



Landscape features drive dispersal patterns in the vulnerable Yellow-spotted Mountain Newt, *Neurergus derjugini* (Caudata: Salamandridae)

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Manuscript received: 9 September 2024

Accepted: 1 December 2025 by STEFAN HERTWIG

Abstract. The study investigates the impact of landscape features on the dispersal patterns of the vulnerable Yellow-spotted Mountain Newt, *Neurergus derjugini*. By integrating population genetics and geospatial data, the research aims to identify potential movement corridors among populations. The mitochondrial DNA marker NADH Dehydrogenase Subunit 2, along with genetic subdivision (θ_{ST}) and least-cost path (LCP) analyses, is utilized based on data collected from six fragmented highland streams and spring ponds, representing the southern range of the species' distribution area in the Zagros mountains of Iran. The study explores five dispersal routes: straight line, stepping stone, least cost slope, stream likelihood, and a combination of least cost slope and stream likelihood. Genetic and LCP analyses reveal evidence of potential dispersal facilitated by aquatic corridors in the least-cost slope. The findings have crucial implications for informing conservation priorities for *N. derjugini*, offering valuable estimates of the species' potential dispersal activity in response to climate change and ongoing habitat destruction linked to human activities.

Key words. Landscape features, habitat fragmentation, dispersal routes, population genetics, GIS, conservation priorities.

Introduction

Heterogeneous landscapes, characterized by diverse habitats and fragmented territories, pose significant challenges for species dispersal, population genetics, and genetic structure (GARRIDO-GARDUÑO et al. 2016, JENSEN et al. 2019, BRUNKE et al. 2020). This is especially true for species that exhibit continuous interaction with their environments, such as small vertebrates, where the spatial distribution of landscape features profoundly influences their movement across these landscapes (CUSHMAN et al. 2006, TURNER et al. 2015). Consequently, the consideration of landscape heterogeneity and the precise arrangement of features on a landscape provides crucial insights into our understanding of gene flow and population structure (LOZIER et al. 2013, VAN STRIEN 2017, BALKENHOL et al. 2019).

Amphibians, with their intricate life cycles and limited dispersal abilities, are highly sensitive to changes in their environment (CAYUELA et al. 2020). Habitat fragmentation, a growing threat in diverse landscapes, poses significant challenges for amphibian populations by disconnecting breeding sites and impeding gene flow (JOLY et al. 2003, CUSHMAN 2006, TAN et al. 2023). This can lead to reduced genetic diversity and increased vulnerability to inbreeding

depression, compounding the challenges faced by small, isolated populations (WILK et al. 2020, NOLAN et al. 2023). Climate change further exacerbates these threats, potentially leading to habitat loss and changes in moisture distribution, adding another layer of complexity to amphibian conservation efforts (BERANEK et al. 2022, INMAN, ESQUE & NUSSEAR 2023, NOLAN et al. 2023).

This study focuses on the Yellow-spotted Mountain Newt (*Neurergus derjugini*), a vulnerable amphibian endemic to the high-altitude streams of the Zagros mountains in western Iran and northeastern Iraq (YOUSEFI et al. 2023). These mountains present a unique ecological setting with diverse microclimates, ranging from warm and humid valleys to cold and dry higher altitudes (HEYDARI-GURAN & GHASIDIAN 2024). *Neurergus derjugini* thrives in this mosaic of habitats, primarily residing in first-order streams, springs, and pools within an altitudinal range of 772 to 2100 m a.s.l. (AFROOSHEH et al. 2016, IUCN 2023). However, despite the ecological significance of the Zagros mountains, this region faces considerable threats from deforestation, water pollution, overexploitation, and habitat fragmentation (HENAREH KHALYANI & MAYER 2013). These challenges are further amplified by climate change, leading to the drying up of streams and potentially isolating *N. derjugini* populations (IUCN 2023).

Understanding *N. derjugini*'s movement patterns and how they navigate these fragmented landscapes is crucial for its conservation. While genetic investigations reveal significant differentiation among populations despite low within-population diversity, indicating restricted gene flow (AFROOSHEH et al. 2019, SALEHI et al. 2019), directly observing their movements across the rugged terrain is impractical. This is where our innovative approach using least-cost path (LCP) analysis comes in. By combining LCP with population genetic data, we can virtually recreate the most likely pathways *N. derjugini* takes between breeding streams, considering factors like topography, distance, and habitat suitability. This powerful tool helps us shed light on the complex interplay between isolation and connectivity that shapes *N. derjugini*'s genetic diversity. This newfound understanding will guide our conservation efforts, allowing us to identify critical corridors for maintaining gene flow and ensuring the long-term survival of these unique and imperiled populations in the face of ongoing threats.

