Research Article

Measuring environmental niche isolation between genetically management units of Goitered gazelle, *Gazella subgutturosa* (Guldenstadt, 1970) in Iran

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Abstract

The interactions between species and their environments can shape distribution of spatial genetic variations. Evaluation of niche overlap and environmental dissimilarity provides valuable opportunities to investigate how niche differences contribute to genetic divergence between populations that differ in their geographical distributions and environment conditions. Nowadays, the formerly large continuous populations of Goitered gazelle in Iran have been confined to fragmented habitats due to natural and anthropogenic factors. A statistical framework based on an ecological niche modeling at genetically management units (MUs) level was used to compare environmental niche and evaluate the effect of niche differentiations on genetic patterns of two management units of Goitered gazelle in Central Iran. We found low values of niche overlap between the management units. The niche equivalency hypothesis revealed that niche of MUs is more significantly distinct than expected by chance. Also niche similarity test for both comparisons falls within the 95% confidence limits of the null distribution. These findings demonstrate that the niche of two MUs is rarely identical, but they tend to be more similar than expected based on random predictions and environmental background, which they occur. We concluded that, besides landscape resistance and geographic distance, ecological niche isolation is another factor affecting the genetic structure of gazelle populations in Iran. Conservation planning of this vulnerable species should focus on isolated populations as separate management units and landscape linkages to maintain gene flow between the genetically similar populations.

Keywords: Goitered gazelle, Management unit, Niche equivalency, Niche overlap, Niche similarity.

Introduction

There are many biological and ecological processes that can shape patterns of genetic structure in continuous or discrete populations of species including geography (Isolation by distance, IBD; Wright 1943), landscape resistance (Isolation by resistance, IBR; McRae and Beier 2007), and environment niche dissimilarity (Isolation by Environment; Wang and Summers 2010). In the recent years, in the field of landscape genetics, several landscape models have been developed to examine the roles of landscape and environmental niche on gene flow (Storfer *et al.* 2010, Balkenhol *et al.* 2017).

Despite to importance of environmental niche dissimilarity as a motivator of genetic differentiations, its dynamism and strength is poorly understood (Kareiva and Marvier 2015). Populations that inhabit different niche may show signature of genetic differentiation due to variety of ecological processes including natural selection against immigrants, sexual selection against immigrants, reduced hybrid fitness and biased dispersal (Wang *et al.* 2013). Hence, populations evolve traits suited to their local conditions. When populations show ecological specialization, natural selection will limit the reproductive success of individuals between different environments (Rasanen and Hendry 2008, Mosca *et al.* 2012). The pairs of populations inhabiting different environment niches will experience reduced gene flow and greater genetic distance (Lee and Mitchell-Olds 2011, Wang *et al.* 2013).

In the absence of gene flow between demes, populations may diverge genetically while inhabiting similar environment, and hence, the species niche is conserved (Wiens and Graham 2005). In the other hands, populations that occupy different environmental niches may show signature of genetic differentiations. A niche includes set of abiotic and biotic conditions that facilitates the persistence of a species (Hutchinson 1957). The two complementary concepts of the environmental niche (Grinnell 1917) and the trophic niche (Elton 1927) serve as a basis for quantifying the ecological niche (Broennimann *et al.* 2012). In the recent years, researchers focused on ecological niche conservatism and niche overlap in different niche dimensions (Svendsen *et al.* 2015).

Ecological niche differences among species or populations can be analyzed to evaluate the possible ecological and evolutionary forces that shape geographical distributions, habitat preferences, and genetic structures (Raxworthy *et al.* 2007). Recently, a variety of approaches have been proposed and applied to quantify niche overlap and niche conservatism (e.g. Steiner *et al.* 2008, Medley 2010). Approaches for quantifying the niche overlap typically rely on either ordination techniques (e.g. Thuiller *et al.* 2005, Hof *et al.* 2010) or ecological niche modeling (Guisan and Thuiller 2005). Recent studies have revealed that bioclimatic variables are very useful in predicting the distribution of species and measuring environmental niche. Here, we used a statistical framework to describe and compare niches in a gridded environmental space using ordination technique.

