




Determining the drivers of population structure in a highly urbanized landscape to inform conservation planning

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Abstract: *Understanding the environmental contributors to population structure is of paramount importance for conservation in urbanized environments. We used spatially explicit models to determine genetic population structure under current and future environmental conditions across a highly fragmented, human-dominated environment in Southern California to assess the effects of natural ecological variation and urbanization. We focused on 7 common species with diverse habitat requirements, home-range sizes, and dispersal abilities. We quantified the relative roles of potential barriers, including natural environmental characteristics and an anthropogenic barrier created by a major highway, in shaping genetic variation. The ability to predict genetic variation in our models differed among species: 11–81% of intraspecific genetic variation was explained by environmental variables. Although an anthropogenically induced barrier (a major highway) severely restricted gene flow and movement at broad scales for some species, genetic variation seemed to be primarily driven by natural environmental heterogeneity at a local level. Our results show how assessing environmentally associated variation for multiple species under current and future climate conditions can help identify priority regions for maximizing population persistence under environmental change in urbanized regions.*

Keywords: adaptive variation, climate change, conservation planning, landscape genetics, population genetics, Santa Monica Mountains, vertebrates

Determinación de los Conductores de la Estructura Poblacional en un Paisaje Altamente Urbanizado para Informar a la Planeación de la Conservación

Resumen: *El entendimiento de los contribuyentes ambientales a la estructura poblacional es de importancia primordial para la conservación en ecosistemas urbanizados. Utilizamos modelos espacialmente explícitos para determinar la estructura genética poblacional bajo condiciones ambientales actuales y futuras a lo*

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largo de un ambiente dominado por humanos y altamente fragmentado en el sur de California para valorar los efectos de la variación ecológica natural y la urbanización. Nos enfocamos en siete especies comunes con diversos requerimientos de hábitat, tamaños de extensión doméstica, y habilidades de dispersión. Cuantificamos los papeles relativos de las barreras potenciales, incluyendo las características ambientales naturales y una barrera antropogénica creada por una gran autopista, en la formación de la variación genética. La capacidad de predecir la variación genética en nuestros modelos difirió entre especies: el 11 - 81% de variación genética intraespecífica se explicó con variables ambientales. Aunque una barrera inducida antropogénicamente (una gran autopista) restringió severamente el flujo génico y el movimiento a escalas grandes para algunas especies, la variación genética pareció estar conducida principalmente por la heterogeneidad ambiental natural a nivel local. Nuestros resultados muestran cómo la valoración ambiental asociada con la variación para múltiples especies bajo condiciones climáticas actuales y futuras puede ayudar a identificar las regiones prioritarias para maximizar la persistencia poblacional bajo el cambio ambiental en regiones urbanizadas.

Palabras Clave: cambio climático, genética de paisajes, genética poblacional, Montañas de Santa Mónica, variación adaptativa, vertebrados

Introduction

Genetic variation is an essential component of biodiversity (Frankel 1974); it provides the building blocks for populations to adapt to changing environmental conditions that are critical for long-term persistence (e.g., Smith et al. 1993; Vandergast et al. 2008; Hoffmann & Sgro 2011). Given rapid habitat modification due to climate change, urban development, and other anthropogenic pressures, it is urgent to protect this environmentally associated variation (EAV), as opposed to protecting variation resulting simply from demographic processes (Thomassen et al. 2011). When populations become increasingly fragmented, their ability to track optimal habitat conditions by dispersing may become limited. In these cases, adaptation is required to prevent extirpation.

Whether and how quickly populations can adapt to changing conditions depends largely on the amount of standing genetic EAV. Understanding the drivers and distribution of EAV is thus an important step in conservation prioritization but has long been limited due to constraints in molecular techniques and spatial modeling. However, with the emergence of the field of landscape genetics (Manel et al. 2003; Storfer et al. 2007), it is now possible to integrate such data in studies for applied management (Thomassen et al. 2011; Manel & Holderegger 2013). Our previous work suggested that areas important for protecting EAV in one species are also important for others (Thomassen et al. 2011). Whether or not these similarities hold at smaller spatial scales, however, has yet to be tested, and it is at least possible that the correlation between diversity patterns may break down due to more localized evolutionary and demographic processes differentially affecting the geographic distribution of EAV in different species.

To better understand these relationships and inform conservation and prioritization more generally (at different spatial scales and levels of disturbance), we applied our approach to species in Santa Monica Mountains

National Recreation Area (SMMNRA), northwest of Los Angeles, California. This region is a 634-km² semiarid area characterized by coastal sage scrub and chaparral vegetation that extends from sea level to 948 m. The landscape is heavily threatened by urbanization, which is estimated to increase from 11% urbanized in 2000 to 47% by 2040 (Syphard et al. 2005). We assessed the distribution of EAV in 7 species to understand how their populations are differentially affected by natural conditions and a highway barrier. We selected species for which genetic data were readily available (Semple Delaney et al. 2010) and that represented diverse taxonomic groups, including reptiles, amphibians, birds, and mammals.