In this study, our main goal was to explore the genetic diversity and relationships of *N. derjugini* within its southern range by utilizing mitochondrial DNA markers. This served as the foundation for our landscape genetic approach, wherein we quantified dispersal costs using the genetic subdivision metric (θ_{ST}) and examined various landscape variables to uncover environmental impacts on gene

flow. Additionally, we conducted a comparison of models, including stepping stone, least-cost slope, stream likelihood, and a combined model, against the conventional isolation-by-distance model. This analysis aimed to pinpoint the most accurate representation of genetic divergence factors in *N. derjugini*.

Materials and methods

Species distribution data and sampling sites

Geographic coordinates and occurrence records for *N. derjugini* were sourced from SALEHI et al., (2019) and carefully cross-verified for spatial accuracy using field-collected GPS data were available (Fig. 1). Coordinates were originally recorded in degrees and minutes and converted to decimal degrees for consistency in spatial analyses. Discrepancies greater than ± 100 meters – based on comparisons between published records and ground-truthed GPS points – were corrected or excluded to ensure locational precision. Dispersal modeling focused on six focal populations in the southern portion of the species' range: Kavat ($34^{\circ}52'$ N, $46^{\circ}30'$ E), Ghoore-ye Ghaleh ($34^{\circ}52'$ N, $46^{\circ}29'$ E), Gholani ($34^{\circ}54'$ N, $46^{\circ}27'$ E), Dorisan ($35^{\circ}01'$ N, $46^{\circ}23'$ E), Darreh-e Najjar ($35^{\circ}05'$ N, $46^{\circ}18'$ E), and Lashgar Gah ($35^{\circ}00'$ N, $46^{\circ}08'$ E). The study area was delineated using a minimum convex polygon (MCP) surrounding these six sites, serv-

