8% (p >0.05) and 3.5% (p >0.05) alleles/locus in current and future disturbance scenarios. This location lost 2.0% (p = 0.025) and 2.5% (p = 0.025) H_o in current and future disturbance scenarios, relative to the neutral landscape. Spatial autocorrelation was present in the neutral landscape, with evidence for two clusters with admixture. Spatial autocorrelation increased in the current disturbance scenario and was further amplified with future projections. In both disturbance scenarios there was a reduction in gene flow compared with the neutral landscape (Fig. 3.2).

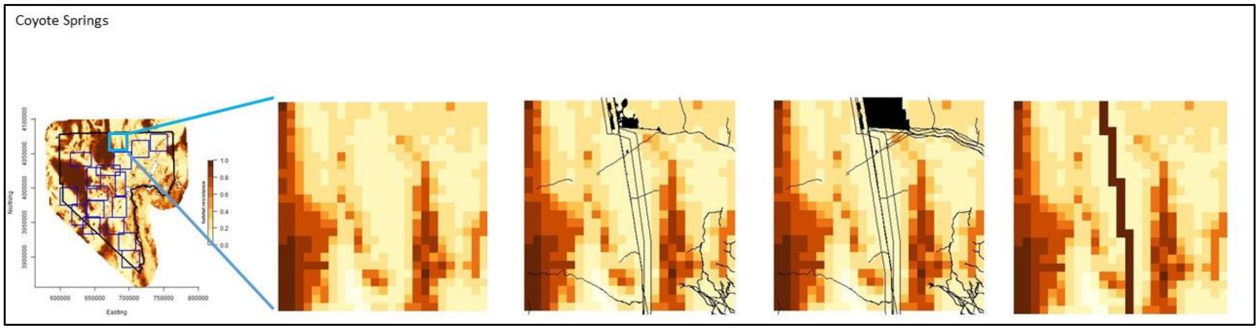


Fig. 2.2 Coyote Springs depicted as a resistance surface (625 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

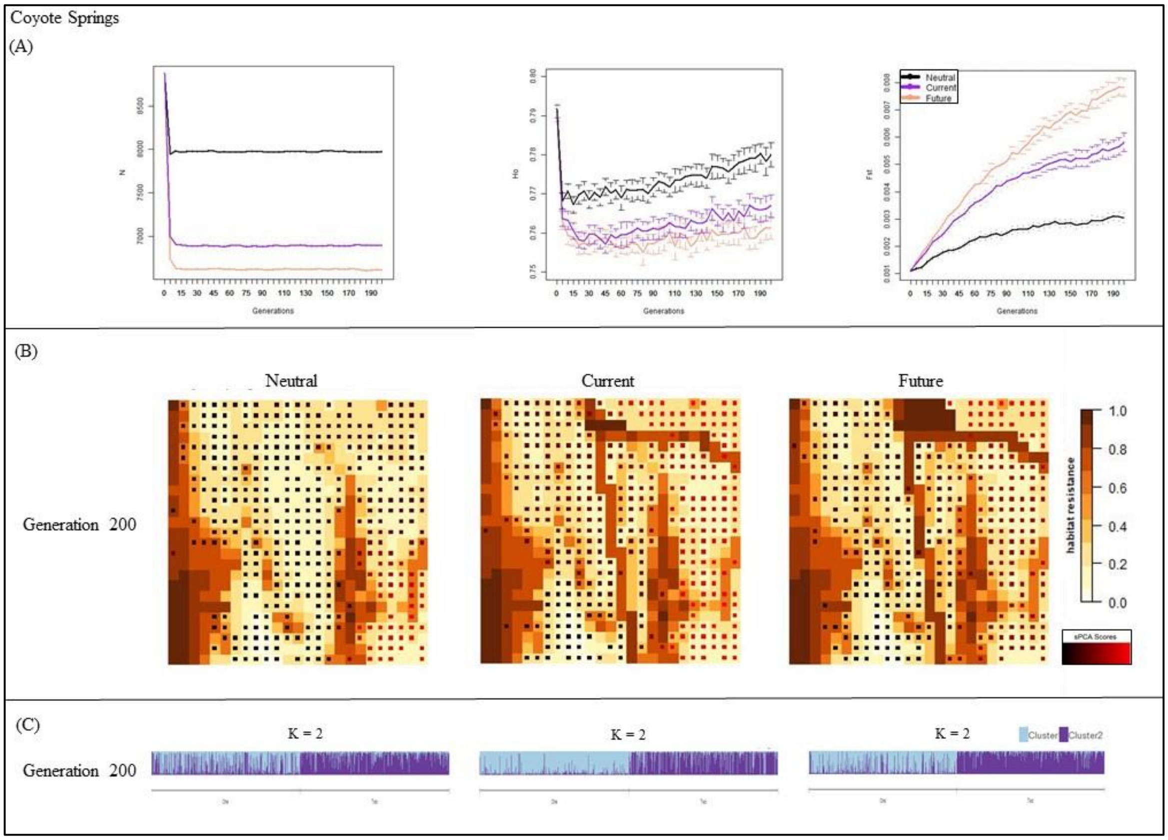


Fig. 3.2 Coyote Springs simulation results. Number of individuals (*N*) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) *N*, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because *Pr(X|K)* may overestimate clusters with IBD we report *ΔK*, except where *Pr(X|K)* = 1.

DRY LAKE (Fig 2.3): A loss of 24.2% in population was predicted in the current disturbance simulation, and 30.2% with future disturbance. Dry Lake ranked 5TH (current disturbance) and 8TH (future disturbance) in terms of loss in population, relative to the 17 locations modeled. The mean number of alleles/locus decreased 4.8% (current disturbance; p >0.05) and 6.0% (future disturbance; p = 0.008) compared with the neutral landscape. Dry Lake lost 3.1% (p = 0.002) and 4.1% ($p = 1*10^{-4}$) H_o in current and future disturbance scenarios, relative to the neutral landscape. Only the neutral landscape showed relatively stable values for genetic differentiation. STRUCTURE and sPCA analyses supported a single cluster with IBD. Strong spatial autocorrelation was apparent in current and future disturbance scenarios with support for population genetic structure related to landscape barriers. Current disturbance is predicted to result in two clusters with admixture. The future disturbance scenario lost connectivity (Fig. 3.3).

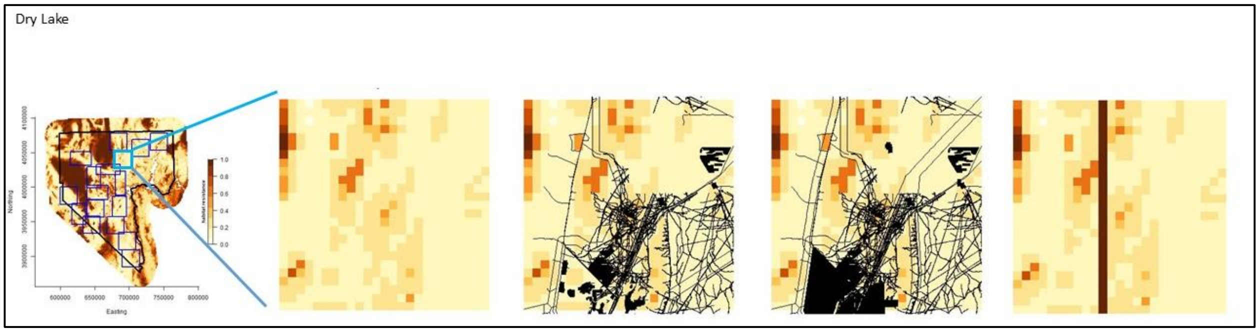


Fig. 2.3 Dry Lake depicted as a resistance surface (625 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

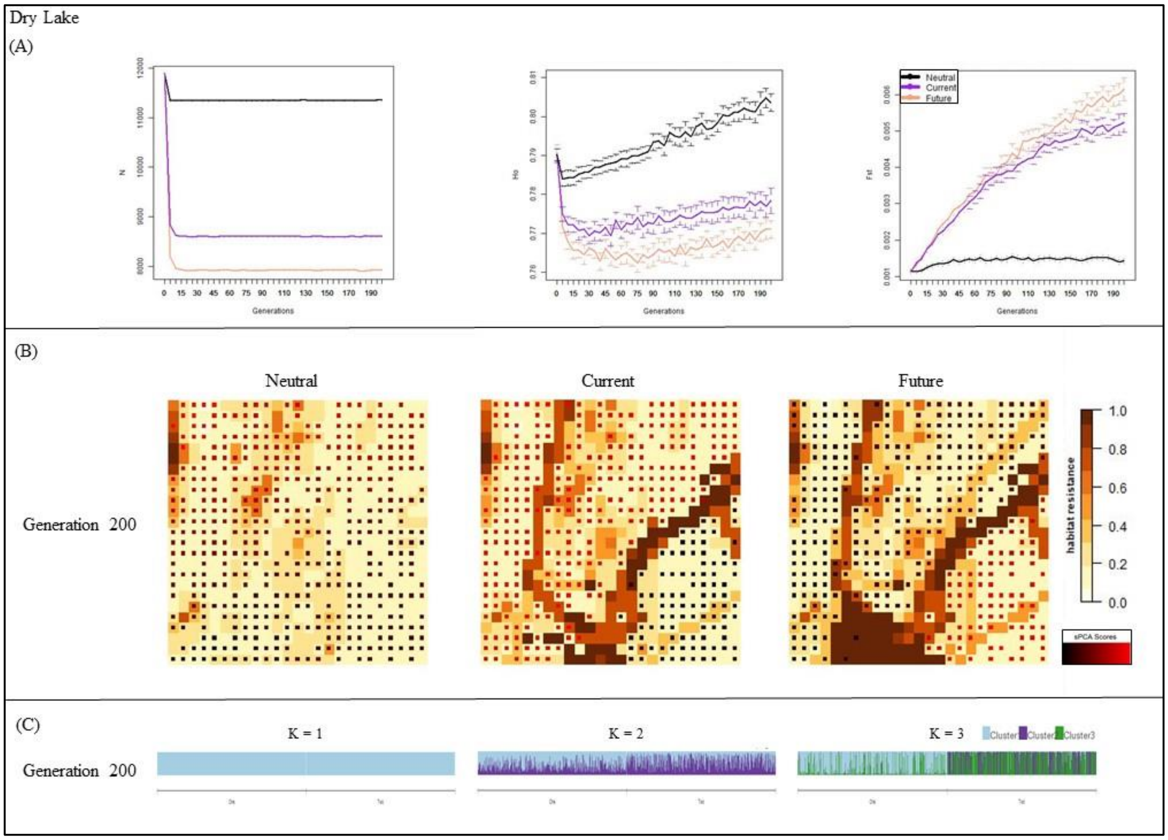


Fig. 3.3 Dry Lake simulation results. Number of individuals (N) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) N, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because $Pr(X|K)$ may overestimate clusters with IBD we report ΔK, except where $Pr(X|K) = 1$.

ELDORADO VALLEY (Fig. 2.4): Population losses of 7.8% were predicted with current disturbance, and 11.7% with future disturbance simulations. This location ranked 15TH (current disturbance) and 16TH (future disturbance) in terms of loss of individuals, relative to the 17 locations modeled. Alleles/locus were predicted to be lost by 1.4% (current disturbance; p >0.05) and 3.4% (future disturbance; p >0.05) compared with the neutral landscape. In current and future disturbance scenarios this location lost 0.7% (p >0.05) and 2.2% ($p = 8*10^{-6}$) H_o through time, relative to the neutral landscape. Genetic differentiation in the neutral landscape was stable through time, and the current and future disturbance scenarios reached relatively steady levels. Spatial autocorrelation was present in the neutral landscape, which displayed weak population genetic structure with admixture as the result of landscape features. Spatial autocorrelation remained in current and future disturbance scenarios, with increased population genetic structure and reduced admixture (Fig. 3.4).

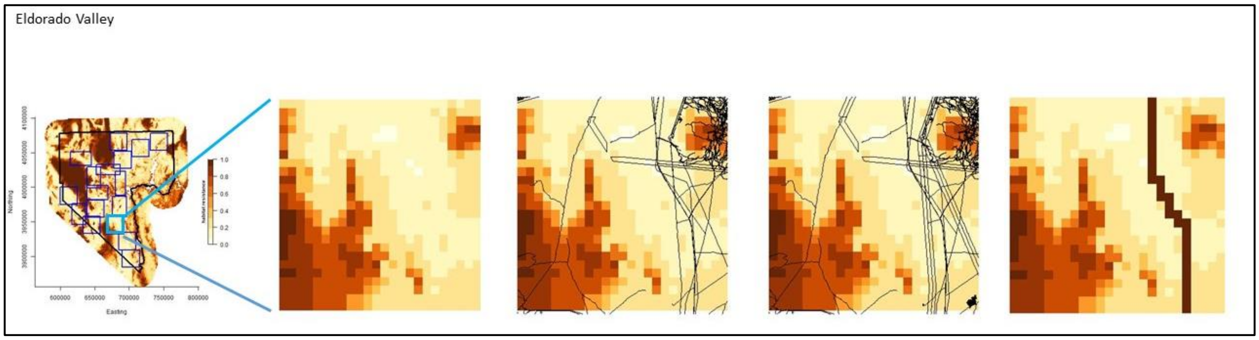


Fig. 2.4 Eldorado Valley depicted as a resistance surface (625 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

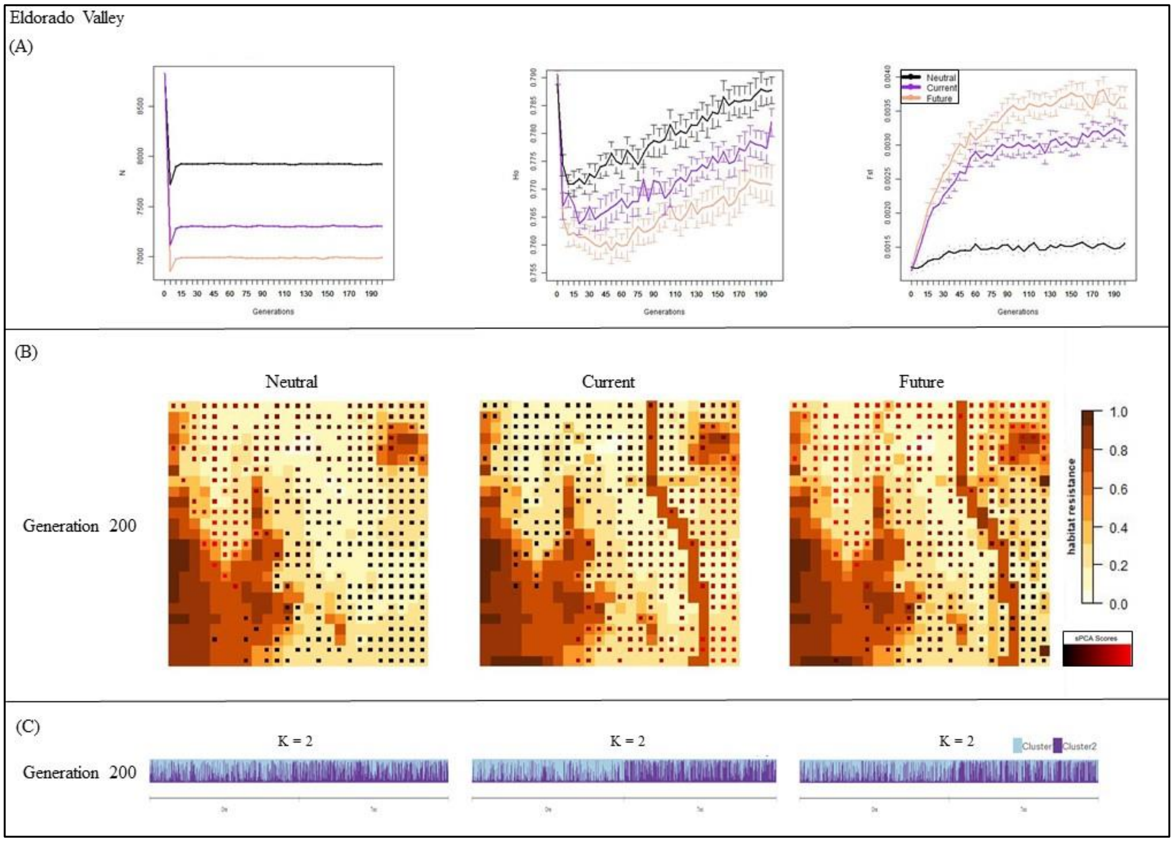


Fig. 3.4 Eldorado Valley simulation results. Number of individuals (*N*) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) *N*, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because $Pr(X|K)$ may overestimate clusters with IBD we report ΔK, except where $Pr(X|K) = 1$.