Our objectives were to determine patterns of population structure in a diverse set of species, identify the main (environmental) drivers of divergence in species in this region, evaluate the concordance between the spatial patterns of EAV among taxa, and investigate how EAV will be affected by future environmental conditions, including climate change.

Methods

Study Species and Modeling Approach

To contrast species-specific spatial patterns of genetic variation, we used existing genetic data (Riley et al. 2006; Semple Delaney et al. 2010; Serieys et al. 2015) on the following species from 15 to 25 sites in SMMNRA (details in Table 1 and Supporting Information): gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), Wrentit (*Chamaea fasciata*), Pacific tree frog (named *Pseudacris regilla* or *Pseudacris hypochondriaca* [see Recuero et al. 2006]), western fence lizard (*Sceloporus occidentalis*), side-blotched lizard (*Uta stansburiana*), and western skink (*Plestiodon skiltonianus*). These species have a variety of mobility patterns, occupy different niches, and represent a range of strata within the

Table 1. Species included, number of microsatellite loci, and sample sizes in a study of 7 species occurring within Santa Monica Mountains National Recreation Area (U.S.A.).

<i>Species name</i>	<i>No. of loci</i>	<i>Total no. samples</i>	<i>No. of locations</i>	<i>Samples per location</i>
Western skink (<i>Plestiodon skiltonianus</i>)	6	225	15	5-29
Western fence lizard (<i>Sceloporus occidentalis</i>)	8	239	17	8-18
Side-blotched lizard (<i>Uta stansburiana</i>)	8	215	15	2-18
Wrentit (<i>Chamaea fasciata</i>)	7	105	10	3-18
Gray fox (<i>Urocyon cinereoargenteus</i>)	8	35	35	1
Pacific tree frog (<i>Pseudacris regilla</i>)	7	299	25	10-15
Bobcat (<i>Lynx rufus</i>)	9	319	319	1

vegetation (Fitch & Pennie 1977; Doughty & Sinervo 1994; Doughty et al. 1994; Baker et al. 1995; Massot 2003; Sinervo et al. 2006). Each species is common and widely distributed within California (Stebbins 1954; Busteed 2003), although Wrentits are limited to coastal chaparral habitat (Geupel et al. 2002).

We first gathered satellite-based elevation, vegetation, and temperature data and long-term climate data from weather stations. We then used spatially explicit ecological-modeling techniques (Thomassen et al. 2010) to relate these environmental conditions to genetic variation and project EAV across the landscape. In accordance with our objectives, we identified spatially explicit population structure across SMMNRA and surrounding areas; tested for correlations between genetic variation with landscape features and habitat characteristics; predicted the distribution of genetic variation across the study landscape; and projected how patterns of genetic variation are likely to shift under climate change.

For each species, this procedure resulted in maps of the spatial distribution of genetic variation under current and future climate conditions. We qualitatively compared these maps to evaluate concordance between species and quantitatively assessed the level of congruence between these regions with Mantel correlations in the *ade4* package in R (R Core Team 2014) and plotted pairwise site differences for each pair of species. Finally, we evaluated whether the most important environmental predictors in our models (GDM models, see below) relating environmental characteristics to genetic composition were similar across species in order to determine whether common environmental drivers were responsible for genetic changes across a wide diversity of taxa.

Genetic Data

We used microsatellite data derived from individuals sampled as part of previous research in SMMNRA for western skink, western fence lizard, side-blotched lizard, Wrentit (Semple Delaney et al. 2010), bobcat (Riley et al. 2006; Serieys et al. 2015), and Pacific tree frog (Pease 2011; Pease & Wayne 2014), and supplemented these with new data for the gray fox (in Supporting Information). The data sets included georeferenced genotypes for each sampled individual. Multiple individuals were sampled

per location for all species, except for bobcats and foxes, which all had unique GPS locations.

Environmental and Anthropogenic Variables

We used data resolved to 200 m–1 km (based on available data resolutions, Table 2 & Supporting Information) because dispersal within one generation for most of these species tends to be within this range (Massot 2003; Sinervo et al. 2006). Temperature was expected to influence genetic variation in these species because four of the study species are ectothermic. Furthermore, precipitation was expected to be important because 2 of the target species (Pacific tree frog and western skink) are at least partially dependent on water resources; the Santa Monica Mountains and surrounding areas are a relatively arid region; and understory growing season and resource use are likely both water limited in this region.

Previous work indicates that U.S. Highway 101 (hereafter US 101) may act as a dispersal barrier (Riley et al. 2006, 2014; Serieys et al. 2015) and thus reduce gene flow between local populations. We included this barrier hypothesis by generating a GIS raster layer in which the areas north and south of US 101 were coded as a binomial variable. This procedure allowed a test of whether US 101 acts as an influential barrier between populations and whether it or environmental conditions can best explain genetic variation in current populations.

