

Diversity, Distribution, and Conservation Challenges of Bats in Georgia

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Statement

As the author of the submitted dissertation, I declare that this work is my original creation and does not include materials previously published, accepted for publication, or submitted for defense by other authors that are not mentioned or cited in accordance with the appropriate rules.

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აბსტრაქტი

საქართველო მდებარეობს გლობალურად აღიარებული ბიომრავალფეროვნების 36 ცხელი წერტილიდან ორის - კავკასიისა და ირან-ანატოლიის - ფარგლებში და გამოირჩევა მაღალი ტოპოგრაფიული და კლიმატური მრავალფეროვნებით. მიუხედავად ქვეყნის ამგვარი მაღალი ეკოლოგიური მნიშვნელობისა, ხელფრთიანები (ღამურები), რომლებიც საქართველოში ძუძუმწოვრებს შორის სახეობრივი მრავალფეროვნებით მეორე ყველაზე მდიდარ ჯგუფს წარმოადგენენ, კვლავ ერთ-ერთ ნაკლებად შესწავლილ ცხოველთა ჯგუფად რჩებიან. წინამდებარე ნაშრომი წარმოადგენს ხელფრთიანების სახეობრივი მრავალფეროვნების, მათ მიერ ჰაბიტატების გამოყენებისა და მათი სივრცითი განაწილების ინტეგრირებული შეფასების პირველ მცდელობას ქვეყნის მასშტაბით, რაც ქმნის საფუძველს მეცნიერულად დასაბუთებული კონსერვაციული ღონისძიებების დაგეგმვისთვის.

კვლევა აერთიანებს ოთხ ურთიერთშემავსებელ კომპონენტს. 1835 წლიდან 2025 წლამდე ხელფრთიანთა დაფიქსირების ყველა არსებული ჩანაწერი თავმოყრილ იქნა ერთიან, გადამოწმებულ ეროვნულ მონაცემთა ბაზაში. აღნიშნული მონაცემთა ბაზა მოიცავს ოთხი ოჯახიდან 30 სახეობის 2003 გადამოწმებულ დაფიქსირების წერტილს და წარმოადგენს 1987 დაფიქსირების წერტილის მომცველი მონაცემთა ბაზის განვრცობილ ვერსიას, რომელიც პირველად გამოქვეყნდა და ხელმისაწვდომი გახდა გლობალური ბიომრავალფეროვნების ინფორმაციის პლატფორმის (GBIF) მეშვეობით 2023 წელს (Natradze et al. 2023). 1999 წლიდან 2024 წლამდე ჩატარდა 300-ზე მეტი საველე გასვლა და გამოკვლეულ იქნა ყველა ტიპის მიწისქვეშა თავშესაფარი. მიწისქვეშა თავშესაფრების კვლევებისას დაფიქსირდა 20 სახეობა, რომელთა ყველაზე მაღალი მრავალფეროვნება დასავლეთ საქართველოს კარსტულ ლანდშაფტებში გამოვლინდა. 107 ინდივიდის COI გენის გამოყენებით შეიქმნა 24 სახეობის დნმ-ბარკოდირების ბიბლიოთეკა მორფოლოგიური იდენტიფიკაციის გადასამოწმებლად, ტაქსონომიურად პრობლემური ჯგუფების დასაზუსტებლად და სამომავლოდ არაინვაზიური მეთოდებით კვლევის ხელშესაწყობად. დნმ-ბარკოდირებამ დაადასტურა მორფოლოგიური იდენტიფიკაციის სისწორე ინდივიდთა უმრავლესობისთვის და გამოკვეთა ორი მნიშვნელოვანი მიგნება; კერძოდ, ორივე

სახეობის - *Myotis tschuliensis* და *M. Nattereri* - შესაძლო თანაარსებობა საქართველოში და ორი განსხვავებული მიტოქონდრიული ხაზი *Eptesicus serotinus* სახეობის შიგნით. ხელფრთიანთა 27 სახეობისთვის შემუშავდა გავრცელების მოდელები მრავალშრიანი მოდელირების გზით, რაც გულისხმობს MaxEnt-ს, Random Forest-ს, mboost-სა და ექსპერტული ცოდნის ინტეგრირებულ გამოყენებას მოდელირებაში. ჰაბიტატების ვარგისიანობის ანალიზისას 27 სახეობისთვის შექმნილი რუკების საშუალო AUC მაჩვენებელმა 0.873 შეადგინა. შედეგების მიხედვით, დასავლეთ საქართველო გამოიკვეთა, როგორც მაღალი პრიორიტეტის მქონე რეგიონი ხელფრთიანთა კონსერვაციისთვის, ხოლო აღმოსავლეთ საქართველო მნიშვნელოვანია მხოლოდ რამდენიმე სახეობისთვის, თუმცა იგი კვლავაც ნაკლებად არის შესწავლილი ვიდრე დასავლეთ საქართველო. ნაშრომში ასევე გამოყენებულია თანაავტორობით შესრულებული რამდენიმე კვლევის შედეგები, რომლებიც ეხება ხელფრთიანების ბაქტერიულ და ვირუსულ პათოგენებზე კვლევას და ხელფრთიანთა კოლონიაში სიკვდილიანობის დაფიქსირების პირველ შემთხვევას.

ნაშრომის შედეგებზე დაყრდნობით, საქართველოს ხელფრთიანთა ფაუნა ხასიათდება მაღალი მრავალფეროვნებით. მაღალია ასევე ხელფრთიანთა მნიშვნელობა როგორც კონსერვაციული თვალსაზრისით, ისე მისი შესაძლო გავლენით ადამიანის ჯანმრთელობაზე, ვიდრე ეს აქამდე იყო მიჩნეული. ნაშრომი გვთავაზობს ხელფრთიანთა გავრცელების დაზუსტებულ მონაცემთა ბაზას, მიწისქვეშა ჰაბიტატების გამოყენების შეფასებას, ბარკოდების ბიბლიოთეკას და სახეობათა ჰაბიტატების მოდელირებულ რუკებს. ყოველივე ეს ქმნის მყარ საფუძველს საქართველოში შესაბამისი კონსერვაციული პრიორიტეტების განსაზღვრისთვის და სამომავლოდ მნიშვნელოვანი კვლევების დაგეგმვისთვის.

საკვანძო სიტყვები: ღამურები; ხელფრთიანები; ბიომრავალფეროვნება; კონსერვაცია; სახეობების გავრცელების მოდელირება; დნმ-ის ბარკოდირება; გამოქვაბულის ეკოლოგია; *Yersinia enterocolitica*.

Abstract

Georgia is located within two of the 36 globally recognized biodiversity hotspots - the Caucasus and Irano-Anatolian - and is characterized by pronounced topographic and climatic heterogeneity. Despite this high ecological significance of the country, bats - the second most species-rich mammalian group in the country, have remained among the least studied mammals in Georgia. This thesis provides the first integrated assessment of bat species composition, habitat use and spatial distribution across the country, establishing a foundation for evidence-based conservation planning.

The research integrates four complementary core components. All available records from 1835 to 2025 were compiled into a single verified national occurrence dataset. This database includes 2003 verified occurrence records of 30 species from four families and represents an expanded version of the dataset comprising 1987 occurrence records, which was first published and made available through the Global Biodiversity Information Facility (GBIF) in 2023 (Natradze et al. 2023). From 1999 to 2024, more than 300 field surveys were conducted, covering all types of underground roosts. These surveys recorded 20 species, with the highest diversity observed in the karst landscapes of western Georgia. A DNA barcode reference library was established for 24 species from 107 individuals using the COI gene, to verify morphological identifications, resolve taxonomically problematic taxa and facilitate future non-invasive monitoring. DNA barcoding confirmed morphological identifications for most sampled individuals and revealed two significant findings: the possible coexistence of *Myotis tschuliensis* and *M. nattereri* in Georgia, and two divergent mitochondrial lineages within *Eptesicus serotinus*. Species distribution models were developed for 27 species using a stacked generalization framework integrating MaxEnt, Random Forest, mboost and expert-knowledge-based range maps. Habitat suitability maps for 27 species achieved a mean AUC of 0.873, identifying western Georgia as the highest-priority conservation zone, while eastern Georgia is important for several species with eastern distributions and remains considerably undersampled. The thesis also draws on several co-authored contributions, including an investigation of Georgia's first documented bat die-off and broader surveys of bacterial and viral pathogens in Georgian bats.

These findings demonstrate that Georgia's bat fauna is considerably more diverse, conservation-relevant, and potentially significant for human health than previously recognized. The thesis provides a verified occurrence database, a national assessment of bat use of underground habitats, a barcode library, and habitat suitability maps, together forming the evidence base required for conservation prioritization and future bat research in Georgia.

Keywords: bats; Chiroptera; biodiversity; conservation; species distribution modelling; DNA barcoding; cave ecology; *Yersinia enterocolitica*.

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Abbreviations

a.s.l - Above sea level

AUC - Area Under the Curve

BOLD - Barcode of Life Data Systems

cgMLST - Core genome multilocus sequence typing

COI - Cytochrome c oxidase subunit I

cytb - Cytochrome b

DNA - Deoxyribonucleic acid

eDNA - Environmental DNA

EUROBATS - Agreement on the Conservation of Populations of European Bats

GBIF - Global Biodiversity Information Facility

IUCN - The International Union for Conservation of Nature

NCDC - National Center of Disease Control and Public Health

NDVI - Normalized Difference Vegetation Index

pYV - Plasmid for Yersinia virulence

SDM - Species distribution model

UTM - Universal Transverse Mercator

VU – Vulnerable

WCBV - West Caucasian Bat Virus

WGS - World Geodetic System

List of Core Publications

1. **Natradze, I.**, Bukhnikashvili, A., Sheklashvili, G., & Mumladze, L. (2023). Bats of Georgia: An occurrence dataset from 1835 through 2022. *Biodiversity Data Journal*, 11, e103181. <https://doi.org/10.3897/BDJ.11.e103181> (IF=1.1)
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Proceedings of the National Academy of Sciences, 117(13), 7255–7262.
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<https://doi.org/10.3390/microorganisms8071000> (IF=4.2)
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1. Introduction

Georgia lies mostly in the Caucasus Biodiversity Hotspot, while its southern part also falls along the northern periphery of the Irano-Anatolian Biodiversity Hotspot, placing the country across two of the 36 globally recognized biodiversity hotspots (Myers et al. 2000; Mittermeier et al. 2011; Habel et al. 2019). Geographically, Georgia is situated on the isthmus between the Black and Caspian Seas, encompassing the southern slopes of the Greater Caucasus and the northern slopes of the Lesser Caucasus, as well as extensive lowlands between these mountain systems - the Kolkheti lowland in the west and the Mtkvari (Kura) River lowland in the east. The designation of these areas as biodiversity hotspots reflects both the exceptional level of endemism characteristic of the region, predominantly among plant species, and the significant loss of natural vegetation cover (Myers et al. 2000; Mittermeier et al. 2011). However, the diversity of most animal taxonomic groups within these hotspots remains poorly understood, and a substantial proportion of existing biodiversity data, including that from Georgia, is outdated and incomplete (Mumladze et al. 2020).

This knowledge gap is evident in the case of bats. With 30 species recorded in the country (Natradze et al. 2023), bats constitute the second-most species-rich group of mammals in Georgia. They are associated with a wide range of natural and human-modified habitats, playing an ecologically significant role across the country. At the same time, bats remain one of the least comprehensively studied vertebrate groups in Georgia in terms of their diversity, distribution and habitat use.

The oldest documented record of bats in Georgia dates back to 1835, when Nordmann (1840) reported four species, followed shortly by surveys conducted by Kolenati (1860). For nearly four decades thereafter, no new data were available until a renewed but still limited contribution of the twentieth century (Radde 1899; Satunin 1896, 1903, 1908, 1912, 1913, 1915), bringing the total number of species recorded in Georgia to 16. Research throughout the twentieth century remained sporadic, with information scattered across Georgian and Russian publications by researchers (Chkhikvishvili 1926; Ognev 1928; Kuzyakin 1950; Janashvili 1953, 1963; Perov 1975, 1980, 1983; Strelkov 1983, 1988; Shidlovsky 2013), while

additional incidental records appeared in works by researchers from other fields (Papava 1949, 1953, 1960; Matsaberidze 1961, 1976; Avaliani 1963, 1969a, 1969b, 1970, 1973, 1976; Matsaberidze and Khotenovsky 1966, 1967), collectively raising the known species count to 22.

More systematic surveys of the Georgian bat fauna began at the end of the twentieth century and resulted in a number of publications (Bukhnikashvili and Kandaurov 2002; Bukhnikashvili et al. 2004, 2008, 2009; Gazaryan and Bukhnikashvili 2005; Ghazaryan et al. 2006; Gazaryan et al. 2008, 2017; Yavruyan et al. 2008; Ivanitsky 2002, 2010, 2015, 2017, 2018; Benda 2011; Smirnov et al. 2016; Imnadze et al. 2020; Urushadze et al. 2021), raising the number of recorded species to 26 (Bukhnikashvili 2004). Beyond changes resulting from taxonomic and molecular revisions, field surveys conducted by our research group as part of thesis work directly contributed to expanding the known bat fauna of Georgia: *Pipistrellus pygmaeus* and *Myotis daubentonii* were added to the national list by Bukhnikashvili (2004), followed by *Rhinolophus blasii* (Ghazaryan et al. 2006), *Tadarida teniotis* (Gazaryan et al. 2017), *Myotis alcatheae* and *M. davidii* (Natradsze et al. 2023), and most recently *Myotis tschuliensis* (Maghlakelidze et al. 2024), bringing the total number of bat species recorded in Georgia to 30. A considerable portion of the survey results accumulated over this period had remained either in grey literature and unpublished project reports (Bukhnikashvili and Kandaurov 1997; Natradsze et al. 2003; Bukhnikashvili et al. 2008; Natradsze and Bukhnikashvili 2014) or entirely unpublished. One of the major focuses of work was therefore to compile and consolidate all existing bat occurrence records into a single, comprehensive, and accessible dataset, published through the Global Biodiversity Information Facility (GBIF), comprising 1987 records spanning the period from 1835 to 2022 (Natradsze et al. 2023). This dataset has since been expanded to 2003 records covering 1835 to 2025, with the underground habitat component published separately (Natradsze et al. 2024).

A key component of the data consolidation was the compilation of bat records from subterranean habitats, which exemplify a broader pattern of initially limited data that have gradually improved through more systematic survey and monitoring efforts. Among the habitats used by bats in Georgia, underground sites, including natural caves and man-made

structures, are of high conservation value, serving as regular roosts, maternity sites, and hibernation shelters for many species, and thereby playing a critical role in their life cycles. At the same time, these habitats are increasingly affected by anthropogenic pressures, including tourism, habitat modification, and light pollution. In Georgia, the study of subterranean bat assemblages long remained limited: by the 1980s, only 13 bat species had been identified from 71 underground sites across the country (Satunin 1912a, 1912b; Papava 1949; Kuzyakin 1950; Perov 1975, 1980, 1983). The more systematic studies of the late twentieth and early twenty-one century, while advancing general knowledge of Georgian bats, addressed underground habitats only to a limited extent (Bukhnikashvili 2004; Bukhnikashvili et al. 2004, 2009; Gazaryan 2005; Ivanitsky 2010, 2015, 2017; Natradze et al. 2023), and publications specifically targeting bats in caves remained rare and confined to individual sites (Ivanitsky 2002; Imnadze et al. 2020). Building on these earlier records, more than 300 surveys of underground sites of all types were carried out across the country over 20 years.

Reliable assessment of bat diversity, however, depends not only on comprehensive occurrence data but also on accurate species identification. Indeed, the knowledge of the increasing number of bat species in Georgia has benefited not only from the intensification of research but from the progressive refinement of taxonomic and molecular methods. In Georgia, several bat taxa (*Myotis mystacinus*, *M. brnadtii*, *M. alcathoe*, *M. davidii*) belong to cryptic or taxonomically difficult groups that cannot be resolved confidently by morphology alone. This indicates the unreliability of old distribution data on one hand, and making integrative taxonomic approaches increasingly necessary for accurate diversity inventories on the other. DNA barcoding - a molecular method for species identification based on a standardized short fragment of DNA (typically cytochrome oxidase subunit 1 – CO1) - represents an important complementary tool in this context, both for confirming morphological identifications and for detecting hidden diversity (Hebert et al. 2003). A local DNA barcode reference library is particularly valuable in regions such as the Caucasus Biodiversity Hotspot, where global databases, including Barcode of Life Data (BOLD) Systems (Ratnasingham and Hebert 2007) and GenBank (Sayers et al. 2022) have limited coverage of regional taxa (Zhou et al. 2011; Weigand et al. 2019; Specchia et al. 2020). Before 2021–2024, no broad molecular assessment

of Georgian bats had been conducted, and as part of the thesis work, a DNA barcode reference library was therefore developed for bat species occurring in Georgia, with the aims of testing morphology-based identifications, clarifying taxonomically problematic records, and strengthening the reliability of the occurrence dataset used in subsequent analyses. At the same time, the molecular data obtained highlighted that some taxonomic assumptions require continued revision, confirming that an integrative approach combining morphological and genetic evidence is essential for an accurate understanding of bat diversity in Georgia (Maglakelidze et al. 2024).

With a consolidated, field-verified, and taxonomically reliable occurrence dataset in place, it became possible to address the broader question of how bat species are distributed across Georgia's diverse landscapes. Occurrence records alone, however, do not provide a complete picture of species distributions across a country as topographically and ecologically diverse as Georgia. The Wallacean shortfall, the widespread lack of detailed distributional knowledge for many regions and taxa (Hortal et al. 2015), represents not only a gap in biogeographic understanding but also a practical barrier to conservation planning (Hochkirch et al. 2021). Species distribution models (SDMs) have become a central tool for addressing this shortfall, allowing species' niches to be characterized by combining occurrence records with environmental predictors to predict distributions across unsampled areas (Elith and Leathwick 2009; Guisan and Thuiller 2005). For this reason, species distribution modelling formed another major component of the present thesis, applying the stacked generalization framework of Oeser et al. (2024), which integrates predictions from multiple SDM algorithms with expert-based range maps. Applied to Georgia, this framework provides fine-scale habitat suitability maps for bat species and supports a more detailed analysis of their spatial distribution across the country.

Robust occurrence data and predictive distribution maps are only one part in the process of effective bat conservation. Despite the gradual accumulation of knowledge on Georgia's bat fauna, important conservation shortfalls remain. Although bats are highly prioritized animals and protected under national legislation and many species are listed under international frameworks such as the IUCN Red List, The Emerald Network (an ecological network of Areas

of Special Conservation Interest across Europe and the Caucasus), The Berne Convention (Convention on the Conservation of European Wildlife and Natural Habitats) and the Agreement on the Conservation of Populations of European Bats (EUROBATS), on-the-ground conservation measures lag substantially behind these formal protections. Practical conservation action has so far been limited to occasional initiatives, such as for instance, the development of a site-specific management plan for a single cave, or conducting sporadic state monitoring of bat populations and roosts (Natradsze and Bukhnikashvili 2014). Disease surveillance has likewise received limited attention despite mounting global evidence that bats can host bacterial, viral and fungal pathogens of conservation- and public health relevance (Mühldorfer et al. 2011; Bai et al. 2017; Hoyt et al. 2020; Urushadze et al. 2022). The isolation of *Yersinia enterocolitica* from bats during the first documented bat die-off in Georgia, recorded during fieldwork for this thesis, illustrates this gap directly.

2. Aims and Objectives

The main aim of the thesis research is to study bat species composition and spatial distribution in Georgia, establishing a robust foundation for better conservation planning, future monitoring and advanced research on bats in Georgia. The objectives of the work included:

- Assessment of bat species distribution and composition in Georgia.
- Assessment of the use of underground habitats by bats and identification of critical roosts.
- Modelling of habitat suitability and spatial distribution across Georgia.
- Development of a DNA barcode reference library for bat species occurring in Georgia, and application of molecular evidence to improve the reliability of species identification and clarify taxonomically problematic records.
- Identification of knowledge gaps and conservation challenges.

3. Overview of the Included Studies

This thesis is based on four core interrelated studies that together provide a progressively more complete understanding of bat diversity, distribution and conservation in Georgia. Rather than

representing isolated publications, these studies form a connected research framework in which each component addresses a major knowledge gap and creates the foundation for the follow-up activities. Several additional co-authored publications and reports complement the core studies and are described separately below.

In the first study, we established the empirical basis for understanding bat distribution in Georgia by consolidating all available occurrence records from 1835 to 2022 into a single verified national dataset. The publication associated with this study provided a comprehensive overview of long-term trends in bat research in Georgia. This knowledge forms a basis for addressing conservation challenges and provides essential data for shaping future research priorities. In addition, the consolidated dataset enables the assessment of habitat use across the country, the evaluation of bat assemblages in underground sites, and the development of species distribution models (Natradze et al. 2023).

In the second study, we investigated the distribution of bat species across the underground sites of Georgia, refined this baseline by focusing on subterranean habitats, demonstrating that existing survey coverage remains far from complete and identifying underground environments as a clear conservation priority (Natradze et al. 2024).

In the third study, we explored small mammal diversity in Georgia through DNA barcoding. Within this study, we established the first DNA barcode library for bat species occurring in Georgia (along with other small mammals), which strengthens the taxonomic reliability of the occurrence dataset and provides a molecular basis for resolving cryptic and taxonomically problematic taxa (Maghlakelidze et al. 2024).

In the fourth study, we used verified occurrence records to model habitat suitability. Using the stacked generalization approach of Oeser et al. (2024) — an ensemble integrating MaxEnt (Phillips et al. 2006), Random Forest (Breiman 2001), boosted GAMs (Bühlmann and Hothorn 2007), and expert knowledge — we generated spatially explicit habitat suitability maps relevant for conservation planning. This study demonstrated the importance of methodological refinement in obtaining accurate predictions and showed that expert-informed ensembles produced marginal improvements in predictive performance over SDM-

only ensembles across most modelled species. The approach was then applied to Georgia in the present thesis, generating habitat suitability maps for 27 bat species. (Oeser et al. 2024).

In addition to these four core studies, during the doctoral work, I contributed to a number of further bat research and conservation activities, the resulting publications and reports of which are listed in the publication section. These include a national bat monitoring effort (Natradze and Bukhnikashvili 2014), a molecular survey of bacterial zoonotic agents in Georgian bats (Bai et al. 2017), a site-specific conservation management plan for Ghliana Cave (Campester 2019), the investigation of the first documented bat die-off in Georgia and the isolation of a novel *Yersinia enterocolitica* lineage (Imnadze et al. 2020), global work on white-nose syndrome (Hoyt et al. 2020), and the first cross-sectional survey of coronaviruses in Georgian bat populations (Urushadze et al. 2022). While the four core studies address what bat species occur in Georgia, how they use underground habitats, how reliably they can be identified, and how their distributions can be predicted, this additional co-authored work adds further dimensions related to disease ecology, applied monitoring, and site-based conservation planning. Together, these additional contributions fall outside the core area of the thesis but broaden the evidence base and create an important foundation for bat conservation in Georgia.

4. Materials and Methods

The methodological framework used in the thesis covers historical data compilation, systematic field surveys, molecular identification, and species distribution modelling. Because the thesis is cumulative and each component is described in full detail in the respective appended publications, the sections below summarize the principal approaches and key methodological decisions specific to the Georgian context. Methods relating to the additional co-authored papers and reports are not described separately here, and the reader is referred to the corresponding publications.

4.1 Study Area

The thesis study area encompasses the entire territory of Georgia, reflecting its primary objectives related to bat species diversity and distribution in the country. It should be noted,

however, that Abkhazia and the Samachablo region (so-called South Ossetia) are currently outside the control of the Georgian authorities, and direct fieldwork in these regions was not possible during the thesis period. Records from these regions used in the present work derive from previously published sources and historical museum collections, and any conclusions concerning these areas should be interpreted with the given assumption.

Georgia covers an area of 69,700 km², with elevations ranging from sea level to approximately 5,203 m at Mount Shkhara. Two-thirds of the country is mountainous, with an average elevation of 1,200 m a.s.l.

Climatic conditions across Georgia range from humid subtropical with extensive mountain forests in the west, to dry arid woodland and semi-deserts in the east, and glaciated nival belts in the high-mountain north. Georgia encompasses two zoogeographic subzones and three provinces: The Circumboreal subzone (Caucasus district of the European forest province) and the Mediterranean subzone (Anterior Asia district of the Mediterranean province and the Kura district of the Iran-Turan province) (Verestchagin 1959). Overall, approximately 72 landscape types have been identified in the country, ranging from humid subtropical landscapes in the west and alpine landscapes in the north-east, to Middle Eastern-type treeless uplands in the south and Turanian semi-deserts in the south-east (Beruchashvili 2000).

Subterranean environments are an important component of Georgia's landscape. Karstic outcrops cover approximately 6.4% of the total territory (4,475 km²) and support more than 1,500 known karst and conglomerate caves (Asanidze et al. 2017). These are concentrated primarily in the western part of the country, in the peripheral zone of the southern slope of the Greater Caucasus and on the hilly zones north of the Colchis lowland (Ukleba 1981). In eastern Georgia, karstic outcrops are less developed, occurring as limestone deposits with only small grottos and crevices.

4.2 Data compilation and consolidation

All available published and unpublished records of bats in Georgia were systematically compiled. Published sources were identified through a snowball survey method, beginning

with a set of known references, including peer-reviewed articles, grey literature and museum records, and tracing additional references cited within each source. This process incorporated materials published in Georgian, Russian and English, held in scientific libraries of Georgian and Russian research institutions, as well as Georgian and Russian museum collections, including the collection of the Zoological Institute of the Russian Academy of Sciences (Saint Petersburg) and the Zoological Museum of Moscow State University. European databases, including GBIF and the EUROBATs underground habitats database, were also searched. The reference list was additionally verified through consultation with colleagues working on bat fauna across the Caucasus, Russia and Europe.

Records were included only if identification to the species level was possible. Georeferencing was based on provided geographic coordinates where available, or on locality names and descriptions of subterranean objects for older literature records. The dataset, spanning records from 1835 through 2025, was originally published and made accessible through GBIF as the first version, with 1987 records covering 1835–2022 (Natradze et al. 2023). This data was then enriched by additional records collected during 2023–2025 and this expanded dataset forms the basis of the analyses presented in this thesis. Full details of data compilation and quality control procedures are provided in Natradze et al. (2023).

To visualize spatial patterns in survey effort and species richness, a 50×50 km grid was overlaid on Georgia in UTM Zone 38N (EPSG:32638). For each cell, the number of unique occurrence points (U) — defined as the number of distinct localities with bat records, irrespective of how many times each was surveyed, and the number of species (S) were calculated from the occurrence dataset. Cells with $S \geq 20$ were designated as high-diversity cells for visualization purposes. For mapping, the grid was reprojected to WGS84 (EPSG:4326).