INDIAN SPRINGS (Fig 2.5): Population losses of 22.2% were predicted with current disturbance, and 23.7% with future disturbance. In terms of population loss through time this location ranked 9^{TH} (current disturbance) and 10^{TH} (future disturbance), relative to the 17 locations modeled. Compared with the neutral landscape this location lost 4.4% (p >0.05) and 5.8% (p >0.05) alleles/locus in current and future disturbance scenarios. Relative to the neutral landscape this location lost 4.0% (p = 0.011) and 4.3% ($p = 4*10^{-4}$) H_o in current and future disturbance scenarios. Genetic differentiation in the neutral landscape was stable. Spatial autocorrelation was present in all landscape scenarios. Population genetic structure was weakly present in the neutral landscape, and amplified by anthropogenic disturbance in both current and future scenarios. All landscapes provided support for admixture; however, it was reduced by disturbance (Fig. 3.5).

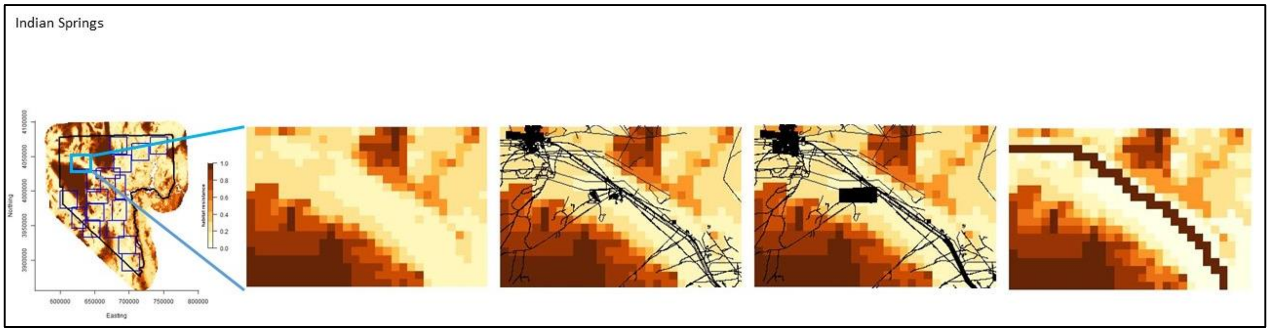


Fig. 2.5 Indian Springs depicted as a resistance surface (600 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

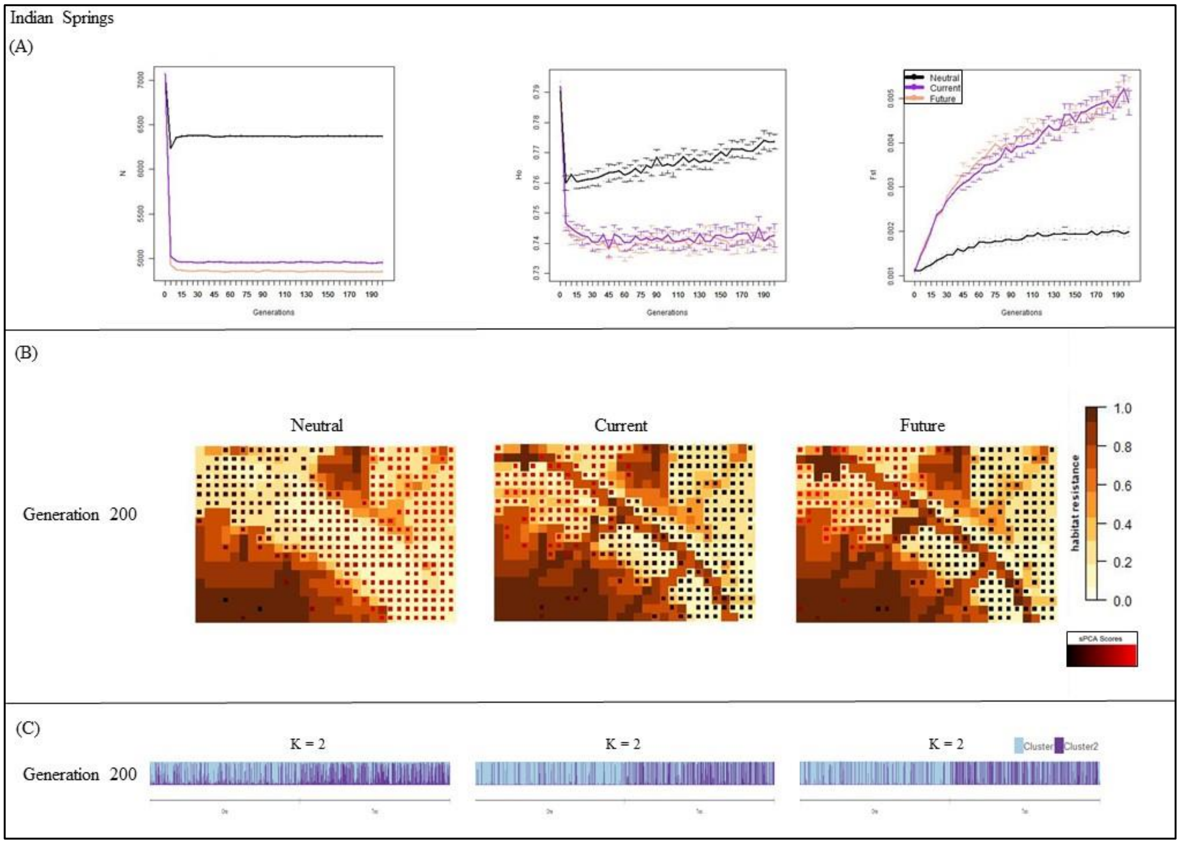


Fig. 3.5 Indian Springs simulation results. Number of individuals (*N*) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) *N*, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because *Pr(X|K)* may overestimate clusters with IBD we report *ΔK*, except where *Pr(X|K)* = 1.

IVANPAH VALLEY (Fig 2.6): A population loss of 23.7% was predicted in current disturbance simulations. Future disturbance predicted a loss of 29.6%. Based on the 17 locations modeled, this location ranked 6^{TH} (current disturbance) and 9^{TH} (future disturbance) in terms of loss in individuals. This location lost 6.0% (current disturbance; $p > 0.05$) and 6.6% (future disturbance; $p > 0.05$) alleles/locus compared with the neutral landscape. Relative to the neutral landscape, this location lost 4.0% ($p > 0.05$) and 4.6% ($p = 0.017$) in current and future disturbance scenarios. Only the neutral landscape showed indications of steady genetic differentiation through time. The neutral landscape exhibited spatial autocorrelation, with genetic structure supporting two clusters. The disturbance scenarios are expected to result in an almost complete loss of connectivity, with the current disturbance landscape suggesting an increase in clustering and the future disturbance landscape resulting in two isolated clusters (Fig. 3.6).

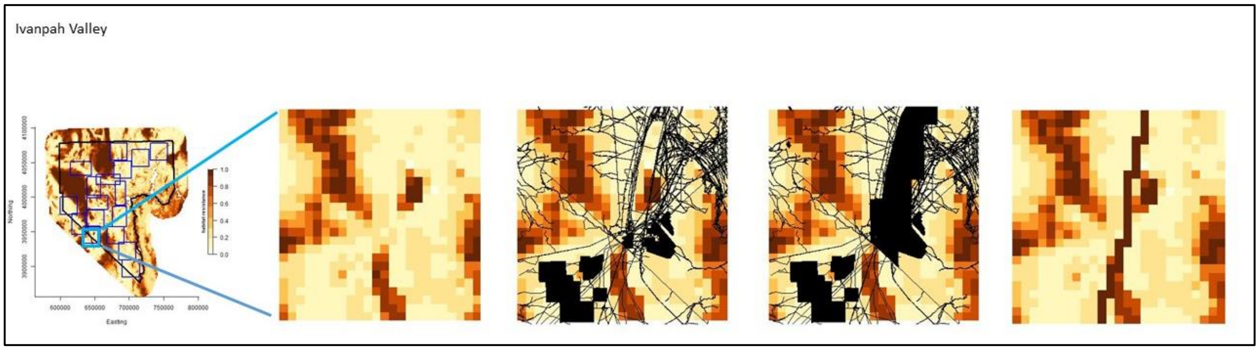


Fig. 2.6 Ivanpah Valley depicted as a resistance surface (625 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

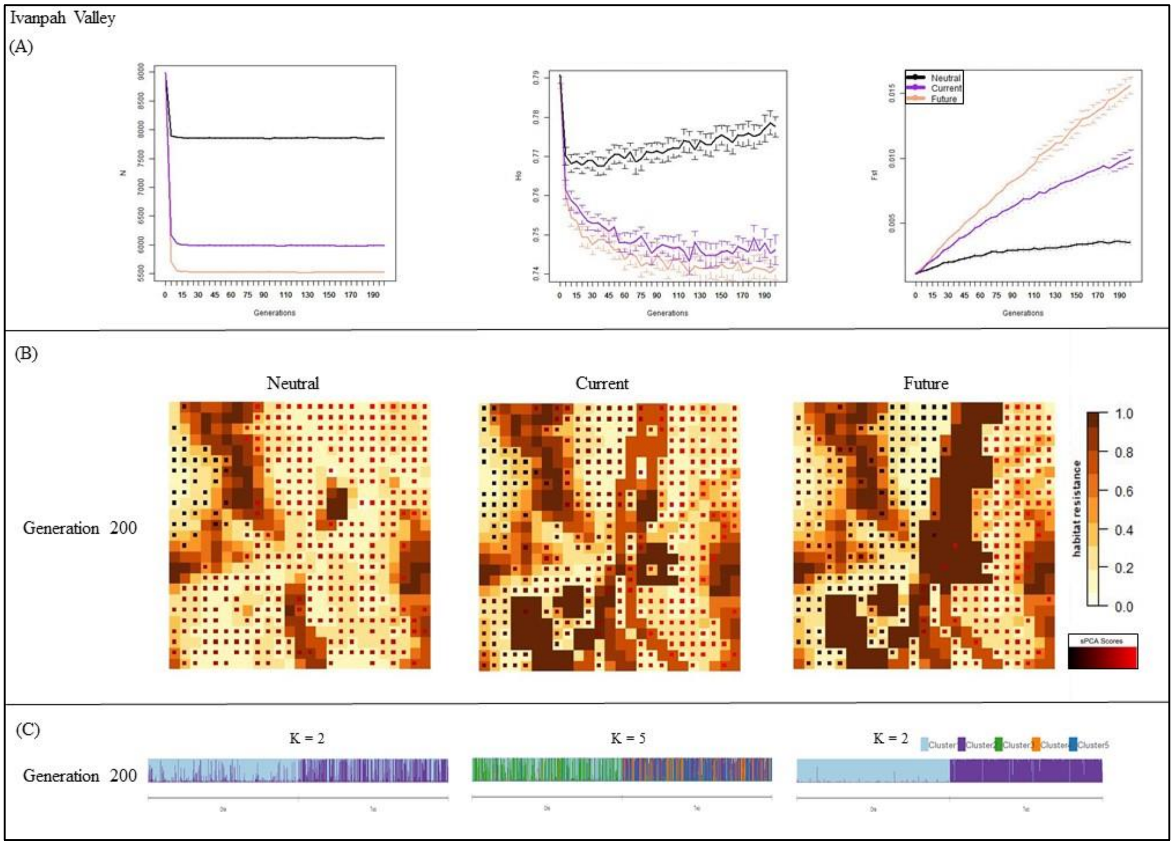


Fig. 3.6 Ivanpah Valley simulation results. Number of individuals (*N*) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) *N*, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because $Pr(X|K)$ may overestimate clusters with IBD we report ΔK, except where $Pr(X|K) = 1$.

JEAN/ROACH (Fig 2.7): Population losses of 21.2% and 39.0% were predicted with current and future disturbance simulations, ranking this location 10^{TH} (current disturbance) and 6^{TH} (future disturbance), based on the 17 locations modeled in terms of population loss through time. Compared with the neutral landscape the Jean/Roach location lost 4.5% ($p > 0.05$) and 8.6% ($p > 0.05$) alleles/locus in current and future disturbance scenarios. This location lost 3.5% ($p > 0.05$) and 10.3% ($p = 2*10^{-5}$) H_o in current and future disturbance scenarios, relative to the neutral landscape. Only the neutral landscape exhibited stable genetic differentiation through time, with support for a cline. Spatial autocorrelation was present in the disturbance scenarios, with support for increased genetic clustering with little to no admixture (Fig. 3.7).

