

Habitat connectivity analysis of the endangered Sardinian grass snake reveals priority areas for conservation

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Keywords: circuit theory, connectivity models, ecological modelling, landscape connectivity, *Natrix helvetica cetti*, Sardinia.

SUMMARY

We studied functional habitat connectivity for *Natrix helvetica cetti*, a rare and endangered island endemic taxon with a highly fragmented range on Sardinia. Using the habitat suitability model recently developed for this species as input, we applied circuit-theory based connectivity analyses in Julia, combining pairwise runs among all known occurrence localities with an omnidirectional analysis independent of focal nodes. Both approaches converged in identifying the eastern mountain chain as the main connectivity backbone, with a particularly strong corridor linking the Sarrabus reliefs in the south-east to the Barbagia region and, more weakly, to the Monte Limbara area in the north. Additionally, fainter routes were detected along the Iglesiente ranges in south-western Sardinia. Pinch point extraction based on the 95th percentile further identified the main priority connectivity corridors along this eastern backbone. The highest current flow generally connected areas previously predicted to have high habitat suitability, and also highlighted sectors with no confirmed records, suggesting priorities for targeted surveys. Of the identified priority areas, only about 50% fell within protected areas in Circuitscape, whereas this proportion increased to 65% in Omniscape. Our results indicate that corridors in eastern Sardinia are likely to be crucial for maintaining gene flow and long-term persistence of *N. h. cetti* and provide a spatial basis for integrating this island-restricted reptile into regional connectivity planning and future genetic and health assessments.

INTRODUCTION

The world's biodiversity is currently facing a crisis, with extinction rates estimated to be up to 1000 times higher than historical values (Pimm et al. 1995, 2014). However, extinction risk is higher for species

with a limited geographic range, especially for those endemic to small areas and with limited dispersal ability (Fontaine et al. 2007; Burlakova et al. 2011). Species with small geographic ranges and narrow habitat breadth are generally more vulnerable to

extinction (Chichorro et al. 2019), and endemic taxa are projected to be disproportionately affected by ongoing climate change, particularly on islands and mountains (Manes et al. 2021). In insular systems, island endemics show elevated threat status and account for a disproportionate share of documented global extinctions (Spatz et al. 2017; Fernández-Palacios et al. 2021; Llorente-Culebras et al. 2024). Among reptiles, for example, island-restricted species display especially high proportions of threatened taxa and documented historical extinctions (Nunes et al. 2025).

Sardinia, Italy, is a Western Mediterranean island that, together with Corsica, represents one of the most important biodiversity hotspots in the Mediterranean Basin (Blondel 2010). Regarding herpetofauna, it hosts 19 reptile and 12 amphibian species (see Supplementary Table S1), with many taxa endemic to Sardinia exclusively ($n = 7$; 20.6%) or to the Sardinian-Corsican islands ($n = 3$; 8.8%), thus requiring special conservation attention. Among them, the Sardinian grass snake, *Natrix helvetica cetti* Gené 1839, is a rare, endangered taxon endemic to Sardinia's main island with a highly fragmented and restricted geographic distribution (Schultze et al. 2020; Di Nicola et al. 2021, Rondinini et al. 2022). Because of its restricted range and threatened status, this taxon represents a particularly relevant case for spatially explicit conservation assessments. Likely due to its low density and elusive nature (Capula et al. 1994; Lunghi et al. 2018), important knowledge gaps still remain regarding its ecology, population structure and spatial conservation needs (Di Nicola et al. 2023). Accordingly, understanding how suitable habitat patches are functionally connected across the island is especially important for conservation planning in such a rare and fragmented insular taxon.

A recent work by Di Nicola and colleagues (2023) compiled an updated distributional map of this snake, highlighting the concerning sparse and isolated nature of *N. h. cetti* populations, with a consequent potential risk of genetic loss. Habitat suitability modelling revealed eastern Sardinia, especially in the centre-south, as the most suitable area for the species, while only a few small suitable areas are present in western Sardinia (Di Nicola et al. 2023). Species with small, fragmented populations often show reduced gene flow among populations and are thus more susceptible to decline in fitness caused by limited genetic diversity (Frankham 2005, 2015), which makes the identification of potential dispersal pathways a key conservation priority.