4.3 Field data collection

Field surveys were conducted from 1999 to 2025 across all major regions of Georgia. To collect presence records, several methods were employed, including mist-netting, harp trapping, and visual inspection of natural and man-made underground and overground shelters (Dietz and Kiefer 2016). Acoustic detection was carried out using hand-held ultrasound bat detectors

(Pettersson D 200, Pettersson D240, Pettersson D240x), with detector records included only when bat presence was visually confirmed and species-level identification was possible. Morphological measurements for species identification followed Kuzyakin (1950) and Dietz and Kiefer (2016). After measurements, bats were released at the site of capture. Tissue samples for molecular analysis were taken from the wing membrane, a non-lethal procedure, and stored in 96% ethanol. All field research and primary morphological analyses were carried out by the staff of the Vertebrate Animal Research Group of the Institute of Zoology, Ilia State University. For underground habitats specifically, more than 300 surveys were conducted during all seasons from 1999 to 2025, contributing to a total of 115 underground sites reported across the country. Both natural and man-made subterranean structures were surveyed. In western Georgia, man-made sites consisted primarily of mines. In eastern Georgia, man-made sites included caves with built-in walls, small grottoes and adits, located in the gorges of the Mtkvari (Kura), Iori, Khrami, Algeti and Mashavera rivers, formed in sandstone or by widening of volcanic caverns. During the swarming period, bats were additionally mist-netted in front of underground sites. Where bat colonies were encountered, colony size was estimated using direct counts for small visible groups, subgroup extrapolation for larger aggregations, and photographic methods where direct counting was not possible.

Bat species were classified by their degree of association with subterranean habitats, and potential threats were assessed at selected sites with colonies. Many sites, particularly those hosting bat colonies, were surveyed repeatedly across multiple years and seasons to confirm species occurrence and monitor population trends. Coordinates of sensitive roost sites were masked or generalized to prevent disturbance to vulnerable colonies. Full methodological details of data compilation and underground surveys are provided in Natradze et al. (2023) and Natradze et al. (2024).

4.4 Molecular identification and DNA barcoding

From 2007 to 2022, tissue samples were collected from 107 bat individuals representing 24 species from 32 localities across Georgia. Samples were taken from the wing membrane using a non-lethal procedure, stored in 96% ethanol and transported to the Institute of Zoology, Ilia

State University, where voucher specimens and tissues are deposited. A small number of individuals were euthanized for detailed morphological and genetic study.

Molecular-genetic analysis was carried out within the framework of the Caucasus Barcode of Life Project (Thormann et al. 2019). Genomic DNA was extracted from preserved tissues, and a fragment of the mitochondrial cytochrome c oxidase subunit 1 (COI) gene was amplified and sequenced following standard barcoding protocols (Folmer et al. 1994). Resulting sequences were uploaded to the Barcode of Life Data System (Ratnasingham and Hebert 2007) and compared with the reference sequences available in BOLD and GenBank (Sayers et al. 2022) to test morphology-based identifications and clarify taxonomically problematic records. Where available, Georgian sequences were also cross-checked against published GenBank entries for closely related species to identify possible mitochondrial introgression or cryptic divergence. Full methodological details are provided in Maghlakelidze et al. (2024).

4.5 Species distribution modelling

Presence records were prepared for modelling through a series of filtering steps. All occurrence records before 1970 were excluded to ensure temporal consistency with environmental predictors. Duplicate records and points located within less than 1 km of each other were removed through a thinning procedure, retaining one presence point per 1 km grid cell.

Species distribution models were developed following the stacked generalization framework proposed by Oeser et al. (2024). Environmental predictors were prepared at 1 km resolution and included bioclimatic variables, monthly NDVI, topographic variables, and a land-cover layer, all masked to Georgia. For the expert-informed component, distance-to-range layers derived from IUCN expert range maps were obtained from the supporting dataset of Oeser et al. (2024), aligned to the study grid, and prepared for the 27 bat species occurring in Georgia before inclusion in the expert-informed ensemble.

Background points were generated using two approaches. First, a target-group bias background was created based on kernel density estimation of all available bat occurrence records, with the resulting density surface used as a probability layer for sampling background points.

Second, a random background was generated by sampling points uniformly across the study area. In contrast to the original Oeser et al. (2024) implementation, a fixed number of 10,000 background points per species was used for both approaches, following the widely adopted convention in presence-background modelling (Phillips et al. 2006; Merow et al. 2013), ensuring comparability among species with differing sample sizes and producing consistent habitat suitability maps across taxa. Models were fitted using MaxEnt, Random Forest, and boosted generalized additive models (gamboost, implemented through the mboost package), and final model variants were selected for presentation based on the area under the receiver operating characteristic curve (AUC). Continuous habitat suitability maps were produced for each species, and binary maps were additionally derived using the maximum sum of sensitivity and specificity (MaxSSS) threshold.

All analyses were conducted in R (R Core Team, 2024). Species distribution modelling and raster processing were conducted using the packages terra (Hijmans, 2024), dismo (Hijmans et al., 2024), Random Forest (Liaw & Wiener, 2002), mboost (Hothorn et al., 2024), brglm2 (Kosmidis, 2024), and pROC (Robin et al., 2011). Data preparation and file handling used dplyr (Wickham et al., 2023), tidyr (Wickham et al., 2024), readr (Wickham et al., 2024), readxl (Wickham & Bryan, 2023), purrr (Wickham & Henry, 2023), and magrittr (Bache & Wickham, 2022). Spatial vector processing and visualisation used sf (Pebesma, 2018), ggplot2 (Wickham et al., 2024), and patchwork (Pedersen, 2024). The MaxEnt implementation through dismo additionally relied on rJava (Urbanek, 2024), and R.utils (Bengtsson, 2023) was used for runtime control.

5. Results

5.1 Bat species composition and distribution

Field surveys and literature compilation documented 30 bat species belonging to 11 genera and four families across Georgia (Table 1): Rhinolophidae (5 species), Vespertilionidae (23 species from nine genera), Miniopteridae (1 species) and Molossidae (1 species).

Table 1. Bat species of Georgia with occurrence records and conservation status

#	Species	Total records	Literature & Museum data	Our records	IUCN status	Georgia Red List	Emerald Network
Rhinolophidae							
<i>Rhinolophus</i>							
1	<i>Rhinolophus ferrumequinum</i> (Schreber, 1774)	185	57	128			+
2	<i>Rhinolophus hipposideros</i> (Borkhausen, 1797)	168	86	82			+
3	<i>Rhinolophus euryale</i> Blasius, 1853	51	20	31		VU	+
4	<i>Rhinolophus blasii</i> Peters, 1866	6	0	6			+
5	<i>Rhinolophus mehelyi</i> Matschie, 1901	5	5	0		VU	+
Vespertilionidae							
<i>Myotis</i>							
6	<i>Myotis blythii</i> (Tomes, 1857)	123	34	89			+
7	<i>Myotis bechsteinii</i> (Kuhl, 1817)	25	4	21		VU	+
8	<i>Myotis daubentonii</i> (Kuhl, 1817)	41	6	35			
9	<i>Myotis nattereri sensu lato</i> (Kuhl, 1817)	66	12	54			
10	<i>Myotis emarginatus</i> (E. Geoffroy, 1806)	72	15	57			+
11	<i>Myotis alcathoe</i> von Helversen & Heller, 2001	25	1	24			
12	<i>Myotis brandtii</i> (Eversmann, 1845)	28	3	25			
13	<i>Myotis davidii</i> (Peters, 1869)	3	0	3			
14	<i>Myotis mystacinus</i> (Kuhl, 1817)	89	33	56			
<i>Nyctalus</i>							
15	<i>Nyctalus noctula</i> (Schreber, 1774)	89	16	73			
16	<i>Nyctalus leisleri</i> (Kuhl, 1817)	86	12	74			
17	<i>Nyctalus lasiopterus</i> (Schreber, 1780)	26	10	16	VU		
<i>Eptesicus</i>							
18	<i>Eptesicus nilssonii</i> (von Keyserling & Blasius, 1839)	4	1	3			
19	<i>Eptesicus serotinus</i> (Schreber, 1774)	163	51	112			
<i>Pipistrellus</i>							
20	<i>Pipistrellus pipistrellus</i> (Schreber, 1774)	288	65	223			
21	<i>Pipistrellus pygmaeus</i> (Leach, 1825)	74	0	74			
22	<i>Pipistrellus kuhlii</i> (Kuhl, 1817)	83	11	72			
23	<i>Pipistrellus nathusii</i> (von Keyserling & Blasius, 1839)	17	15	2			
<i>Hypsugo</i>							
24	<i>Hypsugo savii</i> (Bonaparte, 1837)	23	4	19			
<i>Barbastella</i>							
25	<i>Barbastella barbastellus</i> (Schreber, 1774)	63	8	55		VU	+
<i>Plecotus</i>							
26	<i>Plecotus auritus</i> (Linnaeus, 1758)	62	26	36			
27	<i>Plecotus macrobullaris</i> Kuzyakin, 1965	21	10	11			
<i>Vespertilio</i>							
28	<i>Vespertilio murinus</i> Linnaeus, 1758	38	15	23			
Miniopteridae							
<i>Miniopterus</i>							
29	<i>Miniopterus schreibersii</i> (Kuhl, 1817)	65	35	30	VU		
Molossidae							
<i>Tadarida</i>							
30	<i>Tadarida teniotis</i> (Rafinesque, 1814)	14	1	13			

Total	2003	556	1447			
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Notes: "Literature & Museum data" includes 11 records from an unpublished survey report by the Behavioral Ecology and Evolution Research Group, University of the Basque Country (2011). IUCN: global IUCN Red List status (VU = Vulnerable); National Red List of Georgia status; Emerald Network: + indicates species listed under the Emerald Network.

The species list expanded progressively through the survey period, with seven species added to the national fauna through fieldwork conducted by our research group: *Pipistrellus pygmaeus* and *Myotis daubentonii* (Bukhnikashvili 2004), *Rhinolophus blasii* (Ghazaryan 2006), *Tadarida teniotis* (Gazaryan et al. 2017), *Myotis alcathoe* and *M. davidii* (Natradze et al. 2023), and *Myotis tschuliensis* (Maghlakelidze 2024). Several taxonomic uncertainties remain in the Georgian fauna, particularly within morphologically similar or cryptic species complexes; these are addressed in the Discussion and in the DNA barcoding section.

The compiled dataset spans records from 1835 through 2025, comprising 2003 verified occurrences. Temporally, 52 records (2.6%) date from the nineteenth century, 196 records (9.8%) from the twentieth century, and 1556 records (77.7%) from the twenty-first century and 199 records (9.9%) without dates. Of all records, 1447 (72.2%) were collected by our research group, with the great majority published either through GBIF as part of Natradze et al. (2023) or in earlier group publications, and two records (one *Plecotus macrobullaris* and one *Nyctalus lasiopterus*) representing novel unpublished field observations. An additional 11 records were drawn from an unpublished survey report by the Behavioral Ecology and Evolution Research Group, University of the Basque Country (2011). The remaining 545 records were compiled from published literature. The geographic distribution of all records is shown in Appendix 3, Figure 31.

The 50×50 km grid analysis across 40 cells covering Georgia revealed considerable spatial variation in both the number of unique occurrence points (U) and the number of species (S). Species richness increased with the natural logarithm of the number of unique occurrence points, showing a strong positive log-linear relationship ($R^2 = 0.81$, $n = 40$; where R^2 , the coefficient of determination, indicates the proportion of variation in species number explained by survey coverage; Fig. 2). This relationship indicates that observed spatial patterns in species richness partly reflect the uneven geographic distribution of survey effort. Cells in the northern high-mountain zone showed the lowest values for both metrics, with some recordings fewer than two species and a single occurrence point, consistent with both

genuinely lower diversity at high elevations and limited survey coverage in these areas. The highest species richness values were distributed across both western and eastern Georgia, with eight cells reaching or exceeding 20 species - the threshold used to designate high-diversity cells. The single cell with the highest species richness reached 28 species, equivalent to 93% of the country's entire known bat fauna.

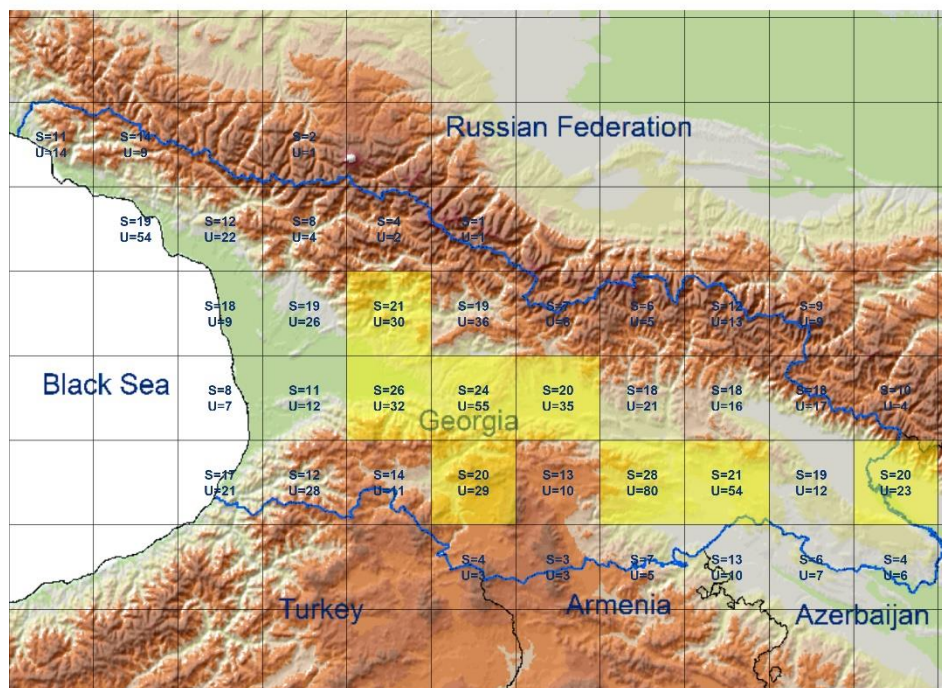


Figure 1. Bat species richness (S) and the number of unique occurrence points (U) across 50×50 km grid cells in Georgia. Yellow cells indicate high-diversity areas ($S \geq 20$).

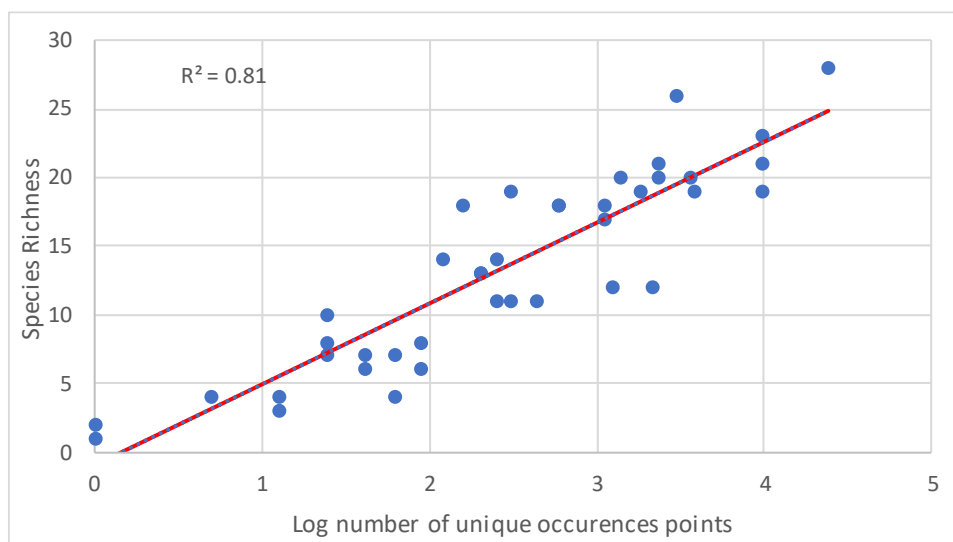


Figure 2. Scatterplot showing the relationship between species richness (S) and the natural logarithm of the number of unique occurrence points ($\ln U$) across 50×50 km grid cells in Georgia ($n = 40$, $R^2 = 0.81$). The fitted line indicates a positive log-linear relationship.

Species richness and record density were also assessed across elevation bands. Species richness was highest in the 401–800 m and 801–1200 m elevation bands with 29 species recorded in each, closely followed by the 0–400 m band with 28 species (Fig. 4). Record density was concentrated in the 401–800 m band ($n = 699$), followed by 0–400 m ($n = 640$) and 801–1200 m ($n = 422$) (Fig. 3). Both metrics declined with increasing elevation above 1200 m a.s.l., with 23 species recorded in the 1201–1600 m band, 20 in the 1601–2000 m band, 10 in the 2001–2400 m band, five in the 2401–2800 m band and one above 2800 m (fig 4).

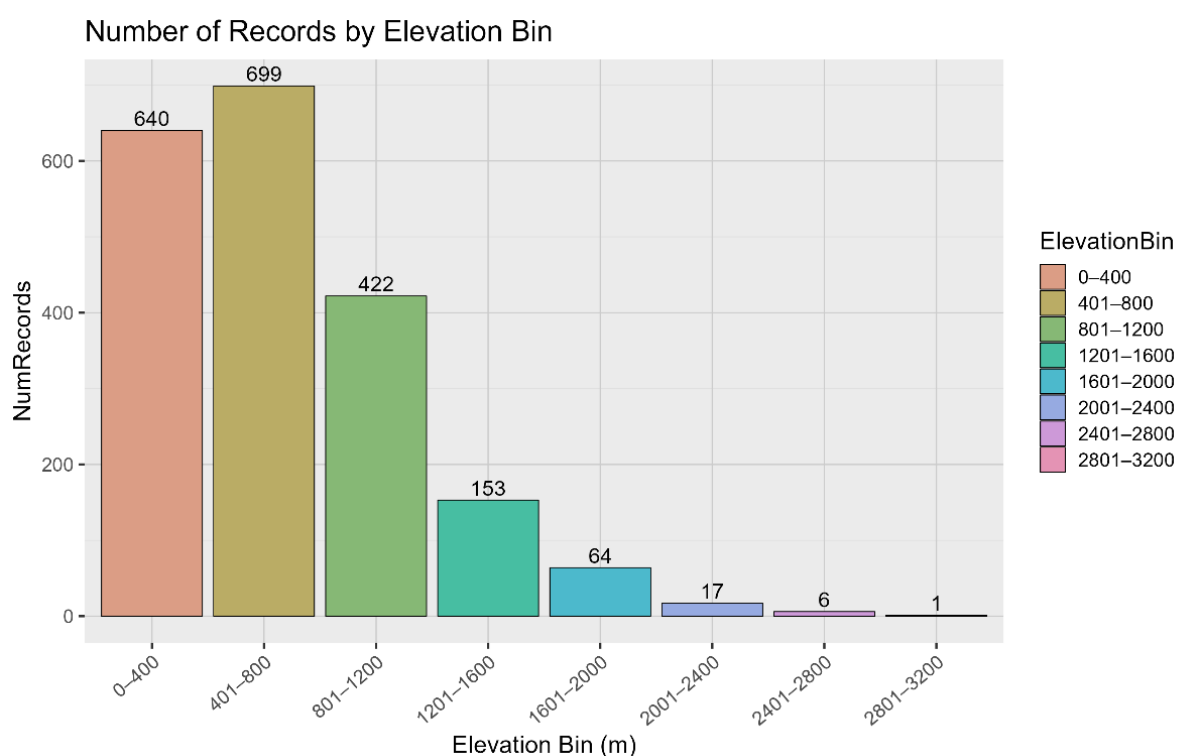


Figure 3. Number of bat occurrence records by elevation band (m a.s.l.) in Georgia.

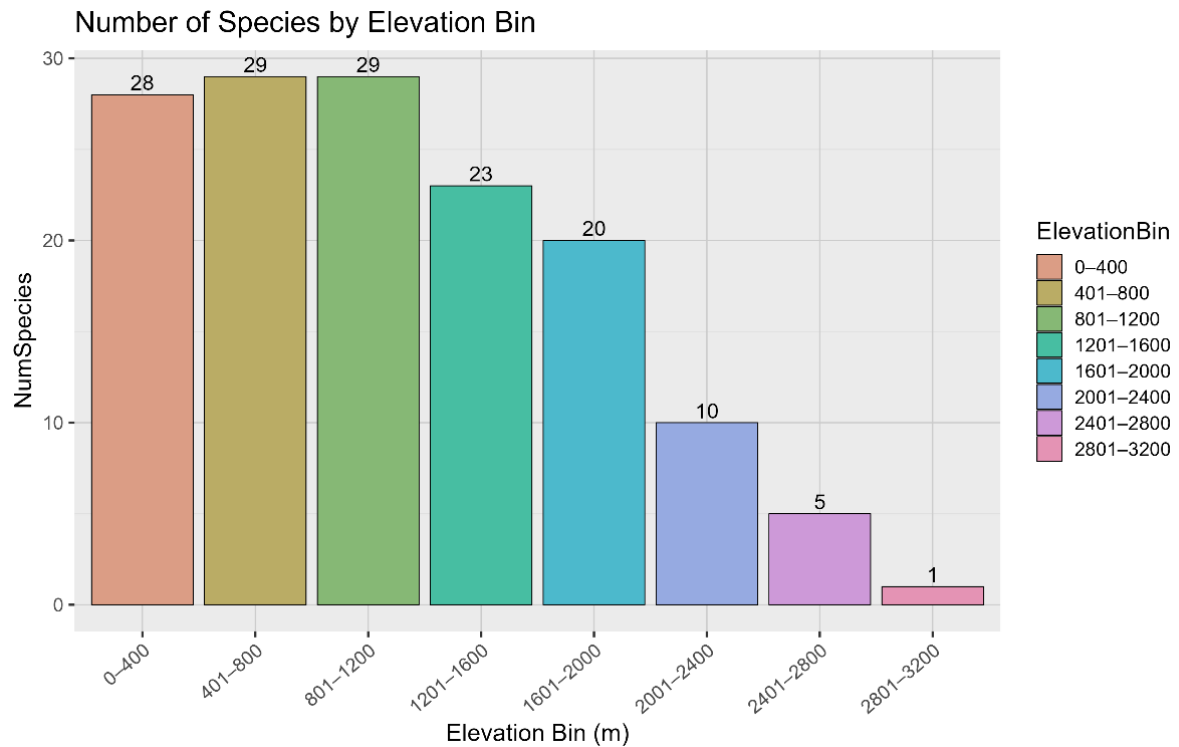


Figure 4. Number of bat species recorded per elevation band (m a.s.l.) in Georgia.

Species-specific elevation ranges varied considerably across the bat species recorded in Georgia (Fig. 5). *Pipistrellus nathusii*, *Myotis bechsteinii*, *Myotis daubentonii* and *Miniopterus schreibersii* showed the lowest median elevations, with records concentrated in the lowland and submontane zones. In contrast, *Plecotus macrobullaris* showed the highest median elevation among all recorded species, followed by *Tadarida teniotis*. *Nyctalus lasiopterus* showed a wide elevation range, with records spanning from lowlands to approximately 2700 m a.s.l. *Eptesicus serotinus*, although typically associated with lowland and submontane habitats, included a high-elevation record of four males captured at 2950 m a.s.l. at Abano Pass (Behavioral Ecology and Evolution Research Group 2011) — the highest elevation record for any bat in the Georgian dataset.

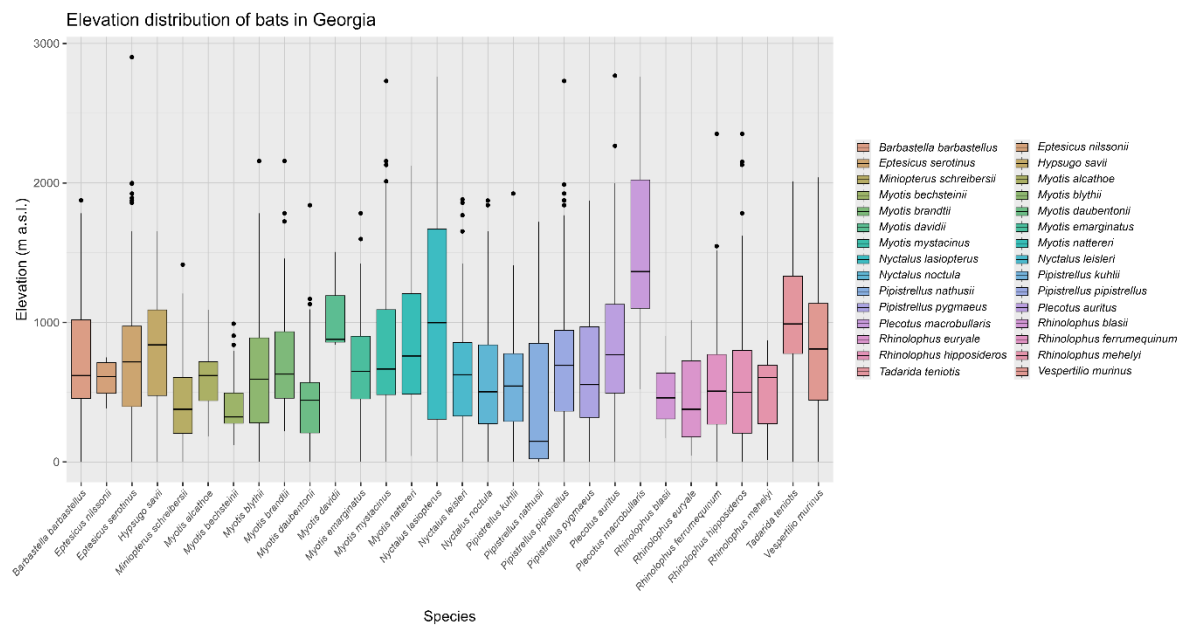


Figure 5. Elevation distribution of bat species in Georgia. Boxes show the middle 50% of elevations, the line inside each box shows the median, and dots indicate outliers.

5.2 Bat diversity in underground habitats

Publications from 1912 to 2010 recorded 13 bat species from 71 underground sites. Surveys conducted between 1999 and 2025, also covering 44 additional sites, recorded a total of 20 species from 115 sites, comprising 331 records. Of the 20 species recorded, one — *Rhinolophus blasii* — was documented in Georgia for the first time; twelve overlapped with previously published reports; six species were recorded from underground sites in addition to their typical overground roosts; and the presence of previously recorded *R. mehelyi* could not be confirmed.

The most frequently recorded species were *Rhinolophus ferrumequinum*, *R. hipposideros*, *Miniopiterus schreibersii*, *Myotis blythii* and *R. euryale*, with *R. ferrumequinum*, *M. blythii*, *R. euryale* and *M. schreibersii* persisting in substantial numbers at specific cave sites (Appendix 3, Fig. 32). Six primarily cave-dwelling species were most commonly encountered: *R. ferrumequinum*, *R. hipposideros*, *R. euryale*, *M. blythii*, *M. emarginatus* and *M. schreibersii*. Seven partially cave-dwelling species were also recorded: *M. mystacinus*, *M. brandtii*, *M. daubentonii*, *M. nattereri sensu lato*, *Barbastella barbastellus*, *Plecotus auritus* and *P. macrotis*. *Rhinolophus blasii* was the only species recorded exclusively in caves.

Additionally, two forest species (*M. bechsteinii* and *Nyctalus leisleri*), three crevice-dwelling species (*Hypsugo savii*, *Eptesicus serotinus* and *Vespertilio murinus*) and one species with no clear roosting preference (*Pipistrellus pipistrellus*) were recorded from underground sites. Full results are provided in Natradze et al. (2024).

5.3 Molecular identification and DNA barcoding

From the bat component of the barcoding study, 24 bat species were successfully barcoded from 107 individuals collected across 32 localities (Appendix 1). A total of 107 unique COI sequences were generated, with an average length of 631 bp. All barcode data are available through BOLD (<https://bench.boldsystems.org/>) project - SMGEO (Caucasian small mammal barcode library). Barcoding results confirmed morphology-based identifications for the majority of sampled individuals. Both *Myotis tschuliensis* and *M. nattereri* were tentatively identified from Georgian material, providing molecular evidence suggesting the possible coexistence of these two cryptic species in Georgia, a finding that requires further confirmation as reference sequences become available. *Eptesicus serotinus* samples formed two distinct barcode clusters. Full results are provided in Maghlakelidze et al. (2024).