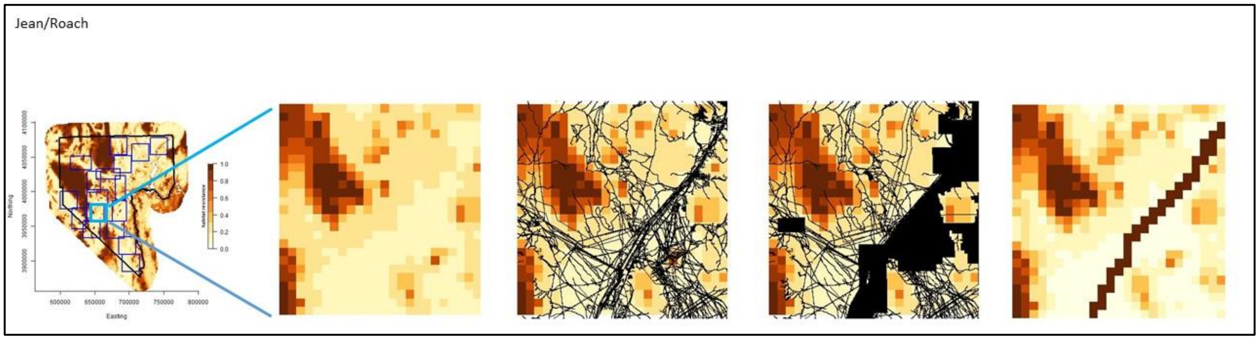


Fig. 2.7 Jean/Roach depicted as a resistance surface (625 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

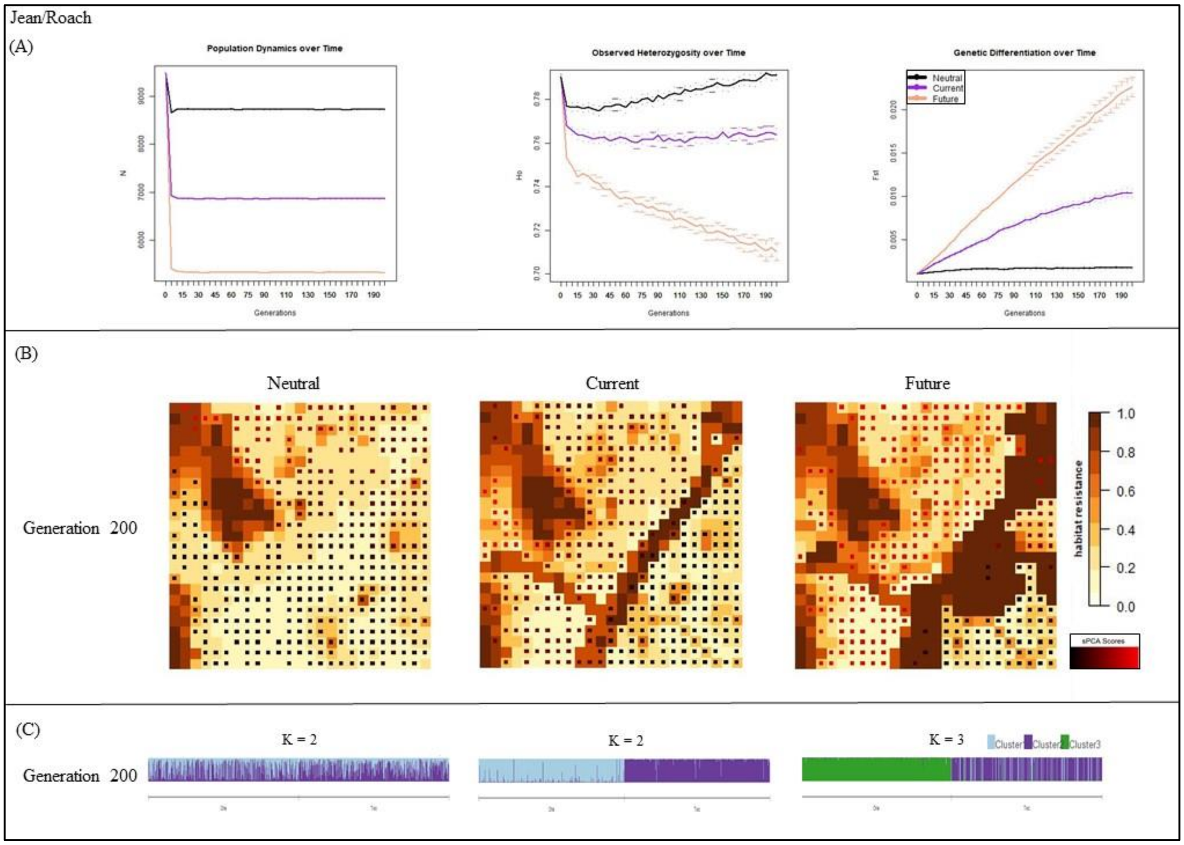


Fig. 3.7 Jean/Roach simulation results. Number of individuals (N) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) N, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because $Pr(X|K)$ may overestimate clusters with IBD we report ΔK, except where $Pr(X|K) = 1$.

LAS VEGAS EAST (Fig 2.8): A population loss of 28.9% was predicted in the current disturbance simulation, and 37.3% with future disturbance. In terms of loss of individuals, this location ranked 3RD (current disturbance) and 7TH (future disturbance), relative to the 17 locations modeled. Compared with the neutral landscape 8.1% ($p > 0.05$) and 8.7% ($p = 0.010$) alleles/locus were lost in current and future disturbance scenarios. This location lost 5.6% ($p = 0.003$) and 7.2% ($p = 2*10^{-5}$) H_o, relative to the neutral landscape in current and future disturbance scenarios. Genetic differentiation in the neutral landscape was predicted to rise through time as the result of rugged terrain; however, genetic differentiation increased to a lesser degree than in current or future disturbance scenarios. Spatial autocorrelation remained in current and future disturbance scenarios with amplified population genetic structure caused by increased landscape barriers, resulting in populations with almost no admixture (Fig. 3.8).

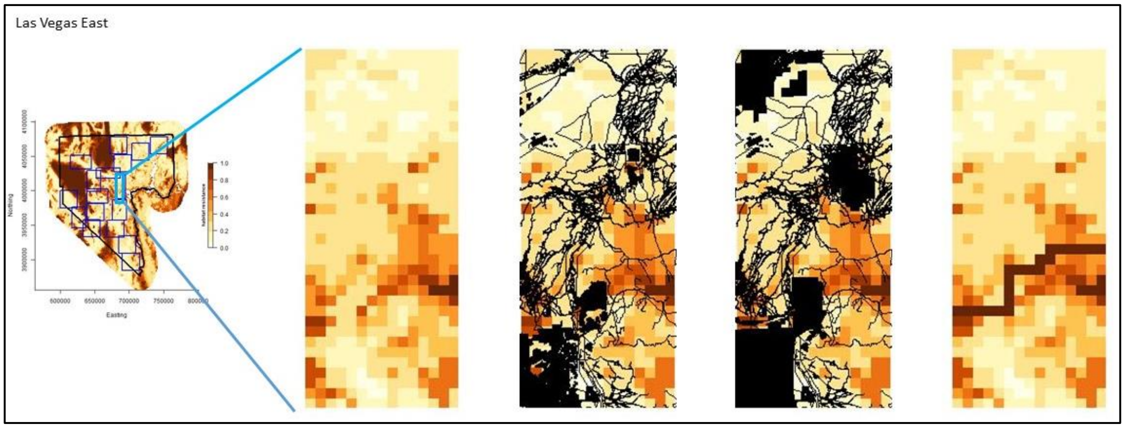


Fig. 2.8 Las Vegas East depicted as a resistance surface (525 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

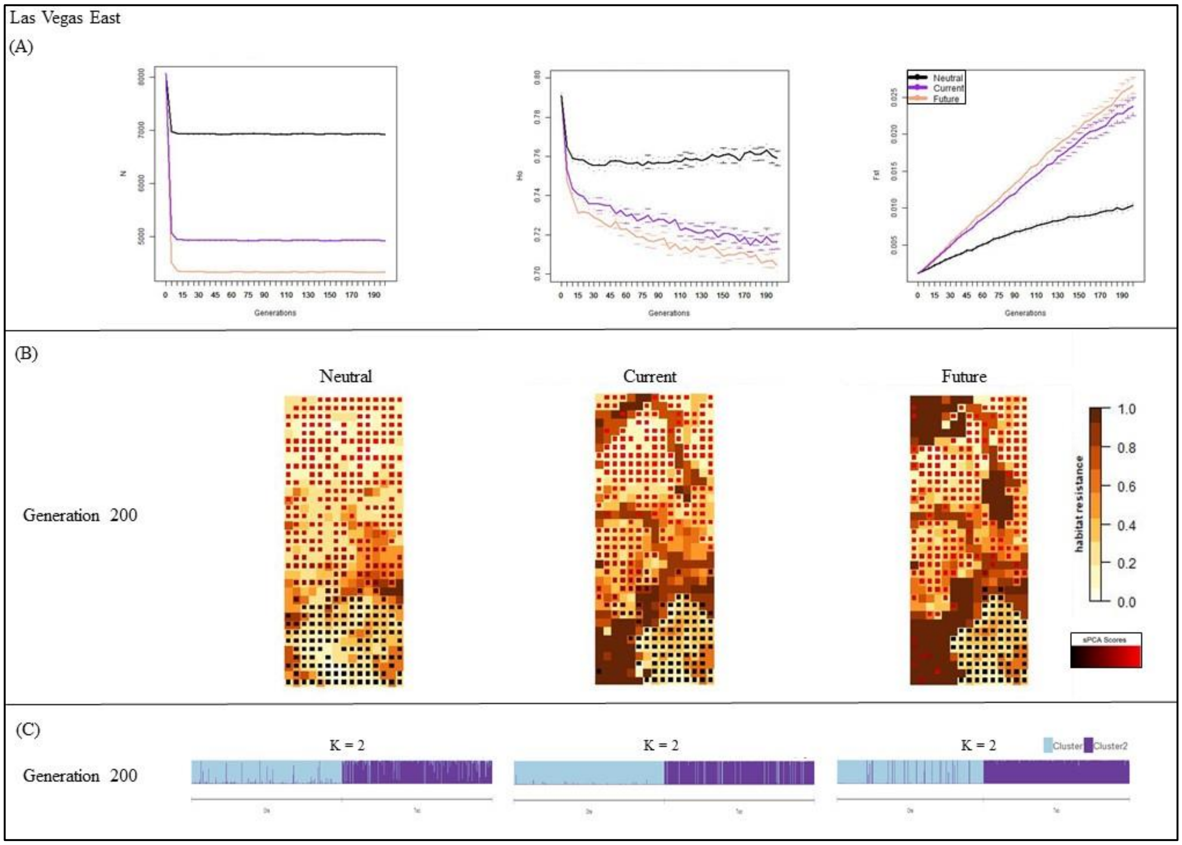


Fig. 3.8 Las Vegas East simulation results. Number of individuals (*N*) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) *N*, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because *Pr(X|K)* may overestimate clusters with IBD we report *ΔK*, except where *Pr(X|K)* = 1.

LAS VEGAS NORTH (Fig. 2.9): Current disturbance simulations predicted a 23.3% loss in population, with future disturbance predicted at a 43.3% loss. Based on the 17 locations modeled, this location ranked 7TH (current disturbance) and 4TH (future disturbance) in terms of loss in population. This location lost 5.7% (current disturbance; $p = 0.002$) and 10.8% (future disturbance, $p = 0.001$) alleles/locus compared with the neutral landscape. Heterozygosity was predicted to be lost by 2.6% ($p = 0.010$) and 8.2% ($p = 1*10^{-5}$) in current and future disturbance scenarios, relative to the neutral landscape. In the neutral landscape genetic differentiation increased and resulted in population genetic structure as the result of constricted habitat. As suitable habitat decreased with anthropogenic disturbance, spatial autocorrelation increased. Population genetic structure was predicted to be stronger with current disturbance, and strongest with future disturbance, which also exhibited increased genetic clustering (Fig. 3.9).

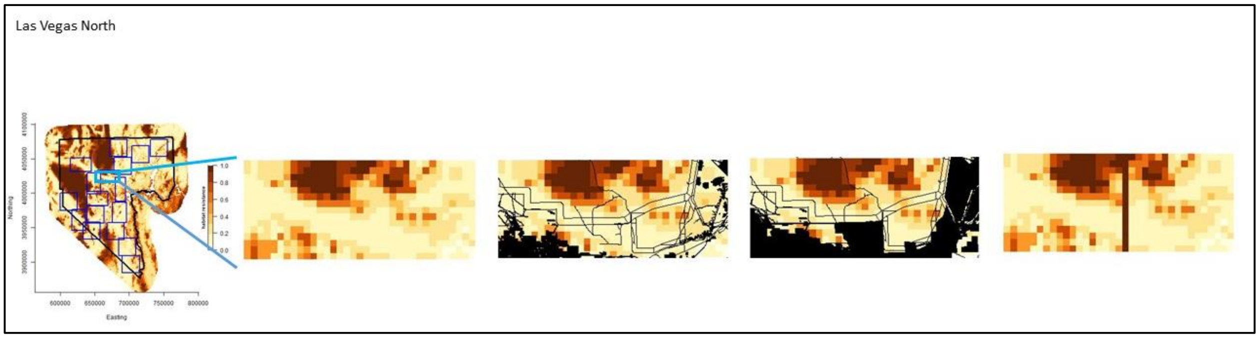


Fig. 2.9 Las Vegas North depicted as a resistance surface (525 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

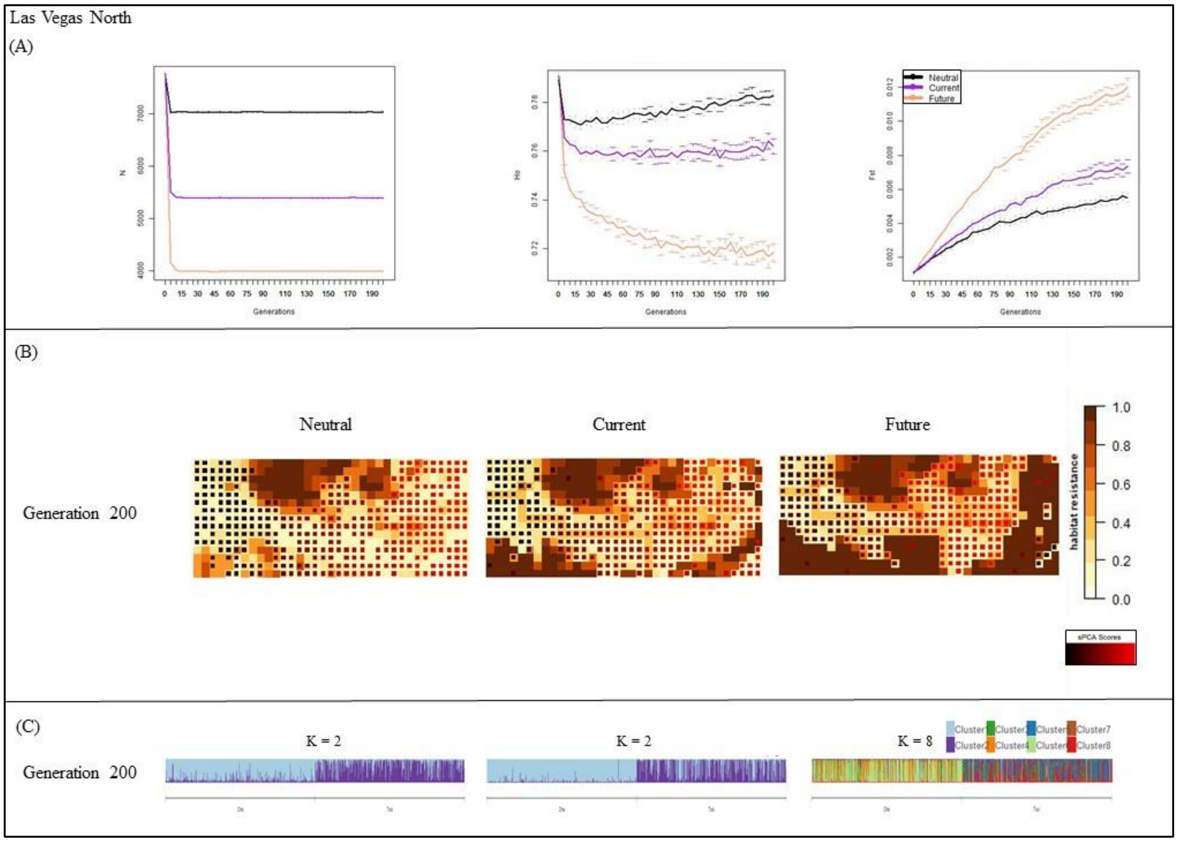


Fig. 3.9 Las Vegas North simulation results. Number of individuals (*N*) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) *N*, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because *Pr(X|K)* may overestimate clusters with IBD we report ΔK, except where *Pr(X|K)* = 1.