Although *N. h. cetti* has been included in broad-scale phylogeographic and genomic studies of the *N. helvetica* complex (e.g., Schultze et al. 2020; Schöneberg et al. 2023), a dedicated population genetic study explicitly targeting the fine-scale genetic structure and connectivity of Sardinian populations is still lacking. In this context, landscape connectivity modelling can provide a useful spatial proxy to identify the sectors most likely to facilitate movement among known occurrence areas, highlight potential barriers or bottlenecks requiring conservation attention, and translate habitat suitability predictions into spatial conservation priorities.

While the importance of understanding species distributions for conservation is well recognised (Guisan et al. 2013) and integrated in several studies (e.g., Mizsei et al. 2016; Ficetola et al. 2020; Colla et al. 2025), habitat connectivity, a fundamental feature for biodiversity conservation (Thompson et al. 2017), is less studied, with the majority of works coming only from recent years (Correa Ayram et al. 2016; Brodie et al. 2025). Connectivity influences population persistence, and both natural and man-made corridors have been proven to positively affect fitness, abundance and diversity (Resasco 2019) by enhancing dispersal (Gilbert-Norton et al. 2010). Conversely, loss of habitat connectivity is associated with increased extinction risk (Valenzuela-Aguayo et al. 2020; Brodie et al. 2025). It is therefore crucial to assess connectivity for spatial conservation planning (Beger et al. 2022).

Identifying the most critical corridors for maintaining large-scale connectivity requires an integrated assessment of both habitat suitability and landscape connectivity (e.g., Iannella et al. 2024). Accordingly, in this study we integrated the distributional and habitat suitability framework provided by Di Nicola et al. (2023) with circuit theory-based connectivity analyses to: (i) identify the main functional corridors potentially linking known populations of *N. h. cetti* across Sardinia; (ii) detect the principal connectivity pinch points by focusing on cells with the highest current density values; and (iii) assess the spatial overlap between these key connectivity sectors and the existing protected-area network. By doing so, we aimed to provide a spatially explicit basis for the conservation prioritisation of one of Sardinia's most range-restricted reptile taxa.

MATERIALS AND METHODS

The potential corridors between *N. h. cetti* populations were identified using connectivity modelling, integrating both directional and omnidirectional approaches in Julia 1.11.6 (Bezanson et al. 2017). For the directional approach, connectivity analysis was performed with the Circuitscape v5.15.0 Julia package (Hall et al. 2021), which is considered to outperform other methods (Anantharaman et al. 2020). Circuitscape uses electrical circuit theory within an ecological framework (McRae et al. 2008) to model the net probability of species movement across the landscape under a random-walk assumption, treating the landscape as an electrical circuit whose cells possess resistance (or conductance) values, with current flowing from sources to grounds. Circuitscape was run using the “cg+amg” solver in “pairwise” mode, where current flows between each pair of focal nodes (i.e., points between which connectivity was modelled). One of the two nodes was connected to a 1-amp current source, while the other was connected to ground. For the purpose of this study, all *N. h. cetti* occurrence points reported in Di Nicola et al. (2023) were used as focal nodes.

The omnidirectional connectivity approach was also employed to test a scenario without the influence of focal nodes (i.e., *N. h. cetti* occurrence points). Omnidirectional connectivity was estimated using the Omniscape v0.6.2 Julia package (Landau et al. 2021). This algorithm applies Circuitscape in “advanced mode”. A circular moving window with a user-specified radius is generated iteratively for every pixel; the pixel at the centre is set to ground, while, according to user specifications, all other pixels inside the window can act as current sources. The window radius was set to six cells (i.e., ~ 6 km), as this represents a reasonable dispersal distance for grass snakes (see Ward 2017, paragraph 5.5.2). Within this buffer, all non-NA cells were set as potential source.

Since both algorithms require a resistance (or conductance) layer as input (McRae et al. 2008, 2016), the habitat suitability

output from Di Nicola et al. (2023) was transformed into a resistance map of ~ 1 km resolution; hence, the final connectivity raster also had an approximately 1 km resolution. The negative exponential function of Keeley et al. (2016) is considered the best-performing option; it produces a steep increase in resistance as suitability decreases, according to a constant. However, in this study the resistance map was generated by means of a reciprocal transformation (i.e., resistance layer = 1/suitability layer; Figure 1). This alternative approach has already been applied (e.g., Falaschi et al. 2025; Rafeai et al. 2025) and avoids the need to define external parameters. The habitat suitability map used as input included 18 bioclimatic variables and the altitude (see the best performing model in Di Nicola et al. 2023).