Determining Spatially Explicit Population Structure

We used Geneland (Guillot et al. 2005) in R (R Core Team 2014) to examine spatially explicit population structure for each of the target taxa. Geneland is a Bayesian clustering algorithm that takes into account the geographic location and orientation of samples. Models were run for 500,000 iterations with a thinning interval of 100 for all genetic data. Geneland and its inference methods are not used to relate genetic structure to environmental predictors. Rather, the genetic structure and geographic coordinates of each location's samples are compared and used to infer a number of homogenous groups corresponding to putative populations within the study region and the most likely membership in each of those groups for every pixel within the study region.

Table 2. Environmental and anthropogenic variables used in modeling intraspecific variation in Santa Monica Mountains National Recreation Area (U.S.A.).

<i>Data record</i>	<i>Instrument</i>	<i>Ecological attributes</i>	<i>Variables derived*</i>	<i>Resolution</i>
Normalized difference vegetation index (NDVI)	advanced spaceborne thermal emission and reflection radiometer (ASTER)	vegetation density, SD	NDVI mean, NDVI SD	200 m
Vegetation cover fraction (VCF)	satellite MODIS	percent tree cover	trees	250 m
Scatterometer backscatter	satellite Quick Scatterometer (QSCAT)	surface moisture	QSCAT	30 arcsec (~ 750 × 900 m)
Digital elevation model (DEM)	ASTER	elevation, steepness of terrain, direction of slope	elevation, slope, aspect	200 m
Temperature WorldClim	ASTER station network	temperature in August bioclimatic variables	temperature Bio 1, Bio 2, Bio 4, Bio 5, Bio 6, Bio 12, Bio 15, Bio 18, Bio 19	200 m 30 arcsec (~ 750 × 900 m)
California road map		Highway US 101 as a barrier to gene flow	US 101	200 m

* Abbreviations: Bio 1, mean annual temperature; Bio 2, mean temperature range; Bio 4, temperature seasonality; Bio 5, maximum temperature; Bio 6, minimum temperature; Bio 12, mean annual precipitation; Bio 15, precipitation seasonality; Bio 18, precipitation of warmest quarter; Bio 19, precipitation of coldest quarter; SD, standard deviation.

Predicting Genetic Variation

To assess correlations of genetic data with environmental variables, geographic distance, and the barrier US 101, we used generalized dissimilarity modeling (GDM) (Ferrier et al. 2007) in the R package *gdm* (Manion et al. 2015). We used GDM to predict the relationship between predictor variables and pairwise genetic distances (F_{ST} , as response variables) in each of the target taxa.

Four types of models were run. They varied only in the predictor variables used: best fit (including all environmental variables, US 101 barrier, and geographic distance); environmental variables and US 101 barrier only; straight-line geographic distance only; and a set of 1000 models with randomized environmental variables. Results of these models were compared to evaluate the significance of the variation explained by the model with the best fit. The model with the best fit was not significant if the variation explained fell below the upper 95% confidence interval of the random models.

In a subsequent step, the spatial distribution of the response variable was projected across the study area based on the known environmental conditions (obtained from the predictor variables) and the previously computed relationship between the environment and genetic variation. We visualized this genetic variation with a color gradient, where different colors represented different genetic compositions. To do so, we first extracted the values of the environmental variables included in the model from all grid cells across our study region. The response (i.e. genetic distance) was then predicted for each pair of grid cells, resulting in a dissimilarity matrix. We then reduced the dimensionality of this matrix to one coordinate axis ($k = 1$) through classic multidimensional

scaling (MDS) with the *cmdscale* command in R (R Core Team 2014).

Predicting Genetic Change under Climate Change

Assuming the relationship between genetics and environment does not change in the future, current predictions of genetic diversity can be used to understand spatiotemporal dynamics under future climate scenarios. Whereas the exact nature of changes will remain unknown, under a scenario of isolation by adaptation (Nosil et al. 2008), or linkage of microsatellites to genes under selection, predictive maps can highlight areas where populations will likely be at high risk of being affected by climate change. To assess the potential for such an effect of future climate change on genetic diversity, we created a model based solely on current climatic conditions (i.e. without vegetation and elevation variables); projected these F_{ST} -climate associations onto predicted future climate layers from the IPCC (Intergovernmental Panel on Climate Change) 5th Assessment Report Representative Concentration Pathway (RCP) 6.0 and 8.5 scenarios for 2050–2060 and 2080–2090; and created maps that showed changes between current and future conditions with the *predict* function in R (R Core Team 2014).