LAS VEGAS WEST (Fig. 2.10): This location experienced expected population losses of 40.9% with current disturbance, and 55.6% in future disturbance simulations. This location ranked 2^{ND} in both current and future disturbance scenarios in terms of relative loss of individuals through time, relative to the 17 locations modeled. Compared with the neutral landscape this location lost 3.7% ($p > 0.05$) and 0.8% ($p > 0.05$) alleles/locus in current and future disturbance scenarios. The Las Vegas West location lost 10.8% ($p = 3*10^{-7}$) and 30.0% ($p = 4*10^{-13}$) H_o, relative to the neutral landscape in current and future disturbance scenarios. Only the neutral landscape showed indications of reaching steady genetic differentiation values. A natural corridor between rugged terrain created genetic structure and spatial autocorrelation was present in all landscape scenarios. Loss of suitable habitat within and surrounding the natural corridor in disturbance scenarios intensified population isolation, with notable reductions to gene flow (Fig. 3.10).

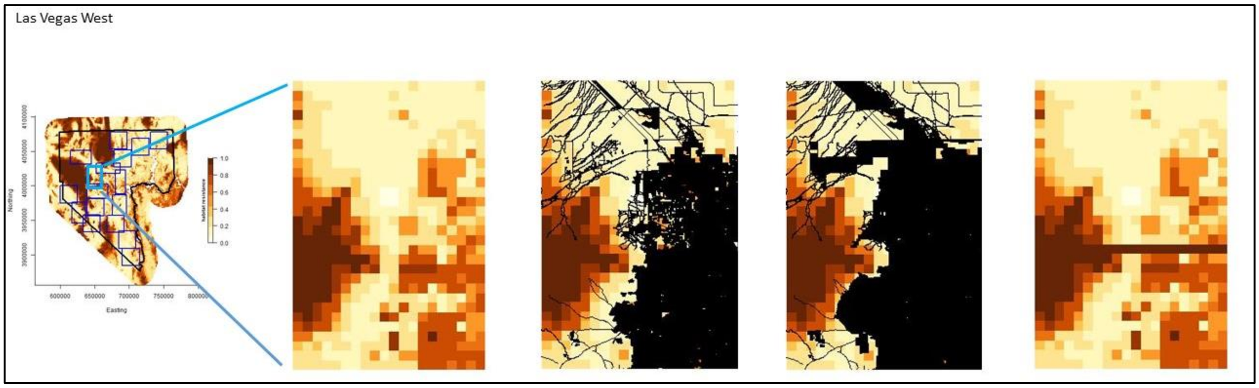


Fig. 2.10 Las Vegas West depicted as a resistance surface (600 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

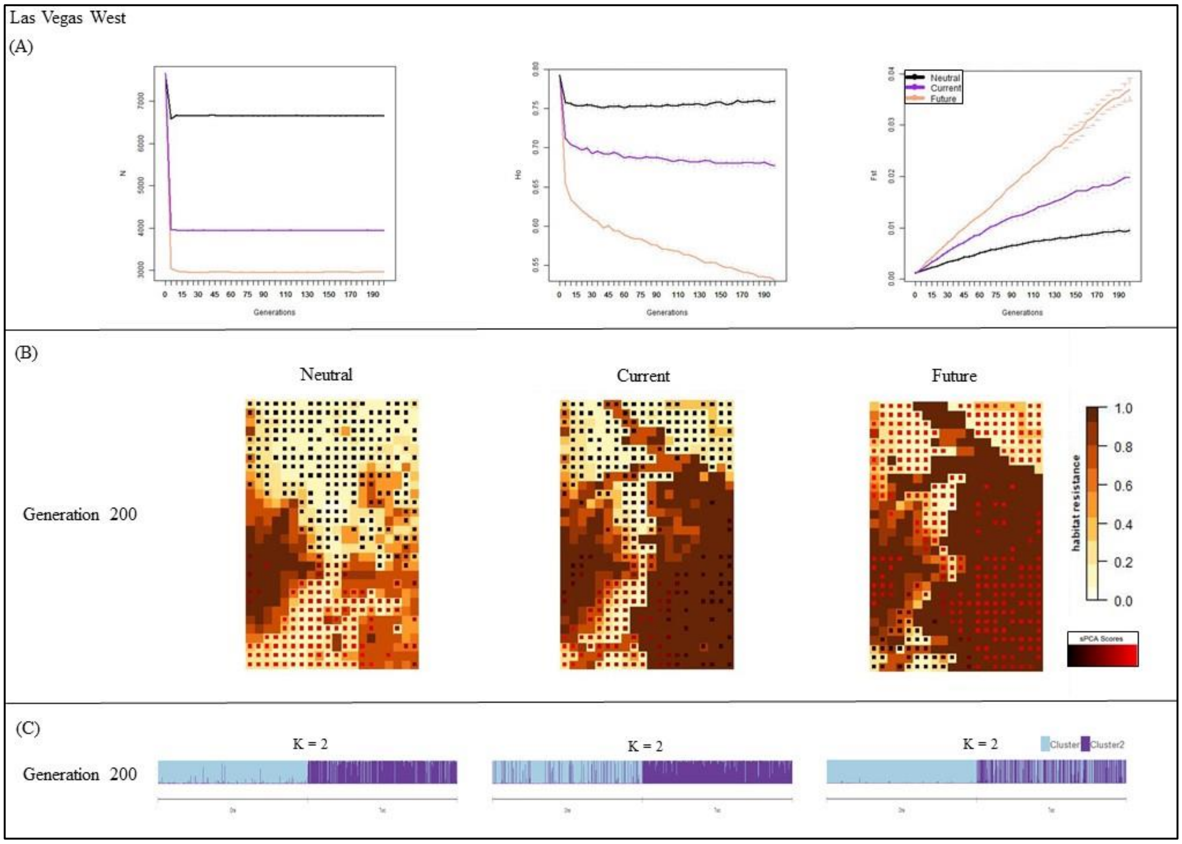


Fig. 3.10 Las Vegas West simulation results. Number of individuals (*N*) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) *N*, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because *Pr(X|K)* may overestimate clusters with IBD we report *ΔK*, except where *Pr(X|K)* = 1.

LAUGHLIN (Fig 2.11): A loss of 4.3% of individuals was predicted in the current disturbance simulation. A loss of 9.0% was predicted with future disturbance projections. This location ranked 16^{TH} (current disturbance) and 17^{TH} (future disturbance) in terms of loss in the population, relative to the 17 locations modeled. The Laughlin location lost 1.1% (current disturbance; $p > 0.05$) and 1.3% (future disturbance; $p > 0.05$) alleles/locus compared with the neutral landscape. Heterozygosity was predicted to be lost by 0.4% ($p > 0.05$) and 0.9% ($p = 0.002$), relative to the neutral landscape, in current and future disturbance scenarios. The neutral landscape, current, and future disturbance scenarios all showed signs of achieving steady levels of genetic differentiation. Spatial autocorrelation was present in all landscape scenarios. Population genetic structure was weakly present in the neutral landscape as the result of natural landscape features in the northeast. Anthropogenic disturbance strengthened this structure in both current and future scenarios. All landscapes are predicted to support admixture (Fig. 3.11).

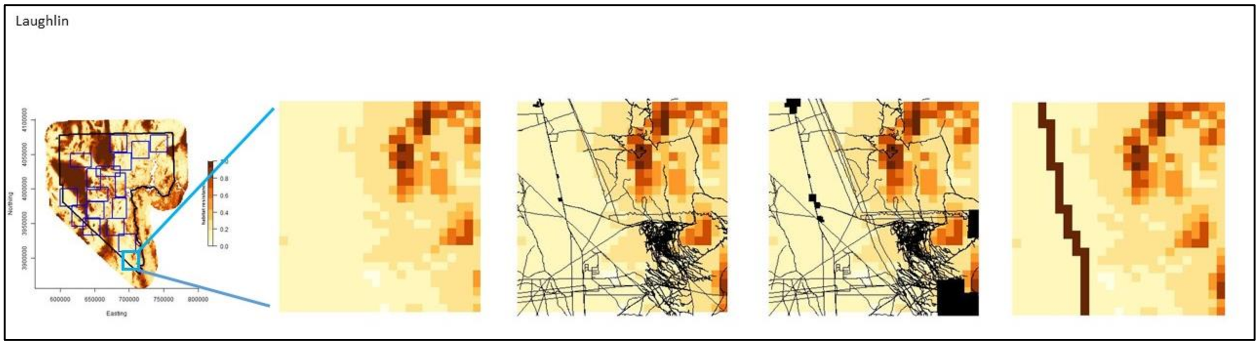


Fig. 2.11 Laughlin depicted as a resistance surface (625 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

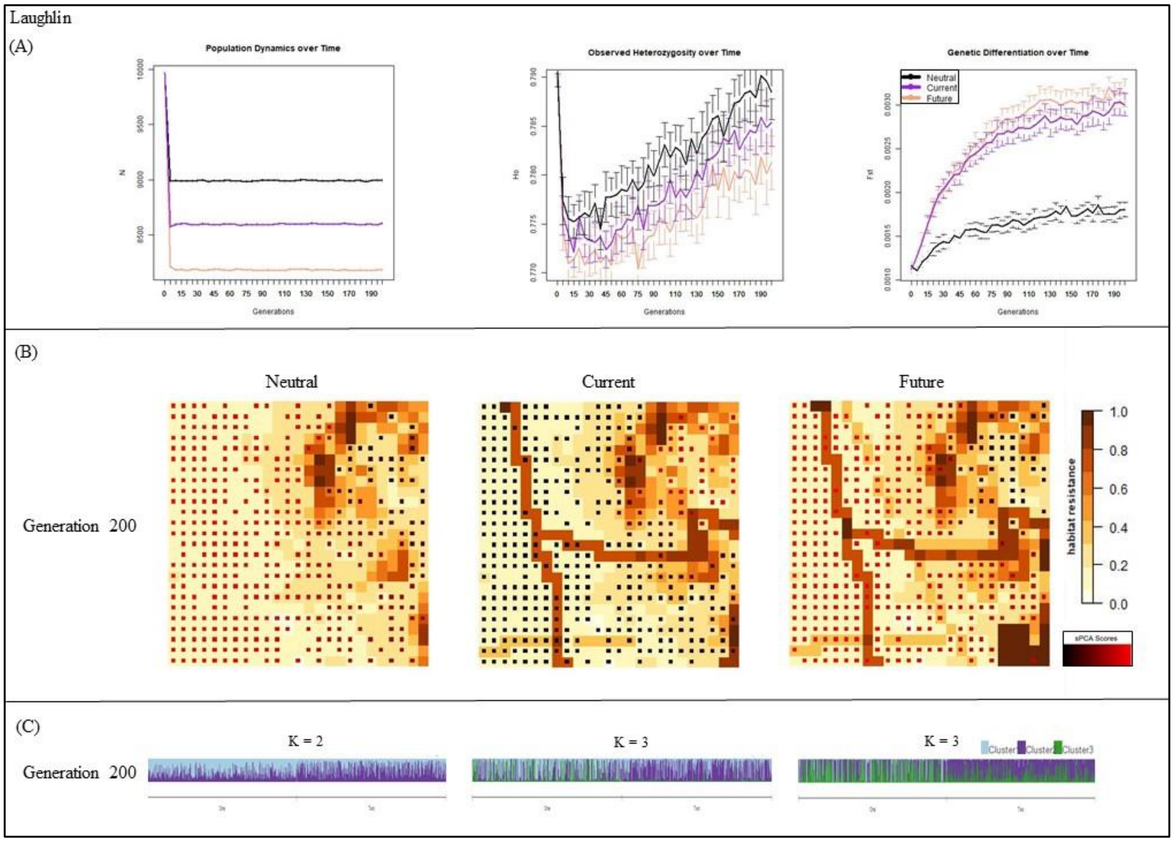


Fig. 3.11 Laughlin simulation results. Number of individuals (*N*) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) *N*, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because $Pr(X|K)$ may overestimate clusters with IBD we report ΔK, except where $Pr(X|K) = 1$.

MESQUITE (Fig. 2.12): Population losses of 11.9% and 15.7% were predicted with current and future disturbance simulations. In terms of population loss through time, this location ranked 13^{TH} in both current and future disturbance scenarios, based on the 17 locations modeled. Compared with the neutral landscape this location lost 1.9% ($p > 0.05$) and 2.5% ($p > 0.05$) alleles/locus in current and future disturbance scenarios. This location lost 1.0% ($p > 0.05$) and 1.1% ($p > 0.05$) H_o in current and future disturbance scenarios, relative to the neutral landscape. The neutral landscape showed indications of reaching stable levels of genetic differentiation and exhibited spatial autocorrelation, with genetic structure analyses supporting two clusters, one on either side of the Virgin River. Both current and future disturbance scenarios increased population genetic structure. Admixture was present in all scenarios, but decreased with disturbance (Fig. 3.12).