5.4 Species distribution modelling

Species distribution models were developed for 27 bat species with sufficient occurrence records for reliable modelling, following the exclusion of three species after temporal and spatial filtering (Wisz et al. 2008). *Myotis davidii* and *Eptesicus nilssonii* did not meet the minimum threshold of five records, while *Rhinolophus mehelyi*, although represented by five records, was excluded because all records pre-date 1970 and therefore fell outside the temporal range of the environmental predictors. No post-1970 records exist for *R. mehelyi* in Georgia, and no modelled distribution map is therefore available for this species. Presence-only locality maps are provided separately for *R. mehelyi*, *M. davidii* and *E. nilssonii*.

Expert-informed ensembles were selected for 16 species (59%) and SDM ensembles for the remaining 11. Mean AUC of the selected maps across all 27 species was 0.873, ranging from 0.79 (*Plecotus auritus*) to 0.972 (*Myotis alcathoe*). The highest AUC values were obtained for

Myotis alcathoe (0.972), *Rhinolophus blasii* (0.957), *Rhinolophus euryale* (0.939) and *Myotis bechsteinii* (0.936). The lowest AUC values were recorded for *Plecotus auratus* (0.790), *Myotis nattereri sensu lato* (0.792), and *Vespertilio murinus* (0.793). Full species-specific AUC values are provided in appendix 2.

Mapped distributions showed considerable variation in predicted range extent and spatial pattern across species (Appendix 3, Figures A1–A27). Several species — including *Pipistrellus pipistrellus*, *Eptesicus serotinus*, *Myotis blythii* and *Vespertilio murinus* — were predicted to have broad suitable habitat extending across lowlands, foothills and mid-elevation zones in both the west and east of the country. A second group, including *Pipistrellus nathusii*, *Miniopterus schreibersii* and *Rhinolophus hipposideros*, showed predicted suitability concentrated in western Georgia, associated with the Colchic lowland and the southern slopes of the Greater Caucasus. *Myotis alcathoe*, *Myotis brandtii* and *Myotis mystacinus* showed predicted distributions concentrated in eastern and south-eastern Georgia. Species of the genus *Rhinolophus* showed habitat suitability concentrated along mountain foothills and river valleys, particularly in western Georgia. *Plecotus macrobullaris* had the most restricted predicted distribution, confined to the central highland zone. *Tadarida teniotis* showed broad suitability across the western lowlands and central valleys but was largely absent from the high-mountain north.

The stacked binary distribution maps of 27 bat species revealed a pronounced spatial pattern of predicted species richness across Georgia (Fig. 6). Predicted richness was not distributed uniformly, but instead showed clear concentration in several parts of the country where suitable habitat for multiple species overlapped. The highest richness values formed a large continuous zone in western Georgia, extending across the Kolkheti lowland and the foothills of the Greater Caucasus in Imereti and Samegrelo. Additional areas of elevated richness were distributed across eastern Georgia, including the Mtkvari and Alazani river valleys. In contrast, lower richness values were predicted in more peripheral parts of the country, particularly the high-mountain north and the drier southern uplands.

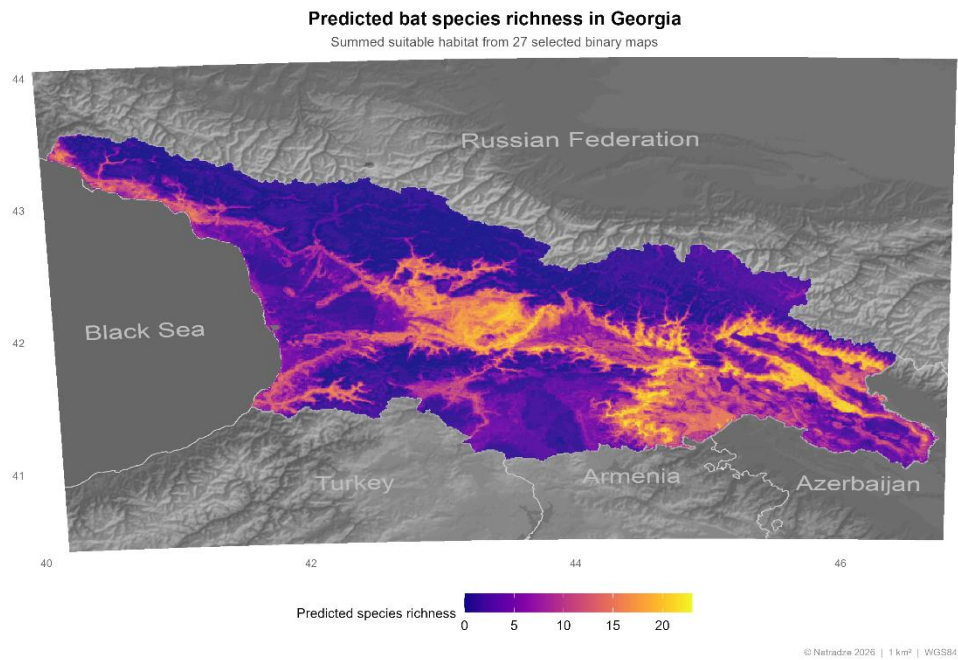


Figure 6. Predicted bat species richness map

The hotspot analysis further highlighted this pattern by identifying the richest 10% of cells, corresponding to areas with predicted richness of at least 15 species (Fig. 7). These hotspot cells formed several spatially connected clusters rather than isolated patches, with the largest continuous hotspot occurring in western Georgia and additional clusters distributed along river valleys in eastern Georgia.

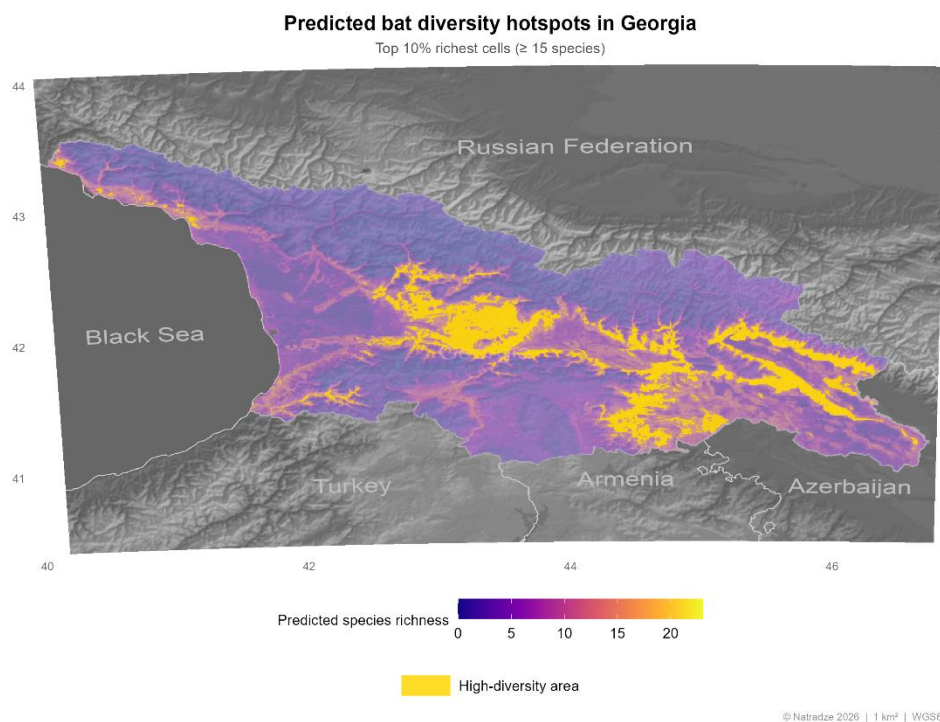


Figure 7. Predicted bat diversity hotspots map

6. Discussion

6.1 Bat Species Composition

The consolidation of bat occurrence records for Georgia into a single publicly accessible dataset addresses a long-standing gap in regional chiropterology. With 30 species from four families documented across 2003 verified records, Georgia's bat fauna proves notably diverse for a country of its size, reflecting its position at the intersection of two global biodiversity hotspots and the exceptional topographic, landscape and climatic heterogeneity of the Caucasus region.

The temporal distribution of records reveals that systematic knowledge of Georgian bats is largely recent, with the majority of records deriving from the twenty-first century and a substantial proportion collected by our research group. Much of this material was not available in the published literature prior to its compilation and publication through GBIF (Natradze et al. 2023), reflecting both the recent intensification of survey effort and the extent to which earlier field data had remained inaccessible, underscoring the value of the consolidation undertaken here.

Several taxonomic uncertainties remain that may affect the known species count. The status of *Myotis nattereri* versus *M. tschuliensis*, some records attributed to *M. mystacinus* may pertain to *M. davidii* due to their morphological similarity, and the unconfirmed occurrence of *Miniopterus pallidus* in eastern Georgia all require resolution through targeted molecular work. The publication of the dataset through GBIF (Natradze et al. 2023) provides an updatable baseline that can accommodate future records and taxonomic revisions as knowledge develops.

The strong positive log-linear relationship between the number of unique occurrence points and species richness confirms that survey coverage substantially shapes observed diversity patterns at the national scale. It should be noted that U represents the number of distinct localities recorded within a cell, not the number of survey visits; repeated visits to the same site do not increase U , since the location remains unchanged. U therefore reflects the spatial spread of sampling within a cell rather than total survey intensity, and cells with few unique

localities — particularly in the northern Greater Caucasus and parts of eastern Georgia — are likely to underrepresent local bat diversity and should be prioritized for future survey effort.

The concentration of high-diversity cells in western and central Georgia is consistent across the occurrence dataset, the underground habitat surveys and the species distribution models, and is maintained even in cells with moderate record densities, indicating that it reflects genuine ecological conditions - particularly the concentration of karstic habitats - rather than sampling bias alone. The recording of 28 species in a single 50×50 km cell highlights the exceptional local conservation importance of this area and reinforces the identification of western and central Georgia as the highest priority zone for bat conservation in the country.

6.2 Bat diversity in underground habitats

Three species — *Rhinolophus ferrumequinum*, *Myotis blythii* and *Miniopterus schreibersii* — have been consistently recorded in Georgian underground habitats from pre-1999 literature through to recent surveys, indicating long-term stability in the core composition of the subterranean bat fauna. The highest species richness in underground habitats was recorded in western Georgia, particularly within the karstic outcrops of the Imereti, Samegrelo and Abkhazeti regions (Natradze et al. 2024). This concentration reflects the density of suitable karstic formations in western Georgia, while in eastern Georgia natural caves are scarce and subterranean habitats were dominated by smaller grottoes, crevices and man-made structures, which were also systematically surveyed. The pattern therefore underscores the conservation importance of Georgia's western karstic landscapes for bat populations.

The most frequently encountered species - *R. ferrumequinum*, *R. hipposideros*, *R. euryale*, *M. blythii* and *M. schreibersii* - were classified as mainly cave dwelling. Of these, *R. euryale* is listed as Vulnerable (VU) on the Georgian Red List, and *M. schreibersii* carries VU status on the IUCN Red List. All five species are included in the Emerald Network priority species list, further highlighting these underground sites as critical microhabitats for their survival. *Rhinolophus blasii*, the only species recorded exclusively in caves and first documented in Georgia in 2006, has since been confirmed at three additional cave sites (Tarokldis cave; Tskaltubo II (Kumistavi, Promethe); Gogoleti cave; Samertskhle klde Cave). Despite extensive

surveys, *Rhinolophus mehelyi* - last recorded in 1964 (Matsaberidze and Khotenovskii 1967) and classified as a mainly cave-dwelling species - was not encountered, though its continued presence in the country cannot be conclusively ruled out, underlining the need for targeted monitoring of suitable subterranean habitats.

Among the most significant roost sites documented (Appendix 3, Fig. 32), Ghliana Cave hosts one of Georgia's largest mixed maternity colonies, with annual populations ranging from 4,000 to 8,000 individuals of *M. blythii*, *M. schreibersii*, *R. ferrumequinum*, *R. euryale* and, in some years, *M. emarginatus* (CAMPESTER 2019). Samertskhle Klde Cave supports a nursery colony of several thousand individuals, primarily consisting of *M. blythii* and *M. schreibersii*, while Sakishore Cave hosts the largest known wintering colony, with more than 1,000 *M. schreibersii*.

Threat assessments across surveyed sites were conducted using a standardized scoring approach described in Natradze et al. (2024), and revealed considerable variation in vulnerability. Ghliana Cave received the highest threat score despite being covered by a conservation action plan developed by the author for the Ministry of Environmental Protection and Agriculture of Georgia in 2019 (CAMPESTER 2019), while most other caves with colonies were assessed as moderately threatened. At present, only 18 caves or cave complexes in Georgia hold legal protection status, and of these Ghliana and Melouri caves host large bat colonies. The gap between the known conservation value of subterranean habitats and their formal protection status represents one of the most pressing conservation challenges identified by this thesis, and is addressed further in the Conservation Implications chapter.

6.3 Molecular identification and DNA barcoding

Molecular analysis confirmed morphological identifications for the large majority of barcoded individuals, supporting the overall reliability of the occurrence dataset assembled for this thesis. Two exceptions are of particular taxonomic significance (Maghlakelidze et al. 2024). Two specimens morphologically assigned to *Myotis* sp. from Chobalauri village were identified as *M. tschuliensis* Kuzyakin, 1965 through COI sequencing and comparison with unpublished reference material. Although COI sequences for this species were not available in BOLD or

GenBank at the time of analysis, genetic validation was achieved in consultation with Emrah Çoraman, whose work on the *M. nattereri* complex first proposed *M. tschuliensis* as a valid species (Çoraman et al. 2019). Crucially, the present study extends understanding beyond taxonomic confirmation: the identification of both *M. tschuliensis* and *M. nattereri* from Georgian material documents the coexistence of these two taxa in the country, a finding not previously reported.

The second notable finding concerns *Eptesicus serotinus*, for which barcoded individuals formed two distinct COI clusters with a mean intraspecific distance of 4.38% and a maximum of 8.37% — well above the 2.5–3% threshold typically accepted for well-separated bat species (Ditchfield 2000; Bradley and Baker 2001; Mayer and von Helversen 2001). One group of seven individuals showed 99% similarity with both *E. serotinus* and *E. nilssonii* reference sequences from GenBank, while morphological examination clearly assigned all collected individuals to *E. serotinus*. The most parsimonious explanation for this pattern is the presence of two mitochondrial lineages within *E. serotinus* in Georgia, consistent with evidence of historical hybridisation between *E. serotinus* and *E. nilssonii* in the western Palearctic, whereby mitochondrial DNA from *E. nilssonii* was introgressed into *E. serotinus* populations without detectable effects on nuclear markers or morphology (Currat et al. 2008; Artyushin et al. 2009; Juste et al. 2013). Notably, Artyushin et al. (2009) suggested that most Caucasian *E. serotinus* populations escaped this introgression event, making the presence of two divergent COI lineages in Georgian material an observation that warrants further investigation with nuclear markers. These findings reinforce the conclusion that integrative morphological and molecular approaches are essential for accurate bat diversity assessments in Georgia, and that several taxonomic questions in the regional fauna remain open.

Despite the progress represented by this reference library, some of the 30 bat species known from Georgia remain unbarcoded — *Rhinolophus hipposideros*, *R. blasii*, *R. mehelyi*, *Eptesicus nilssonii*, *Nyctalus lasiopterus*, *Plecotus macrobullaris* and *Tadarida teniotis* — reflecting both technical challenges and the difficulty of physically capturing species known only or mainly from acoustic records.

6.4 Species distribution modelling

The application of the stacked generalisation framework to Georgian bat occurrence data demonstrated its practical utility for generating fine-scale habitat suitability maps in a topographically and ecologically complex country with an uneven survey history. Consistent with the findings of Oeser et al. (2024), random background outperformed bias background across the majority of modelled species, and SDM ensembles generally matched or exceeded single-algorithm models in predictive performance. The addition of expert range information through the expert-informed ensemble produced marginal but consistent improvements for most species, reflecting the general pattern described by Oeser et al. (2024) whereby incorporating range limits helps constrain overprediction of suitable habitat in areas outside a species' realized range. Overall, the mean AUC of selected maps across all 27 modelled species was 0.873, indicating good predictive performance across a taxonomically and ecologically diverse assemblage.

The strong performance advantage of random over bias background in the Georgian dataset likely reflects the spatially clustered nature of occurrence records, which are concentrated in well-surveyed cave systems and accessible lowland areas. Under these conditions, a bias-corrected background that upweights heavily sampled areas may inadvertently reduce the contrast between presence and background, diminishing model discrimination. The exceptional performance of the expert-informed ensemble for *Plecotus macrobullaris*, for which it outperformed the SDM-only model, illustrates the value of incorporating range constraints for species with strongly localized distributions.

The pattern of model selection across species is ecologically interpretable. Expert-informed ensembles were selected predominantly for cave-associated species — including all four modelled *Rhinolophus* species, *Miniopterus schreibersii* and several *Myotis* species — for which IUCN expert range maps provide well-calibrated range limits that effectively constrain predictions to areas of known occurrence. In contrast, SDM ensembles were selected for more generalist or wide-ranging species such as *Barbastella barbastellus*, *Myotis blythii* and *Myotis alcathoe*, for which occurrence data capture the ecological niche more effectively without the constraint of expert range boundaries. The high AUC achieved for *Myotis alcathoe* (0.972)

using the SDM ensemble suggests a particularly well-defined ecological niche for this species, with its predicted range concentrated in the eastern and south-eastern part of the country.

The comparatively low AUC values obtained for *Plecotus auritus* (0.790) and *Myotis nattereri sensu lato* (0.792) reflect different sources of modelling difficulty. For *M. nattereri sensu lato*, the low performance likely reflects the fact that this taxon encompasses two molecularly distinct species in Georgia — *M. nattereri* and *M. tschuliensis* — whose occurrence records cannot be systematically separated in the dataset. Combining records of two ecologically distinct taxa in a single model introduces incoherence into the presence data, reducing predictive performance, and underscores the importance of resolving taxonomic uncertainties before modelling. For *P. auritus*, the low AUC more likely reflects its broad habitat use across forest, karst and agricultural landscapes combined with a relatively limited number of occurrence records, making it difficult to characterize a well-defined ecological niche — a challenge common to habitat generalists in SDM applications.

Spatially, the west-east contrast in predicted suitability observed across multiple species reflects the steep environmental gradient between Georgia's humid western lowlands and drier eastern landscapes. The concentration of predicted suitability for cave-associated *Rhinolophus* species along karstic foothills and river valleys in western Georgia is consistent with the distribution of subterranean roost sites documented in the underground habitat surveys and aligns with the higher species richness observed in that region. The spatial concordance between field-based and model-based evidence for western Georgia as the primary bat conservation zone strengthens the prioritization set out in the Conservation Implications chapter.

The stacked richness map (Fig. 6) suggests that bat diversity in Georgia is likely structured by broad environmental gradients and by the spatial coincidence of suitable conditions for multiple species. Areas of high predicted richness may reflect the combined influence of favorable climatic conditions, topographic heterogeneity, habitat diversity, and the availability of suitable roosting and foraging environments. The largest continuous hotspot in western Georgia reinforces the conservation importance of the karstic and foothill landscapes identified by the underground habitats' surveys, while additional high-richness areas along

the river valleys of eastern Georgia point to complementary conservation priorities that extend beyond the western karst. At the same time, these results should be interpreted with caution, as they represent modelled potential richness derived from the overlap of binary suitability maps rather than direct field-based estimates of species numbers. Nevertheless, the consistency and spatial coherence of the identified hotspots suggest that the maps provide a valuable framework for guiding future survey efforts, prioritizing field validation, and identifying areas that may warrant particular attention in conservation planning and habitat management.

6.5 Bat health and disease ecology in Georgia

Disease ecology was not a primary focus of this thesis, but the doctoral work also contributed to several studies on the health of Georgian bats. The first documented bat die-off in the country, recorded at Tkibula-Dzevrula cave in April 2018, led to the isolation of *Yersinia enterocolitica* from the intestinal tissues of three *Miniopterus schreibersii* individuals (Imnadze et al. 2020). Advanced decomposition of carcasses and the impossibility of pathomorphological evaluation meant that a causal role for this bacterium could not be confirmed. The Georgian isolates were characterized as biotype 1A and placed in a distinct phylogenetic cluster within this biotype, most closely related to an environmental isolate from Japan. Before this study, only one report of *Y. enterocolitica* in bats existed in the literature — a single isolation from a common pipistrelle in Germany (Mühldorfer et al. 2011).

Other studies have shown that Georgian bats are exposed to a range of bacterial and viral pathogens. A molecular survey detected *Bartonella* in 35% of 218 bats, *Leptospira* in 13% (including a variant 98.6% identical to the zoonotic *L. interrogans*), and *Brucella* in four bats from Imereti, at the time the first reported detection of *Brucella* in bats worldwide (Bai et al. 2017). A cross-sectional coronavirus survey detected an overall positivity rate of 24.5% and revealed several novel putative species-level lineages (Urushadze et al. 2022). Active disease has not been documented in any of these cases, but together these findings show that Georgian bats, especially in the large mixed roosts of western Georgia, carry diverse pathogens whose role in bat health remains unstudied.

The condition of the cave environment itself can also matter. Global work on white-nose syndrome has shown that environmental pathogen reservoirs in hibernacula strongly influence infection patterns and population impacts (Hoyt et al. 2020). *Pseudogymnoascus destructans*, the causative agent of white-nose syndrome, has not been documented in Georgia, but the country's many karstic caves provide environments broadly suitable for cave-associated pathogens. This points to the value of monitoring roost condition and unusual mortality events alongside species occurrence and colony size, particularly in the large mixed roosts where pathogens are most likely to circulate. Taken together, these results indicate that disease surveillance, covering bacteria, viruses and fungi, should be part of long-term bat conservation monitoring in Georgia.

7. Conservation Implications

The findings of this thesis, taken together, provide the comprehensive evidence base yet assembled for bat conservation planning in Georgia. Several priorities emerge consistently across the different components of the work and are outlined here.

7.1 Priority areas for conservation

Different lines of evidence highlight complementary priority areas. Underground habitat surveys identify western Georgia, particularly the karstic landscapes of Imereti, Samegrelo and Abkhazeti, as the most important area for cave-dwelling bats. The grid-based analysis of occurrence records identifies eastern Georgia as supporting the highest observed species richness, with one 50×50 km cell reaching 28 species (93% of Georgia's known bat fauna). The SDM-based summed richness map identifies the largest continuous predicted diversity hotspot in western Georgia, with additional hotspots along the river valleys of eastern Georgia. Together, these converging but not identical patterns indicate that both western and eastern Georgia should be treated as priority regions for bat conservation, with western Georgia emphasizing cave-associated fauna and eastern Georgia supporting a broader community that includes tree-dwelling, crevice-dwelling and generalist species.

7.2 Subterranean habitat protection

The most urgent conservation need identified by this thesis concerns the legal protection of key underground roost sites. Of the more than 1,500 known caves and karst structures in Georgia, only 18 currently hold legal protection status, and of these, only Ghliana and Melouri caves host large bat colonies. This represents a severe gap between the known conservation value of subterranean habitats and their formal protection. We recommend that legal protection be urgently extended to at least four additional caves — Samertskhle Klde, Vardigora (both in Imereti region), Becho (in Samegrelo region) and Sakishore (in Racha region) — which collectively support key colonies of *Rhinolophus euryale*, *Myotis blythii* and *Miniopterus schreibersii*, all of which carry national or international conservation status. Protection measures should not be limited to cave entrances but must include the surrounding foraging and commuting habitats on which bat colonies depend.

7.3 Species-specific priorities

Rhinolophus euryale and *Miniopterus schreibersii* are listed as Vulnerable in the Georgian Red Lists and IUCN respectively, yet both are among the most frequently recorded species in Georgian caves, present across numerous sites throughout the country. The wide distribution and frequency of these species in Georgian underground habitats suggests that the country holds an important role in supporting their regional populations, strengthening the case for their active protection at the national level. *Barbastella barbastellus* and *Myotis bechsteinii*, both listed as Vulnerable on the Georgian Red List, are recorded predominantly from our own surveys, suggesting that knowledge of their distribution in Georgia has until recently remained limited. *Rhinolophus mehelyi*, unconfirmed since 1964, requires targeted survey effort in suitable subterranean habitats.

7.4 Disease ecology and monitoring

The documented presence of *Yersinia enterocolitica* in dead *Miniopterus schreibersii*, alongside earlier evidence of bacterial agents such as *Bartonella*, *Leptospira* and *Brucella* (Bai et al. 2017) and a diverse coronavirus community (Urushadze et al. 2022) in Georgian bats, highlights the need to include disease surveillance in bat monitoring programs. Future surveys should sample for bacterial, viral and fungal pathogens, particularly in the large mixed roosts

of western Georgia where pathogen circulation is most likely, and any future die-offs should be investigated quickly while fresh tissue samples can still remain available for pathological and microbiological analyses. Surveillance should also continue to target lyssaviruses. Only a few dozen Georgian bats have so far been examined for lyssaviruses, and none had detectable antigen consistent with active infection by rabies virus or other related lyssaviruses (unpublished data). This limited screening is a concern given the proximity of the West Caucasian Bat Virus (WCBV), a divergent lyssavirus first isolated from *M. schreibersii* in the West Caucasus region adjacent to Georgia (Botvinkin et al. 2003; Kuzmin et al. 2008) — its association with the same host species recorded throughout Georgian caves, and the limited cross-protection offered by conventional rabies vaccines. Roost conditions themselves should also be considered, given the demonstrated role of environmental pathogen reservoirs in influencing infection outcomes in bats globally (Hoyt et al. 2020).

7.5 Molecular reference resources and future applications

The DNA barcode library compiled as part of this work (Maghlakelidze et al. 2024) covers 24 of the 30 bat species known from Georgia. Completing the reference library is a priority for future work, particularly for *Rhinolophus mehelyi*, *Eptesicus nilssonii* and *Tadarida teniotis*, which are either unconfirmed in recent decades or known only from acoustic records and therefore require targeted field sampling. Establishing a complementary reference library for the cytochrome b (cytb) gene would strengthen identification of taxonomically problematic taxa — particularly within the *Myotis nattereri* complex and provide an additional molecular marker for phylogeographic and conservation genetic studies. Beyond species identification, these reference libraries open applications in non-invasive monitoring, particularly through environmental DNA (eDNA) approaches from guano samples, which could substantially expand the detection of cryptic or rarely captured species.

7.6 Data and knowledge gaps

The occurrence dataset assembled for this thesis represents the most complete national baseline currently available, but important gaps remain across four main dimensions.

Taxonomic gaps. Several taxonomic uncertainties remain that may affect the known species count. These include the status of the *Myotis nattereri*/*M. tschuliensis* complex, the difficulty of reliably separating *M. davidii* and *M. mystacinus*, the unconfirmed occurrence of *Miniopterus pallidus* in eastern Georgia, and the presence of two divergent COI lineages within *Eptesicus serotinus* which requires resolution with nuclear markers. Resolving these uncertainties requires continued molecular work alongside careful morphological re-examination of available material.

Distributional gaps. Survey coverage is geographically uneven, with eastern Georgia, high-elevation zones (above 1200 m a.s.l.), and man-made subterranean structures in the east particularly underrepresented. The strong correlation between survey effort and recorded species richness at the 50×50 km grid scale confirms that cells with few records likely underrepresent local bat diversity rather than reflecting genuine species poverty. The SDM results further indicate that suitable habitat exists across large parts of Georgia for many species. Yet occurrence records remain sparse or absent in many of these areas, indicating a systematic survey deficit that limits both conservation planning and scientific understanding.