To further unravel the role of human impact on *N. h. cetti* functional connectivity, the resistance map was also merged with a vector layer including Sardinia’s main roads, urban areas, and industrial areas using QGIS 3.34 (QGIS Association 2025), assigning a very high resistance value of 1000 ohms to the corresponding cells. Nevertheless, given the limited spatial overlap of these features with the species’ known range and inferred connectivity network, and considering that the major roads intersecting this range are mostly single-carriageway roads that may in some cases serve as crossing areas and basking sites for snakes (M.R. Di Nicola pers. obs.), this alternative resistance map is provided only in the Supplementary Material (Supplementary Figure S1).

Finally, to identify functional connectivity “pinch points” (i.e., highest connectivity corridors) falling within protected areas, the connectivity rasters were converted into a binary layer by extracting cells whose connectivity values exceeded the 95th percentile. These binary rasters were then intersected with protected-area polygons, and the proportion of pinch-point cells occurring within protected areas was calculated relative to the total number of pinch-point cells in the study area. These

operations were carried out with the terra package (Hijmans 2025) in R 4.4.1 (R Core Team 2024). Protected areas included Natura 2000 sites (SCIs/SACs and SPAs), national protected areas, the regional system of parks, reserves and natural monuments, and permanent wildlife protection oases, which were merged into a single layer.

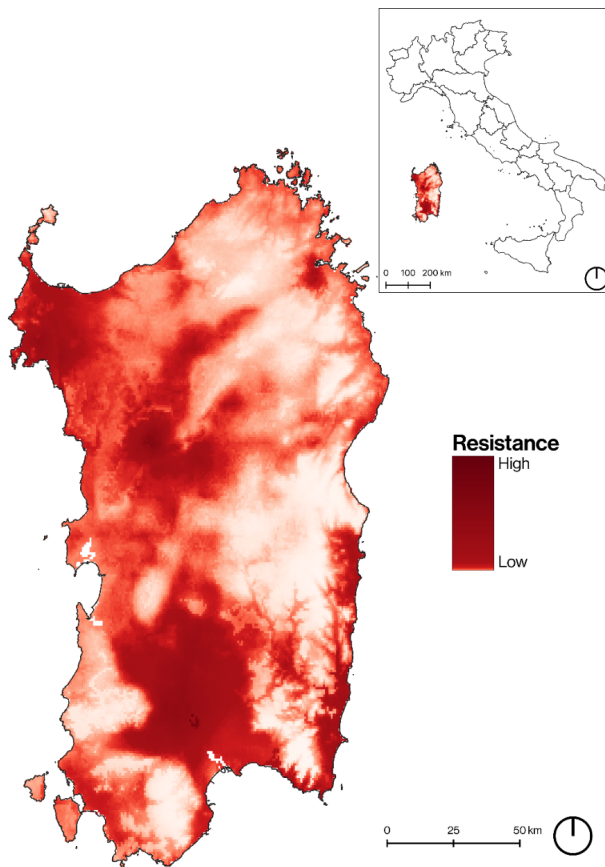


Figure 1. Resistance map used as input for connectivity modelling. Light colours represent low resistance cells, whereas red and darker red tones indicate high-resistance cells.

RESULTS

As expected from the transformation technique, areas presenting higher resistance values mirrored areas of lower suitability (see Figure 1 and Di Nicola et al. 2023: Figure 3).

Landscape connectivity, as estimated in Circuitscape pairwise mode, revealed higher connectivity among the mountain ranges of the eastern sector of the island. A particularly prominent corridor in the south-eastern part of Sardinia

connects the Sarrabus reliefs with the Barbagia region. Weaker corridors are also apparent further north, extending towards Monte Limbara. A further faint pathway is visible in the south-western sector along the Iglesias ranges. These latter areas appear to be weakly connected to the central eastern Barbagia highlands by a weak dispersal route running from the south-west towards the centre-east of the island (Figure 2A).

The Omniscape algorithm, which investigates omnidirectional connectivity without considering focal nodes (i.e., *N. h. cetti* presence records), confirmed the presence of highly connected areas (Figure 2B) in the sectors traversed by the previously identified corridors, namely those linking the main high-suitability zones (see Di Nicola et al., 2023: Figure 3).

Models that additionally incorporated anthropogenic disturbance as a resistance factor showed a broadly consistent pattern, supporting the same main connectivity signal (Supplementary Figure S2).