Results

Population Structure

All study species, with the exception of the western skink, showed population structure north and south of US 101 (Fig. 1 & Supporting Information). In 5 of our

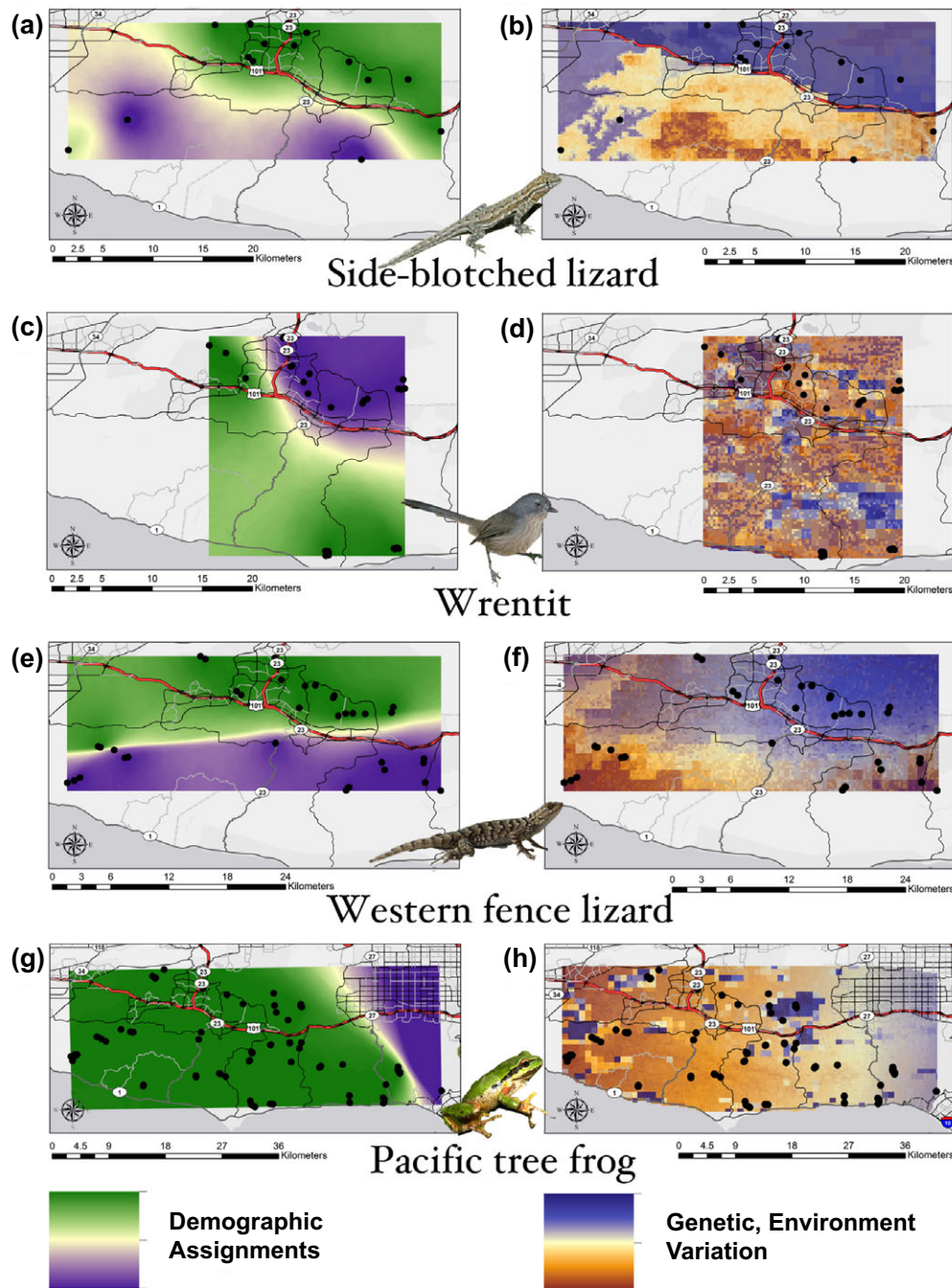


Figure 1. Results from Geneland and best fit models (from GDM) for 4 species. Panels on the left (a, c, e, g) show genetic differences between populations as measured by demographic models (Geneland) and panels on the right (b, d, f, h) show the genetic differences between populations as they relate to GDM. The larger the color difference, the larger the genetic difference. Colors in the Geneland maps represent the probability of membership in 1 of 2 populations (range 0–1). In the GDM maps, a comparison of the colors of any 2 sites on the map along the color bar represents the populations' pairwise genetic distance (F_{ST}). The color bars are stretched across the largest observed F_{ST} values for each species: side-blotched lizard, 0.234; Wrentit, 0.288; and western fence lizard, 0.109. See Supporting Information for maps of remaining species.

7 target taxa, populations were clustered into 2 major groupings according to Geneland results ($K = 2$), and this split occurred along a horizontal axis, largely concordant with US 101. The gray fox was assigned to 4 groups and the western skink to 6. There was some evidence of movement between areas north and south of US 101 for each of these species (Supporting Information).