The Goitered gazelle (*Gazella subgutturosa*) inhabits large numbers of steppes, semi-arid and arid environments of Iran (Zachos *et al.* 2009). Gazelle populations have experienced periods of decline due to illegal hunting, drought, and habitat degradation (Zachos *et al.* 2010). Currently, almost all the existing gazelle populations are confined to protected areas surrounded by areas of human settlements and road networks. Khosravi *et al.* (2017) adopted a landscape genetics approach to investigate spatial genetic structure and the effects of landscape features on gene flow among populations of Goitered gazelle in Iran. Their findings revealed three genetically homogeneous groups with restricted dispersal including Biduiyeh, Kolah-Qazi/Kahyaz, and Ghamishloo/Mooteh/Kalmand. They suggested that conservation measures on this vulnerable species could consider some isolated population as separate MUs (e.g. Biduiyeh and Ghamishloo/Mooteh). The results of this study showed that a combination of IBD and IBR are affecting the genetic structure and gene flow between populations.

While they revealed new insights into the effects of landscape resistance and geographic distance on spatial genetic structure of the populations, but they did not evaluate the effects of niche isolation on genetic differentiations. We adopted a new statistical framework based on genetically informed ecological niche approach to describe and compare niches of two gazelle's MUs including Biduiyeh and Ghamishloo/Mooteh in a gridded environmental space. Given the large distance

between the MUs, we hypothesized that a difference in climate niche is one of the motivators of genetic differentiations between MUs besides of IBD and IBR. Therefore, the main objective of the present work was to explore the hypothesis of the effect of climate niche differentiations on the genetic distances and the degree of niche conservatism within the Goitered gazelle's MUs in Iran.

Material and methods

Study area

The central Iran, with an elevation ranging from 117 to 4429 m, covers most of the distribution range of the Goitered gazelle. Mean annual temperature and precipitation is 17.6 °C and 117 mm respectively. Human activity within the landscape includes farming and livestock herding. Paved roads are one of the most important fragmenting features in this landscape (Moqanaki and Cushman 2016). Dwarf scrub vegetation is common in large areas and the dominant vegetation is composed of *Artemisia siberi*, *Astragalus gossypius*, *Zegophyllum* sp. and *Amygdalus* sp. Despite the arid environmental conditions, this part of Iran is rich in biological diversity.

There are seven Goitered gazelle populations in this area confined to the protected areas. We sampled two genetically MUs of Goitered gazelle including BID-Biduiyeh (E56º 20′ N29º 53′), and GHAM-Ghamishloo (E49º 95′ N36º 14′)/ MOT-Mooteh (E50º 10′ N33º 20′, Fig.1). Based on Moritz's (1994) definition, management units are "populations with significantly divergent alleles at either nuclear or mitochondrial loci. The previous studies (e.g. Khosravi *et al.* 2017) have confirmed that population of Goitered gazelle in Biduiyeh, Mooteh and Ghamishloo have significantly different alleles at either nuclear and can be considered as separate management units. The species occurrence data were obtained from a variety of sources including field surveys during genetic sampling, opportunistic direct observation, and environmental guards` direct

sighting. The coordinates of all the presence points were recorded using a hand-held multichannel Global Positioning System (GPS) receiver.
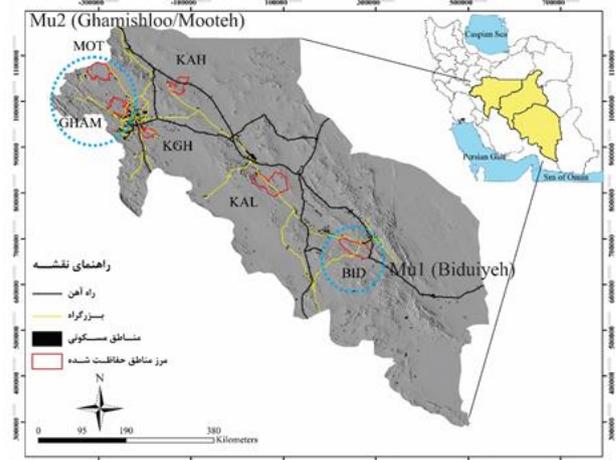

Figure 1. Location of the two genetically management units of *G. subgutturosa* in the study area (dash lines). MU1= Biduiyeh (BID), and MU2= Ghamishloo/Mooteh (GHAM/MOT). The red polygons show location of protected areas and populations of Goitered gazelle. KAL=Kalmand, KGH=Kolah-Qazi, KAH=Kahyaz.