The pinch points extraction following the 95th percentile approach identified the main priority connectivity corridors along the eastern backbone, linking the Sarrabus reliefs with the uplands of east-central Sardinia. In Circuitscape, this corridor appears continuous (Figure 3A), whereas in Omniscape it shows a clear separation between the southern and northern portions of the range; in Omniscape, an additional area of high connectivity also emerges in the eastern reliefs of the Sulcis-Iglesiente (Figure 3B). Of these areas, only about 50% fall within protected areas in Circuitscape (Figure 3A), whereas 65% do so in Omniscape (Figure 3B).

DISCUSSION

Our connectivity analyses identify eastern Sardinia as the main backbone of functional habitat connectivity for the endangered Sardinian grass snake *N. h. cetti*. The directional Circuitscape model revealed a network of corridors linking the main mountain ranges in the eastern part of the island, with a particularly prominent pathway connecting the Sarrabus reliefs in the south-east to the Barbagia region and, more weakly, to the Monte Limbara area in the north. Additional, fainter corridors were

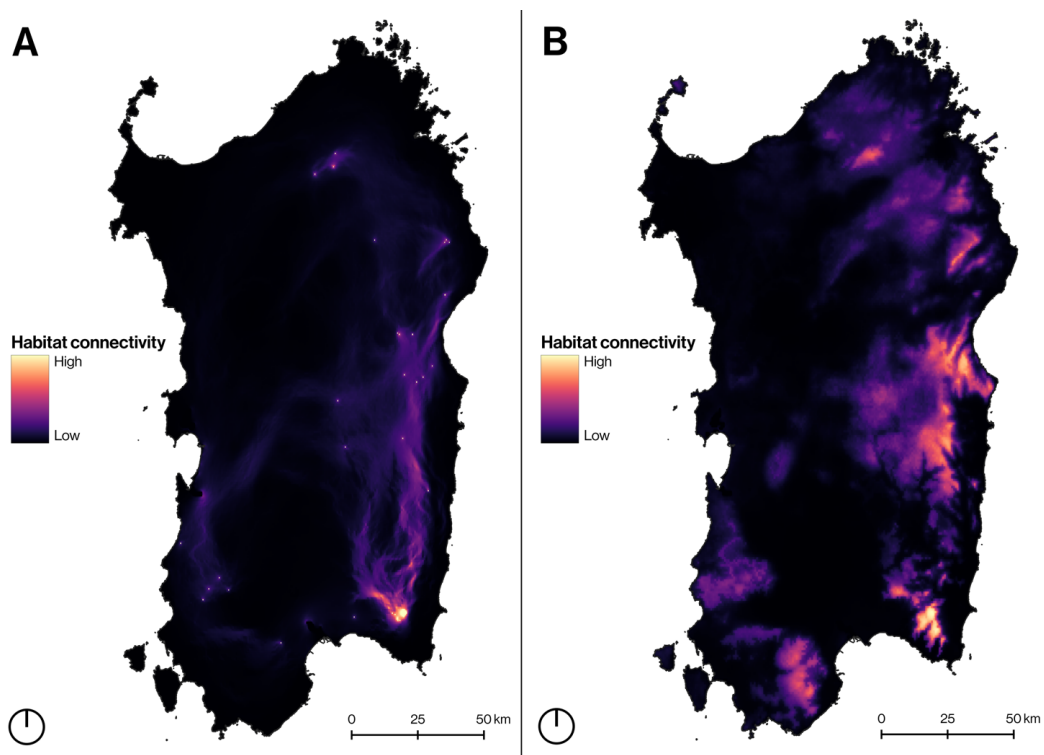


Figure 2. Predicted landscape connectivity estimated using a directional approach with Circuitscape (A) and an omnidirectional approach with Omniscape (B). Lighter colours indicate higher connectivity.