Ecological gaps. Basic ecological knowledge of Georgian bat populations remains limited. Although general information on habitat requirements, roosting behavior, diet, and parasite fauna is available from studies in other regions, region-specific data from Georgia, including how species share roosts and foraging areas locally, how diet composition varies across Georgia's diverse landscapes, and which parasites and pathogens occur in Georgian populations, remain largely undocumented. Filling these gaps is needed to complement existing regional knowledge with evidence directly applicable to Georgian conservation and monitoring.

Conservation gaps. Several applied conservation gaps also require attention. Systematic monitoring of anthropogenic pressures on key colonies and habitats — including cave tourism, unregulated access to underground sites, infrastructure development near roosts, and forestry practices affecting tree-dwelling species — is largely absent, and their long-term effects on bat populations remain unquantified. Some foundations already exist, including the 2014 national bat monitoring effort (Natradze and Bukhnikashvili 2014) and the Ghliana Cave Management

Plan (Campester 2019), but these need to be expanded into a coordinated, repeated and adequately resourced national framework. Public awareness of bats and their conservation value remains limited, and coordination between researchers, protected area managers, cave tourism operators, and local communities is not systematically established. Addressing these gaps will require not only additional scientific work but also investment in institutional capacity, long-term monitoring infrastructure, and sustained engagement with stakeholders.

A particular conservation challenge concerns the regions of Abkhazeti and the Samatchablo regions, which fall outside the effective control of the government. Field surveys, monitoring activities and assessment of anthropogenic impacts on bat populations in these regions are not feasible under the current political circumstances. As a result, knowledge of the bat fauna in these areas relies almost entirely on literatures sources and remains outdated, and the conservation status of potentially important sites and populations cannot be evaluated. These regions therefore represent a persistent and unresolved gap in the national scale assessment of bat diversity and conservation in Georgia, originating not from scientific limitations but from political constraints on access.

8. Conclusions

This thesis provides a comprehensive and integrated assessment of bat diversity, habitat use and spatial distribution in Georgia, addressing a long-standing gap in knowledge about one of the most species-rich but least studied mammals in the country, being part of two, the Caucasus and Irano-Anatolian biodiversity hotspots.

The four core studies that form the basis of this thesis collectively move knowledge of Georgian bats from a fragmented and partly inaccessible literature to a verified, accessible and analytically grounded evidence base. The occurrence dataset established the first national baseline, documenting 30 species across 2003 records and revealing that the majority of existing knowledge derives from the past two decades of systematic survey effort. The underground habitat study demonstrated that subterranean environments are used by two-thirds of the country's bat species, that western Georgia concentrates the highest diversity and the most important roost sites, and that current legal protection is insufficient relative to

conservation needs. The DNA barcoding component confirmed the general reliability of morphological identifications while revealing two taxonomically significant findings: the possible coexistence of *Myotis tschuliensis* and *M. nattereri* in Georgia, and the presence of two mitochondrial lineages within *Eptesicus serotinus*, underscoring the importance of integrative approaches for accurate diversity assessment in this region. The species distribution modelling component used verified occurrence records to generate fine-scale habitat suitability maps for 27 species, providing the first spatially mapped predictions of bat distributions across Georgia and demonstrating that the stacked generalization framework performs robustly at the national scale. Aggregating these individual maps into a predicted species richness map identified the largest continuous hotspot in western Georgia, alongside additional hotspots in the river valleys of eastern Georgia, providing an independent spatial synthesis that complements the field-based evidence.

Alongside these core studies, the work also contributed to several co-authored studies and conservation reports that further broaden the evidence base for Georgian bats. The first documented bat die-off in Georgia led to the isolation of a novel *Yersinia enterocolitica* lineage (Imnadze et al. 2020), and complementary surveys have shown that Georgian bats are exposed to a range of bacterial agents (Bai et al. 2017) and a diverse coronavirus community (Urushadze et al. 2022). Together with global work on environmental disease reservoirs (Hoyt et al. 2020), the Ghliana Cave Management Plan (Campester 2019), and the national bat monitoring report (Natradze and Bukhnikashvili 2014), these contributions extend the relevance of bat research in Georgia beyond biodiversity alone into disease ecology, applied conservation planning, and long-term monitoring.

Taken together, these findings demonstrate that Georgia's bat fauna is more diverse, ecologically significant, and conservation-relevant than the existing literature suggests. The thesis provides a foundation for evidence-based conservation planning that was previously lacking. A verified occurrence baseline, assessment of underground habitat use, a barcode library, habitat suitability maps, a disease-ecology dimension show that meaningful advances in bat research in the Georgia require the integration of classical faunistic approaches with modern analytical and molecular methods.

Several limitations should be acknowledged. Taxonomic uncertainties remain unresolved for a subset of records. Geographic survey coverage is uneven, and the SDM results for species with few records should be interpreted with caution. The role of *Y. enterocolitica* in the observed bat mortality remains unconfirmed. And the occurrence dataset, while the most comprehensive yet assembled, still underrepresents eastern Georgia and high-elevation habitats.

Despite these limitations and remaining knowledge gaps, this thesis substantially advances the understanding of bat diversity, distribution, and conservation in Georgia, and establishes a solid foundation for future conservation planning, monitoring, and targeted survey efforts.

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Appendices

Appendix 1: Summary of barcoded species

Sample ID	Species	COI-5P Seq. Length	Place	Lat	Lon
CaBOL_1022307	<i>Plecotus auritus</i>	658[0n]	Mskheta	41.845	44.757
CaBOL_1022247	<i>Rhinolophus ferrumequinum</i>	658[0n]	Gremi, Grdzeli chala	42.017	45.625
CaBOL_1022249	<i>Miniopterus schreibersii</i>	658[0n]	Gremi, Grdzeli chala	42.017	45.625
CaBOL_1022252	<i>Miniopterus schreibersii</i>	658[0n]	Gremi, Grdzeli chala	42.017	45.625
CaBOL_1022253	<i>Miniopterus schreibersii</i>	658[0n]	Vardigora	42.248	43.09
CaBOL_1007581	<i>Rhinolophus euryale</i>	595[0n]	Qvemo qartli, Tetritskaro	41.589	44.532
CaBOL_1007385	<i>Pipistrellus pipistrellus</i>	624[0n]	Tbilisi	41.817	44.694
CaBOL_1007386	<i>Pipistrellus pipistrellus</i>	604[0n]	Tbilisi	41.817	44.694
CaBOL_1007387	<i>Nyctalus leisleri</i>	604[0n]	Tbilisi	41.817	44.694
CaBOL_1007388	<i>Nyctalus leisleri</i>	631[0n]	Tbilisi	41.817	44.694
CaBOL_1007389	<i>Pipistrellus pipistrellus</i>	583[0n]	Tbilisi	41.817	44.694
CaBOL_1007390	<i>Pipistrellus pipistrellus</i>	664[0n]	Tbilisi	41.817	44.694
CaBOL_1007582	<i>Rhinolophus euryale</i>	621[0n]	Qvemo qartli, Tetritskaro	41.589	44.532
CaBOL_1007392	<i>Myotis blythii</i>	662[0n]	Tbilisi	41.817	44.694
CaBOL_1007393	<i>Nyctalus leisleri</i>	634[0n]	Tbilisi	41.817	44.694
CaBOL_1007394	<i>Eptesicus serotinus</i>	664[0n]	Tbilisi	41.817	44.694
CaBOL_1007395	<i>Miniopterus schreibersii</i>	605[0n]	Tbilisi	41.817	44.694
CaBOL_1007397	<i>Nyctalus leisleri</i>	639[0n]	Tbilisi	41.809	44.656
CaBOL_1007399	<i>Eptesicus serotinus</i>	573[0n]	Kaspi	41.971	44.399
CaBOL_1007400	<i>Eptesicus serotinus</i>	638[0n]	Kaspi	41.971	44.399
CaBOL_1007401	<i>Myotis blythii</i>	660[0n]	Tbilisi	41.813	44.666
CaBOL_1007402	<i>Pipistrellus pipistrellus</i>	626[0n]	Qutaisi	42.219	42.784
CaBOL_1007403	<i>Myotis blythii</i>	663[0n]	Tbilisi	41.812	44.665
CaBOL_1007404	<i>Nyctalus leisleri</i>	617[0n]	Tbilisi	41.813	44.68
CaBOL_1007405	<i>Nyctalus leisleri</i>	631[0n]	Tbilisi	41.813	44.68
CaBOL_1007406	<i>Nyctalus leisleri</i>	672[0n]	Tbilisi	41.813	44.68
CaBOL_1007407	<i>Nyctalus noctula</i>	576[0n]	Tbilisi	41.813	44.68
CaBOL_1007408	<i>Plecotus auritus</i>	658[0n]	Tbilisi	41.813	44.68
CaBOL_1007409	<i>Nyctalus noctula</i>	584[0n]	Tbilisi	41.813	44.68
CaBOL_1007410	<i>Barbastella barbastellus</i>	661[0n]	Kaspi	41.983	44.307

CaBOL_1007411	<i>Barbastella barbastellus</i>	665[0n]	Kaspi	41.983	44.307
CaBOL_1007384	<i>Pipistrellus pipistrellus</i>	621[0n]	Tbilisi	41.817	44.694
CaBOL_1007423	<i>Plecotus auritus</i>	634[0n]	Tsageri	42.679	42.921
CaBOL_1007424	<i>Rhinolophus ferrumequinum</i>	595[0n]	Kvareli	42.002	45.66
CaBOL_1007391	<i>Eptesicus serotinus</i>	665[0n]	Tbilisi	41.817	44.694
CaBOL_1007437	<i>Pipistrellus kuhlii</i>	660[0n]	Shida Qartli, Kaspi	42.012	44.298
CaBOL_1007439	<i>Myotis tschuliensis</i>	610[0n]	Shida Qartli, Kaspi	42.012	44.298
CaBOL_1007461	<i>Pipistrellus kuhlii</i>	589[0n]	Shida Qartli, Kaspi	42.012	44.298
CaBOL_1007463	<i>Myotis tschuliensis</i>	594[0n]	Shida Qartli, Kaspi	42.012	44.298
CaBOL_1007467	<i>Miniopterus schreibersii</i>	662[0n]	Kvareli	42.002	45.66
CaBOL_1007470	<i>Miniopterus schreibersii</i>	581[0n]	Mtskheta	41.844	44.767
CaBOL_1007471	<i>Eptesicus serotinus</i>	598[0n]	Mtskheta	41.844	44.767
CaBOL_1007374	<i>Nyctalus leisleri</i>	579[0n]	Tkibuli	42.308	42.891
CaBOL_1007580	<i>Rhinolophus euryale</i>	620[0n]	Qvemo qartli, Tetritskaro	41.589	44.532
CaBOL_1007578	<i>Rhinolophus euryale</i>	567[1n]	Qvemo qartli, Tetritskaro	41.589	44.532
CaBOL_1007520	<i>Rhinolophus ferrumequinum</i>	626[0n]	Martvili	42.53	42.37
CaBOL_1007521	<i>Rhinolophus euryale</i>	541[2n]	Martvili	42.53	42.37
CaBOL_1007379	<i>Pipistrellus pipistrellus</i>	622[0n]	Khashuri	42.068	43.69
CaBOL_1007575	<i>Rhinolophus euryale</i>	586[0n]	Qvemo qartli, Tetritskaro	41.589	44.532
CaBOL_1007579	<i>Rhinolophus euryale</i>	556[0n]	Qvemo qartli, Tetritskaro	41.589	44.532
CaBOL_1007558	<i>Myotis mystacinus</i>	649[0n]	Khoni	42.342	42.504
CaBOL_1007559	<i>Pipistrellus kuhlii</i>	624[0n]	Khoni	42.342	42.504
CaBOL_1007560	<i>Pipistrellus nathusii</i>	632[0n]	Khoni	42.342	42.504
CaBOL_1007561	<i>Pipistrellus nathusii</i>	658[0n]	Khoni	42.342	42.504
CaBOL_1007562	<i>Pipistrellus pipistrellus</i>	647[0n]	Khoni	42.342	42.504
CaBOL_1007563	<i>Pipistrellus pipistrellus</i>	661[0n]	Khoni	42.342	42.504
CaBOL_1007564	<i>Pipistrellus pygmaeus</i>	621[0n]	Khoni	42.342	42.504
CaBOL_1007565	<i>Miniopterus schreibersii</i>	660[0n]	Qvemo qartli, Tetritskaro	41.589	44.532
CaBOL_1007375	<i>Eptesicus serotinus</i>	617[0n]	Tkibuli	42.308	42.891
CaBOL_1007376	<i>Eptesicus serotinus</i>	681[0n]	Tkibuli	42.297	42.893
CaBOL_1007377	<i>Eptesicus serotinus</i>	627[0n]	Tkibuli	42.297	42.893
CaBOL_1007378	<i>Eptesicus serotinus</i>	665[0n]	Tkibuli	42.297	42.893
CaBOL_1007574	<i>Rhinolophus euryale</i>	576[0n]	Qvemo qartli, Tetritskaro	41.589	44.532

CaBOL_1007380	<i>Myotis blythii</i>	660[0n]	Khashuri	42.068	43.69
CaBOL_1007381	<i>Rhinolophus ferrumequinum</i>	614[0n]	Kaspi	41.988	44.358
CaBOL_1007382	<i>Eptesicus serotinus</i>	624[0n]	Kaspi	41.988	44.358
CaBOL_1007383	<i>Nyctalus leisleri</i>	576[0n]	Tbilisi	41.817	44.694
CaBOL_1022378	<i>Pipistrellus pipistrellus</i>	658[0n]	Dmanisi	41.33	44.207
CaBOL_1022383	<i>Myotis davidii</i>	658[0n]	Khrami II	41.474	44.237
CaBOL_1022384	<i>Pipistrellus pipistrellus</i>	658[0n]	Areshi	41.898	46.066
CaBOL_1022413	<i>Vespertilio murinus</i>	658[0n]	Bakuriani	41.727	43.529
CaBOL_1022416	<i>Miniopterus schreibersii</i>	658[0n]	Gremi	42.019	45.63
CaBOL_1022417	<i>Miniopterus schreibersii</i>	658[0n]	Gremi	42.019	45.63
CaBOL_1022419	<i>Vespertilio murinus</i>	658[0n]	Tbilisi	41.723	44.776
CaBOL_1022431	<i>Miniopterus schreibersii</i>	658[0n]	Becho cave	42.535	41.999
CaBOL_1022432	<i>Myotis blythii</i>	658[0n]	Becho cave	42.535	41.999
CaBOL_1022433	<i>Myotis blythii</i>	658[0n]	Becho cave	42.535	41.999
CaBOL_1022436	<i>Myotis daubentonii</i>	658[0n]	Mtsdziri	41.9	46.07
CaBOL_1022437	<i>Hypsugo savii</i>	658[0n]	Tskhvarichamia	41.885	44.924
CaBOL_1022439	<i>Myotis nattereri</i>	658[0n]	Gudarekhi	41.586	44.463
CaBOL_1022440	<i>Pipistrellus pipistrellus</i>	658[0n]	Khopisi	41.566	44.507
CaBOL_1022442	<i>Barbastella barbastellus</i>	658[0n]	Lagodekhi	41.845	46.278
CaBOL_1022443	<i>Myotis alcathoe</i>	658[0n]	Dmanisi	41.343	44.203
CaBOL_1022444	<i>Myotis daubentonii</i>	658[0n]	Dmanisi	41.311	44.165
CaBOL_1022448	<i>Myotis emarginatus</i>	658[0n]	Dmanisi	41.343	44.203
CaBOL_1022449	<i>Myotis daubentonii</i>	658[0n]	Alazani, Eretiskari	41.676	46.082
CaBOL_1022450	<i>Myotis bechsteinii</i>	658[0n]	Gudarekhi	41.586	44.463
CaBOL_1022451	<i>Myotis emarginatus</i>	658[0n]	Dmanisi	41.343	44.203
CaBOL_1022452	<i>Myotis mystacinus</i>	658[0n]	Dmanisi	41.343	44.203
CaBOL_1022453	<i>Plecotus auritus</i>	658[0n]	Kazreti	41.366	44.47
CaBOL_1022455	<i>Myotis mystacinus</i>	658[0n]	Mtsdziri	41.9	46.07
CaBOL_1022457	<i>Myotis mystacinus</i>	658[0n]	Kolagiri Monastery	41.444	45.66
CaBOL_1022458	<i>Eptesicus serotinus</i>	658[0n]	Tsutskhvati	42.298	42.892
CaBOL_1022459	<i>Eptesicus serotinus</i>	658[0n]	Tsutskhvati	42.298	42.892
CaBOL_1022460	<i>Eptesicus serotinus</i>	658[0n]	Tsutskhvati	42.298	42.892
CaBOL_1022255	<i>Myotis brandtii</i>	658[0n]	Bakhmaro	41.865	42.306
CaBOL_1022275	<i>Nyctalus leisleri</i>	658[0n]	Bakhmaro	41.865	42.306
CaBOL_1022277	<i>Nyctalus leisleri</i>	658[0n]	Bakhmaro	41.865	42.306
CaBOL_1022294	<i>Myotis mystacinus</i>	658[2n]	Sasireti	42.074	43.958
CaBOL_1022300	<i>Myotis daubentonii</i>	658[0n]	Koghoto	41.499	46.098
CaBOL_1022303	<i>Myotis daubentonii</i>	658[0n]	Koghoto	41.499	46.098
CaBOL_1022304	<i>Myotis daubentonii</i>	658[0n]	Koghoto	41.499	46.098

CaBOL_1022306	<i>Myotis davidii</i>	658[0n]	Koghoto	41.499	46.098
CaBOL_1022309	<i>Myotis mystacinus</i>	658[0n]	Koghoto	41.499	46.098
CaBOL_1022311	<i>Pipistrellus pipistrellus</i>	658[0n]	Koghoto	41.499	46.098
CaBOL_1022322	<i>Myotis daubentonii</i>	658[0n]	Koghoto	41.499	46.098
CaBOL_1022325	<i>Myotis daubentonii</i>	658[0n]	Koghoto	41.499	46.098

Appendix 2: Species specific AUC values

Species	AUC
<i>Barbastella barbastellus</i>	0.884
<i>Eptesicus serotinus</i>	0.813
<i>Hypsugo savii</i>	0.920
<i>Miniopterus schreibersii</i>	0.905
<i>Myotis alcathoe</i>	0.972
<i>Myotis bechsteinii</i>	0.936
<i>Myotis blythii</i>	0.845
<i>Myotis brandtii</i>	0.905
<i>Myotis daubentonii</i>	0.855
<i>Myotis emarginatus</i>	0.849
<i>Myotis mystacinus</i>	0.886
<i>Myotis nattereri</i>	0.792
<i>Nyctalus lasiopterus</i>	0.819
<i>Nyctalus leisleri</i>	0.886
<i>Nyctalus noctula</i>	0.841
<i>Pipistrellus kuhlii</i>	0.893
<i>Pipistrellus nathusii</i>	0.833
<i>Pipistrellus pipistrellus</i>	0.816
<i>Pipistrellus pygmaeus</i>	0.889
<i>Plecotus auritus</i>	0.790
<i>Plecotus macrobularis</i>	0.921
<i>Rhinolophus hipposideros</i>	0.868
<i>Rhinolophus blasii</i>	0.957
<i>Rhinolophus euryale</i>	0.939
<i>Rhinolophus ferrumequinum</i>	0.850
<i>Tadarida teniotis</i>	0.923
<i>Vespertilio murinus</i>	0.793

Appendix 3: Species Distribution Maps

Maps show binary habitat suitability maps are presented for 27 bat species in Georgia. For three species for which suitability modelling was not possible, presence-only distribution maps are provided.