Models under Current Environmental Conditions

The total amount of variation explained ranged from 11.0% in gray fox to 81.3% in side-blotched lizards. Models for species with the highest dispersal ability (bobcat and gray fox) underperformed. In these cases, the spatial extent of our study may have been too small to find significant genotype–environment associations, or the spatial resolution (250 m–1 km) may have been too fine-scaled for species with a high capacity for dispersal. For the gray fox, sample size was relatively low, potentially reducing statistical power. Despite the clear splits in population structure, genetic variation between populations was not best explained by geographic location or distance alone. Although geographic distance was included in the best fitting models for the gray fox, Pacific tree frog, and western fence lizard, in each of these cases, geographic distance explained only a small proportion of total genetic variation (0–5.2%) when it was the only predictor variable included (Table 3). This suggests distance alone contributed little to explaining observed variation in these species, whereas environmental variation explained a much greater amount of population divergence. The environmental variables that most affected divergence, however, varied between species (Table 3 & Supporting Information). The highway US 101 was included in the best fitting model only for the side-blotched lizard, suggesting the road is a primary driver of population structure for this species because it acts as a major barrier to dispersal and gene flow.

A visual inspection of the genetic dissimilarities in each species (Fig. 1) showed how genetic profiles differ across the study area. There appeared to be little concordance among species. This observation was supported by low Mantel correlation coefficients (0.18–0.48) (Supporting Information) and by scatterplots of site pairs for each pair of species (Supporting Information). Comparisons between predictive maps of genetic variation and maps of individual environmental variables (Fig. 1 & Supporting Information) provided insight into the underlying drivers of genetic variation. For the western skink, there was no clear pattern that could be attributed to one or a few environmental variables. For the gray fox, there was a slight southwest to northeast gradient that tracked precipitation gradients (Bio 15) and a more pronounced pattern related to aspect (a measure of elevational differences). For the Pacific tree frog, the pattern of EAV was mostly related to deviations in vegetation (normalized

difference vegetation index [NDVI] SD). For the western fence lizard, there was a west-east distance component, and a coast-to-inland pattern related to surface moisture (QSCAT). The spatial distribution of genetic variation in the side-blotched lizard was the result of a combination of a north-south differences across US 101, an east-west gradient of temperature (Bio 1), and a scattered pattern of elevation. Finally, the pattern for the Wrentit seemed to be driven by changes in vegetation (NDVI SD).

Genetic Change under Future Climate Conditions

We computed the change in the genetic makeup of each species between current and future conditions (Fig. 2). Only small differences were observed between RCPs and time periods. However, both the magnitude and the spatial patterns of predicted changes varied greatly among species. Despite these interspecific differences in the spatial distribution of genetic changes, a broad trend appeared to indicate that the most severe changes to genetic variation were observed in the south-central and northeastern part of SMMNRA.

Discussion

We found that the spatial patterns of EAV in a diverse set of species in an urbanized landscape at a small geographic scale were largely discordant. Population divergence was driven primarily by natural environmental heterogeneity, but we also found evidence for a barrier effect by US 101. In cases where environmental variables were responsible for the observed patterns, future climate change is likely to have distinct effects on different species.

Population Structure and Drivers of Divergence

Genetic structure was broadly consistent with habitat fragmentation by major highways and urban areas in 5 of the 7 target taxa investigated, suggesting US 101 acts as a geographic barrier to individual animal movement and gene flow between populations. More detailed models suggested there was further substructuring within species, where environmental variables explained the largest amount of the observed genetic variation. From this we conclude that natural selection at small spatial scales plays an important role in population divergence in these species. This conclusion is particularly striking in the side-blotched lizard, where > 80 % of genetic variation was explained by environmental variables. For all species, a proportion of the observed genetic variation remained unexplained, however. One potential reason for this lack of explanatory power may be that habitat conditions other than those included may be causing strong divergent selection or limiting dispersal between populations. For instance, we did not

Table 3. Generalized dissimilarity modeling results showing the associations between genetic variation and environmental variation for 7 species in Santa Monica National Recreation Area (U.S.A.).*

Species	Best fit	Variables > 50% of max.	Env only	Dist only	Random	Right 95% CI of random models
Western skink (<i>P. skiltonianus</i>)	45.2	QSCAT, Temp, NDVI, Bio 19	45.2	0.0	20.6	21.1
Western fence lizard (<i>S. occidentalis</i>)	35.1	QSCAT, Dist, Aspect, Bio 6	31.1	5.2	16.4	16.9
Side-blotched lizard (<i>U. stansburiana</i>)	81.3	Bio 1, Elev, US Highway 101	81.3	0.0	19.9	20.2
Wrentit (<i>C. fasciata</i>)	70.3	NDVI SD	70.3	0.0	37.8	38.3
Pacific tree frog (<i>P. regilla</i>)	30.2	NDVI SD, Dist	28.6	2.9	7.1	7.2
Gray fox (<i>U. cinereoargenteus</i>)	11.0	aspect, Bio 15, slope	10.9	3.2	3.4	3.5
Bobcat (<i>L. rufus</i>)	2.9	n.t.	n.t.	n.t.	n.t.	n.t.