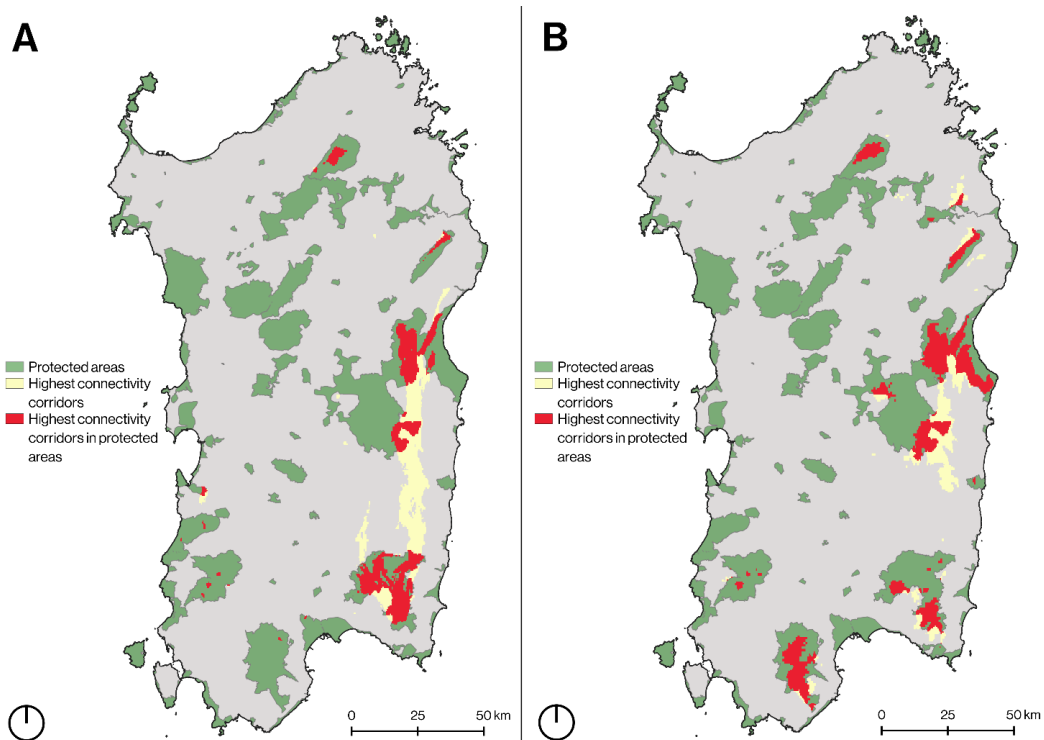


Figure 3. Spatial overlap between protected areas and the highest functional connectivity corridors identified as pinch points (i.e., above 95th percentile) estimated with a directional approach using Circuitscape (A) and an omnidirectional approach using Omniscape (B).

detected along the Iglesiente ranges in south-western Sardinia and towards the central-eastern highlands. The omnidirectional Omniscape model, which is independent of current occurrence records, highlighted broadly similar areas of high current flow, indicating that the eastern mountain system forms a structurally well-connected landscape that could facilitate dispersal even beyond the currently documented range of the species. Both results were consistent with models including anthropogenic disturbance (i.e., main roads, urban areas, and industrial areas) as a further resistance factor (Supplementary Figure S2).

The connectivity patterns are highly consistent with the bioclimatic suitability estimates obtained by Di Nicola et al. (2023), who identified eastern and south-eastern Sardinia as the core of suitable habitat for *N. h. cetti*, with only scattered patches of medium suitability in the south-western sector. In our study, the highest connectivity values tend to link precisely those high-suitability areas, especially between Sarrabus-Gerrei and the Ogliastra-Barbagia complex, whereas areas predicted to be only moderately suitable in south-western Sardinia show mainly weak or diffuse corridors. The agreement between suitability and connectivity suggests that the eastern chain is the main axis along which a metapopulation structure could be sustained. At the same time, the Omniscape outputs point to highly connected sectors where the species has not yet been reported, which may represent priority areas for targeted surveys, as already shown for other range-restricted snakes where habitat suitability models helped to locate new populations (Mizsei et al. 2016; Ficetola et al. 2020; Colla et al. 2025).

Connectivity is a key element for population persistence, especially when distributions are naturally restricted or fragmented (Thompson et al. 2017; Valenzuela-Aguayo et al. 2020; Brodie et al. 2025). *Natrix h. cetti* has a small and highly fragmented range, with scattered and often isolated populations (Schultze et al. 2020; Di Nicola et al. 2023). Under these conditions, gene flow is expected to be reduced and genetic drift to be stronger, increasing the risk of inbreeding depression and loss of adaptive potential (Frankham 2005, 2015). The corridors identified in our study, in particular those forming a south-east to central to north-east axis, highlight areas where maintaining landscape permeability is likely to be most beneficial for

genetic exchange. At present, no dedicated fine-scale population genetic data are available for this taxon, and our maps provide explicit spatial hypotheses that could be tested in future landscape genomic work and used to define management units.