Fig. A1. *Barbastella barbastellus*

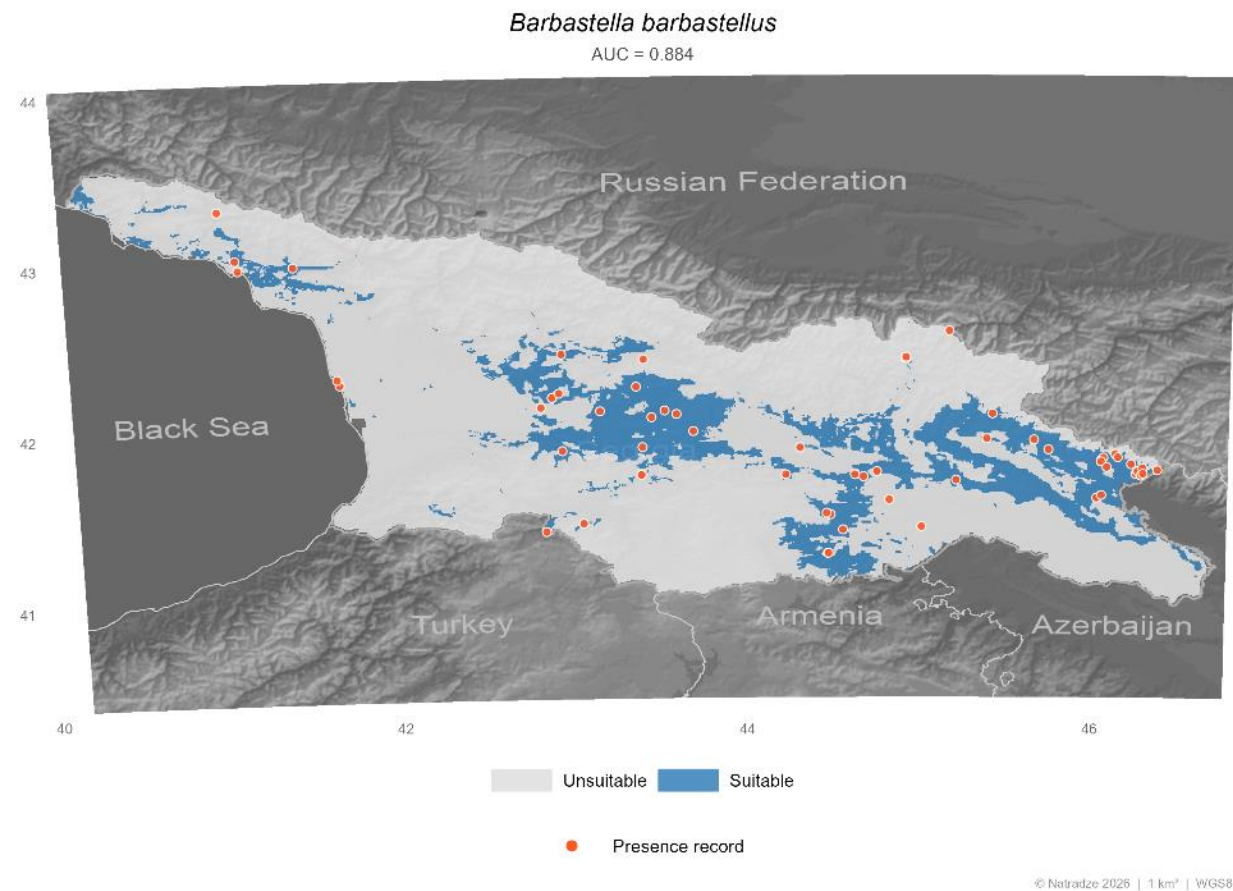


Fig. A2. *Eptesicus nilssonii*

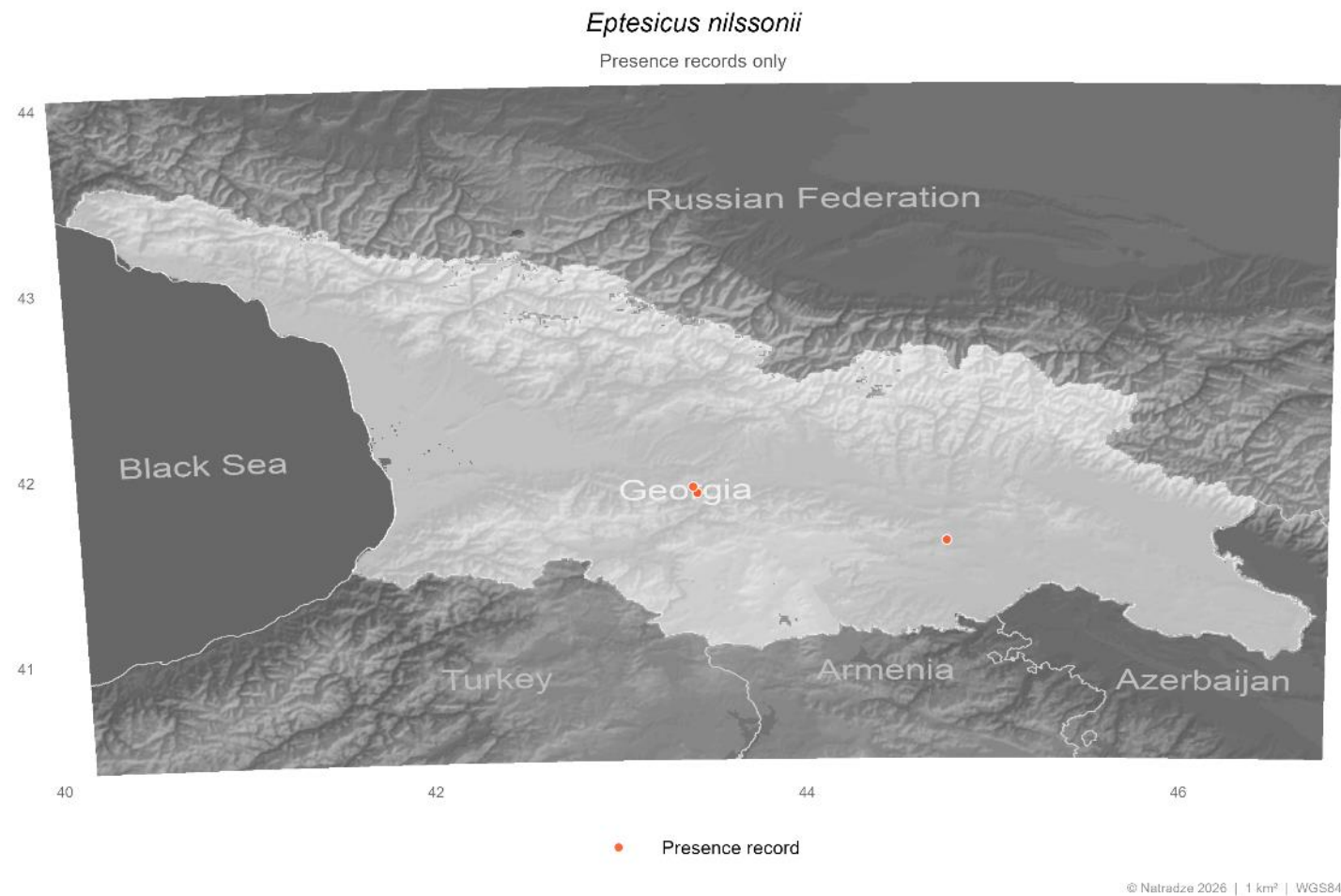
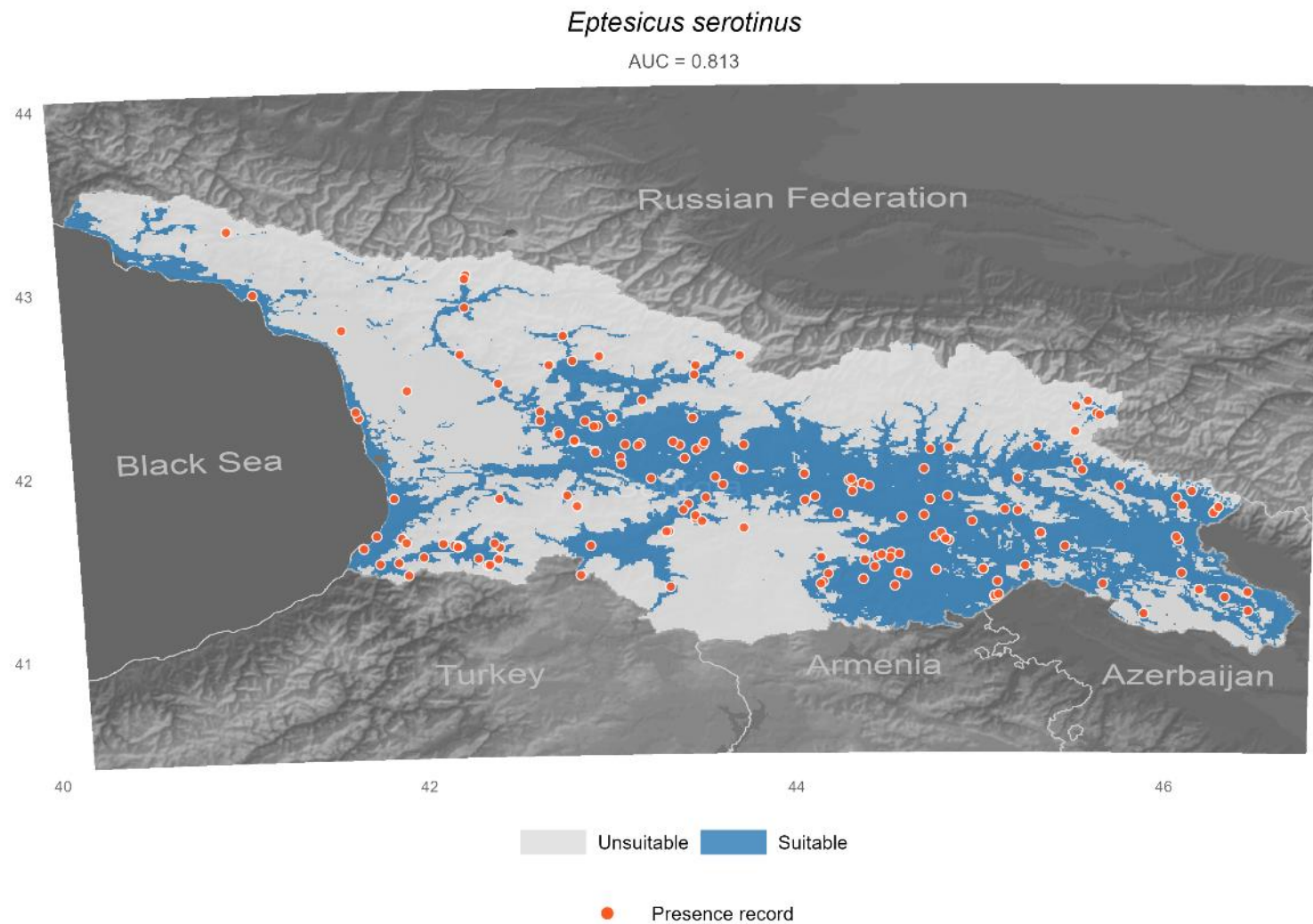
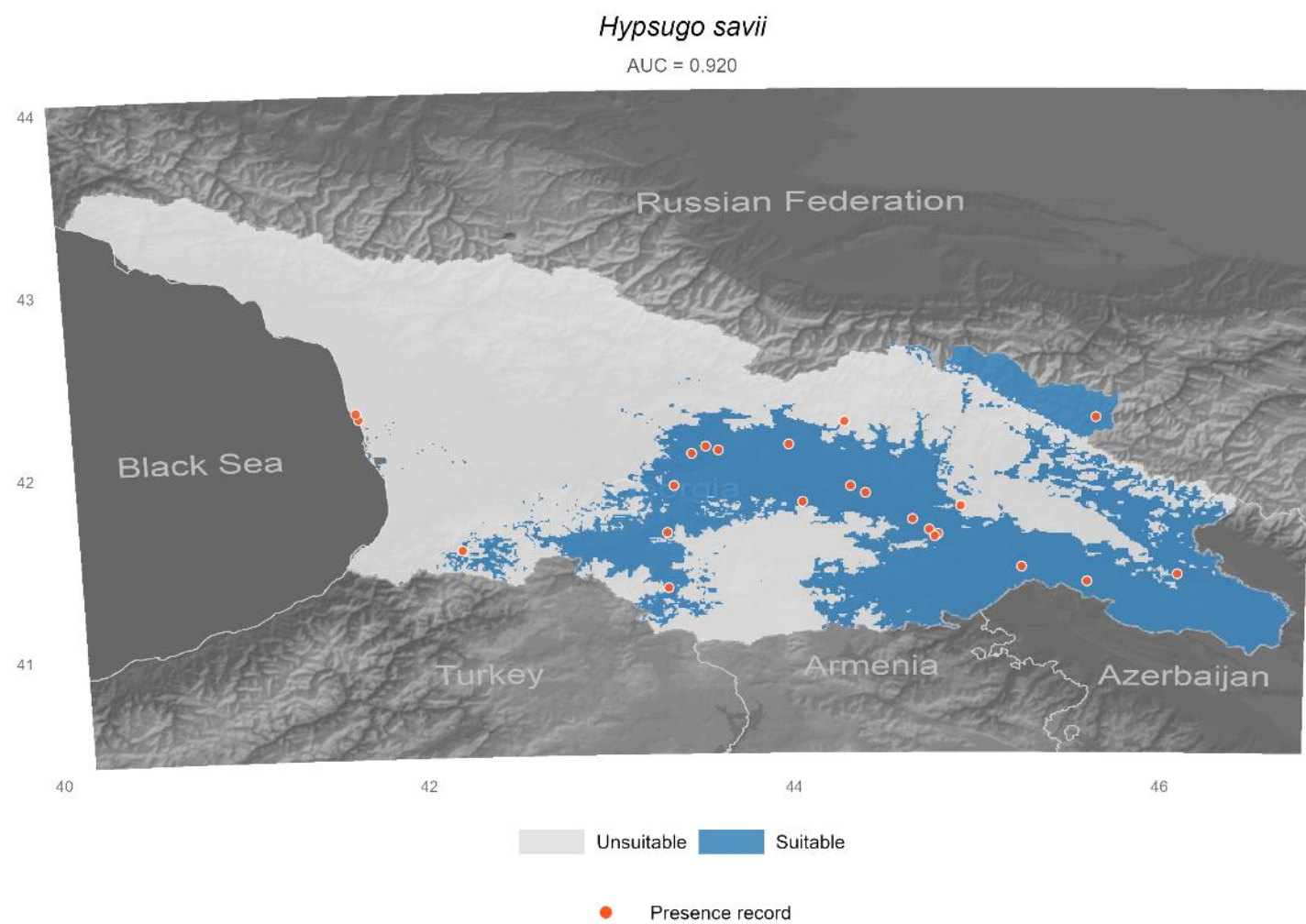


Fig. A3. *Eptesicus serotinus*



© Natradze 2026 | 1 km² | WGS84

Fig. A4. *Hypsugo savii*



© Natradze 2026 | 1 km² | WGS84

Fig. A5. *Miniopterus schreibersii*

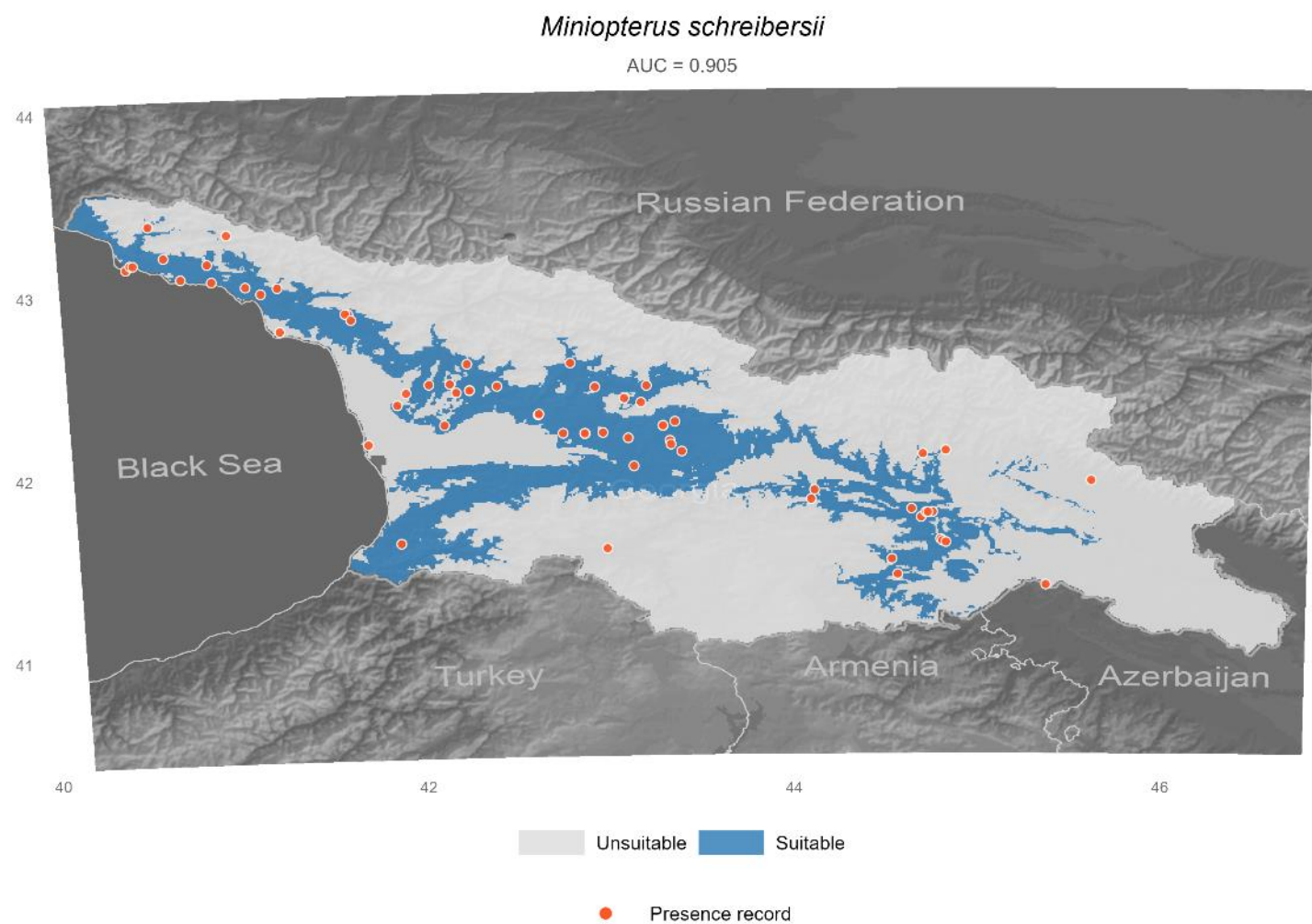
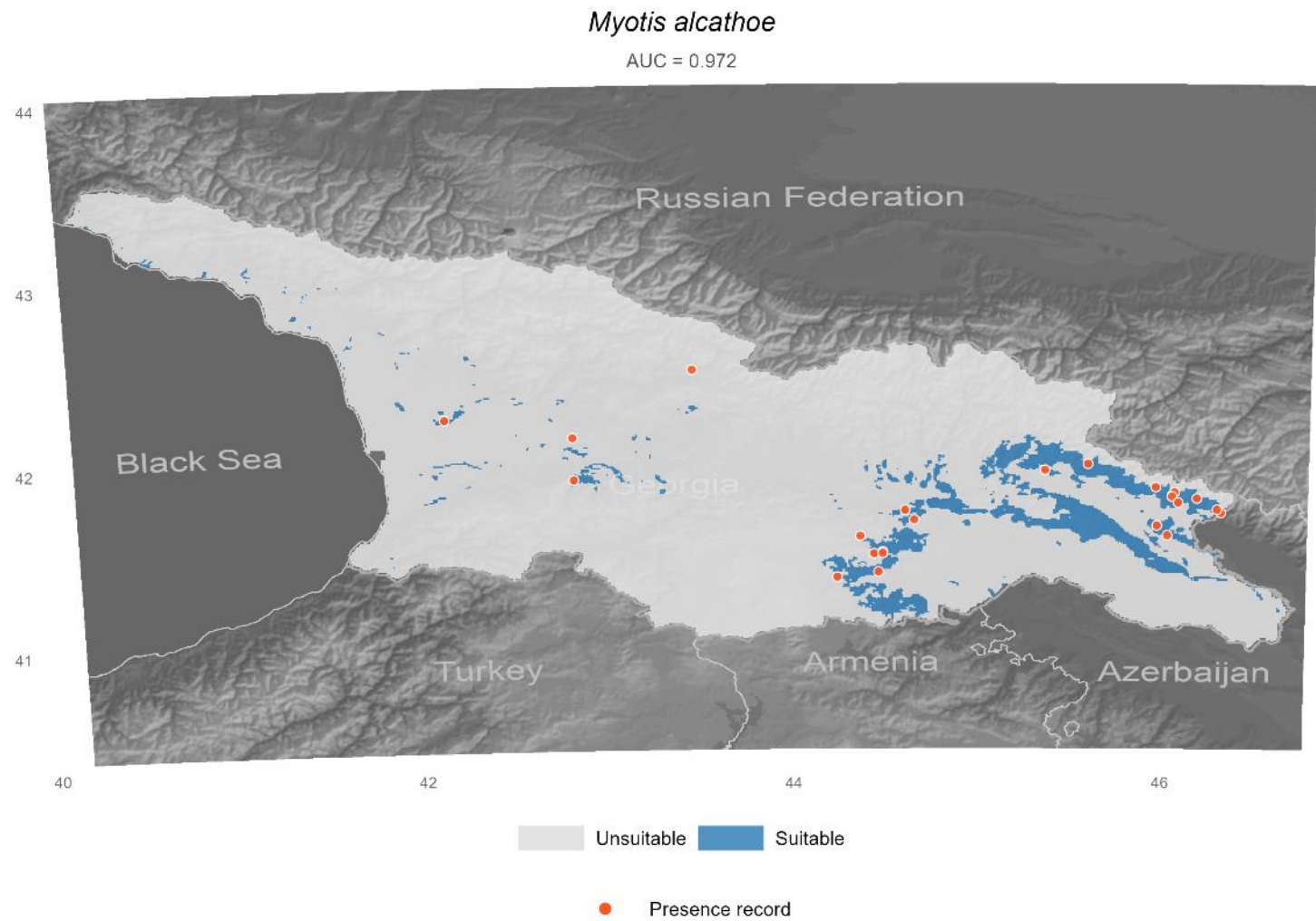
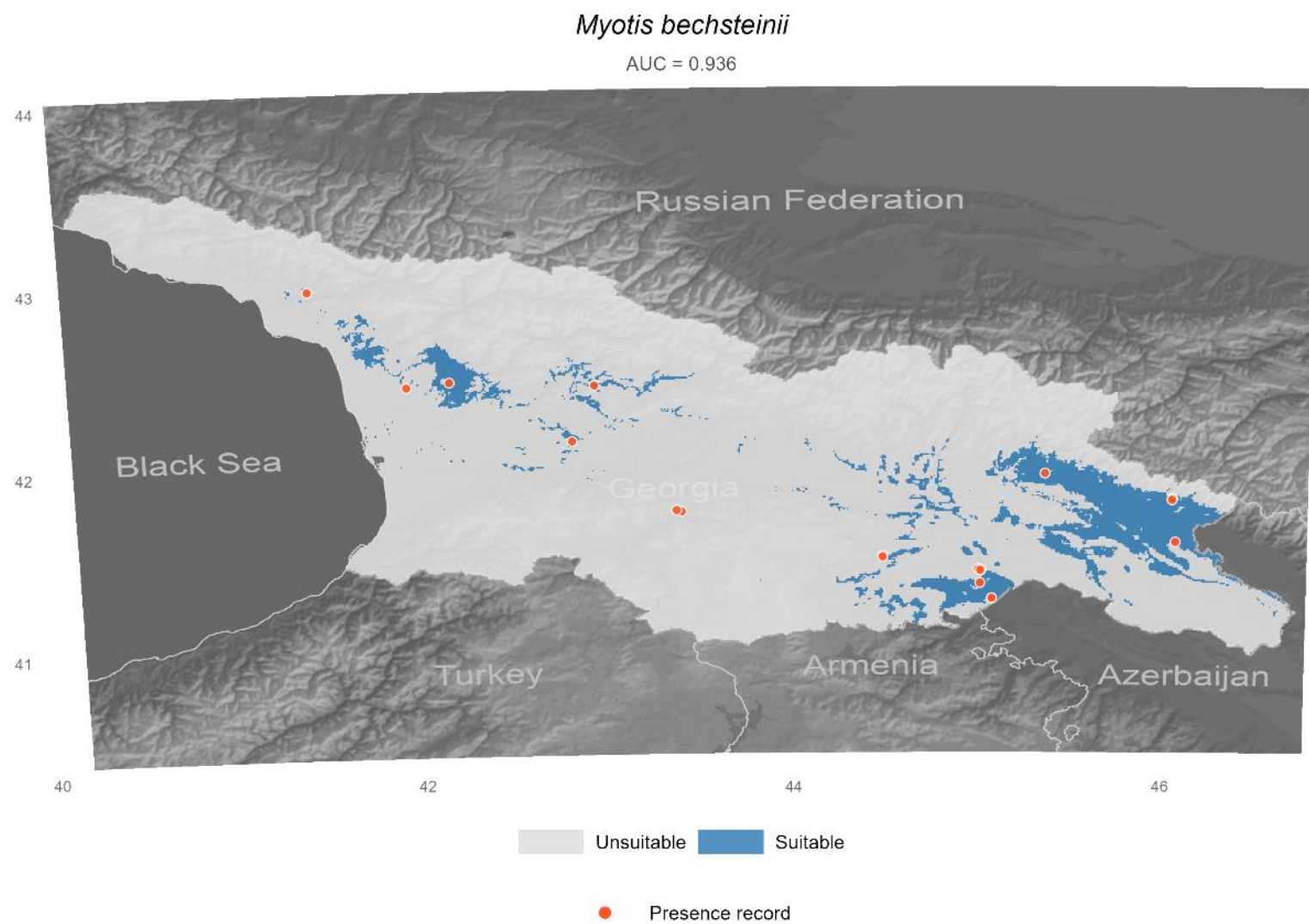