* Abbreviations: Env, Environmental variables; Dist, Euclidean distance between sites; QSCAT, Quick Scatterometer used to measure surface moisture; NDVI, normalized difference in vegetation index, a measure of vegetation greenness; Bio, biological variables defined in Table 2; n.t., not tested.

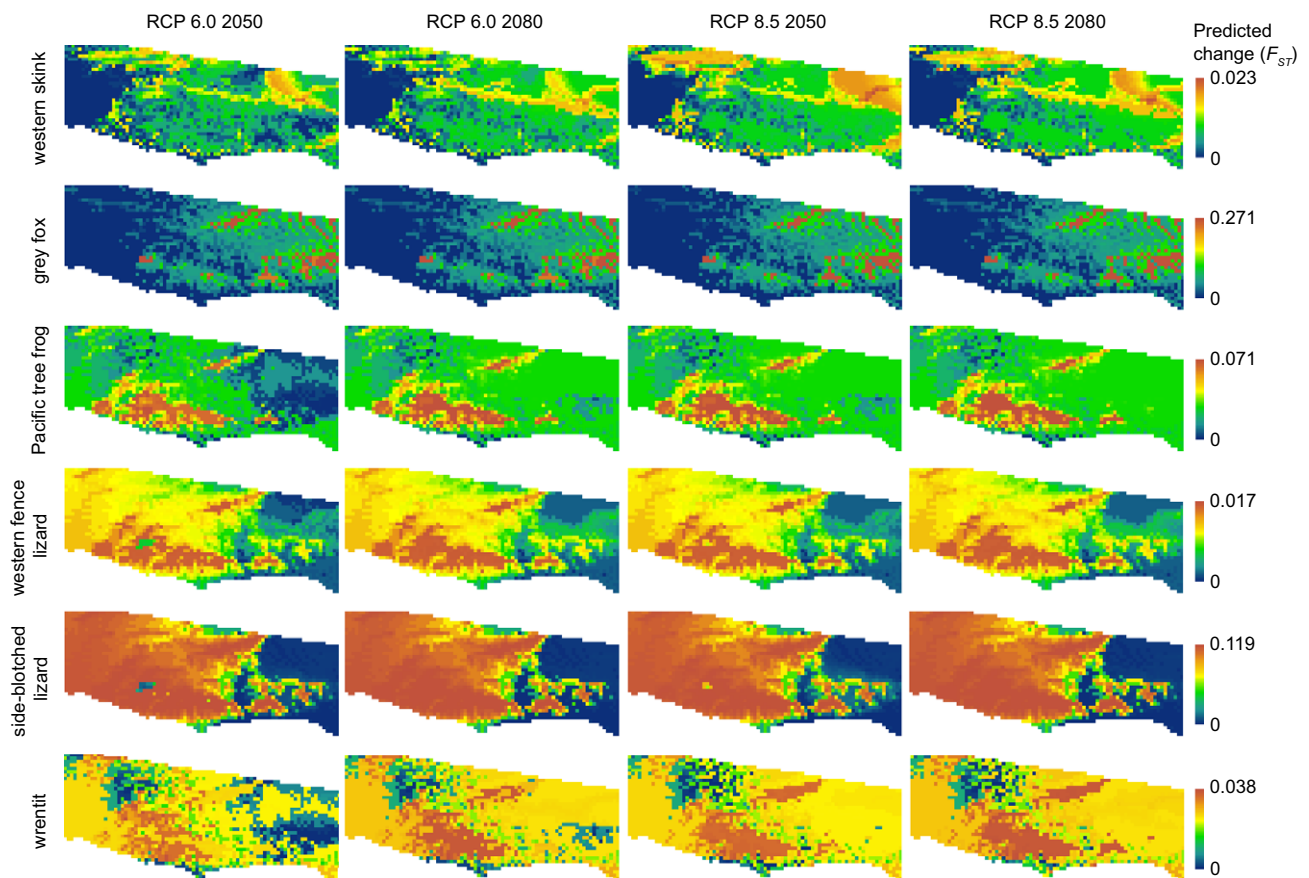


Figure 2. Predicted genetic change (F_{ST}) between current conditions and future climate change scenarios for representative concentration pathway (RCP) 6.0 and 8.5, and for the periods 2050–2060 and 2080–2090. Scales of the color stretch differ among species.

consider isolation by resistance, where unfavorable habitat conditions between populations constrain dispersal and gene flow (McRae 2006). Another explanation for the remaining variation may relate to chance events that are not linked to long-term environmental conditions or

the distance between populations, such as demographic fluctuations due to bottlenecks (Serieys et al. 2015), artificial introductions by human-mediated movements (intentional or accidental), competition with other species, or isolation by colonization (IBC) (De Meester et al. 2002;

Orsini et al. 2013). Under IBC a signal of founder effects can persist over time due to monopolization, where local adaptation is based only on standing genetic variation present in the first colonizers and new dispersers cannot establish themselves. However, such a scenario may be unlikely in species that have inhabited small areas for a relatively long time, as is the case here.