Calculating niche overlap, equivalency and similarity

We assessed the effects of climate niche on the genetic differentiation of the two populations (BID and GHAM/MOT) using ecological niche analysis based on the PCA-env framework proposed by Broennimann *et al.* (2012). We obtained information on climatic conditions from the WorldClim database (http://www.worldclim.org; developed by Hijmans *et al.* 2005). We used a spatial downscaling method to transfer the original 1-km resolution of WorldClim data to the target resolution of 250-m with FORTRAN using Microsoft Visual Studio (Flint and Flint 2012). This model combines a spatial gradient and inverse-distance-squared (GIDS) weighting to WorldClim data with multiple regression. The location and elevation of the new fine-resolution grid cell relative to a coarse-resolution grid cell is used to weight the parameters based on the following equation:

$$Z = \left[\sum_{i=1}^{N} \frac{Z_i + (X - X_i)*C_x + (Y - Y_i)*C_y + (E - E_i)*C_e}{d_i^2} \right] \Bigg/ \left[\sum_{i=1}^{N} \frac{1}{d_i^2} \right]$$

where Z is the estimated climatic variable at the specific location defined by easting (X) and northing (Y) coordinates and elevation (E); Z_i is the climatic variable from the 1-km grid cell i; X_i, Y_i, and E_i are easting and northing coordinates and elevation of the 1-km grid cell i, respectively; N is the number of 1-km grid cells in a specified search radius; C_x, C_y, and C_e are regression coefficients for easting, northing, and elevation, respectively; and d_i is the distance from the 250-m site to 1-km grid cell i (Flint and Flint 2012). We used a 30-km search radius to calculate bioclimatic data at the 250-m resolution (see Khosravi *et al.* 2016 for details).

As inclusion of all 19 bioclimatic variables in model may cause overfitting and uncertainties due to the high degree of correlation among variables, so we conducted PCA to transform the climate layers into a reduced number of components (PCs). Then, the position of a kernel density of presence points in each cell in the environment space for each MUs along the principal components was compared to reflect their ecological niche differentiations and to quantify niche overlap between MUs (Broennimann *et al.* 2012). We used a smoothed density from a kernel density function to ensure that the measured overlap is independent of the resolution of the grid. Environmental space is bounded by the minimum and maximum environmental values found across the entire study region. We considered the first two axes of PCA as environmental space. In this study, the available environmental space of the MUs was defined by all pixels of the 19 climatic variables within a buffer of 20 km enclosing the species occurrence points.

Niche overlap between the MUs was computed by the method proposed by Schoener (1968). Hence, the density grids are used to compute a niche overlap between MUs as fallowing equation:

$$D = 1 - \frac{1}{2} \left(\sum_{ij} \left| Z_{1ij} - Z_{2ij} \right| \right)$$

Where z1ij is entity 1 occupancy and z2ij is entity 2 occupancy. This metric varies between 0 (no overlap) and 1 (complete overlap).

We computed niche equivalency and similarity using the method developed by Warren *et al.* (2008). This method uses statistical randomization (100 repetitions) to determine that if the pairwise comparison of niche differentiation is statistically resulted in by chance. The niche equivalency is a one-tailed randomization test that aims to assess whether the ecological niche of two populations are significantly more equivalent than expected by chance. We also calculated niche similarity between MUs using 100 repetitions to addresses that whether the observed niche overlap among the MUs can be attributed to their available environmental space (Broennimann *et al.* 2012). The MUs level comparisons of PCA-env were computed in R (R Development Core Team 2010) using the method developed by Broennimann *et al.* (2012).