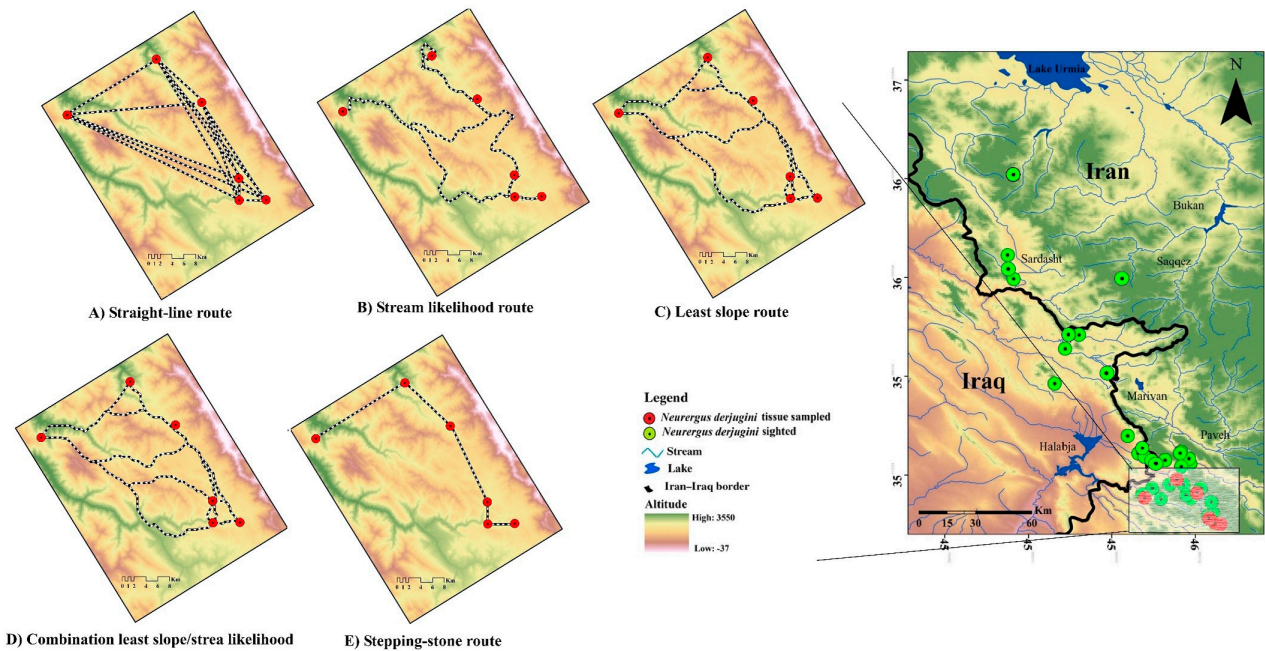


Figure 1. Modeled dispersal routes and geographic context for the vulnerable Yellow-Spotted Mountain Newt (*Neurergus derjugini*) within its southern range in the Zagros mountains of western Iran. Panels A–E illustrate five alternative dispersal models among six focal populations: (A) straight-line (Euclidean) routes; (B) routes following areas of high stream likelihood, derived from flow accumulation analysis; (C) routes minimizing slope; (D) routes combining slope and stream likelihood with equal weighting to represent landscape resistance; and (E) stepping-stone routes linking known aquatic features such as springs, streams, and seasonal pools. All maps (A–E) are north-oriented and based on spatial data from a 30 m resolution digital elevation model (SRTM). The inset map (right panel) provides regional context, showing the full known distribution range of *N. derjugini* across western Iran and eastern Iraq, with key focal populations marked (red circles).

ing as the spatial extent for all connectivity and dispersal modeling analyses.

Dispersal models

To evaluate potential dispersal pathways for *N. derjugini*, five models were constructed following the framework of SPEAR et al. 2005: (1) straight-line (Euclidean) distance, (2) stepping-stone routes via intermediate aquatic habitats, (3) least-slope paths favoring flatter terrain, (4) stream-likelihood routes favoring likely watercourses, and (5) combined least-slope and stream-likelihood paths with equal weighting.

Straight-line distances between the centroids of each population were calculated using the Point Distance tool in ArcGIS v.10.3.1 and served as the null model for isolation-by-distance. For the stepping-stone model, potential intermediate aquatic habitats – specifically streams, springs, and small pools – were identified as stepping-stone features based on field observations. Stepping-stone and Euclidean pathways were then manually digitized as polylines using the Editor tool in ArcGIS by connecting each population to the nearest intermediate aquatic features. The Measure Tool was used solely to confirm segment lengths, not to digitize the routes. Final path lengths were calculated using the Calculate Geometry function.

The least-slope and stream-likelihood models were generated using cost surface rasters derived from slope and hydrological probability, respectively. The combined model was built by averaging these two rasters to account for both topographic and hydrological preferences. Least-cost paths under each model were calculated using the Cost Distance and Cost Path tools in ArcGIS.

Digital elevation model and cost surface construction

To generate topographic and hydrological variables for resistance surface modeling, we used the Shuttle Radar Topography Mission (SRTM) 1 Arc-Second Global Digital Elevation Model (~ 30 m spatial resolution), obtained from the United States Geological Survey (USGS Earth Explorer, <https://earthexplorer.usgs.gov/>).

A slope raster was derived from the DEM using the Slope tool in ArcGIS and expressed in degrees. To estimate stream likelihood, we applied standard hydrological modeling techniques: the Flow Direction and Flow Accumulation tools were used to delineate surface water pathways. The resulting flow accumulation raster was used as a proxy for the likelihood of surface water presence, with higher accumulation values indicating greater stream likelihood.

To construct a resistance surface, each pixel in the landscape (originating from the ~ 30 m DEM grid) was assigned a movement cost based on two environmental variables: (1) slope (in degrees) and (2) the inverse of stream

likelihood ($1 / \text{flow accumulation} + \epsilon$, where ϵ is a small constant to avoid division by zero). Both rasters were normalized to a 0–1 scale using min–max scaling to ensure comparability of values. The two normalized rasters were then linearly combined with equal weighting to produce a composite cost surface, following methods from SPEAR et al. 2005, EMEL & STORFER 2015, VAISSI & SHARIFI 2021.

This composite raster represented the resistance surface, where lower values indicated more favorable conditions for movement (e.g., flatter terrain and proximity to probable watercourses). Least-cost distances between all population pairs were computed using the Cost Distance and Cost Path tools in ArcGIS, based on this resistance surface.