From a management point of view, our results underline the importance of eastern Sardinia as both a stronghold of suitable habitat and as a connectivity hub. This part of the island is already covered by a dense network of protected areas, including regional parks such as Sette Fratelli-Monte Genis and Tepilora, and several Natura 2000 sites along the Sarrabus-Gerrei and Gennargentu-Supramonte ranges. This general pattern is consistent with the overlap analysis of connectivity pinch points, which showed that ~50% of the highest-connectivity cells identified by Circuitscape and 65% of those identified by Omniscape fall within protected areas. Given that these values refer only to cells above the 95th percentile of connectivity, they suggest that the existing protected-area network includes a relevant share of the most critical linkage zones, especially within the eastern mountain systems, but does not cover them completely. Some of the most constrained connectivity sectors remain outside, or only marginally within, protected areas. This is noteworthy because land-cover analyses indicate that, within protected and Natura 2000 areas, recent changes have largely involved transitions among natural and semi-natural classes, whereas unprotected land has experienced stronger increases in artificial and agricultural surfaces (Lai et al. 2017). Accordingly, those pinch points and corridor sections that are not fully included within the current protected network may deserve particular attention when evaluating future land-use changes or infrastructure development, in line with recent recommendations to integrate species distributions and connectivity into spatial planning (Iannella et al. 2024).

Ecological corridors can increase movements, gene flow and local diversity in many taxa (Gilbert-Norton et al. 2010; Fletcher et al. 2016; Resasco 2019; Brodie et al. 2025). For an island-restricted, range-limited reptile such as *N. h. cetti*, functional links between populations may be particularly important, as opportunities for natural recolonisation after local extinctions are limited. At the same time, increased connectivity is not automatically positive. Corridors may also promote the spread of invasive species, fire or pathogens (Simberloff and Cox 1987). In our case, a relevant

concern is the fungal pathogen *Ophidiomyces ophidiicola*, which is emerging in Europe and in Italy is mainly associated with natricine snakes (Di Nicola et al. 2025a, 2026). So far, all the sampled *N. h. cetti* individuals tested negative (Di Nicola et al. 2025a,b). However, if the pathogen were introduced, higher levels of movement could favour its spread along the main corridors. For this reason, any future interventions aimed at reinforcing connectivity should be coupled with continued health surveillance, in particular in high connectivity areas highlighted by our results.

Given the low detectability and elusive behaviour of the species (Capula et al. 1994; Lunghi et al. 2018; Di Nicola et al. 2023), some of these areas may harbour undetected populations. Fieldwork guided by the overlap between high suitability and high connectivity could therefore refine our understanding of the distribution of *N. h. cetti*, improve estimates of its area of occupancy and provide a more solid basis for future conservation assessments. Identifying highly connected sites that are currently unoccupied may also help to identify potential stepping stone habitats that could be crucial for long term persistence under climate and land use change.

Some limitations should be acknowledged. The Omniscape radius (about 6 km) was chosen from dispersal estimates available for other grass snakes (Ward 2017), because dispersal distances for *N. h. cetti* remain unknown, and no genetic data are currently available to validate the predicted corridors. More generally, the still limited ecological knowledge of this taxon constrains inference on its dispersal behaviour across different landscape features, including the extent to which hydrographic networks may facilitate movement. The lack of temporal data on the potential arrival and spread of *Natrix maura* in Sardinia (see Guicking et al. 2008; Di Nicola et al. 2023) also prevents a robust assessment of whether, and to what extent, ecological interactions with this species may influence the distribution and functional connectivity of *N. h. cetti*.

Nevertheless, our study provides the first island wide assessment of functional connectivity for the Sardinian grass snake and complements recent information on its distribution, ecology and conservation status (Di Nicola et al. 2023, 2025b,c). By combining the existing habitat suitability model with a circuit theory framework, we identify corridors that connect the main clusters of suitable

habitat in eastern Sardinia; these areas should be priority targets for conservation planning, genetic and health assessments and further field surveys, and the same workflow can be applied to other insular endemics and narrow-ranged reptiles facing similar problems.

AUTHOR CONTRIBUTIONS

Conceptualisation: L.C., and M.R.D.N.; Data curation: L.C., and M.R.D.N.; Formal analysis: L.C., and M.R.D.N.; Investigation: L.C., and M.R.D.N.; Methodology: L.C., and M.R.D.N.; Resources: L.C., and M.R.D.N.; Supervision: M.R.D.N.; Visualisation: L.C., and M.R.D.N.; Writing – original draft: L.C., and M.R.D.N.; Writing – review and editing: L.C., and M.R.D.N..

DATA AVAILABILITY

The data supporting the findings of this study have been deposited in Zenodo. Access is provided at the following DOI: 10.5281/zenodo.18954984

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Submitted: 7 January 2026

First decision: 20 February 2026

Accepted: 17 March 2026

Published online: 24 March 2026

Edited by Federico Marrone