Results

The results of the multivariate environmental space occupied by two MUs of Goitered gazelle based on PCA-env approach are shown in figure 2. The analysis of environmental niche properties based on PCA showed that first axis explained 51.93% of the total variation in environmental conditions. The PC1 mainly loaded by mean diurnal range, isothermality, temperature seasonality, precipitation seasonality, and temperature annual range. The second axis explained 34.35 % of the total variation and was loaded by max temperature of warmest month, mean temperature of driest quarter and precipitation of wettest quarter variables (Fig. 2 b). Niche overlap results showed a great variability in the environmental space inhabited by the two populations (Fig. 3 a). In this regard, results of niche divergent

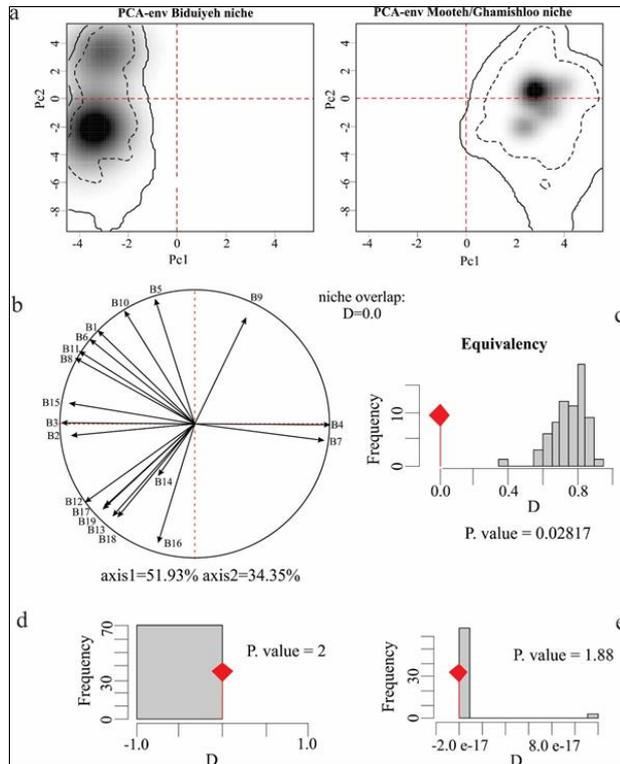analysis did not show overlap between Biduiyeh and Mooteh/Ghamishloo. (Schoener's D = 0.00; Fig. 2a).

Figure 2. The results of niche overlap, similarity and equivalency between two genetically populations of Goitered gazelle in climatic space using PCA-env. The PCA-env results show the niche of the MUs in two main axes with the climate conditions of the complete landscape area. (a) Niche of Biduiyeh and Mooteh/Ghamishloo along the PC1 and PC2 of the PCA analysis. Grey shading shows the kernel density of the presence points of Goitered gazelle. Also the solid and dashed lines show 100% and 50% of the background environment space respectively. (b) The contribution of each variable on the two axes of the PCA. (c) The results of niche equivalency based on the observed and simulated niche overlap between the populations. (d) and (e), respectively, illustrate the niche similarity of BID to MOT/GHAM and niche similarity of MOT/GHAM to BID calculated from 100 iterations.

Using D metric, we rejected the hypothesis of niche equivalency between the MUs (P < 0.05, Fig 2c) revealing that niche of two populations is more significantly distinct than expected by chance. The results of niche similarity based on the background similarity test for both comparisons (Biduiyeh points – Mooteh/Ghamishloo background (Fig. 2d) and Mooteh/Ghamishloo point – Biduiyeh background (Fig.2 e)) falls within the 95% confidence limits of the null distributions, leading to non-rejection of the hypothesis of niche similarity (P > 0.05). Considering the results from niche equivalency, these finding demonstrate that the niche of two studied populations is rarely identical, but they tend to be more similar than expected based on random predictions and broad environmental background which they occur.