Genetic data and differentiation

Mitochondrial DNA sequences of the NADH dehydrogenase subunit 2 (ND2) gene for *N. derjugini* were retrieved from GenBank (accession numbers MK035716–MK035719; SALEHI et al. 2019). These sequences corresponded to individuals sampled from the six focal populations used in the landscape connectivity analysis. Sequences were aligned using MUSCLE in MEGA X (KUMAR et al. 2018), and genetic differentiation among populations was quantified by calculating pairwise θ_{ST} values in Arlequin v.3.0 (EXCOFFIER et al. 2005). These θ_{ST} values served as the response matrix in subsequent analyses to assess the degree to which landscape resistance explains genetic structure (VAISSI & SHARIFI 2021).

Connectivity and statistical analyses

To evaluate the relationship between landscape structure and genetic differentiation, we compared pairwise θ_{ST} values to geographic distances derived from five alternative dispersal models. For each model, pairwise cost distances between populations were extracted and assembled into distance matrices using ArcGIS.

We then performed partial Mantel tests in Arlequin with 10,000 permutations to test for correlations between genetic differentiation (θ_{ST}) and the cost distances from each model, while controlling for simple geographic distance (Euclidean) as a covariate. This allowed us to isolate the effect of landscape resistance independent of isolation-by-distance.

To further evaluate model performance, we used linear regression models in R v.4.1.0 to relate θ_{ST} values to cost distances under each dispersal scenario. Model selection was based on three criteria: the coefficient of determination (r^2), the Akaike Information Criterion, corrected for small sample sizes (AICc) and the Bayesian Information Criterion (BIC). Lower AICc and BIC values and higher r^2 values were interpreted as evidence of better model fit. These model comparisons were conducted using the lme4, MuMIn, and usdm packages in R (EMEL & STORFER 2015, VAISSI & SHARIFI 2021).

Results

Figure 1 presents the full distribution range of *N. derjugini* across western Iran and eastern Iraq, along with five modeled dispersal routes among six focal populations in the southern portion of the species' range: (1) straight-line route (Fig. 1A), (2) stream likelihood route (Fig. 1B), (3) least slope route (Fig. 1C), (4) combined least slope and stream likelihood route (Fig. 1D), and (5) stepping-stone route (Fig. 1E).

Pairwise partial Mantel tests revealed statistically significant positive correlations between mitochondrial ND2 genetic distances and all five dispersal models (Table 1), with correlation coefficients (r) ranging from 0.54 to 0.65 (all $p < 0.05$). The strongest correlation was observed for the stepping-stone model ($r = 0.65$, $p = 0.017$), followed closely by the stream likelihood ($r = 0.64$, $p = 0.014$), least slope ($r = 0.60$, $p = 0.018$), and the combined least slope/stream likelihood model ($r = 0.59$, $p = 0.018$). The straight-line model showed the weakest correlation ($r = 0.54$, $p = 0.020$), as expected from its role as a null model.

Despite having a slightly lower correlation coefficient, the combined least slope/stream likelihood model was identified as the best-supported model based on model comparison criteria. It exhibited the lowest AICc (-1.09) and BIC (-26.26) scores, and explained the highest proportion of genetic variance ($r^2 = 0.45$). In contrast, the straight-line model performed the worst overall, with the highest AICc and BIC scores and the lowest explained variance ($r^2 = 0.29$).

Discussion

The landscape genetic approach employed in this study provides valuable insights into the dispersal patterns and genetic connectivity of the vulnerable Yellow-spotted Mountain Newt (*N. derjugini*) within its southern range of distribution in the Zagros mountains of western Iran. The investigation of potential dispersal pathways, considering various landscape features, enhances our understanding of the species' response to habitat fragmentation and aids in formulating effective conservation strategies. The results paint a clear picture of a landscape that profoundly influences the movement and genetic structure of *N. derjugini*. The significant positive correlation between genetic distances and various dispersal routes highlights the non-random nature of their movements. Unlike a simplistic isolation-by-distance model, our findings reveal a nuanced relationship between distance and gene flow, governed by the intricate choreography of environmental factors.