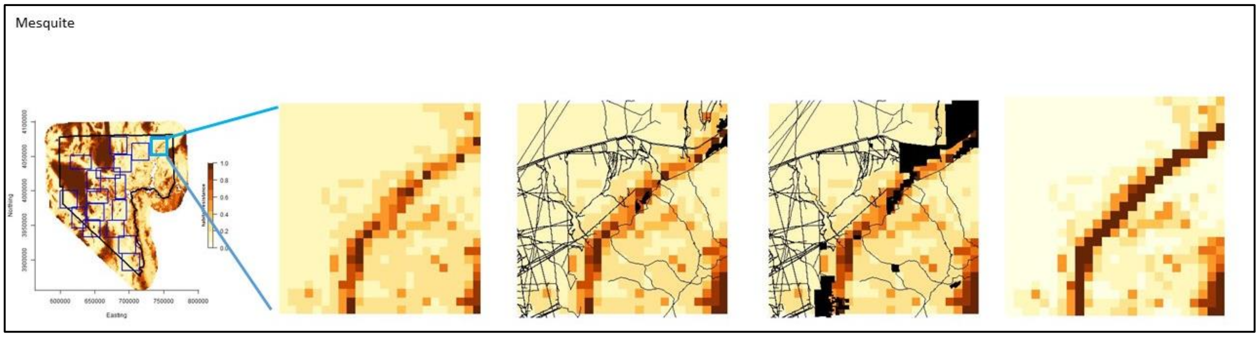


Fig. 2.12 Mesquite depicted as a resistance surface (625 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

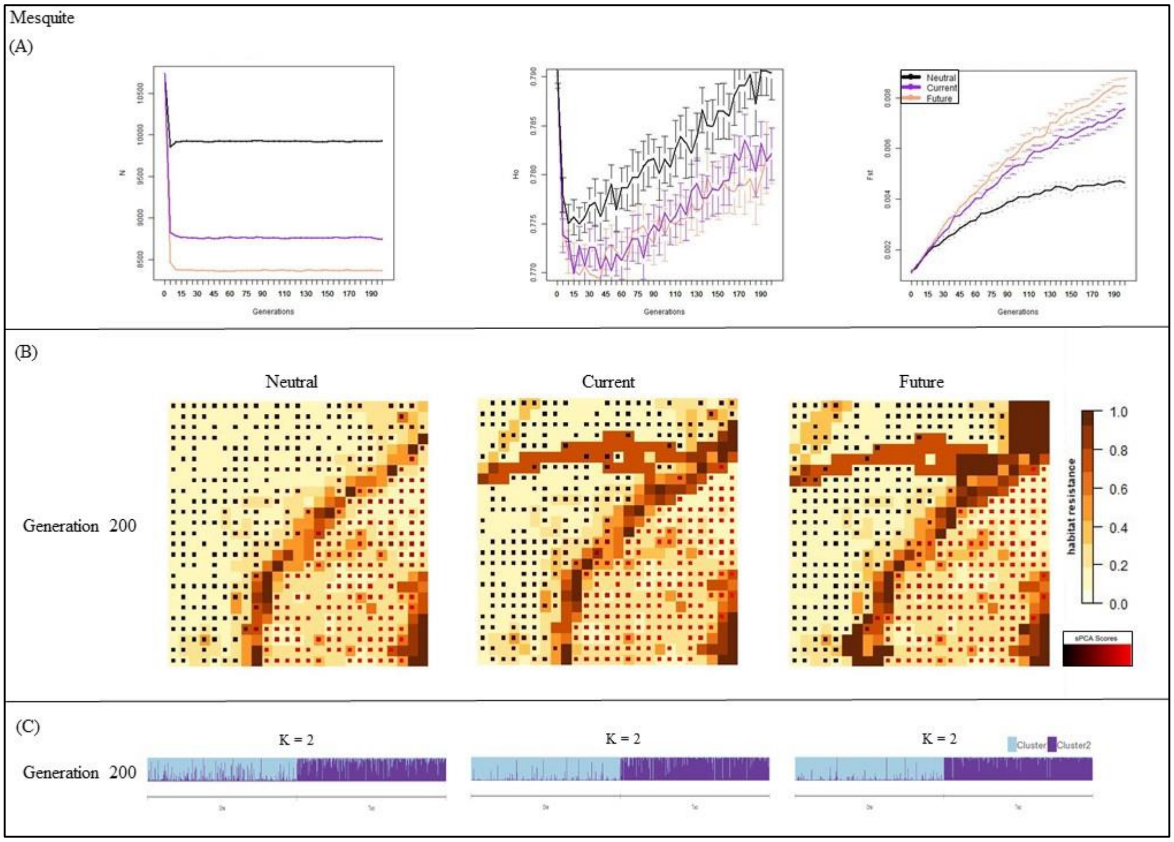


Fig. 3.12 Mesquite simulation results. Number of individuals (N) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) N, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because $Pr(X|K)$ may overestimate clusters with IBD we report ΔK, except where $Pr(X|K) = 1$.

MOAPA VALLEY (Fig. 2.13): A population loss of 27.3% was predicted in the current disturbance simulation, with 43.9% in the future disturbance scenario. Based on the 17 locations modeled, the Moapa Valley location ranked 4^{TH} (current disturbance) and 3^{RD} (future disturbance) in terms of loss in population. Compared with the neutral landscape this location lost 5.3% ($p > 0.05$) and 9.6% ($p > 0.05$) alleles/locus in current and future disturbance scenarios. In current and future disturbance scenarios H_o was predicted to be lost by 3.0% ($p > 0.05$) and 7.0% ($p = 1*10^{-6}$), relative to the neutral landscape. Genetic differentiation in the neutral landscape appeared stable and the current disturbance scenario reached steady levels over time. Spatial autocorrelation was present in all landscape scenarios. Anthropogenic disturbance resulted in genetic structuring in both current and future scenarios (Fig. 3.13).

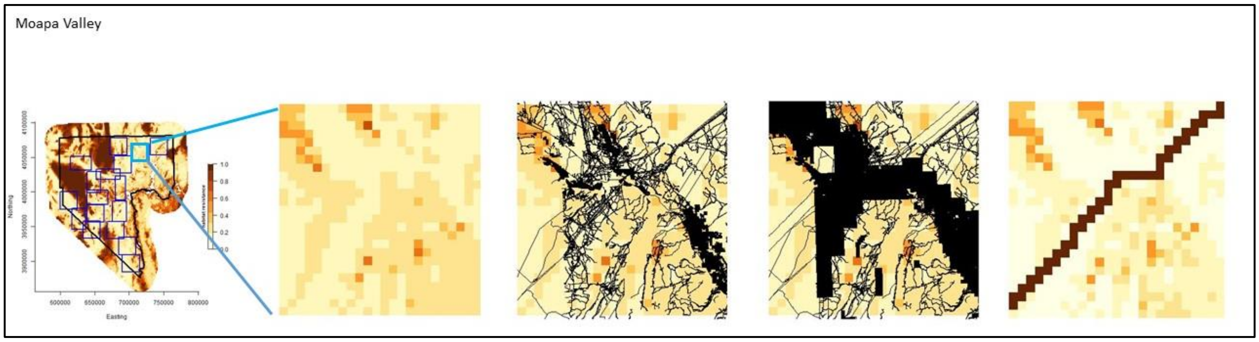


Fig. 2.13 Moapa Valley depicted as a resistance surface (625 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

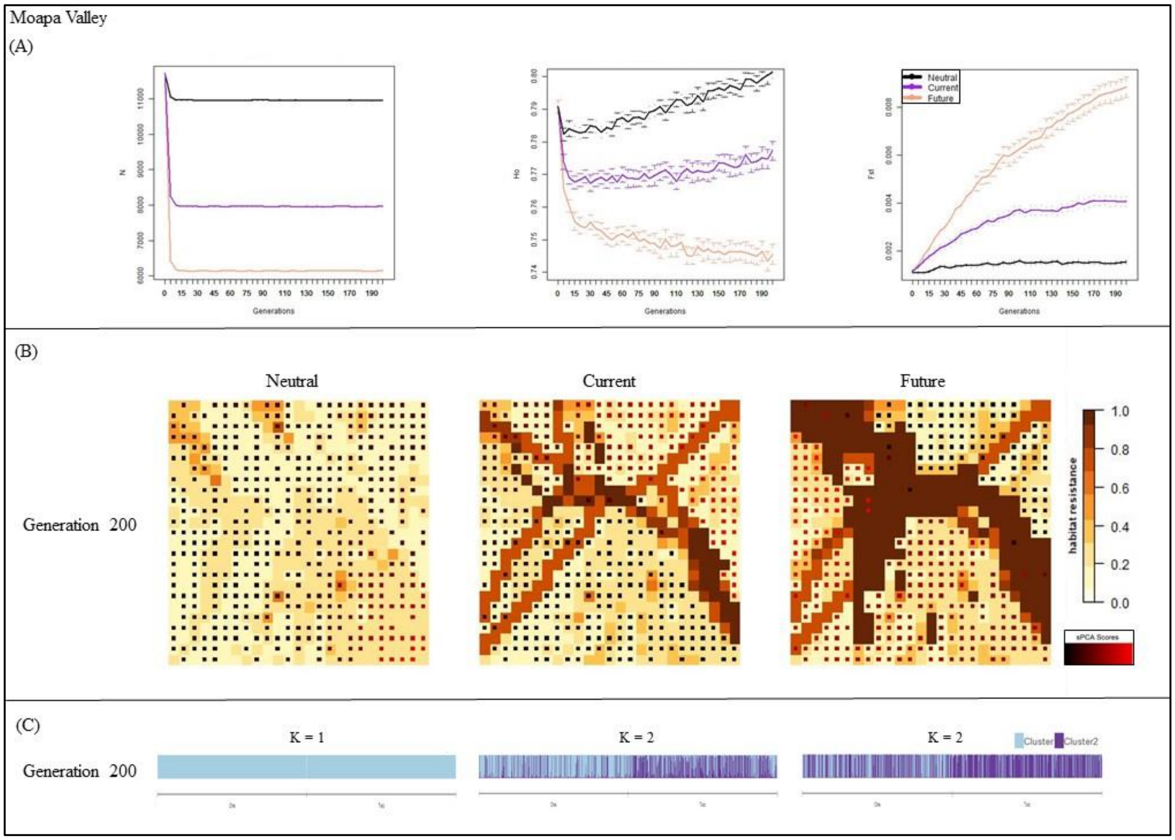


Fig. 3.13 Moapa Valley simulation results. Number of individuals (*N*) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) *N*, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because *Pr(X|K)* may overestimate clusters with IBD we report *ΔK*, except where *Pr(X|K)* = 1.

RED ROCK (Fig. 2.14): This location experienced predicted population losses of 63.6% with current disturbance, and 66.2% with future disturbance simulations. Red Rock ranked 1^{ST} in terms of population loss in both current and future disturbance scenarios, relative to the 17 locations modeled. This location lost 13.5% (current disturbance; $p = 7*10^{-4}$) and 5.1% (future disturbance; $p = 2*10^{-4}$) alleles/locus compared with the neutral landscape. Heterozygosity was predicted to be lost by 16.6% ($p = 2*10^{-10}$) and 23.6% ($p = 2*10^{-13}$) in current and future disturbance scenarios, relative to the neutral landscape. Only the neutral landscape exhibited steady genetic differentiation through time. Spatial autocorrelation was present in the neutral landscape with and weak genetic structure. As habitat amount was dramatically reduced by disturbance, isolation increased and gene flow was restricted (Fig. 3.14).

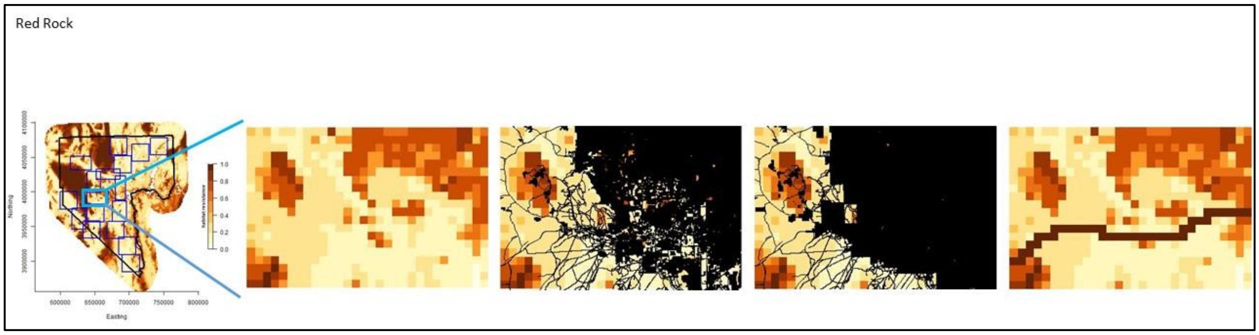


Fig. 2.14 Red Rock depicted as a resistance surface (600 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

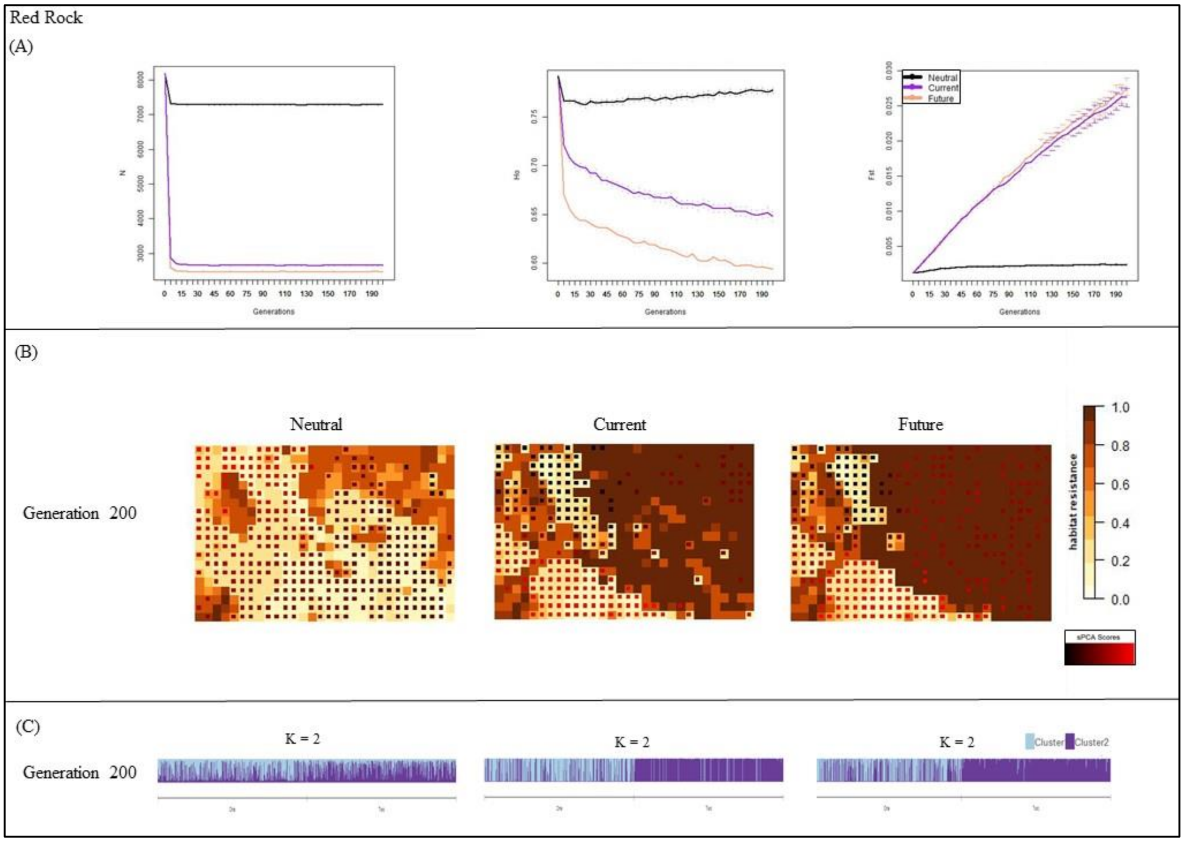


Fig. 3.14 Red Rock simulation results. Number of individuals (N) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) N, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because $Pr(X|K)$ may overestimate clusters with IBD we report ΔK, except where $Pr(X|K) = 1$.