Fig. A6. *Myotis alcathoe*



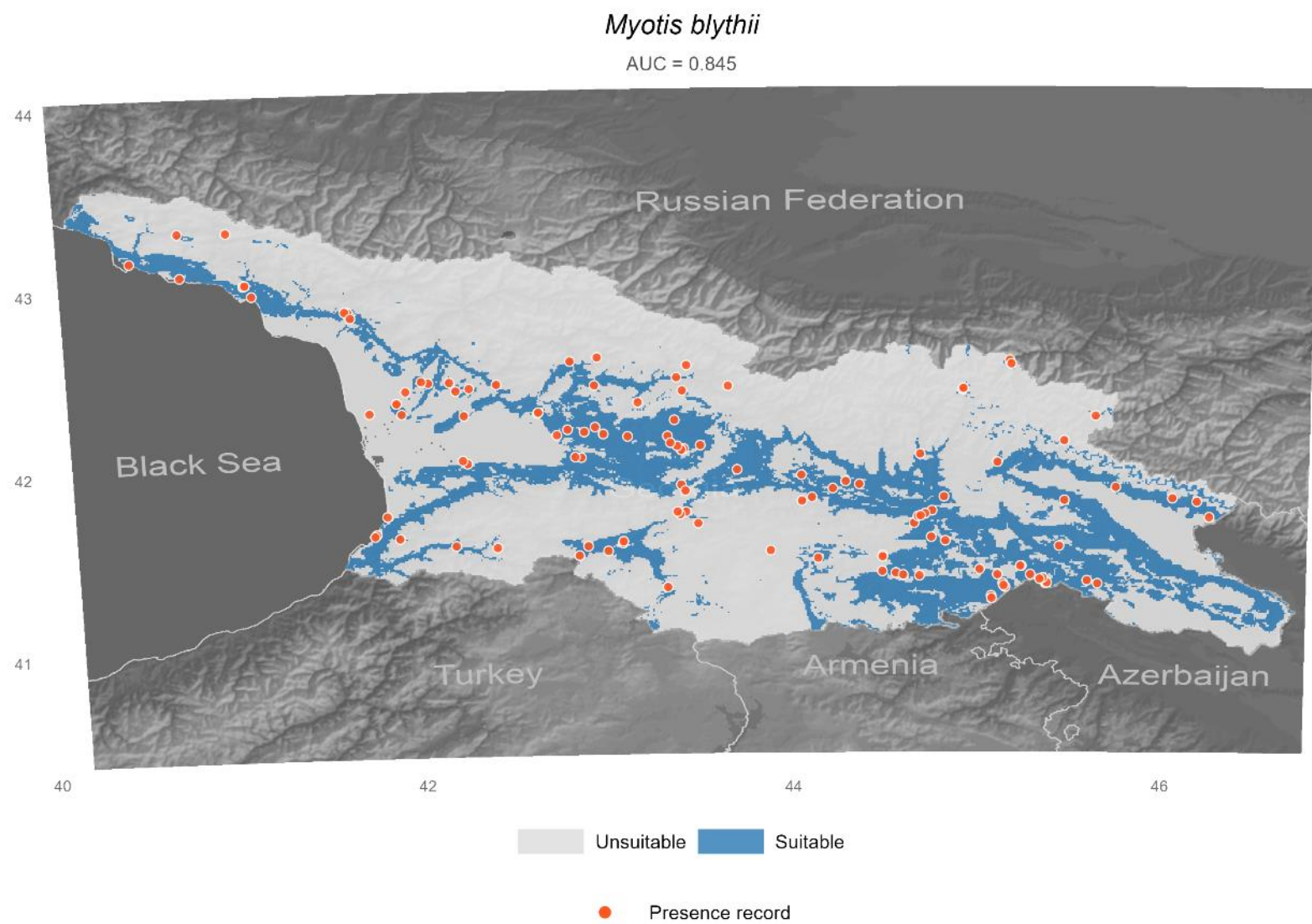
© Natradze 2026 | 1 km² | WGS84

Fig. A7. *Myotis bechsteinii*



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Fig. A8. *Myotis blythii*



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Fig. A9. *Myotis brandtii*

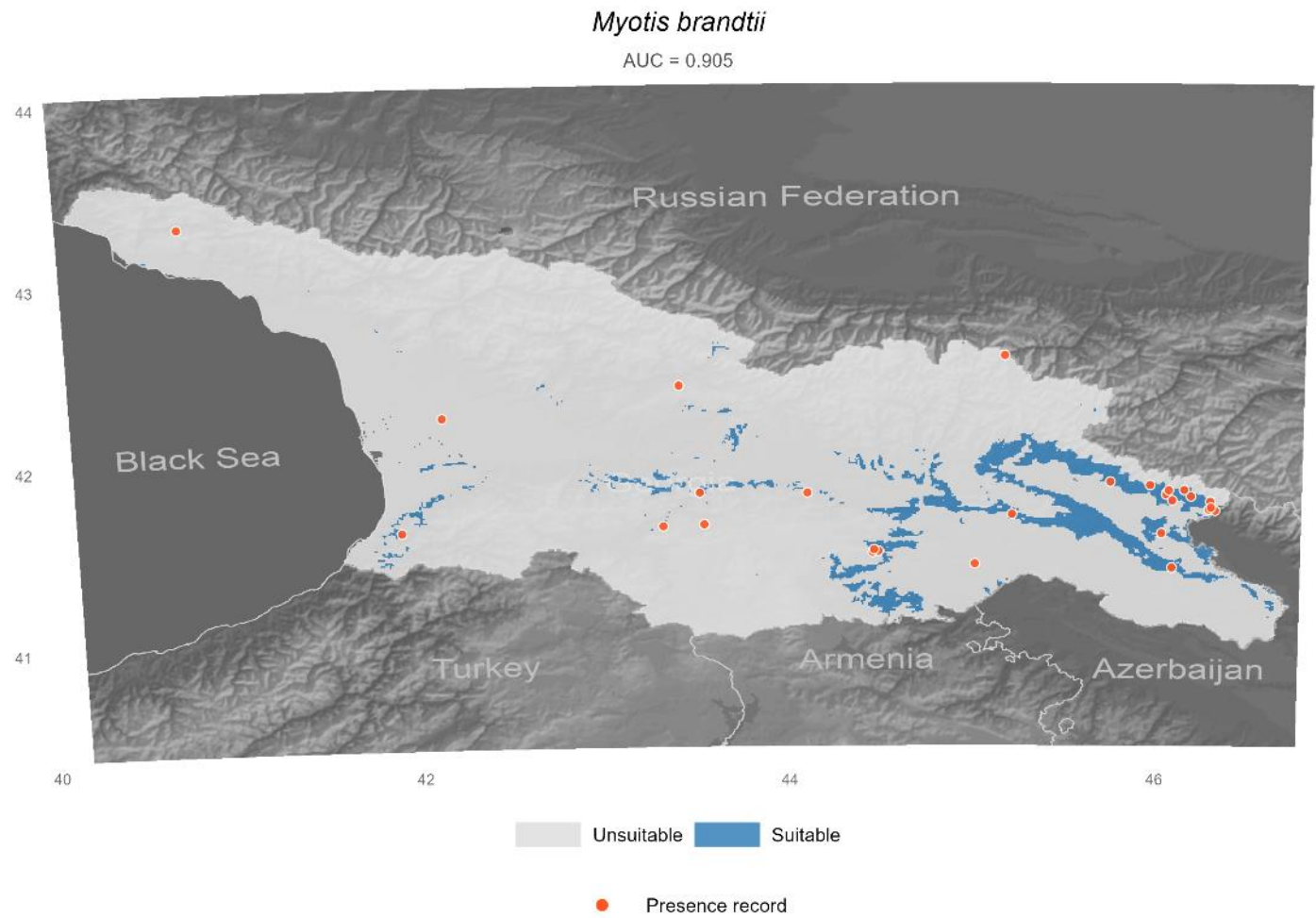


Fig. A10. *Myotis daubentonii*

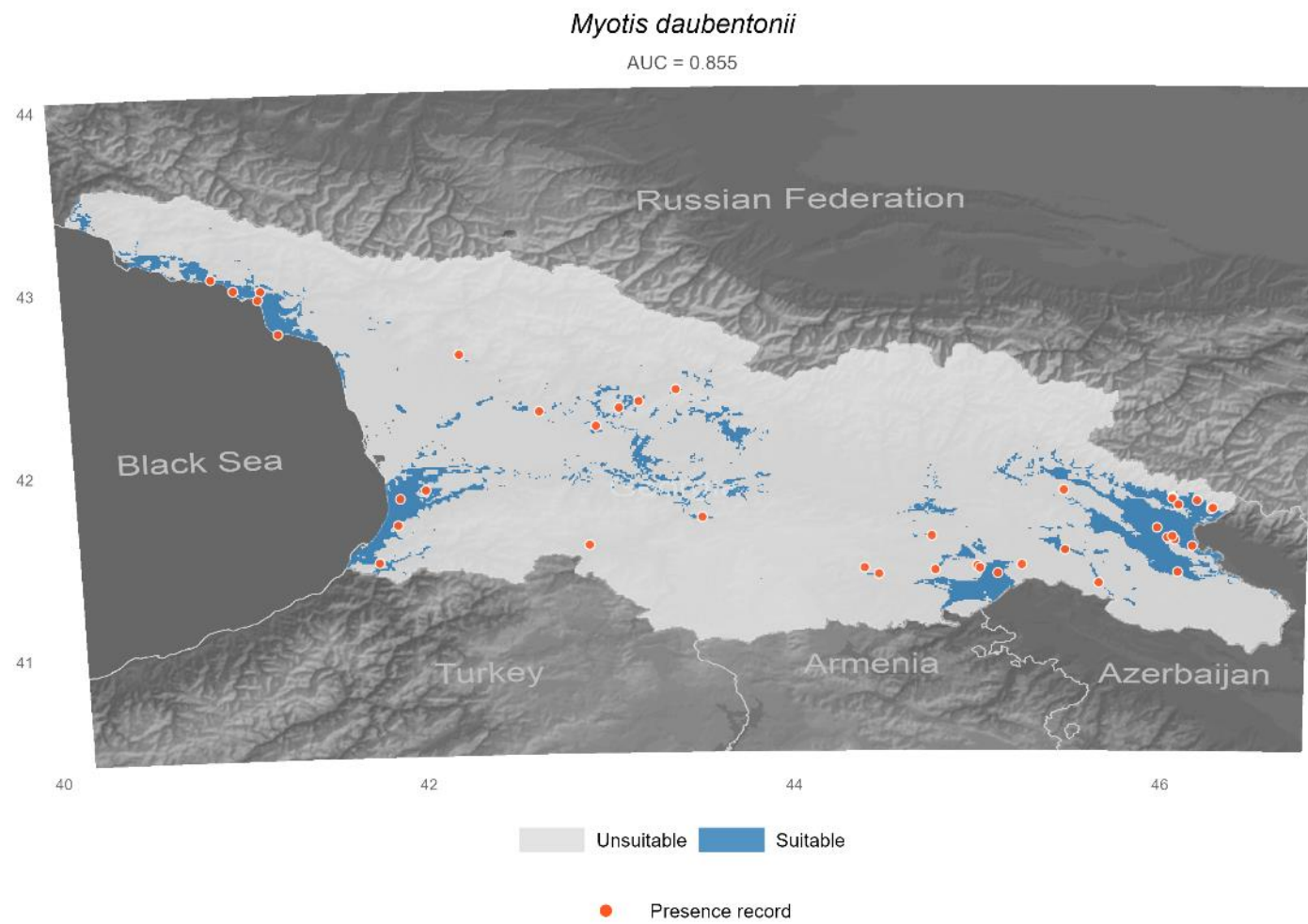


Fig. A11. *Myotis davidii*

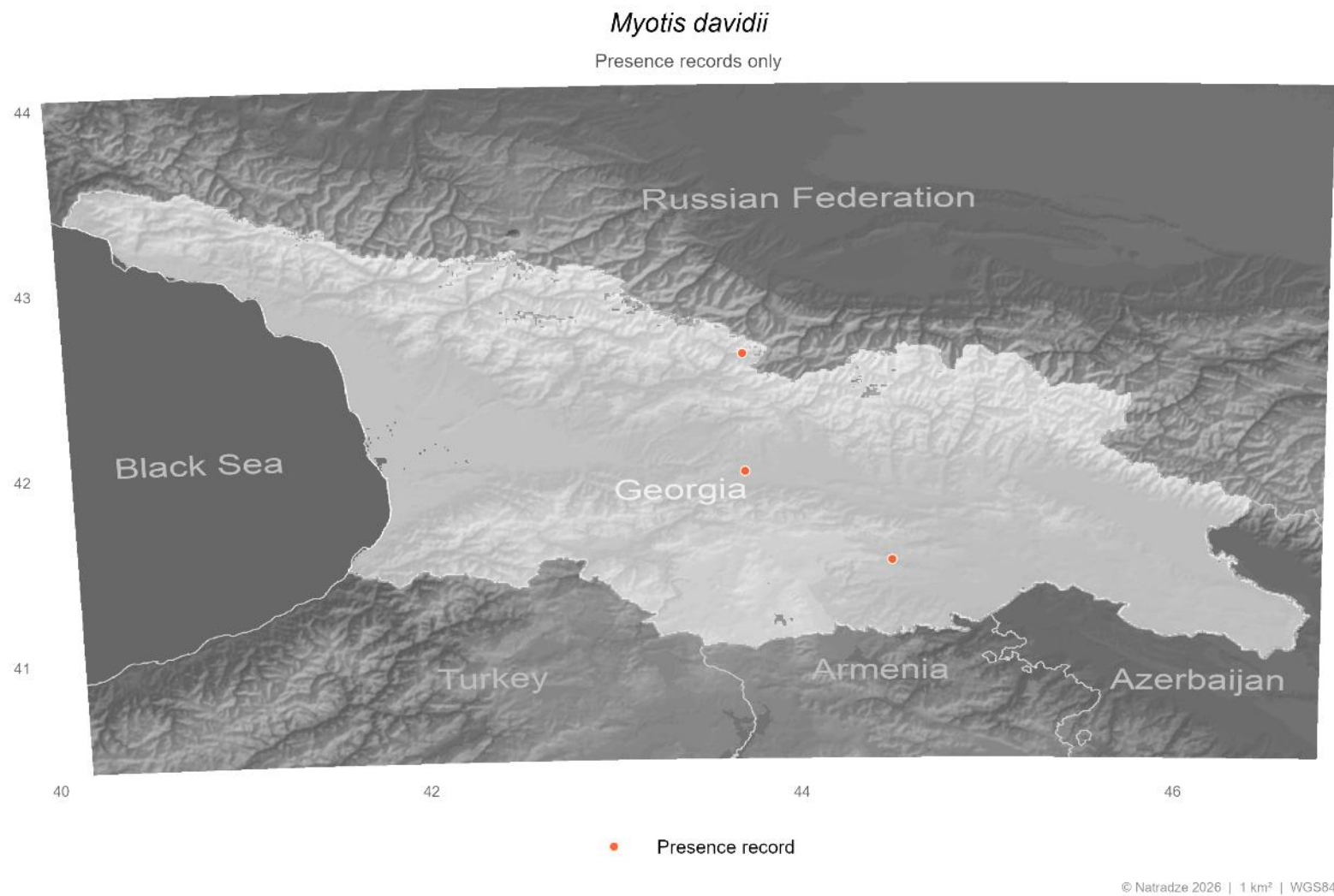
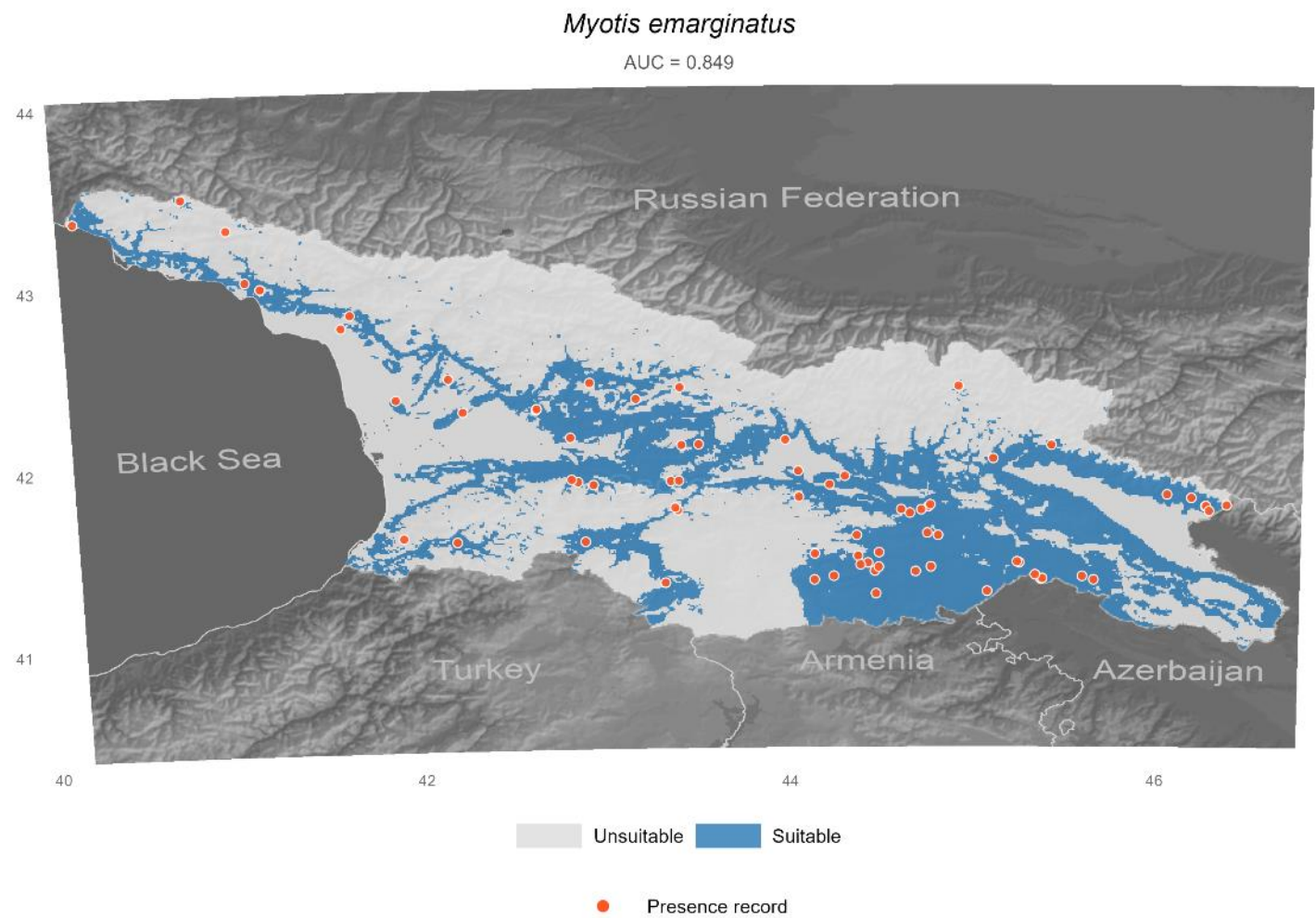
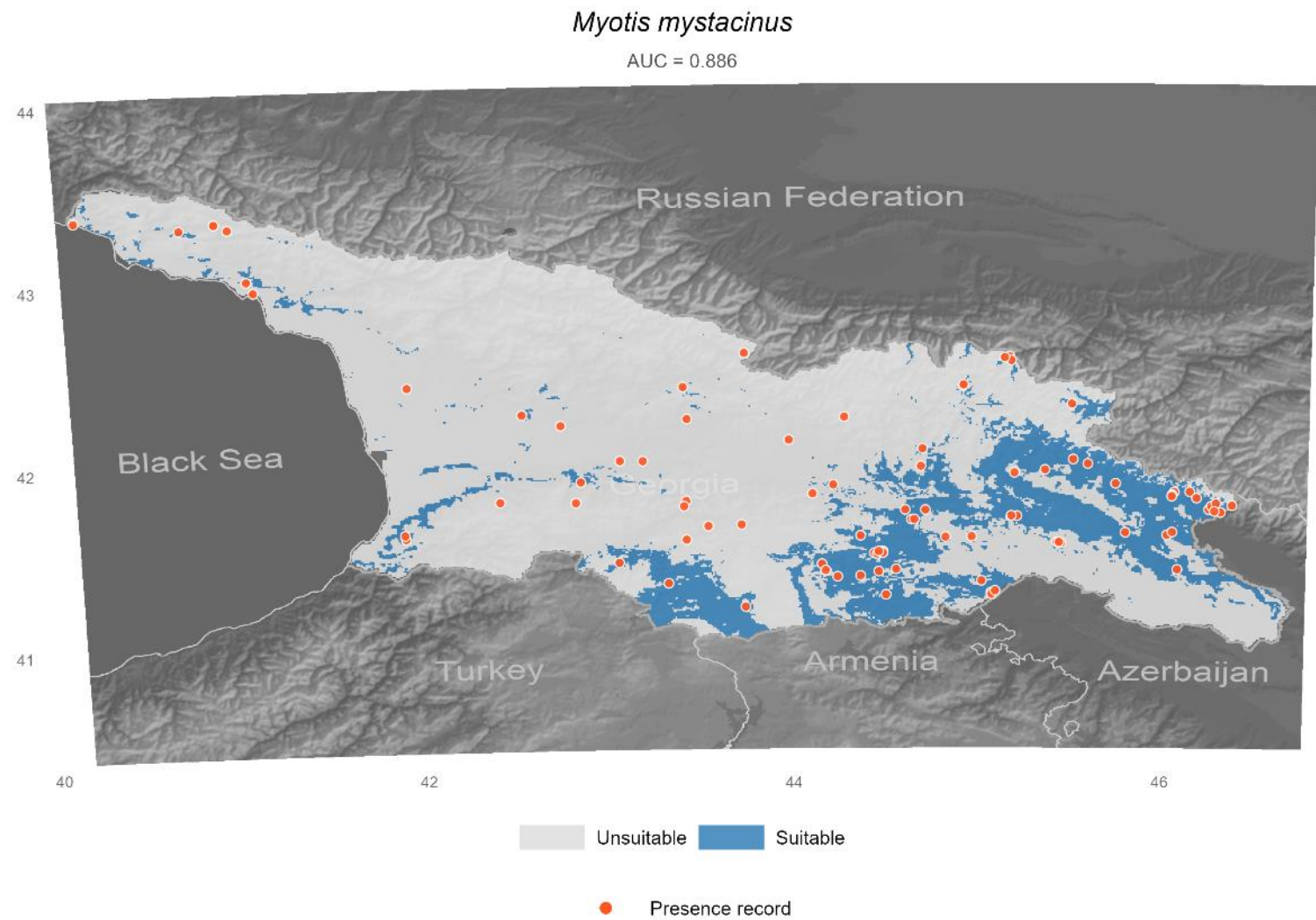


Fig. A12. *Myotis emarginatus*



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Fig. A13. *Myotis mystacinus*



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Fig. A14. *Myotis nattereri*

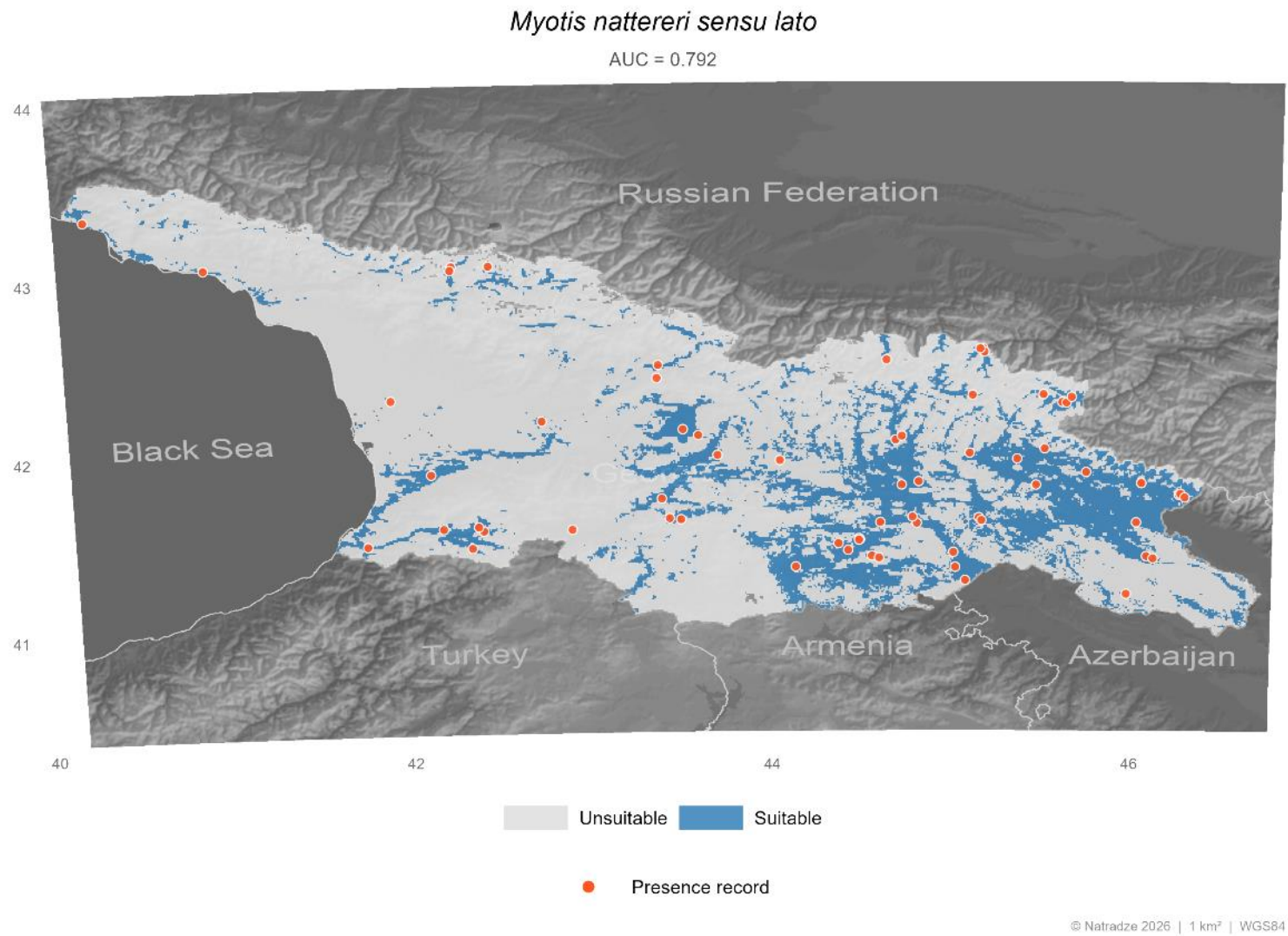
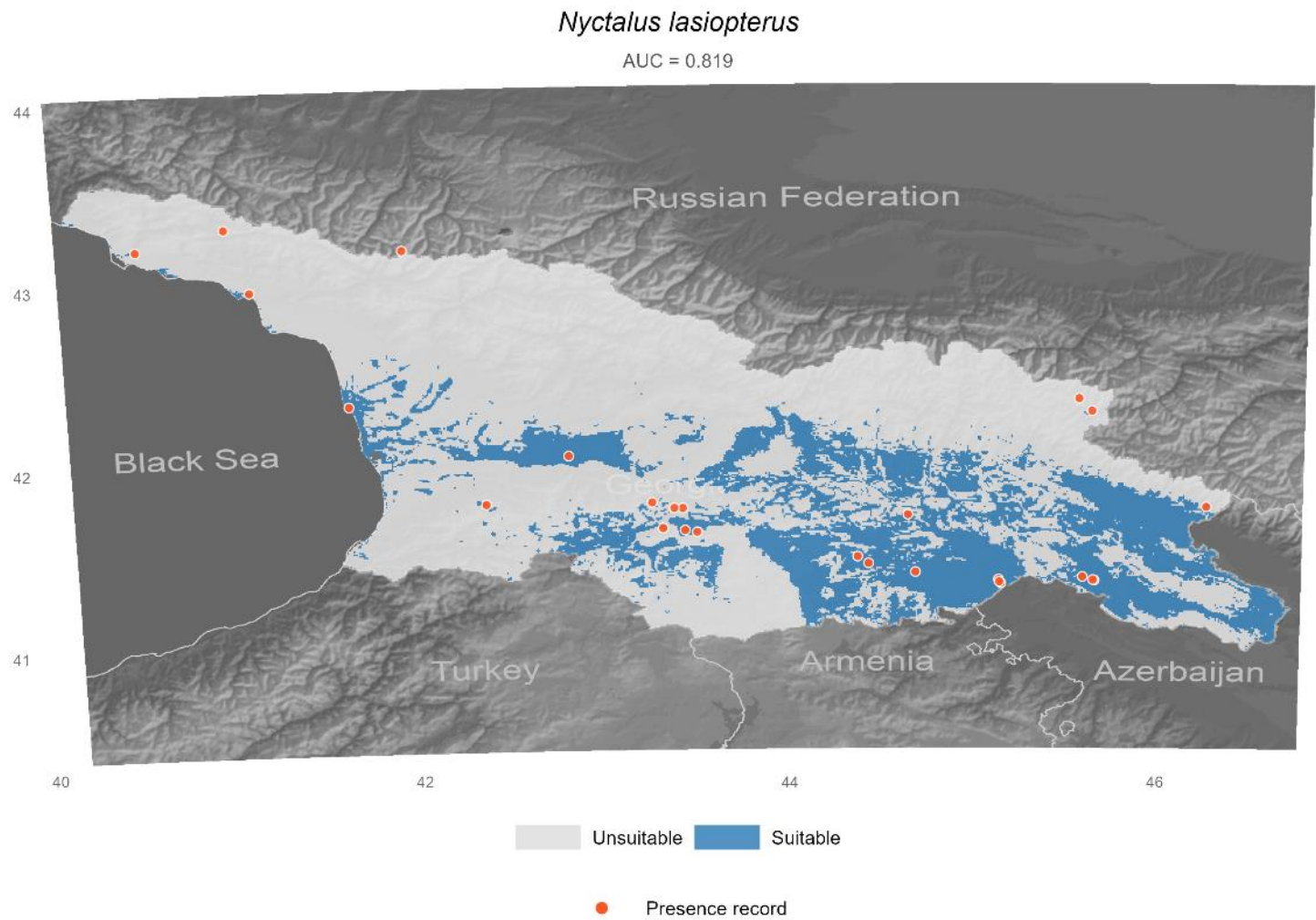
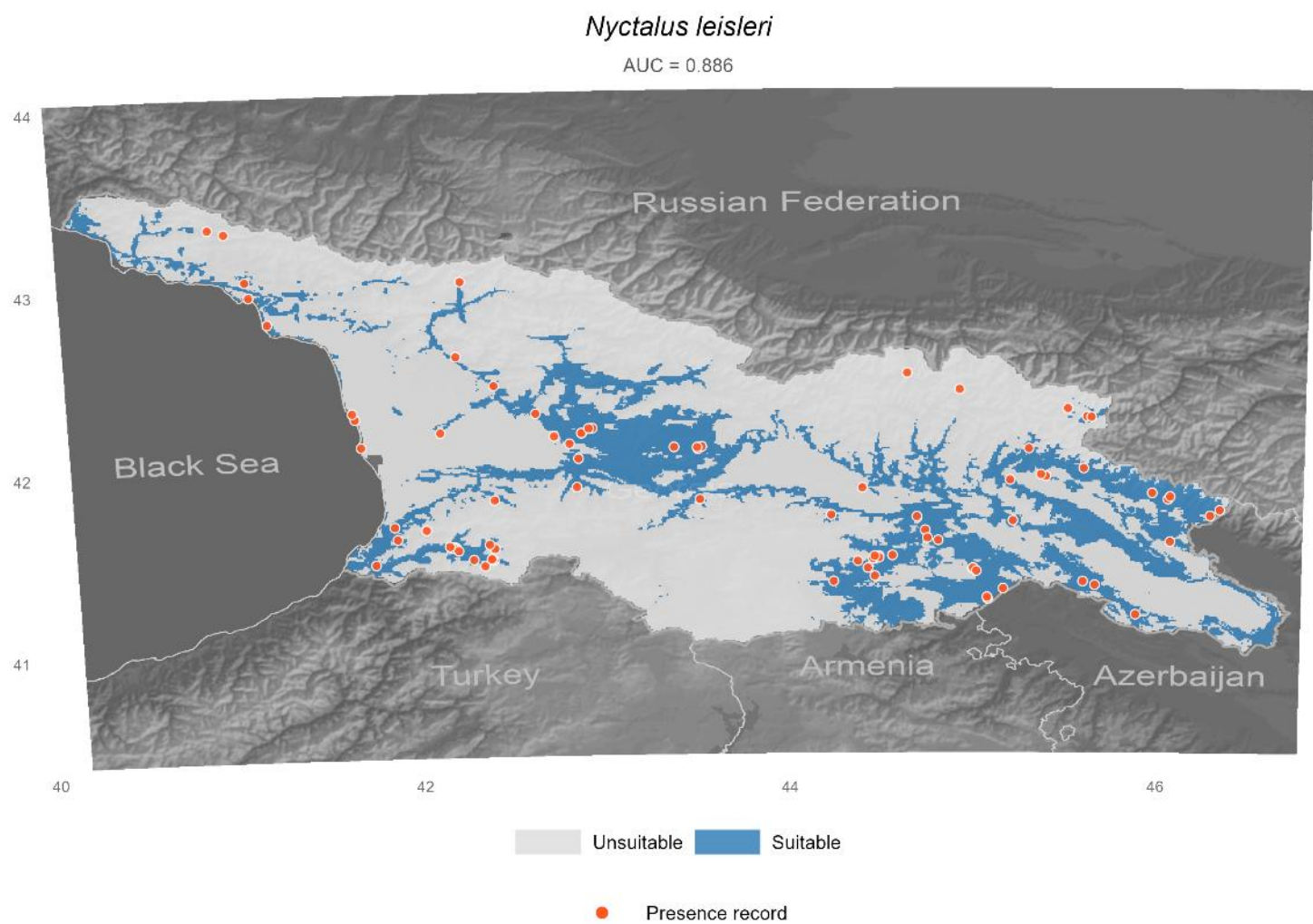


Fig. A15. *Nyctalus lasiopterus*



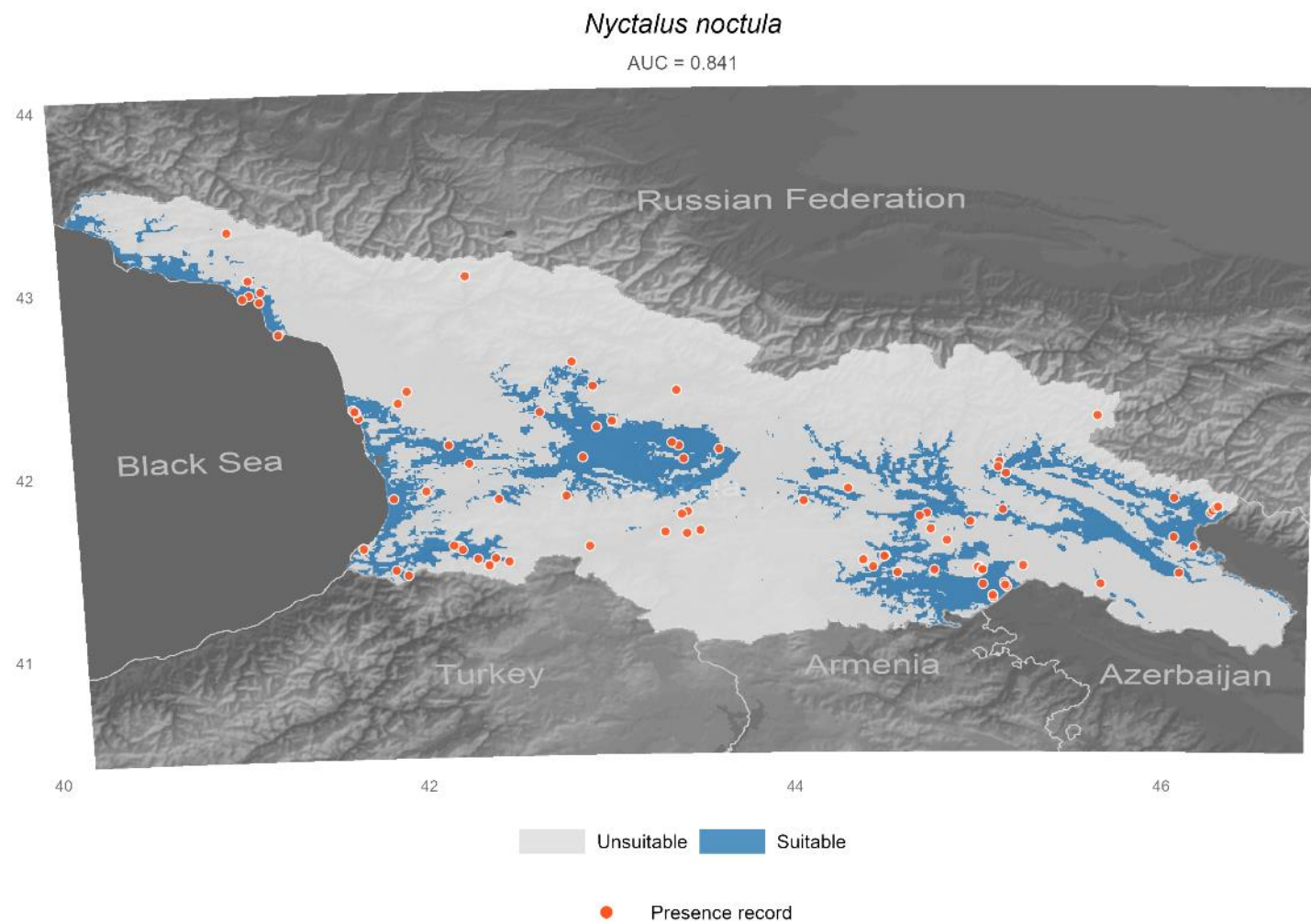
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Fig. A16. *Nyctalus leisleri*