Landscape genetics, particularly least-cost path analysis, has been employed in numerous studies to investigate dispersal pathways based on the minimum cost (SPEAR et al. 2005, WANG et al. 2009, EMEL & STORFER 2015, VAISSI & SHARIFI 2021, GUTIERREZ-RODRIGUEZ et al. 2023, REYNE et al. 2023). They explored the genetic landscape and dispersal pathways in amphibians. In alignment with this meth-

Table 1. Partial mantel test (based on the ND2 gene) for determining the best model (based on AICc, BIC, and r^2) to identify the movement route within the southern range of the vulnerable Yellow-spotted Mountain Newt (*Neurergus derjugini*). Notes: p-value: the statistical significance of the partial correlation coefficient for each variable. r : partial correlation coefficient for each variable. r^2 : total variance explained by the model. AICc: Akaike Information Criterion corrected for small sample sizes. BIC: Bayesian Information Criterion.

Route	p-value	r	r^2	AICc	BIC
Straight-line	0.020	0.54	0.29	-0.47	-25.64
Stream likelihood	0.014	0.64	0.41	-0.32	-24.84
Least slope/stream likelihood	0.018	0.59	0.45	-1.09	-26.26
Stepping stone	0.017	0.65	0.43	-0.48	-25.65
Least slope	0.018	0.60	0.37	-0.85	-26.02

odology, our study focused on the examination of various dispersal routes in amphibians, encompassing straight-line trajectories, stream likelihood routes, least slope routes, a combined model integrating least slopes and stream likelihood, and stepping-stone routes. The correlation observed between genetic distances and different dispersal routes underscores the intricate relationship between landscape features and genetic connectivity within amphibian populations. This integrated approach provides valuable insights into the factors shaping gene flow and population structure, contributing to a more holistic understanding of amphibian ecology and conservation.

Among the various dispersal routes considered, the combination of the "least slope/stream likelihood" model emerged as the champion, showcasing the lowest AICc and BIC values. This implies that *N. derjugini* prioritizes pathways that combine gentle slopes with the proximity of water bodies. This preference is readily understandable, considering their amphibious nature and the energetics of navigating rugged terrain. Steep inclines present a formidable obstacle, while streams offer convenient travel corridors and vital resources for survival and reproduction. The significance of water bodies as facilitators of gene flow aligns with numerous studies on amphibians. Rivers and streams serve as not only highways for movement but also vital lifelines for these moisture-dependent creatures. Our findings further reiterate the critical role of maintaining and restoring waterways within *N. derjugini*'s habitat, ensuring unimpeded dispersal and healthy gene flow among populations.

Beyond topographical considerations, the study also emphasized the importance of habitat connectivity. The stepping-stone model, which assumes movement between connected aquatic habitats, resonated with the observed genetic patterns (LOEHLE 2007). This underscores the vulnerability of *N. derjugini* to habitat fragmentation, a growing threat driven by anthropogenic activities. The potential isolation of populations due to habitat loss reinforces the urgent need for conservation efforts that prioritize the preservation and restoration of interconnected corridors

throughout the species' range. The inclusion of least-cost path analysis proved instrumental in revealing the hidden pathways traversed by *N. derjugini*. This approach surpasses traditional distance-based models by accounting for landscape heterogeneity, providing a more accurate picture of how the species navigates the complexities of the Zagros mountains. This knowledge is invaluable for conservation planning, allowing us to identify crucial corridors that can be prioritized for protection and restoration.

This research moves beyond conventional genetic analyses and makes a significant contribution to the field of amphibian conservation. By employing landscape genetics and highlighting the influence of environmental factors on gene flow, we provide a roadmap for evidence-based conservation strategies for *N. derjugini*. Moreover, these findings can potentially be applied to other amphibian species facing similar challenges, paving the way for more effective conservation interventions on a global scale. In conclusion, our investigation reveals a deep connection between landscape features, dispersal routes, and the genetic destiny of the Yellow-spotted Mountain Newt. This knowledge equips us with the tools to formulate targeted conservation measures that address the specific needs of this vulnerable species, ensuring its long-term survival within the ever-changing environment of the Zagros mountains. By protecting critical corridors, restoring fragmented habitats, and safeguarding vital water resources, we can secure a future where these unique amphibians continue to thrive for generations to come.

Acknowledgements

This research was funded by the Iran National Science Foundation (INSF) (No. 95840118).

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