A previous study on 4 of the 7 species studied here (side-blotched lizard, western skink, western fence lizard, and Wrentit) from sites clustered around Highway 23 showed a significant reduction in gene flow across this smaller highway (Semple Delaney et al. 2010), which intersects US 101 (Fig. 1). Similarly, population structure in bobcats and coyotes (*Canis latrans*) is influenced by US 101 (Riley et al. 2006). We also found that US 101 was a major driver of population structure in the side-blotched lizard (Table 3, Supporting Information). Previous studies suggest urbanization may lead to substructuring of populations, even when strong physical barriers are absent (Hitchings & Beebe 1997; Noël et al. 2007). Such substructuring may lead to smaller population sizes and ultimately to reduced genetic diversity in urbanized areas relative to natural areas (Vangestel et al. 2012; Keely et al. 2015; Munchi-South et al. 2016).

Despite potential impacts of urbanization, for at least some of the species studied, a major urban barrier (US 101) did not play a significant role in structuring populations. There are at least 4 potential reasons this highway did not appear to impede gene flow. First, not enough time may have passed for a major break in genetic structure to evolve in most species, where the signal of environmentally related divergence swamps that of variance across the highway. Nevertheless, the highway was constructed as early as 1949 in some places, and it would be expected that a reduction in gene flow for 50–60 generations would be revealed in estimates of microsatellite variation. Second, the highway runs parallel to the coast, along a natural environmental gradient from coast to inland that can be observed in some environmental variables (Supporting Information), and the road may therefore simply be a good surrogate of environmental variation when no other predictor variables are taken into account. In addition, urbanization occurs to varying degrees along US 101, resulting in different environments and associated genetic variation across the highway (in this sense, anthropogenic changes may drive environmental ones). Finally, US 101 was modeled as a binary factor in GDMs. This approach likely resulted in an oversimplification of the actual environment, in which there are nuanced natural and road barriers in the north and the south that are not captured using a binary predictor. Further investigation of populations along this highway are necessary to tease apart how influential each of these explanations is for the patterns observed. Regardless of which of these potential explanations is more likely, it will be crucial to maintain or reestablish gene flow across

the highways to maximize the probability of long-term survival for these species facing both climate change and continued urbanization in this area.

Variation in Environmental Drivers

In previous studies at larger geographic scales, we have found remarkable concordance in the spatial patterns of EAV among species (Thomassen et al. 2011). However, at the smaller scale of this study, those patterns of EAV varied greatly (Fig. 1). In fact, the small spatial scale and extent of our study may be a reason for this lack of interspecific concordance in the spatial distribution of EAV. The spatial patterns of the large-scale evolutionary processes that generate population divergence (e.g., selection by broad climate conditions or along major topographic features such as mountain ranges) may be common to entire ecological communities and result in similar spatial patterns of EAV among species at such scales. However, at smaller scales population divergence may be caused by processes more mechanistic in nature that differ among species and are more prone to be affected by chance demographic events. Exactly at what scale the concordance between patterns of EAV breaks down depends on the ecology of a species and on the level of environmental heterogeneity and should be a topic for future study.

Genetic Change under Future Climate Conditions

Given the difference between species' adaptive ability and their patterns of EAV under current conditions, it is no surprise that both the magnitude and the spatial distribution of genetic change in the future vary considerably among species. For models with higher RCPs and projected further into the future, environmental conditions increasingly exceed those currently observed, specifically in areas where the biggest changes are predicted (south-central and northeastern regions of SMMNRA). On the one hand, this means interpretation of models in those areas needs to be done cautiously because the gene-environment relationships are extrapolated to extreme conditions (based only on current observable relationships) and may be less accurate. On the other hand, these predictions may be particularly informative because populations in those areas are probably at much greater risk than those in other areas, regardless of the exact magnitude of required change predicted.