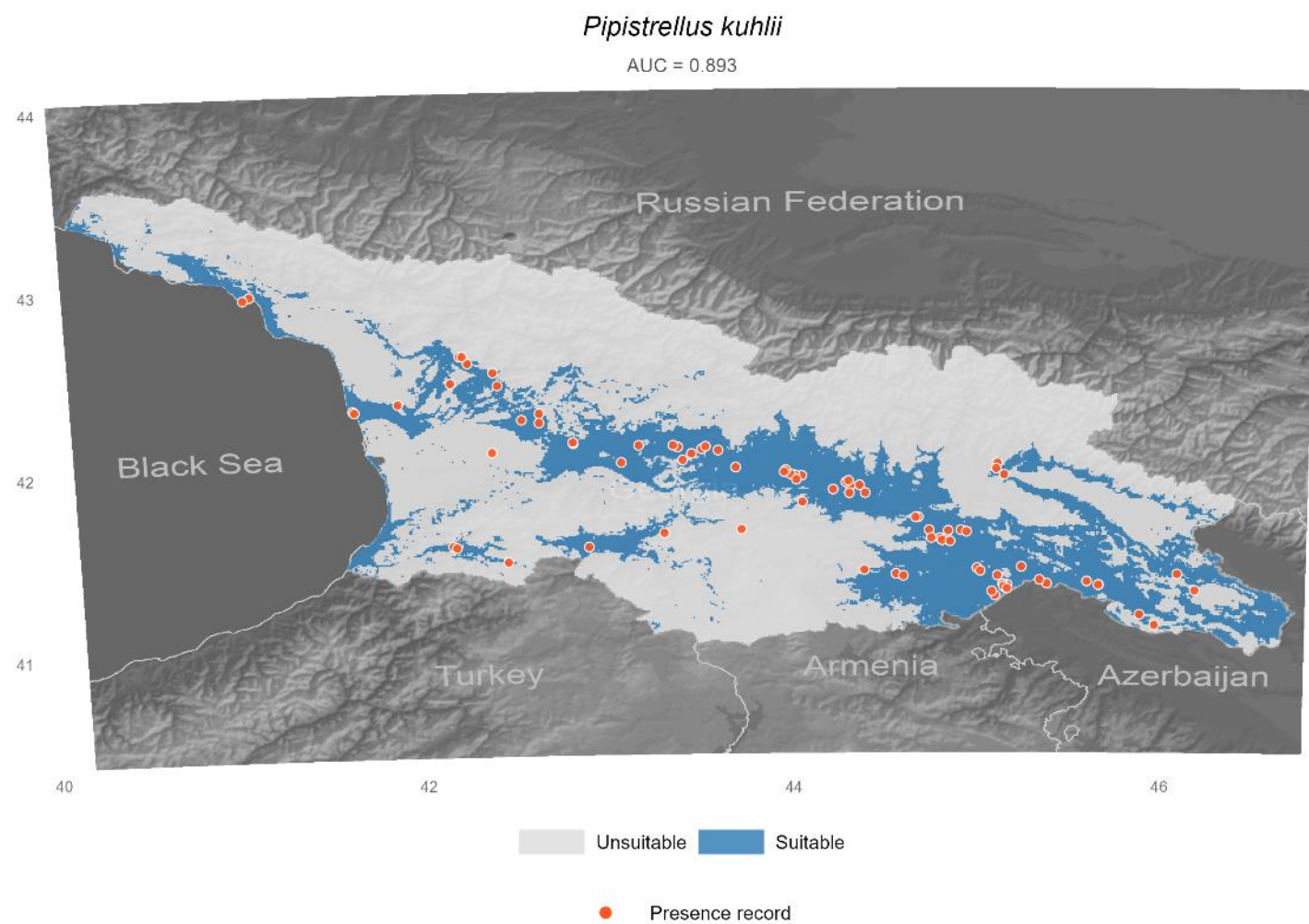
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Fig. A17. *Nyctalus noctula*



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Fig. A18. *Pipistrellus kuhlii*



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Fig. A19. *Pipistrellus nathusii*