Discussion

Here we used a robust method to quantify niche overlap between two genetically populations of Goitered gazelle in Central Iran. PCA-env is an appropriate method for evaluating the difference of niche between populations of the same species that occupy different geographic range and likely different climate conditions (Fitzpatrick *et al.* 2007, Steiner et al. 2008, Broennimann *et al.* 2012). Broennimann *et al.* (2012) revealed that, in comparison to other ordination techniques, PCA-env accurately quantify the level of niche differentiation without substantial bias and is more appropriate than species distribution model (SDMs) for investigating niche overlap. Also, Wielstra *et al.* (2012) showed that both PCA-env and ENFA are powerful methods for evaluating the niche similarity for crested newt (*Triturus cristatus*). We tested the hypothesis of environmental niche isolation as another explanation for genetic differentiation between Biduiyeh and Mooteh/Ghamishloo.

The analysis of genetic structure based on microsatellites show that individuals of Biduiyeh and Mooteh/Ghamishloo are belong to distinct genetically groups. High landscape resistance between two populations and also long geographic distance confirm the genetic differentiations between Biduiyeh and

Mooteh/Ghamishloo (Khosravi *et al.* 2017). The analysis of PCA-env highlighted that there is no niche overlap between two populations (Schoener's D = 0.00). Given the great variations in climate conditions in Iran, it is not surprising the low niche overlap between geographically distant populations of Goitered gazelle. Hence, the low niche overlap value between Biduiyeh and Mooteh/Ghamishloo reflects their different environmental constrains. Our assessment of niche equivalency based on PCA-env rejected the null hypothesis that the climate niche of populations of Goitered gazelle is equivalent. This findings show why it is not accurate to imply niche characteristics for one MU based on the niche of another MU even for populations of same species. In addition, the results showed that the niche of Biduiyeh tends to be more similar to the niche of Mooteh/Ghamishloo than random and, thus, niche similarity cannot be rejected. We concluded that both populations do not significantly retain their environmental niche characteristics from each other. In the other words, the niche similarity results suggest that populations of Goitered gazelle in the studied landscape share more characteristics of their climate niche spaces than randomly expected. These findings suggest that while two MUs are closely related and share climate niche spaces but they are still different MUs.

The observed similarity in climate niche space between two populations suggests that they have similar environmental constrains but that a different set of variables within this environmental niche space restrict their distribution (Aguirre-Gutierrez *et al.* 2015). Niche overlap based on PCA-env analysis, confirmed that there is no sign of niche conservatism or divergent between this two genetically groups. Niche conservatism is allopatric evolution of two evolutionary-closed groups in the past (McCormack *et al.* 2010). Hence, we conclude that there is no sign of

separate evolutionary events because of allopatric adaptation to isolated refuges for Biduiyeh and Moote/Ghamishloo.

A few isolated patches with suitable habitats are available between Biduiyeh population and other populations of Goitered gazelle, which may not be enough to provide a continuous corridor for the gazelle's migration. In addition, road construction and expansion, the close proximity of this protected area to populated residential areas and long distance between Biduiyeh and the nearest gazelle population may have also been responsible for the isolation of this population. Based on the landscape genetics analysis, Khosravi *et al.* (2017) considered Biduiyeh and Mooteh/Ghamishloo as two management units. Based on Moritz's (1994) definition, management units are "populations with significantly divergent alleles at either nuclear or mitochondrial loci". Therefore, according to Moritz (1994), MUs address current structure, making them more useful in addressing short-term management issues. Reduced genetic diversity in isolated populations such as Biduiyeh, will reduce the ability of the population to respond to changing environmental conditions. Hence, in the future conservation plans, it should be considered the role of environmental variables in shaping the ecological niche of focus species.

In conclusion, results of this research indicate that, besides of landscape resistance and geographic distance (Khosravi *et al.* 2017), environmental niche isolation is one of the most motivators of genetic discontinuities in Goitered gazelle populations in Central Iran. In the other words, combination of landscape resistance, geographic distance and ecological niche divergent are affecting the gene flow of gazelle populations. Conservation planning of this vulnerable species should focus on isolated population as separate management units and landscape linkages to maintain the gene flow between the genetically similar populations. In

addition, effective conservation actions must take into account intrinsic requirements of different management units and the main environmental drivers that shape their distributions. Therefore, different conservation interventions may be required for each management unit.

Acknowledgment

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