SANDY VALLEY (Fig. 2.15): Population losses of 4.2% and 13.3% were predicted in the current and future disturbance simulation. This location ranked 17^{TH} (current disturbance) and 15^{TH} (future disturbance) in terms of losses to the population through time, relative to the 17 landscape locations modeled. Compared with the neutral landscape the Sandy Valley location lost 0.9% ($p > 0.05$) and 3.0% ($p > 0.05$) alleles/locus in current and future disturbance scenarios. This location lost 0.7% ($p > 0.05$) and 3.2% ($p > 0.05$) H_o, relative to the neutral landscape in current and future disturbance scenarios. Both of the disturbance landscapes showed indications of reaching steady genetic differentiation values through time. Spatial autocorrelation was present in all landscape scenarios, but increased with disturbance. In the neutral landscape, IBD was apparent with weak population genetic structure. Anthropogenic disturbance amplified population genetic structure with admixture present; albeit reduced by disturbance (Fig. 3.15).

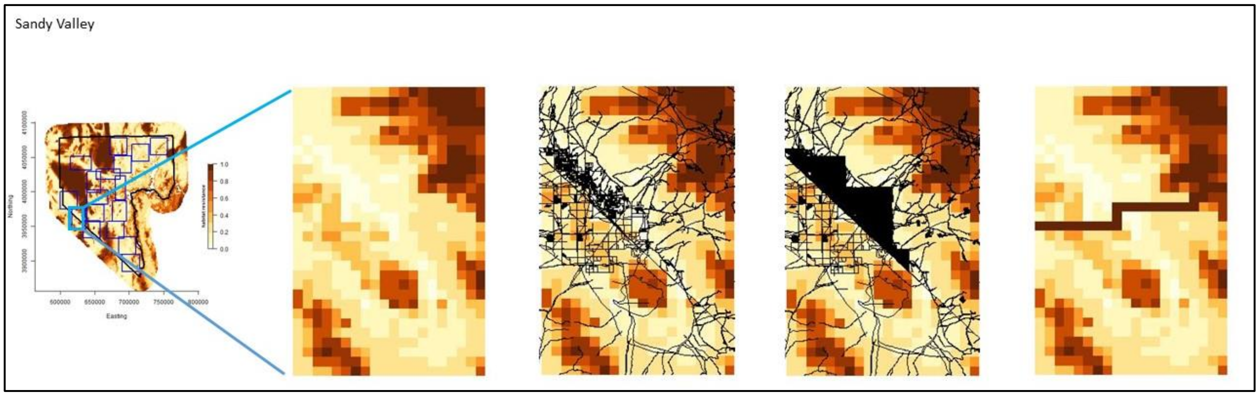


Fig. 2.15 Sandy Valley depicted as a resistance surface (600 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

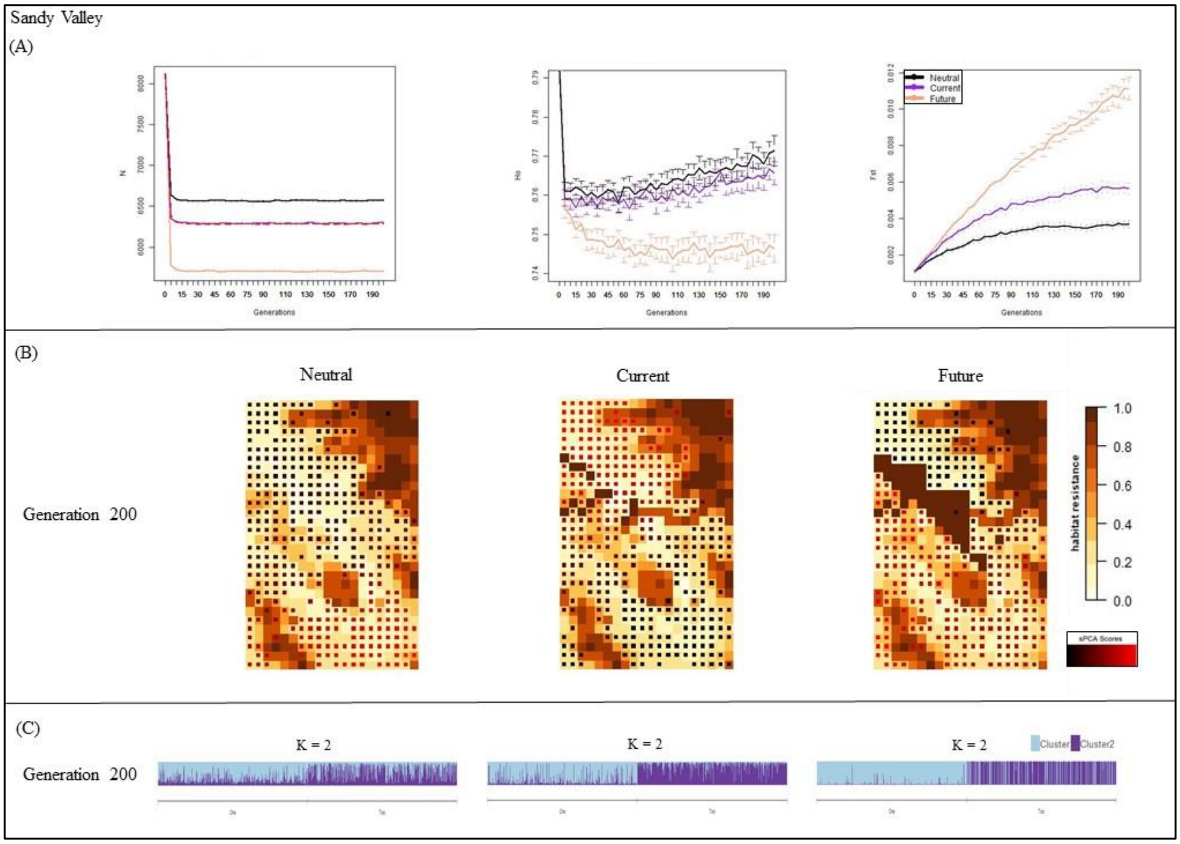


Fig. 3.15 Sandy Valley simulation results. Number of individuals (*N*) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) *N*, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because $Pr(X|K)$ may overestimate clusters with IBD we report ΔK, except where $Pr(X|K) = 1$.

SEARCHLIGHT (Fig. 2.16): A population loss of 9.9% was predicted in the current disturbance simulation, and 13.5% with future disturbance. In terms of relative loss of individuals through time, the Searchlight location ranked 14TH in both current and future disturbance scenarios, relative to the 17 locations modeled. This location lost 3.0% (current disturbance; $p > 0.05$) and 3.2% (future disturbance; $p > 0.05$) alleles/locus compared with the neutral landscape. This location lost 1.7% ($p > 0.05$) and 2.2% ($p = 2*10^{-4}$) H_o, relative to the neutral landscape in current and future disturbance scenarios. All three landscape scenarios appeared to reach stable levels of genetic differentiation. Spatial autocorrelation was present in the neutral landscape, along with weak population genetic structure. Spatial autocorrelation remained in current and future disturbance scenarios and population genetic structure increased. Admixture was predicted in all modeled landscapes; however, it was weakened by anthropogenic disturbance (Fig. 3.16).

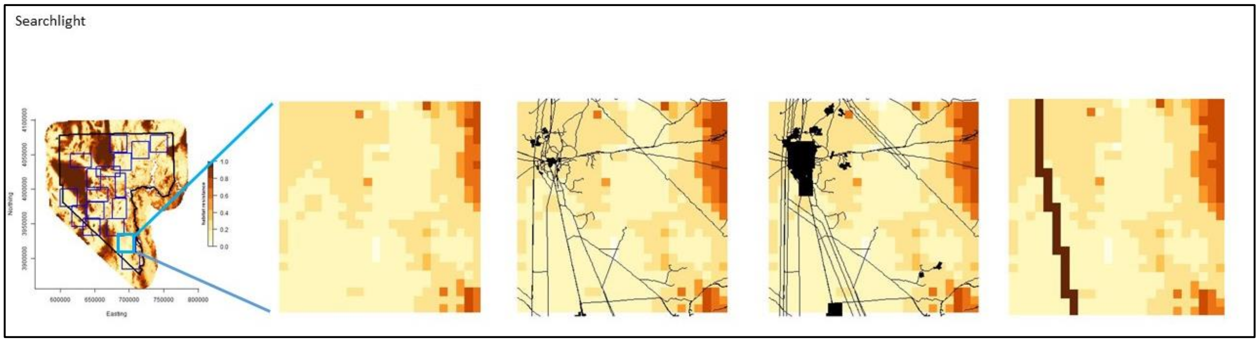


Fig. 2.16 Searchlight depicted as a resistance surface (625 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

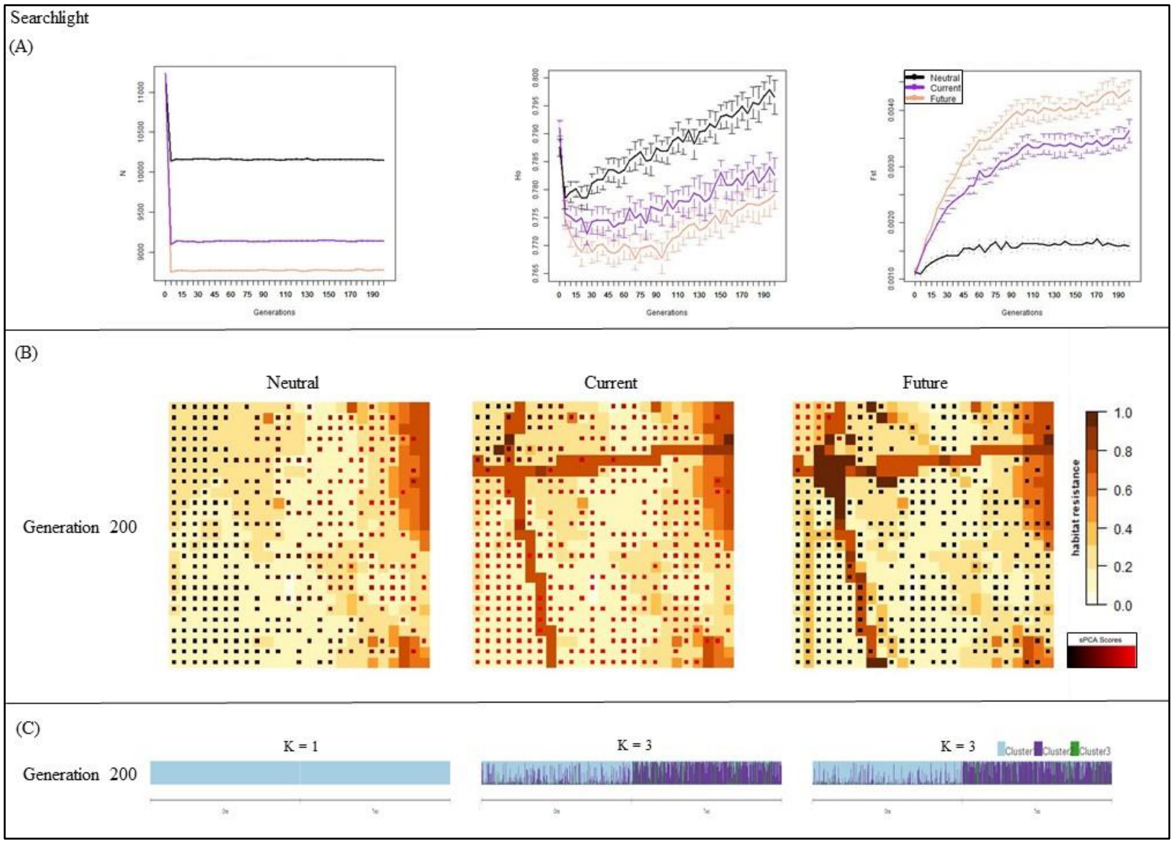


Fig. 3.16 Searchlight simulation results. Number of individuals (N) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) N, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because $Pr(X|K)$ may overestimate clusters with IBD we report ΔK, except where $Pr(X|K) = 1$.

TROUT CANYON (Fig. 2.17): Current disturbance simulations predicted a 16.2% loss in number of individuals, decreasing by 18.1% with future disturbance. Based on the 17 locations modeled, this location ranked 11^{TH} in terms of loss in population in both current and future disturbance scenarios. Compared with the neutral landscape this location lost 3.8% (p >0.05) and 4.7% ($p = 0.036$) alleles/locus in current and future disturbance scenarios. This location lost 1.8% (p >0.05) and 2.4% ($p = 3*10^{-4}$) H_o, relative to the neutral landscape in current and future disturbance scenarios. Genetic differentiation in the neutral landscape was stable and both disturbance scenarios (current and future) showed indications of reaching stability. Spatial autocorrelation was not present in the neutral landscape, and genetic structure analyses revealed panmixia. Spatial autocorrelation formed in disturbance scenarios, with structure predicted to increase in the future disturbance scenario. All scenarios maintained gene flow, with decreases in disturbance landscapes (Fig. 3.17).

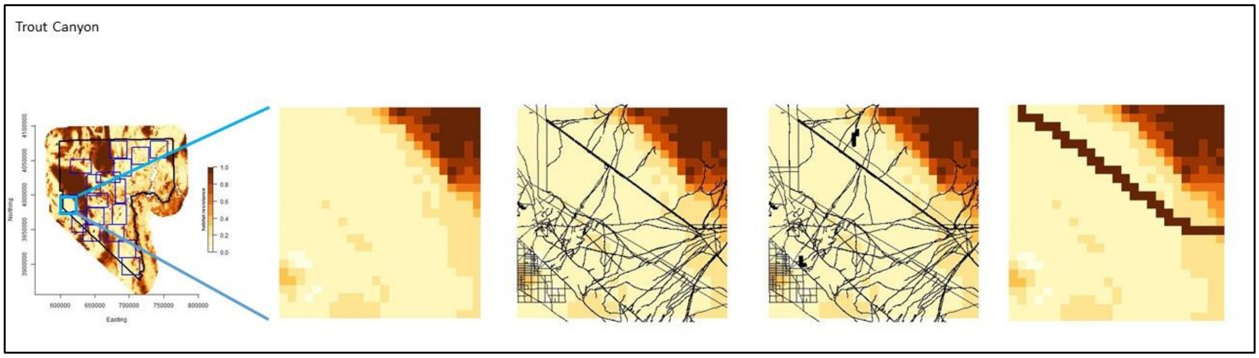


Fig. 2.17 Trout Canyon depicted as a resistance surface (625 km^2). Left to right: Location within Clark County, Nevada; neutral representation without anthropogenic disturbance; current levels of habitat disturbance; future projections of disturbance based on a 50 year forecast; hypothetical absolute barrier landscape.