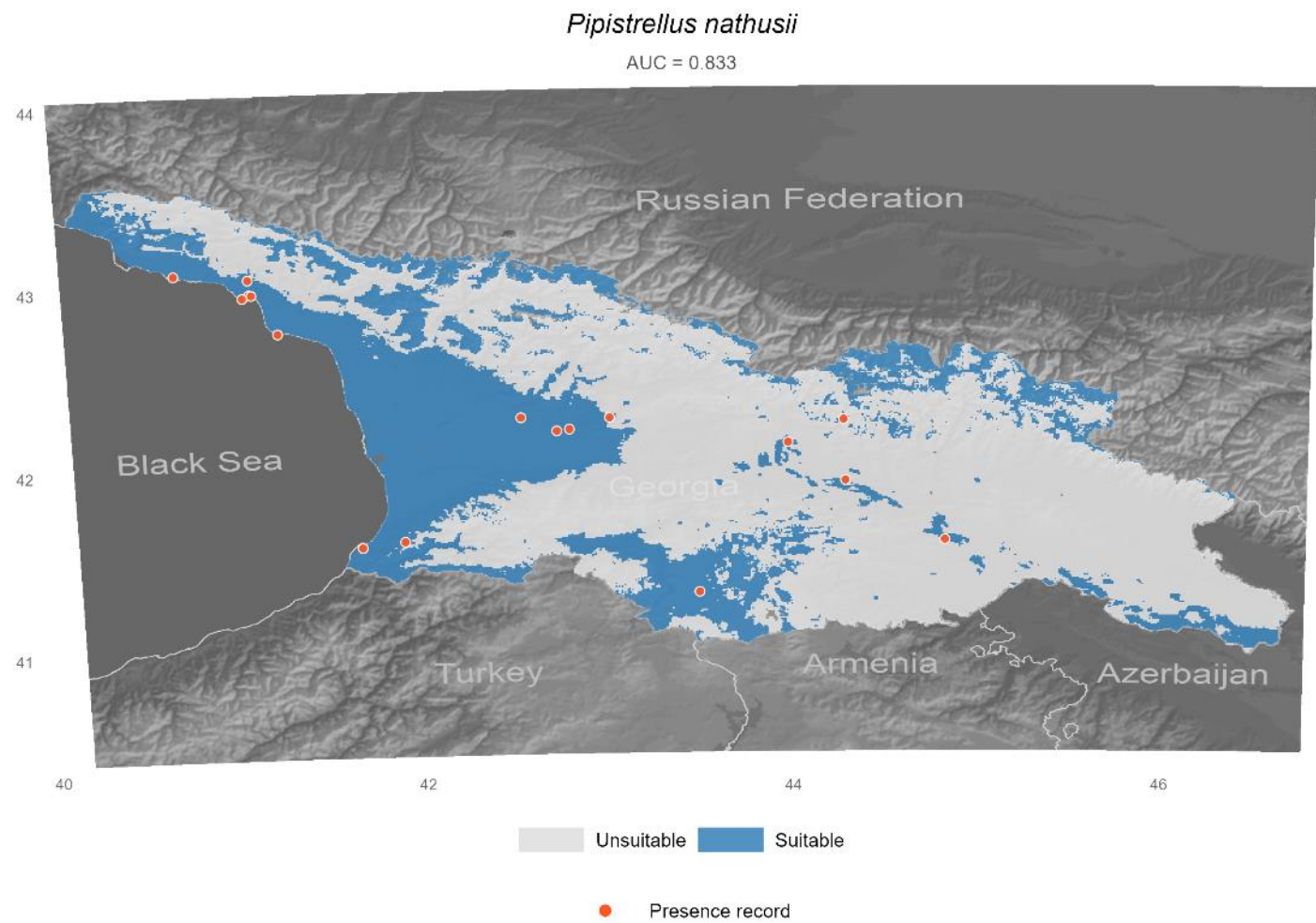


Fig. A20. *Pipistrellus pipistrellus*

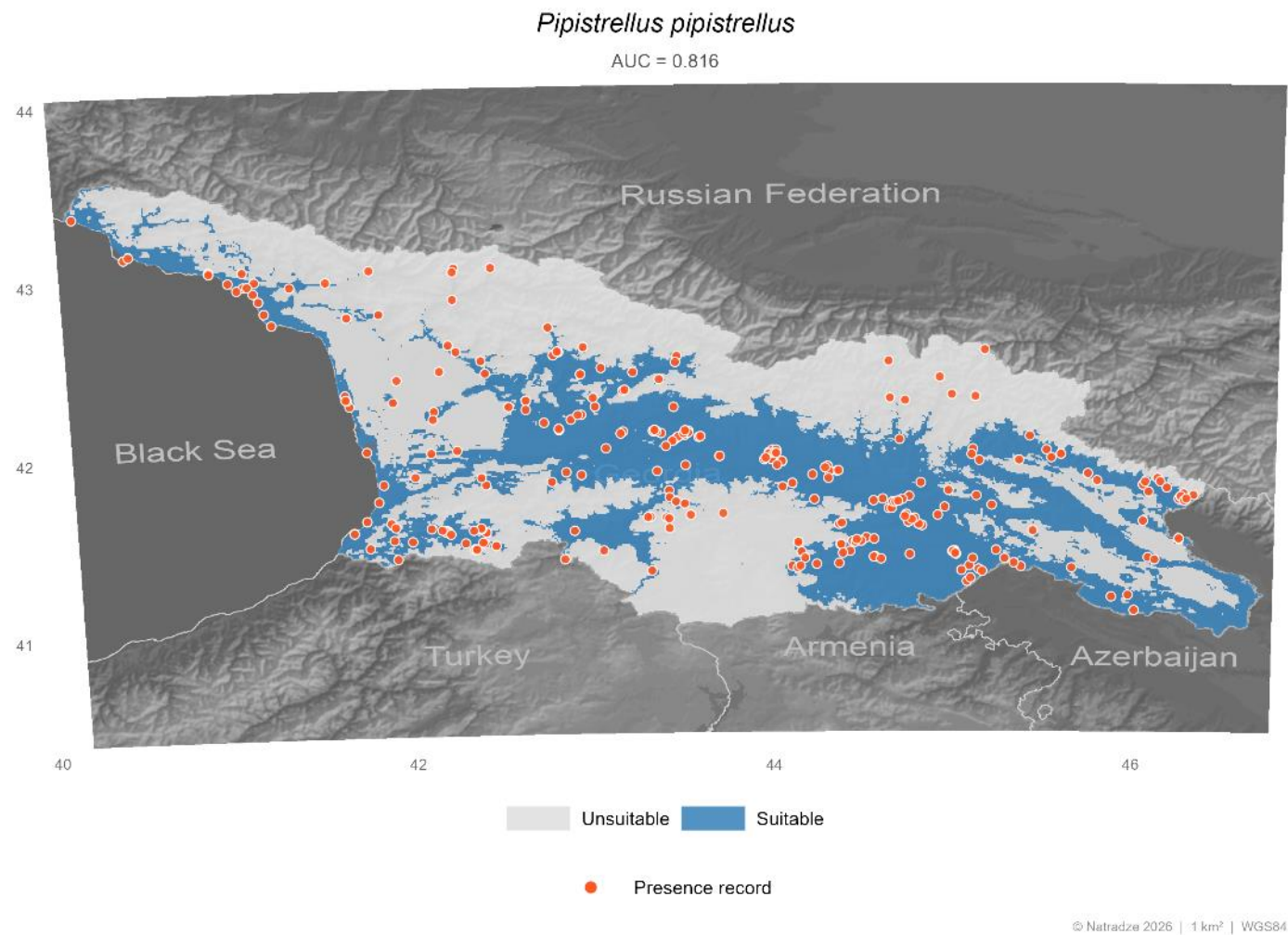


Fig. A21. *Pipistrellus pygmaeus*

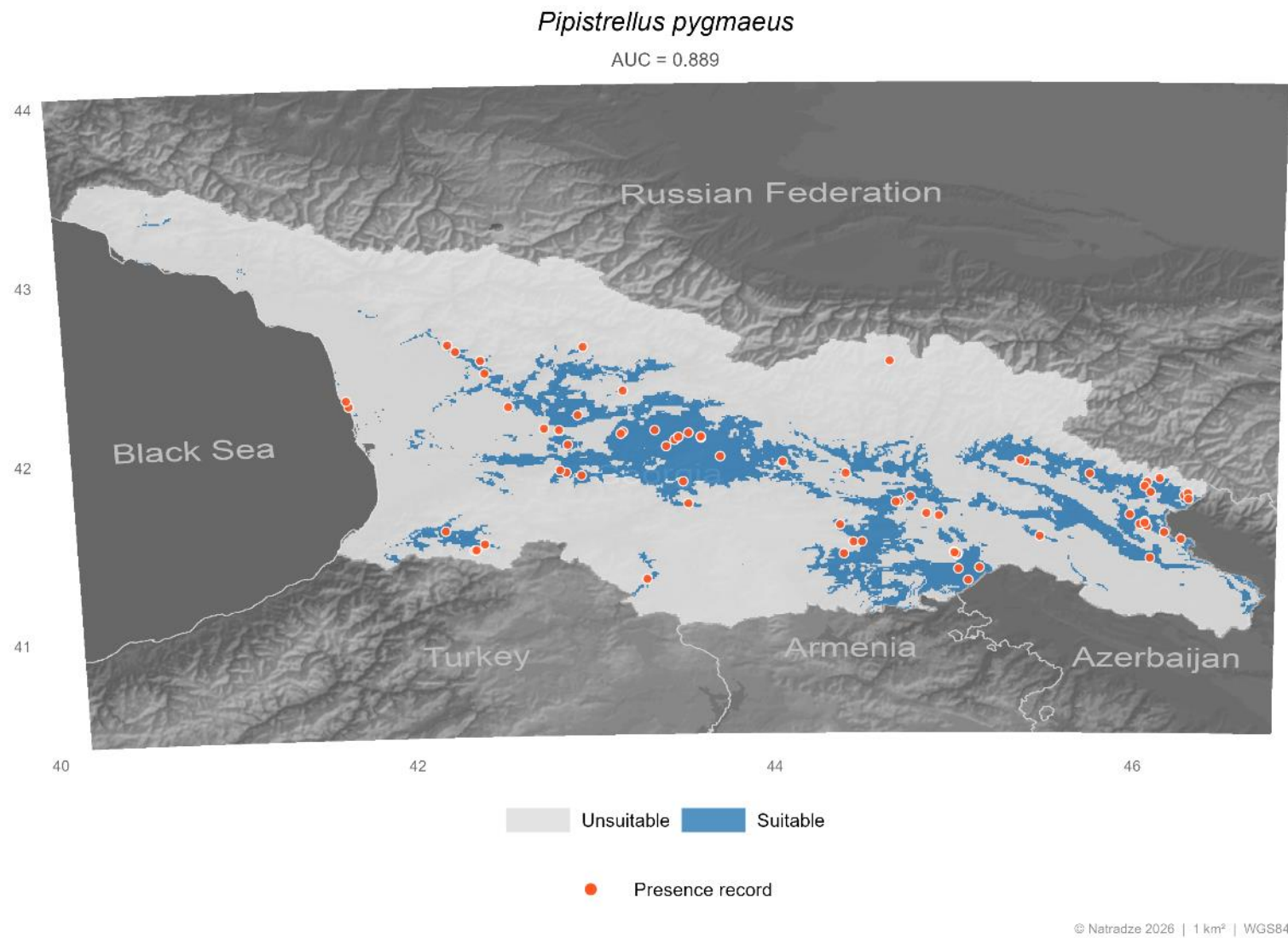


Fig. A22. *Plecotus auritus*

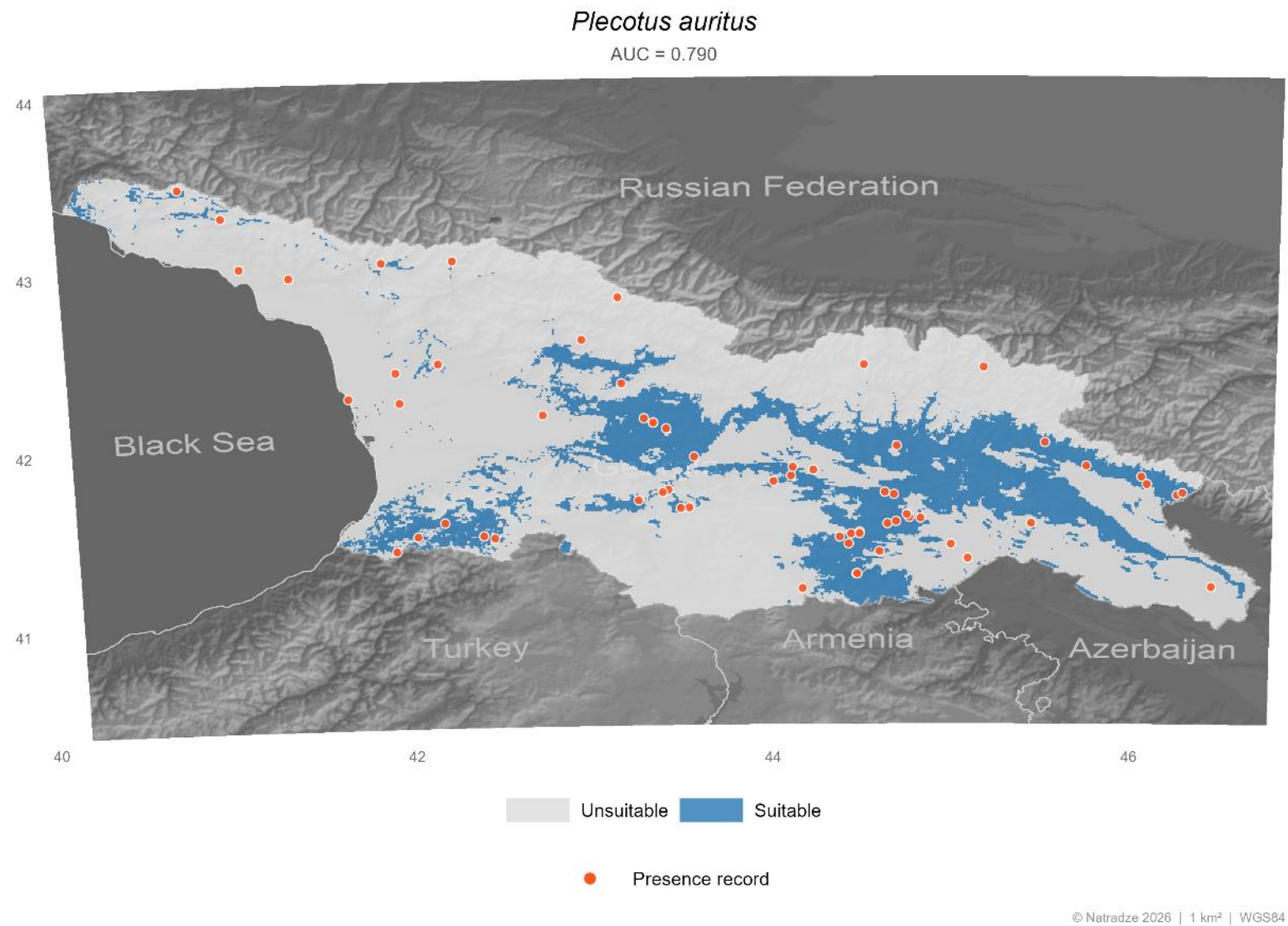


Fig. A23. *Plecotus macrobullaris*

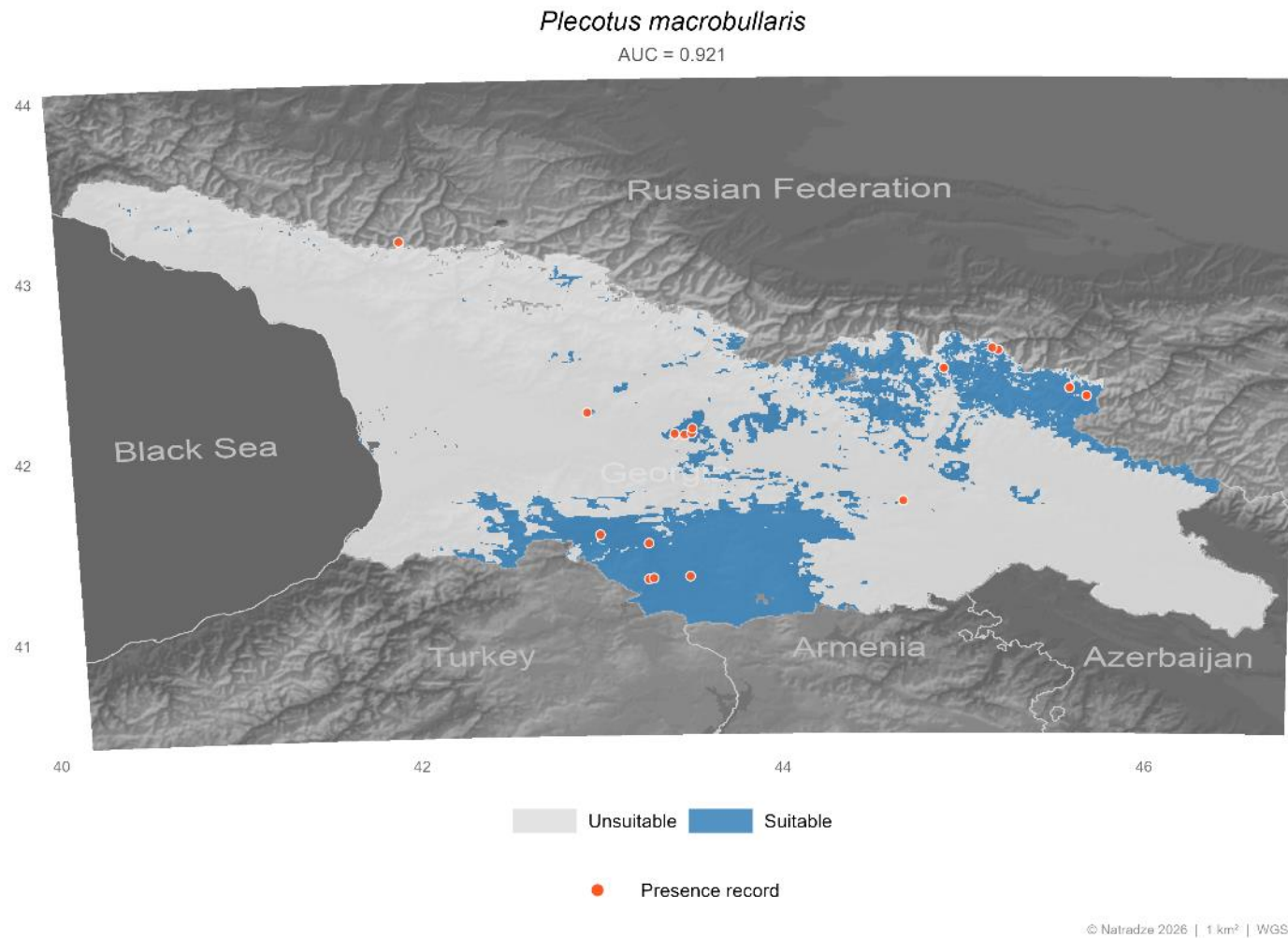


Fig. A24. *Rhinolophus blasii*

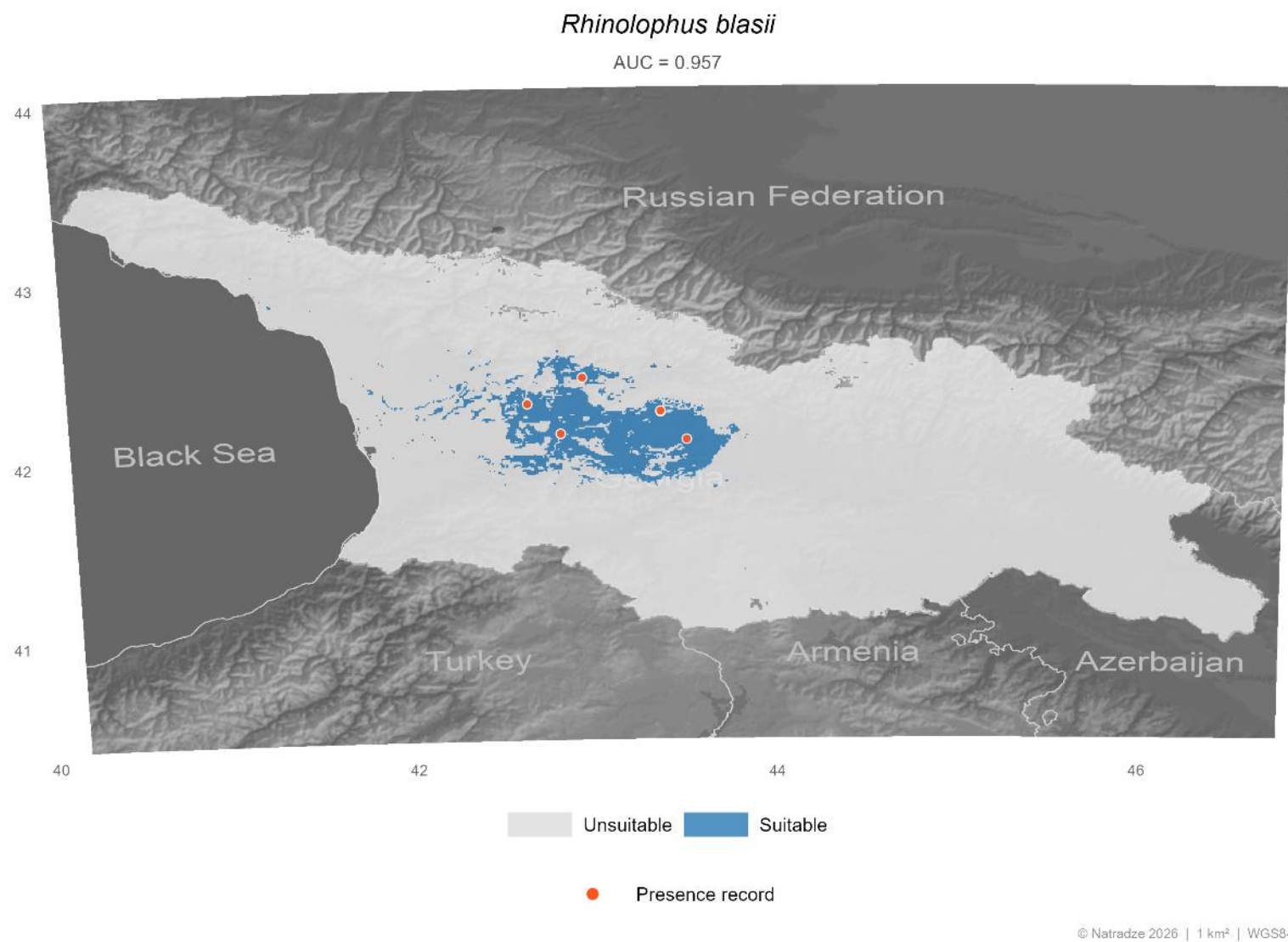


Fig. A25. *Rhinolophus euryale*

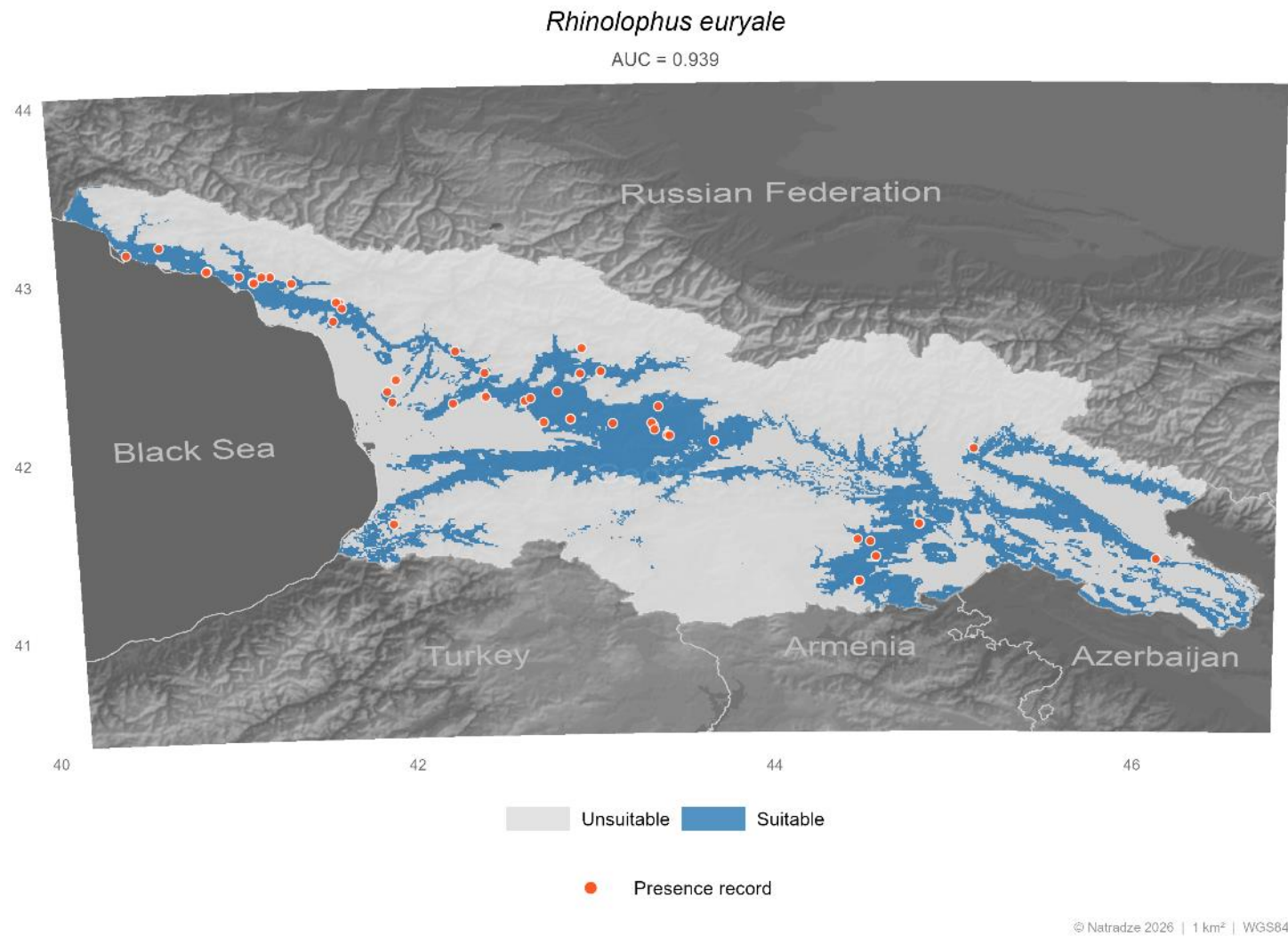
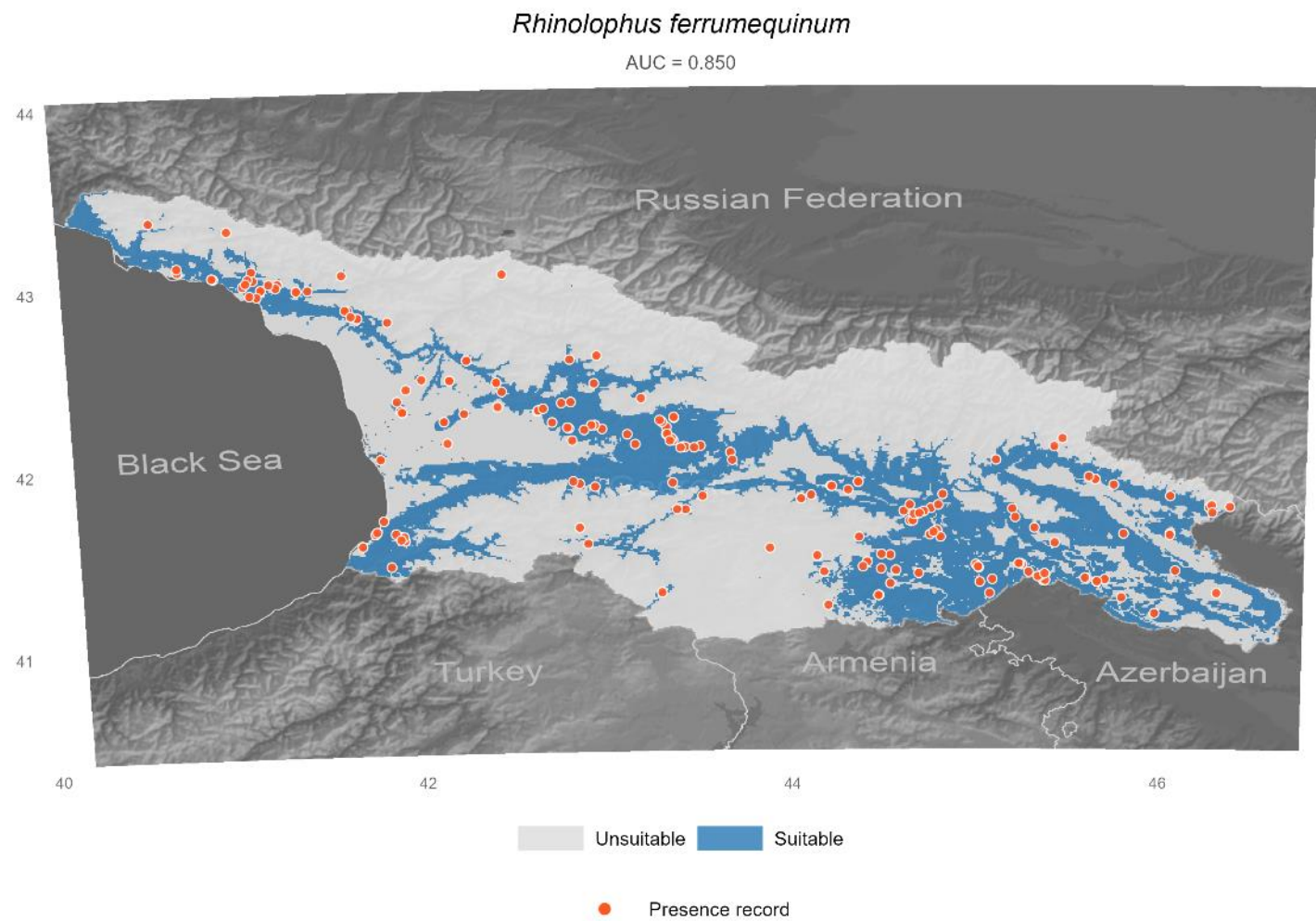
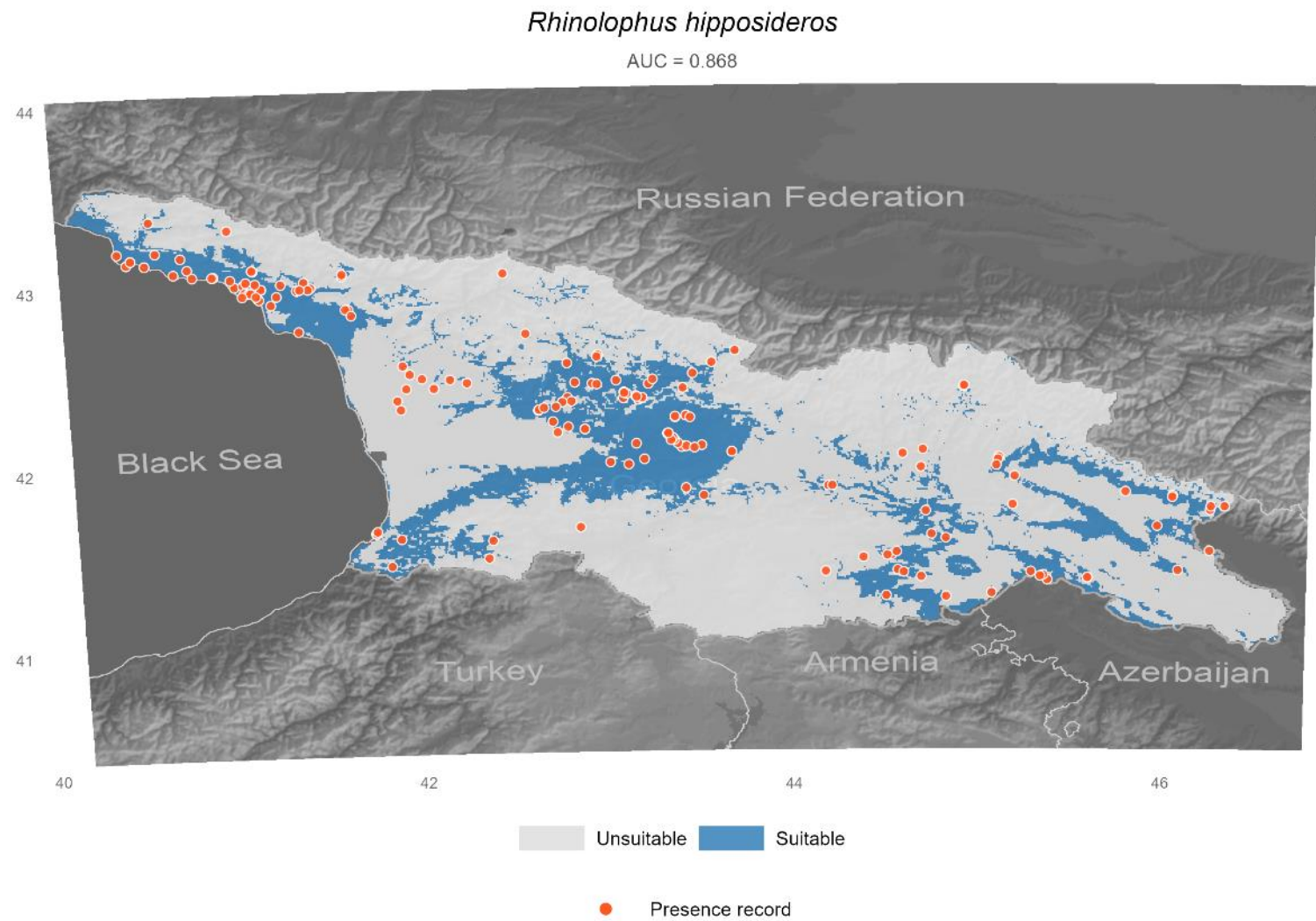


Fig. A26. *Rhinolophus ferrumequinum*



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Fig. A27. *Rhinolophus hipposideros*



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Fig. A29. *Rhinolophus mehelyi*

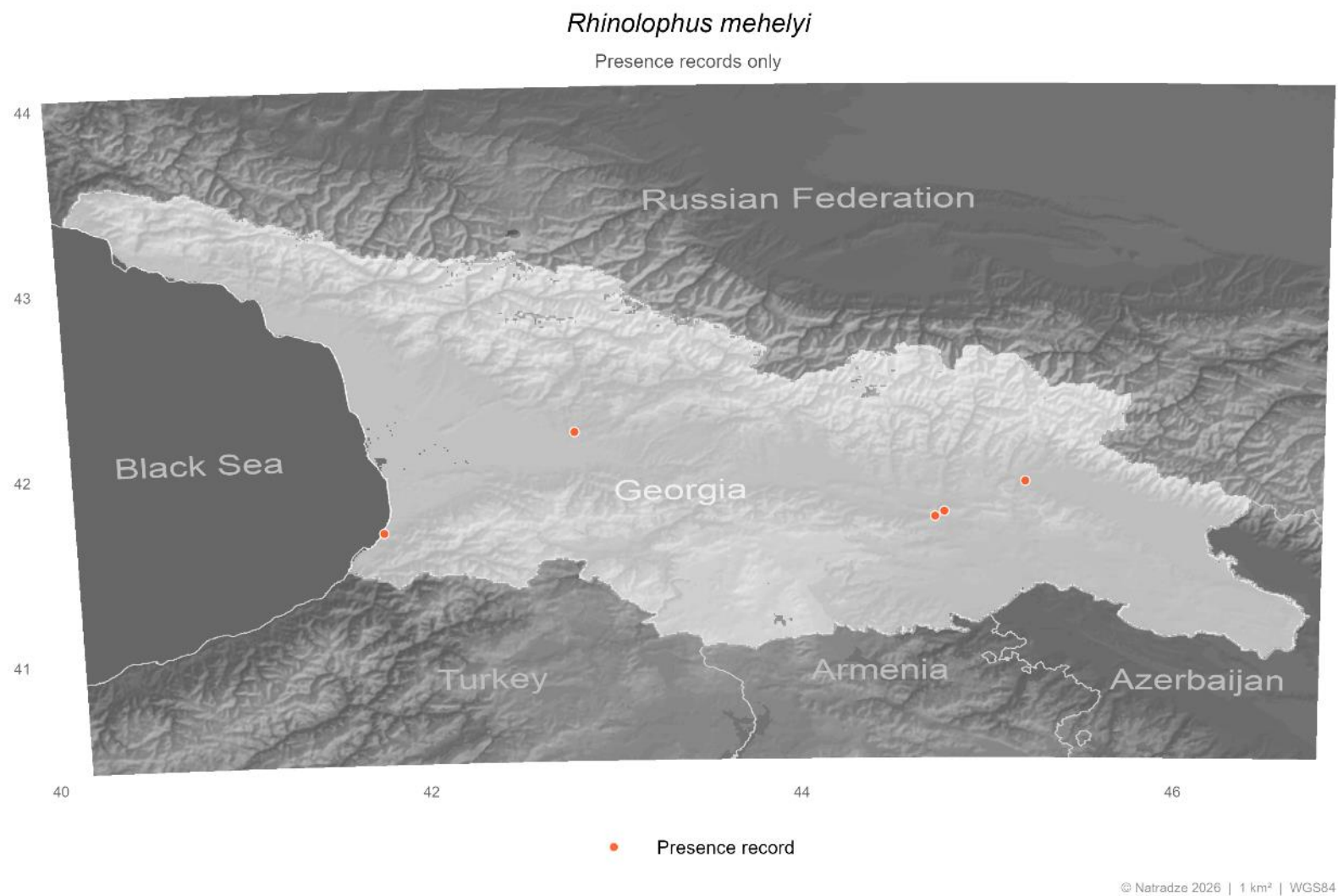
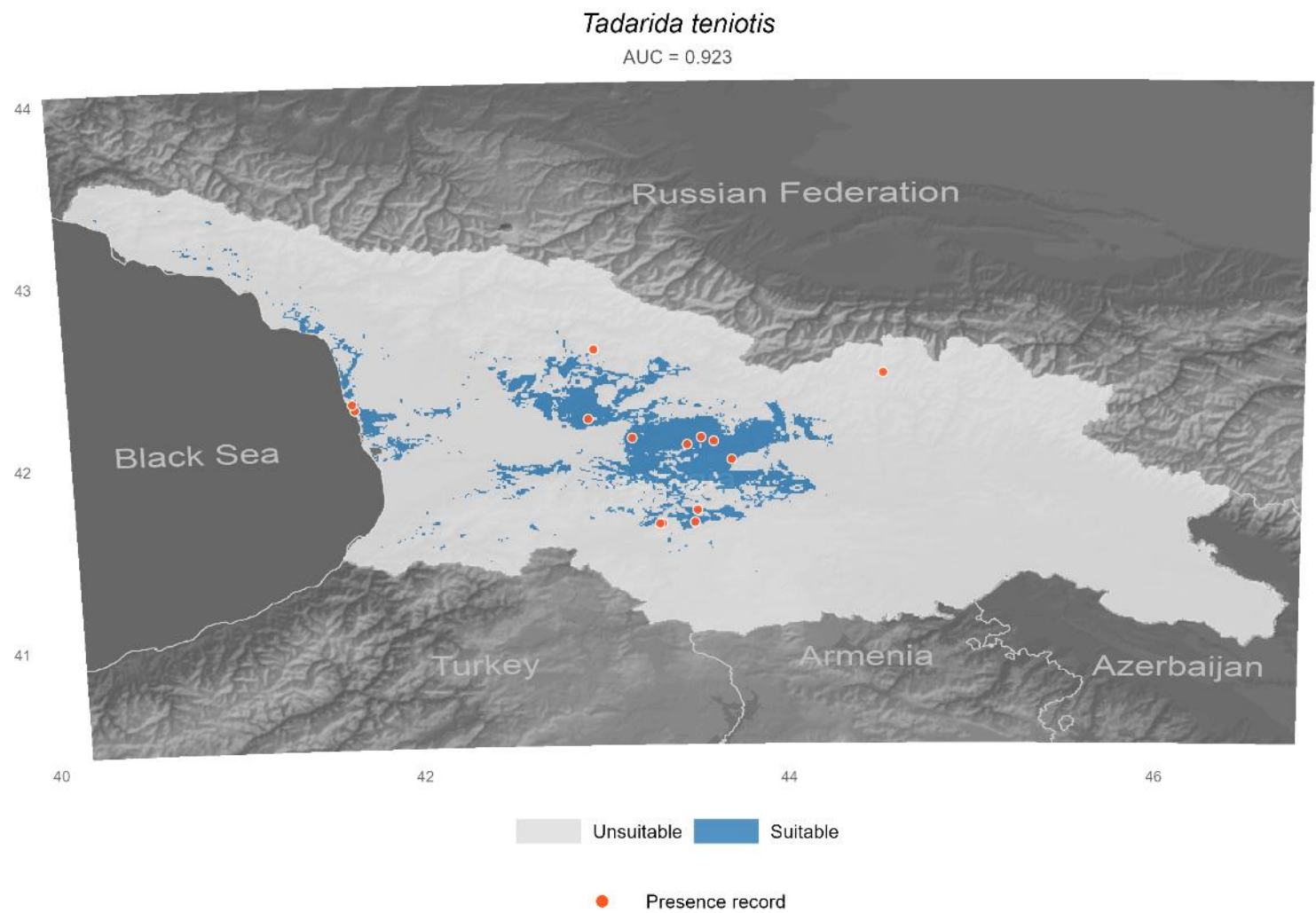
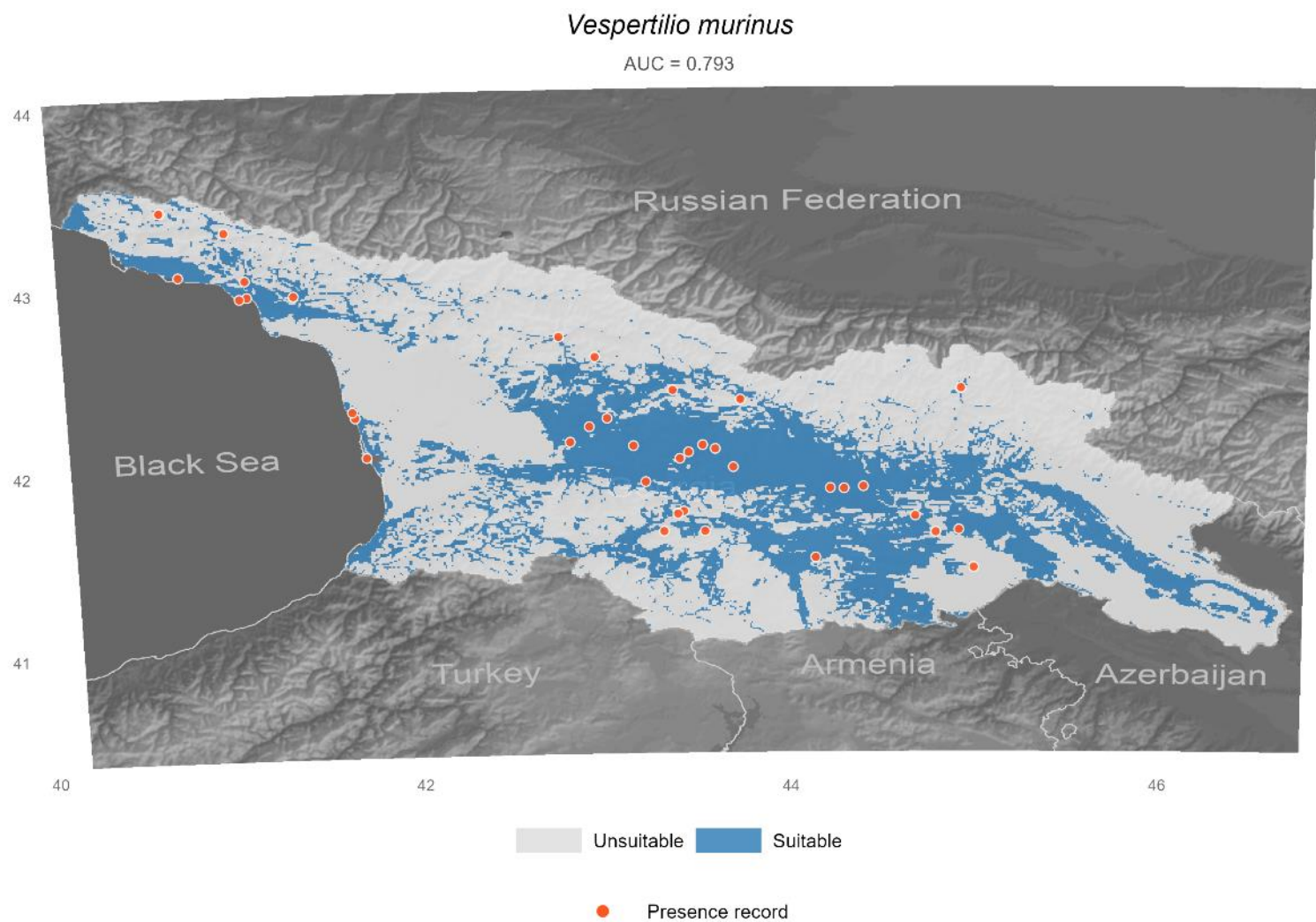


Fig. A29. *Tadarida teniotis*



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Fig. A30. *Vespertilio murinus*



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Fig. 31. Spatial distribution of bat occurrence records in Georgia from 1835 to 2025

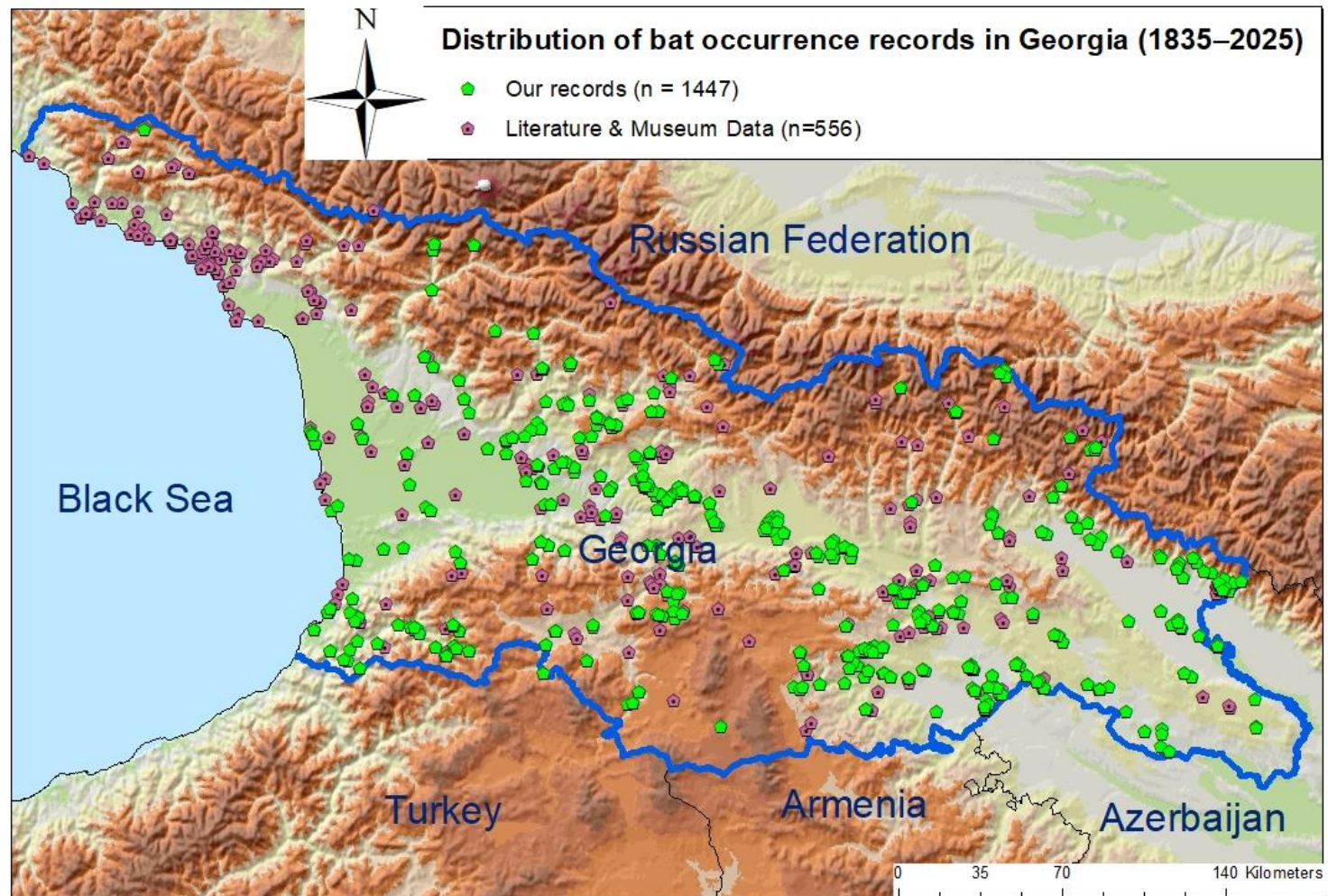


Fig. 32. Most important Underground roosts