Predictions of genetic change under future conditions are made under the assumption that current genotype-environment associations will remain the same in the future and that such spatial associations can be translated across decades. Such predictions ignore the potential for entirely new selective pressures to arise, for instance by environmental conditions that have never been met before, and for changes in community composition

and species interactions. Moreover, scenarios for climate change are specific as to temperature and precipitation variables, but it is much harder to predict how vegetation characteristics (e.g., percent tree cover, NDVI, and NDVI SD) and evapotranspiration (which dictates levels of surface moisture, captured by QSCAT) will change in the future. Vegetation and moisture variables are, therefore, omitted or kept constant for predictions of future EAV, even though they are likely to change themselves as climate conditions change. Despite these caveats, predictions of genetic change under future climate conditions may be a useful first-order assessment of the spatial variation in the magnitude of required genetic adaptations and associated risks for particular populations.

Management Implications and Future Directions

Genetic variation is an important component of biodiversity and should be considered carefully in conservation prioritization efforts (e.g., Frankel 1974; Moritz 2002; Smith & Grether 2008). Advances in association studies and spatial modeling have made it possible to not only take into account overall genetic diversity but also to account for genetic variation associated with the environment that may be particularly relevant for a species' long-term persistence. Ideally, a small set of surrogate species can represent most of the ecological community, and surrogacy is suggested to be sufficient at larger scales (Thomassen et al. 2011). However, our results suggest spatial patterns of EAV at smaller scales may vary considerably among species, reducing the surrogacy of selected species. Under such conditions, the utility of EAV in conservation prioritization could be improved by comparing life history, vagility, morphology, and trophic niche of species occurring in an area and selecting representative species across the range of these traits; increasing the number of different species for which genetic analyses are carried out; and incorporating a larger suite and variety of genetic markers to determine whether patterns observed are reflected genomewide within species.

We also recommend modeling genetic changes under future climate conditions. Using dedicated reserve design software (e.g., Moilanen & Kujala 2008; Ball et al. 2009; Sarkar et al. 2009), 2 sets of prioritized areas can be created: one under current conditions and one under projected future climate conditions. Prioritization scenarios with the highest overlap between current and future reserves may be selected for in a second iteration of reserve design. Here, the set of reserves under future conditions could serve as a starting point for prioritization under current conditions to ensure that the target representation for each level of biodiversity is met under both current and potential future conditions. Despite the discussed caveats of future predictions, such a procedure has the advantage that scenarios for climate change are taken into

account and identification of areas for protection is thus optimized, even if future predictions can be improved as additional data are collected.

Highway US 101 influenced breaks in population structure in nearly all species and was a major explanatory variable of genetic divergence in the side-blotched lizard even when environmental variables were also taken into consideration. Both north and south of the highway, unique genetic variation existed in this species and was related to annual mean temperature (Bio 1) and elevation. Along with evidence from previous studies on these species, and focusing on the influence of major roads on divergence between populations, our results suggest that conservation efforts should consider reestablishing gene flow across US 101 (Riley et al. 2014) that would allow exchange of genetic material that may be important for the long-term survival of these species in SMMNRA. Whereas populations across SMMNRA are predicted to be affected by climate change (Fig. 2), those south of the highway could benefit from gene flow from the north. Southern populations occur in an area that will become warmer and drier (i.e., more similar to current conditions north of US 101). Thus, gene flow between inland (north of US 101) and coastal (south of US 101) populations may allow for an improved adaptive response of the latter. Although not specifically included as a barrier in this study, US 23 reduces gene flow (Semple Delaney et al. 2010), and further studies into its influence on population structure and ways to mitigate its impact should be conducted.

Despite differential patterns of EAV in the species studied, two main gradients in EAV can be recognized: the southern coast to inland, related to surface moisture (QSCAT), and the east to west, mostly related to annual mean temperature (Bio 1) and precipitation seasonality (Bio 15). To maximize the adaptive potential of species, populations should be protected along both gradients and corridors for dispersal and gene flow should be established between protected sites. Final prioritization in this area should also include traditional measures of species richness and complementarity, as well as potentially important socioeconomic factors (e.g., Liu et al. 2007). Such factors may be as divergent as public support for the protection of natural areas, economic conditions, pressure for new commercial developments, costs of land to be acquired for protection, and educational programs that raise awareness of the importance of biodiversity and ecosystem services.

We found that spatial patterns of EAV among a diverse set of species were largely discordant at relatively small geographic scales. We recommend that future studies apply a nested sampling design at multiple scales and use a genomic-level suite of molecular markers to measure adaptive variation. These types of studies will be most effective for understanding the potential relation between spatial scale and concordance of patterns of EAV among

species and could lead to a new understanding of EAV and its utility for conservation prioritization.

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Supporting Information

Sampling and laboratory methods and population genetic analyses (Appendix S1); information on model performance and variable importance (Appendix S2); comparisons of the spatial patterns of genetic variation between species (Appendix S3); supplementary figures showing maps of the environmental variables used, Geneland and GDM maps for bobcat, gray fox, and western skink, GDM response curves for each species, and scatterplots of species-by-species comparisons of F_{ST} values per site pair (Appendix S4); and the location and genotype data for the gray fox (Appendix S5) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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