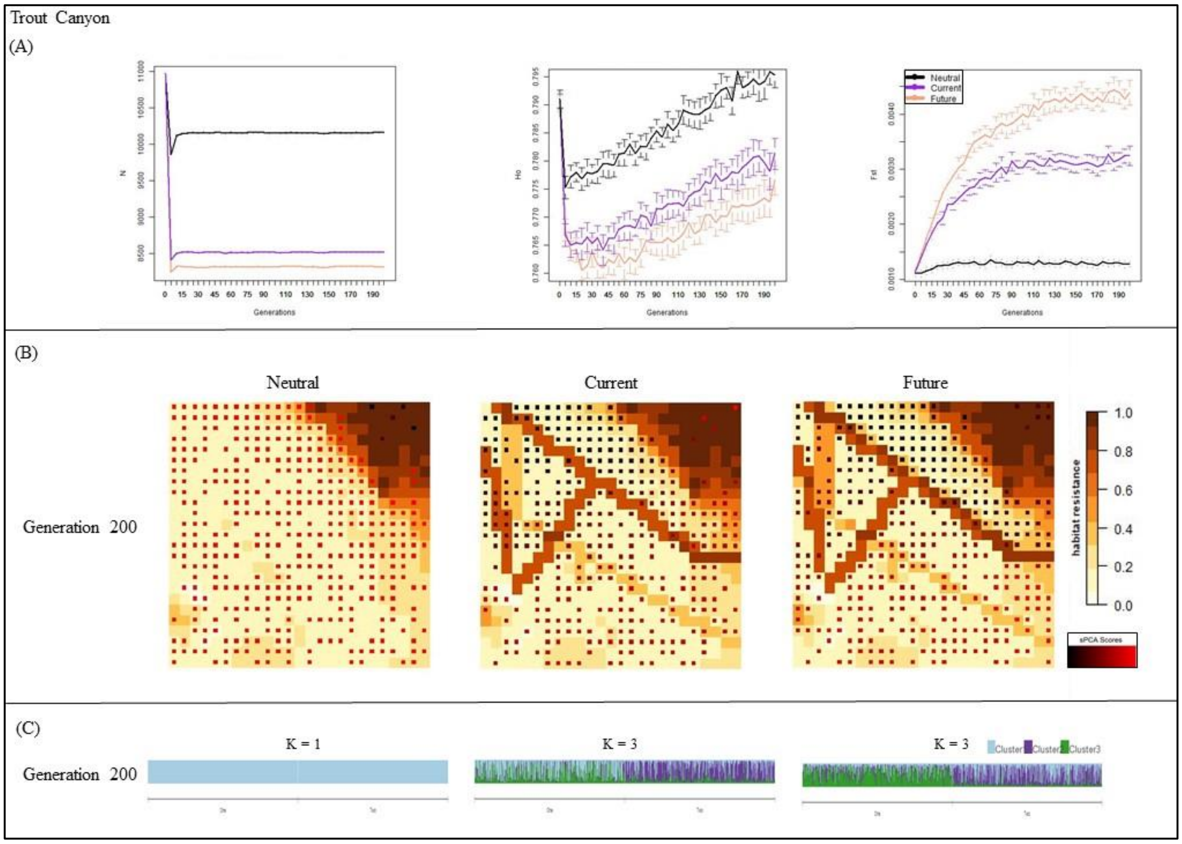


Fig. 3.17 Trout Canyon simulation results. Number of individuals (*N*) dependent on cell resistance in each landscape. Results reported for neutral, current disturbance, and future disturbance landscapes. Left to right: time-series of A) *N*, observed heterozygosity (H_o), genetic differentiation (F_{ST}); B) sPCA genetic patterns; C) STRUCTURE barplots. Because *Pr(X|K)* may overestimate clusters with IBD we report *ΔK*, except where *Pr(X|K)* = 1.

Predicted corridor success

Current disturbance landscapes had 9 of 17 locations that maintained high levels of genetic connectivity (corridor success index values ≥0.7) through time versus future disturbance scenarios, which had 5 of 17 (Table 5). The Laughlin location ranked highest in genetic connectivity in both scenarios. Of the four landscapes that changed ranks from high levels of genetic connectivity between current and future scenarios two became intermediate (Coyote Springs, Sandy Valley) and two lost genetic connectivity (Moapa Valley, Las Vegas North). Current and future disturbance landscapes had a comparable number of locations (3 and 4; respectively) with intermediate genetic connectivity (corridor success index values 0.35 – 0.69). More locations (8 of 17) in future disturbance scenarios did not maintain genetic connectivity (corridor success index values ≥0.34) through time compared with current disturbance landscapes (5 of 17). The Jean/Roach location ranked the lowest in both scenarios. Of the landscapes that failed to maintain genetic connectivity, 77% had negative corridor success index values, meaning they fared worse than scenarios with a hypothetical absolute barrier, likely due to the compounding effects of habitat degradation and loss of individuals. No landscape increased in rank from current to future disturbance scenarios.

Table 5. Corridor success index (CSI) values for current disturbance (CD) and future disturbance projections (FD) based on a 50 year forecast. Predicted F_{ST} values were used in the CSI. Those near 1 indicate gene flow comparable to neutral landscapes; those near or below 0 indicate failure to maintain connectivity. High and low values in bold.

Location	**CSI - CD**	**CSI - FD**
Boulder City	0.61	-0.05
Coyote Springs	0.74	0.55
Dry Lake	0.55	0.44
Eldorado Valley	0.89	0.84
Indian Springs	0.82	0.80
Ivanpah Valley	0.32	-0.25
Jean/Roach	**-50.84**	**-124.30**
Las Vegas East	-0.90	-1.30
Las Vegas North	0.80	0.28
Las Vegas West	-0.18	-2.12
Laughlin	**0.90**	**0.89**
Mesquite	0.55	0.41
Moapa Valley	0.72	0.19
Red Rock	-0.98	-1.11
Searchlight	0.85	0.80
Sandy Valley	0.85	0.44
Trout Canyon	0.88	0.81

Landscape metrics by modeled location supported increased fragmentation and loss of suitable habitat with disturbance (Table 6). The number of patches had a tendency to increase from the neutral landscape to the disturbed landscape (59% current and 76% future disturbance).

Only the Red Rock location predicted more suitable habitat patches with the current landscape than the future scenario, likely because unsuitable habitat patches merged and removed suitable patches. No landscapes experienced an increase in the largest suitable habitat patch size with disturbance. This metric showed a consistent decrease in suitable habitat with disturbance in all landscapes. Conversely, there was a trend for unsuitable habitat to increase from the neutral landscape to current disturbance to future scenarios. The three exceptions were: Coyote Springs, where the largest unsuitable habitat patch remained constant; Jean/Roach, where there was no change between the neutral landscape and current disturbance; and Sandy Valley, where the largest unsuitable habitat patch did not change between current and future disturbance landscapes. These three landscapes also shifted ranks in disturbance scenarios (lost genetic connectivity between scenarios) likely because habitat was degraded, but not completely lost. At all modeled locations suitable habitat decreased in transitioning from the neutral landscape to current disturbance, as would be expected with the inclusion of disturbance. All modeled locations experienced further decreases in suitable habitat from current to future scenarios.

Table 6. Landscape metrics for suitable and unsuitable habitat by modeled locations in neutral landscapes, (CD) current disturbance, and (FD) future disturbance projections. Ranks were established using corridor success index (CSI) values: (1) high genetic connectivity; (2) intermediate genetic connectivity; (3) low/no genetic connectivity. Landscape metrics: (NP) number of patches; (LPI) largest patch index percentage; (Area) percentage of landscape.

	Ranks		**Neutral**			**CD**			**FD**		
	CD	**FD**	**NP**	**LPI**	**Area**	**NP**	**LPI**	**Area**	**NP**	**LPI**	**Area**
Boulder City	2	3									
Suitable Habitat			1	97.8	97.8	2	82.2	86.0	4	59.3	67.5
Unsuitable Habitat			2	1.2	2.2	11	7.2	14.0	6	28.3	32.5
Coyote Springs	1	3									
Suitable Habitat			1	86.1	86.1	1	82.2	82.2	2	72.6	77.9
Unsuitable Habitat			4	10.6	13.9	7	10.6	17.8	7	10.6	22.1
Dry Lake	2	2									
Suitable Habitat			1	99.0	99.0	2	66.4	87.7	3	61.0	82.2
Unsuitable Habitat			1	1.0	1.0	9	8.6	12.3	5	14.4	17.8
Eldorado Valley	1	1									
Suitable Habitat			1	83.2	83.2	1	81.8	81.8	1	81.1	81.1
Unsuitable Habitat			4	15.2	16.8	6	15.4	18.2	9	15.4	18.9
Indian Springs	1	1									
Suitable Habitat			1	72.3	72.3	3	65.2	65.8	3	63.5	64.2
Unsuitable Habitat			5	23.0	27.7	10	25.2	34.2	9	26.3	35.8
Ivanpah Valley	3	3									
Suitable Habitat			2	83.5	83.7	3	72.5	72.8	3	36.5	65.6
Unsuitable Habitat			8	7.0	16.3	14	8.5	27.2	9	20.3	34.4
Jean/Roach	3	3									
Suitable Habitat			1	87.5	87.5	2	79.2	79.4	3	49.1	63.0
Unsuitable Habitat			2	9.9	12.5	7	9.9	60.6	5	22.2	37.0
Las Vegas East	3	3									
Suitable Habitat			1	97.5	97.5	4	42.5	75.4	5	35.2	66.5
Unsuitable Habitat			5	1.3	2.5	6	20.0	24.6	5	21.9	33.5

Las Vegas North	1	3								
Suitable Habitat			1	85.9	85.9	1	73.3	73.3	5	53.0	54.9
Unsuitable Habitat			4	11.0	14.1	10	11.0	26.7	4	16.2	45.1
Las Vegas West	3	3								
Suitable Habitat			1	81.3	81.3	4	44.8	46.0	5	11.3	32.2
Unsuitable Habitat			8	13.2	18.7	8	36.3	54.0	4	67.3	67.8
Laughlin	1	1								
Suitable Habitat			1	97.3	97.3	1	92.5	92.5	1	89.4	89.4
Unsuitable Habitat			3	1.3	2.7	7	2.6	7.5	8	3.2	10.6
Mesquite	2	2								
Suitable Habitat			1	95.0	95.0	2	91.2	91.4	3	85.6	86.4
Unsuitable Habitat			7	1.8	2.7	7	4.6	8.6	4	8.2	13.6
Moapa Valley	1	3								
Suitable Habitat			1	100	100	1	85.0	85.0	3	44.5	64.2
Unsuitable Habitat			0	0	0	10	10.9	15.0	5	33.9	35.8
Red Rock	3	3								
Suitable Habitat			1	92.0	92.0	13	13.7	36.0	6	12.8	27.5
Unsuitable Habitat			13	2.2	8.0	4	63.3	64.0	2	72.2	72.5
Sandy Valley	1	2								
Suitable Habitat			2	80.2	80.5	2	76.5	76.7	2	69.7	69.8
Unsuitable Habitat			6	14.3	19.5	9	15.8	23.3	8	15.8	30.2
Searchlight	1	1								
Suitable Habitat			1	99.0	99.0	2	90.9	93.6	2	88.2	90.7
Unsuitable Habitat			3	0.6	1.0	6	3.8	6.4	10	5.9	9.3
Trout Canyon	1	1								
Suitable Habitat			1	89.4	89.4	1	87.0	87.0	1	85.0	85.0
Unsuitable Habitat			1	10.6	10.6	4	10.6	13.0	6	10.6	15.0

We found substantial overlap in landscape metric values when evaluated by corridor success index rank (high, intermediate, and low/no genetic connectivity; Table 7). The predicted number of suitable habitat patches tended to increase as landscapes decreased in suitable habitat area, indicating an increased number of smaller patches in a more fragmented landscape. Neutral landscapes had no more than two patches of suitable habitat, while those with low/no genetic connectivity ranged from 2 – 13. Edge density was lowest in neutral landscapes (0 – 2.13 m/ha), indicating simplified landscape configurations. Landscapes that did not maintain genetic connectivity showed increasing complexity in configurations (2.38 – 3.98 m/ha). Edge density decreased at three locations (Ivanpah Valley, Moapa Valley, Red Rock) as the number of unsuitable habitat patches decreased and unsuitable habitat area increased in future disturbance scenarios; one (Red Rock) became dominated by unsuitable habitat. Largest patch index values indicated consistent, albeit variable, loss of area to the largest suitable habitat patch as genetic connectivity was lost. The largest patch of suitable habitat in neutral landscapes did not constitute less than 72% of the habitat, while the largest patch of unsuitable habitat was 0% – 23%. In landscapes that did not maintain genetic connectivity the largest suitable habitat patches ranged from 11% – 79%, while the largest unsuitable patches were up to 72%. Generally, percent land area followed a similar pattern, with neutral landscapes having the most suitable habitat (72% - 100%). Landscapes that failed to maintain genetic connectivity maintained less suitable habitat (28% - 79%). The total percent core habitat by class also followed suite, with the largest area of suitable core habitat in neutral landscapes (53% - 85%). The smallest area of suitable habitat remained in landscapes with low/no genetic connectivity (10% - 52%).

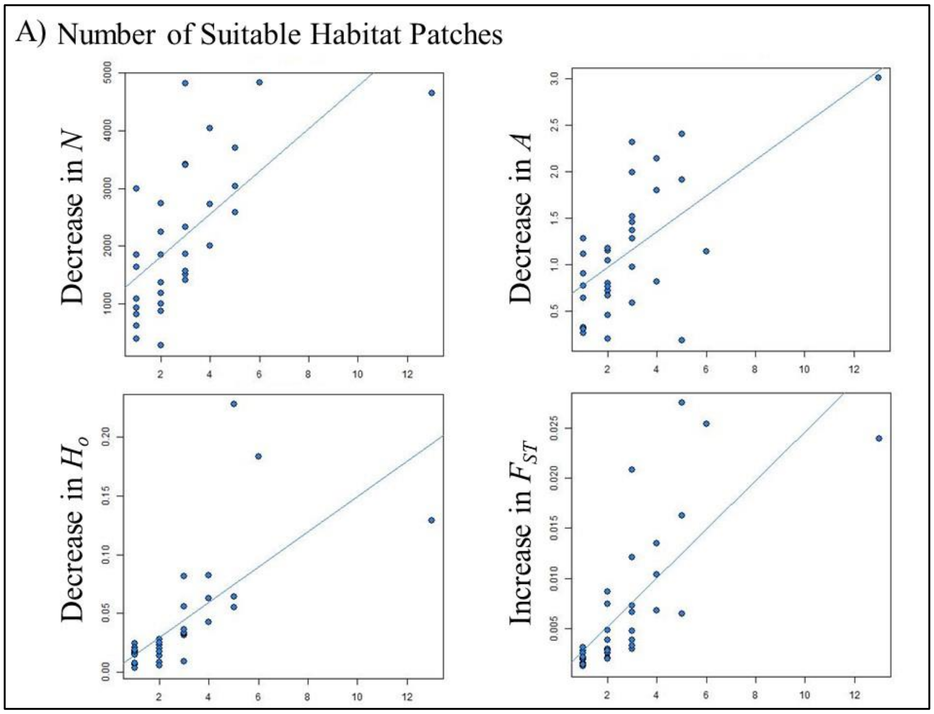
Table 7. Landscape metrics of suitable and unsuitable habitat by ability to maintain genetic connectivity. Assignments were based on ranking corridor success index (CSI) values: high ≥ 0.70, intermediate = 0.35-0.69, low/no genetic connectivity ≤0.34. Landscape metrics: (NP) number of patches; (LPI) largest patch index percentage; (Area) percentage of landscape; (Core) percentage of core area landscape; (Edge) edge density in m/ha. Edge values are equivalent by category.

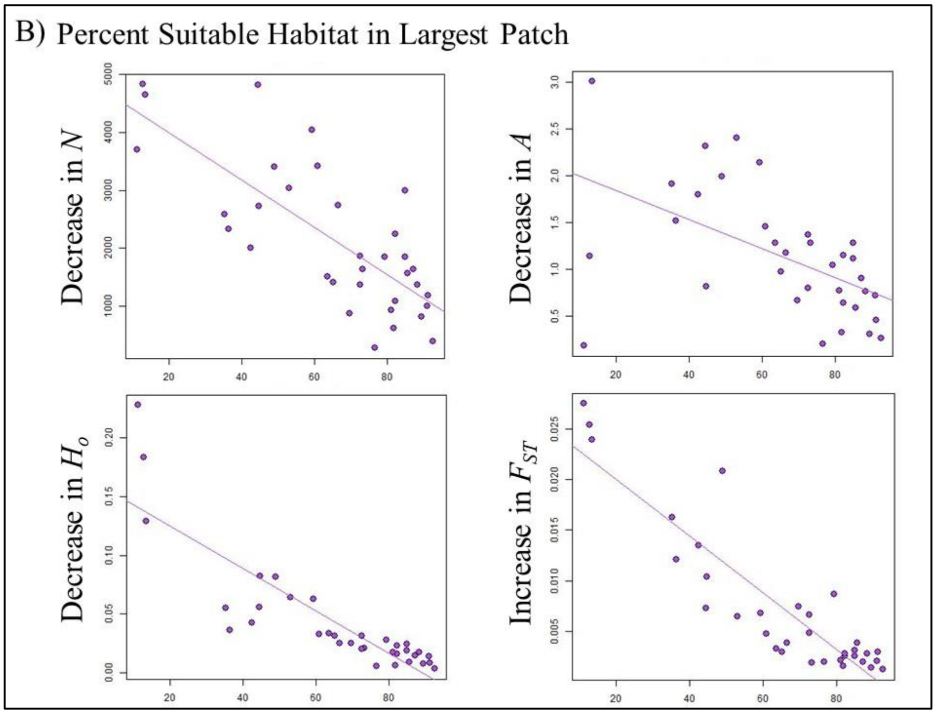
	NP	**LPI (%)**	**Area (%)**	**Core (%)**	**Edge (m/ha)**
Neutral Landscape					
Suitable Habitat	1-2	72.3-100	72.3-100	53.3-84.6	0-2.1
Unsuitable Habitat	0-13	0-23	0-27.7	0-14.5	0-2.1
High Connectivity					
Suitable Habitat	1-3	63.5-92.5	64.2-93.6	35.7-71.0	1.0-3.2
Unsuitable Habitat	4-10	2.6-26.3	6.4-35.8	0.2-15.0	1.0-3.2
Intermediate Connectivity					
Suitable Habitat	2-3	61.0-91.2	69.8-91.4	41.0-68.0	1.6-3.1
Unsuitable Habitat	4-11	4.6-15.8	8.6-30.2	1.3-10.0	1.6-3.1
Low/No Connectivity					
Suitable Habitat	2-13	11.3-79.2	27.5-79.4	9.8-52.0	2.4-4.0
Unsuitable Habitat	2-14	8.5-72.2	20.6-72.5	4.2-48.8	2.4-4.0

The highest ranking AIC models were those with number of suitable habitat patches and alleles/locus, percent area suitable habitat plus largest patch index and H_o, and largest suitable habitat patch index and F_{ST} and N (Table 8). Individual landscapes exhibited a general loss of genetic diversity, but these metrics tended to be less reliable indicators when evaluated across landscapes. Reductions in landscapes that maintained high levels of genetic diversity did not exceed 6%. Landscapes that allowed for intermediate gene flow were also not reduced by more than 6%. Low/no connectivity values tended to be higher; however, loss of genetic diversity could be as low as <1% in these landscapes. Because these estimates are heavily influenced by population size, care should be taken when interpreting results. Overall trends pointed to increased isolation with more complex landscape configuration as connectivity was lost and landscape composition was generally altered, decreasing dominance of the largest patch and amount of suitable habitat (Fig. 4).

Table 8. Akaike's information criterion (AIC) ranks of the strength of relationships. Terms are metrics of landscape disturbance with population or genetic statistics. Population and genetic statistics: (*N*) number of individuals; (*A*) alleles/locus; (H_o) observed heterozygosity; (F_{ST}) genetic differentiation. Landscape metrics: (NP) number of suitable habitat patches; (LPI) suitable habitat largest patch index percentage; (Area) suitable habitat percentage of landscape.

Terms for *N*	**AIC**	**Terms for *A***	**AIC**	**Terms for H_o**	**AIC**	**Terms for F_{ST}**	**AIC**
LPI	557.5	NP	58.6	Area + LPI	-158.0	LPI	-289.2
LPI + NP	558.7	Area + LPI + NP	58.9	Area	-157.5	LPI + NP	-287.8
Area + LPI	559.4	Area + NP	60.0	Area + LPI + NP	-156.2	Area + LPI	-287.4
Area + LPI + NP	560.5	LPI + NP	60.5	Area + NP	-155.5	Area + LPI + NP	-285.9
Area + NP	564.4	LPI	64.4	LPI	-149.3	Area + NP	-274.5
Area	565.8	Area + LPI	64.6	LPI + NP	-147.3	Area	-272.7
NP	567.5	Area	69.7	NP	-124.1	NP	-259.9


A) Number of Suitable Habitat Patches


B) Percent Suitable Habitat in Largest Patch

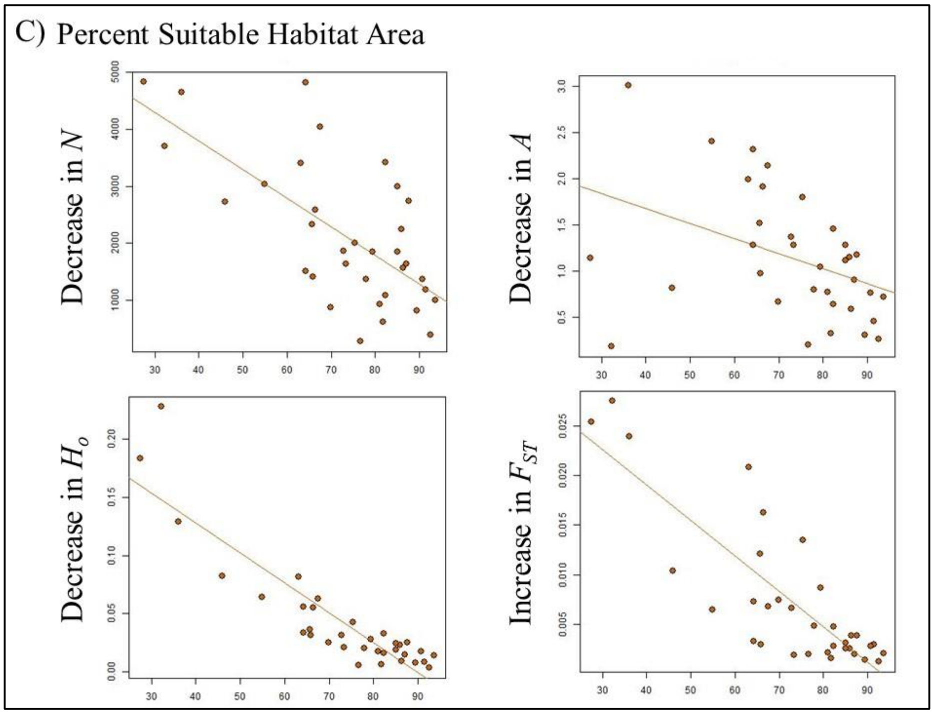


Fig. 4 Landscape metrics of disturbance relative to population and genetic statistics. Each figure compares a landscape metric on the x-axis to the loss of individuals (*N*), loss of alleles/locus (*A*), loss of observed heterozygosity (H_o), and increase in genetic differentiation (F_{ST}) on the y-axis. Top to bottom: A) number of suitable habitat patches (along the x-axis) where *N*, *A*, and H_o are reduced and F_{ST} is increased with greater patchiness on the landscape; B) suitable habitat largest patch index percentage (along the x-axis) where *N*, *A*, and H_o are reduced and F_{ST} is increased as suitable habitat patches decrease in size; C) suitable habitat percentage of landscape (along the x-axis) where *N*, *A*, and H_o are reduced and F_{ST} is increased as suitable habitat area decreases.

Discussion

Connectivity improves with corridors and higher population densities

Understanding how barriers contribute to declines in desert tortoise connectivity is crucial to conservation efforts (Averill-Murray et al. 2012). Even barriers that were not absolute decreased the number of individuals on the landscape and reduced gene flow. The result was the creation of isolated populations that would otherwise not form, ultimately increasing genetic differentiation and reducing overall genetic diversity. Adding limited permeability along absolute barriers (like culverts) allowed for some admixture; but this did not entirely negate genetic effects. Our results demonstrate that low levels of gene flow (i.e. the one-migrant-per-generation rule) may suffice in preventing deleterious effects of inbreeding, but, will not adequately maintain comparable allele frequencies, or genetic connectivity, between populations (Lowe & Allendorf 2010).

The impacts of landscape change on genetic architecture is associated with a considerable lag time in detection (Anderson et al. 2010; Landguth et al. 2010). Our simulations indicate that with any barrier (absolute or semipermeable) structure will be evident within 200 generations of disturbance. Given appropriate conditions (low population density, increased number of loci) the effects of a barrier may be noticeable in as few as five generations. Connectivity on the landscape was found to be heavily influenced by population density, and landscapes with lower density populations experienced greater reductions in population size and genetic diversity (heterozygosity and alleles/locus) with or without barriers (see Appendix I for details). Absolute barriers fragmented populations, increasing genetic differentiation and population genetic structure. When density was moderate to high, genetic diversity was largely unaffected and population size only decreased when a barrier was present or habitat was lost. As density increased barriers resulted in greater genetic differentiation and population genetic structure, but to a lesser degree. Adding permeability to barriers is predicted to improve connectivity at any population density; however, the consequences of low density may result in greater risk of genetic drift and harmful stochastic demographic processes (Dileo et al. 2013; Mateo-Sanchez et al. 2014; Moqanaki & Cushman 2016).

Evaluating the total number of individuals and population genetic structure was useful in detecting changes in scenarios, and genetic diversity was most informative at low population densities. Therefore, in future studies small changes to genetic diversity should be taken as an indication that a population has potentially declined (Barr et al. 2015; Segelbacher et al. 2003; Vandergast et al. 2015; Wood et al. 2016). Altering the population growth rate from0.5% to 1% annual growth did not influence genetic connectivity in this study, but future investigations could benefit from additional research on this parameter, as well as dispersal probability/migration rate estimates. Using more loci did not change the modeling outcomes. However, we were often able to more clearly detect spatial autocorrelation and population genetic structure in fewer generations with more loci (between five and 40 generations following disturbance).

Anthropogenic disturbance reduces gene flow and population size

As anthropogenic disturbance increased, so did demographic and genetic effects. Habitat degradation resulted in population declines, with the most pronounced losses concomitant with increased habitat disturbance (given in the future prediction scenarios). For desert tortoises, genetic diversity was predicted to be highest in undisturbed (neutral) landscapes, and generally decreased as disturbance progressed. Additionally, the greater the disturbance the stronger the population genetic structure (see Results for Fig. 4).

However, outcomes for maintaining genetic connectivity in disturbed landscapes are variable. While neutral landscapes always fared better than disturbance scenarios, the corridor success index (based on genetic differentiation), predicted landscapes that maintain high levels of genetic connectivity experienced no more than a 27% loss in population. Losses as low as 12% were seen in landscapes with intermediate genetic connectivity. These landscapes generally did not lose more than 30% of their population. Losses in low/no genetic connectivity landscapes were often higher, but could start at a 21% reduction. If these numbers hold true, this has significant implications given that Mojave desert tortoises are estimated to have lost roughly 37% of their population range-wide from 2004 – 2014 (Allison & McLuckie 2018).

When genetic connectivity was high, population genetic structure showed substantial admixture when compared with neutral landscapes, while intermediate and low/no genetic connectivity landscapes lost gene flow. Genetic effects (i.e. loss of genetic diversity and increase in population genetic structure) indicate a landscape that lost connectivity roughly five to 40 tortoise generations prior (85 – 680 years). Therefore, careful consideration of population declines and habitat development are needed to prevent deleterious effects to connectivity before they are apparent (Gregory & Beier 2014). In landscapes where increases in genetic structure and/or slight deviations in genetic diversity have been documented, efforts focused on reducing development pressures in tortoise habitat, restoring habitat, and adding permeability to landscape barriers will have the greatest benefit for connectivity.

Corridor success is landscape dependent

Given the challenges of capturing ecological processes with landscape patterns and the overlap we found when sorting landscapes by corridor success index values, it is most appropriate to evaluate landscape locations as individual management units, rather than seek a single metric as a threshold. Disturbance landscapes with high levels of genetic connectivity tended towards low levels of landscape fragmentation and complexity. Suitable habitat amount and dominance of the largest patch remained high. It is important to note that even though high levels of gene flow were maintained in these disturbance landscapes, they all lost genetic connectivity, with 90% being the highest level retained (Laughlin) and -124% being the lowest (Jean/Roach). Clearly, habitat loss and degradation are accelerated by development pressures. It is therefore not surprising that future disturbance scenarios had fewer landscapes that retained high levels of genetic connectivity (29%) and many (47%) failed to maintain genetic connectivity.

Management recommendations

Balance between land use promoting economic and population growth and the long-term conservation and recovery of natural habitats and native species is the key purpose of the Clark County, Nevada Multiple Species Habitat Conservation Plan (MSHCP 2000). Our results indicate that current and planned activities related to economic and urban growth will result in desert tortoise population declines and loss of genetic connectivity, disrupting this balance. For the future development scenarios data were not available regarding disturbance beyond the urban footprint (e.g. increased dirt roads). A literature review found anthropogenic disturbance to have a greater potential for habitat degradation than the development footprint alone (Lovich & Ennen 2011, Hunter et al. 2003). At each modeled location the total number of individuals was always highest with neutral landscape simulations and lowest with future projections of anthropogenic disturbance, with genetic diversity following the same pattern. Genetic differentiation and population genetic structure were always lowest in neutral landscapes and highest with future projections of disturbance. Therefore, we recommend more critical evaluation of proposed developments and reduction of anthropogenic disturbance in Mojave desert tortoise habitat.

Landscapes with high levels of genetic connectivity should be prioritized for conservation to ensure additional habitat is not lost. Landscapes with intermediate genetic connectivity are excellent candidates for strategically restoring habitat and connectivity linkages. Models evaluating landscape change scenarios have shown that reductions in protected habitat results in large declines in connectivity, while corridors between protected areas may serve to increase connectivity (Cushman et al. 2016; Huxel & Hastings 1999; Nowakowski et al. 2015). Landscape scenarios that fail to maintain genetic connectivity would benefit from major reductions in planned development and improvements to habitat in already disturbed areas. Ensuring Mojave desert tortoise habitat is protected could move us towards reversing the trend of continually degrading habitat and reducing connectivity, improving the opportunity for species recovery (Allison & McLuckie 2018; Averill-Murray et al. 2013; Boarman 2002) while preserving our unique natural heritage.

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