DEMOCRATIC AND POPULAR ALGERIAN REPUBLIC الجمهوريـــة الجزائريـــة الديمقراطيـــة الشعبيـــة
MINISTRY OF HIGHER EDUCATION AND SCIENTIFIC RESEARCH وزارة التعليم العالي والبحث العلمي
CHADLI BENDJEDID EL TARF UNIVERSITY
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DEPARTMENT OF AGRONOMY قسم العلوم الفلاحية

THÈSE

Laboratoire de recherche
Agriculture et fonctionnement des écosystèmes

Présentée pour l'obtention du diplôme de :

DOCTORAT LMD

Filière : Sciences Agronomiques

Spécialité : Protection des forêts

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Thème

Caractérisation du peuplement de fauvettes dans différents habitats du Nord-est algérien

Soutenue publiquement le **22 Avril 2026** devant le jury composé de :

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Année universitaire : 2025/2026

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Laboratoire de recherche
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THESIS

Presented for the degree of :

DOCTORATE LMD

Discipline : Agronomic Sciences

Speciality : Forest Protection

By :

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Title

Characterisation of Sylviid Warbler Communities In Different Habitats of Northeastern Algeria

Publicly defended on : **22 April 2026** before the jury composed of :

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Abstract

Transformations induced by global changes, whether climatic modifications, anthropogenic pressures, or land-use changes, are profoundly altering the structure, composition, and distribution of Mediterranean habitats, with direct consequences for the distribution and dynamics of bird populations. On the southern side of the Mediterranean basin, knowledge remains limited, particularly regarding the precise identification of environmental factors structuring seasonal distribution and the joint integration of macro- and micro-habitat scales. This thesis aims to provide useful insights to guide the management and restoration of Mediterranean habitats in Algeria. To achieve this objective, this thesis first applied species distribution modelling (SDM) at the macro-habitat scale to all Mediterranean warblers occurring in Algeria, in order to identify the major environmental determinants of their distribution during the breeding and wintering seasons. This step was complemented by an analysis of ecological niche overlap among species, allowing the characterisation of their ecological similarities and differences. An SDM was then conducted for *Curruca sarda*, a Mediterranean endemic species, to locate and characterise its favourable wintering habitats in North Africa. Finally, for *Curruca deserticola*, a North African endemic species, the study combined a macro-habitat SDM with a micro-habitat analysis based on field surveys, providing an understanding of its ecological requirements across spatial scales. At the macro-habitat scale, seasonal SDMs integrating climatic, enhanced vegetation index, and land-use predictors showed that during the breeding season *C. melanocephala* exhibited a wide distribution across northern Algeria, whereas *C. deserti*, restricted to the southeastern steppes. The other species are mainly concentrated in the northern part of the country. In winter, *C. melanocephala* retains a widespread distribution, *C. deserticola* and *C. conspicillata* cluster in interior mountainous areas. Niche overlap analysis reveals a high similarity between *C. hortensis* and *C. iberiae*; as well as between *C. communis* and *C. melanocephala*, whereas low overlap is observed between *C. deserti* and *C. undata*, and between *C. deserticola* and *C. undata*. For Marmora's Warbler (*C. sarda*), a Mediterranean endemic wintering in Algeria, suitability maps identify two main core areas: Algeria (≈ 44 062 km²) and Tunisia (≈ 4 464 km²), characterised by favourable temperatures ranging between 11 and 13 °C, altitudes from approximately 1 024 to 1 300 m, and precipitation seasonality between 32 and 41%. For Tristram's Warbler (*C. deserticola*), a North African endemic species, SDMs identified maximum suitability in the northeastern Algerian and northwestern Tunisian mountain ranges, characterised by an average elevation of around 1 250 m, an intermediate vegetation index (EVI, 0.15–0.20), and moderate annual temperatures (12–15 °C). At the micro-habitat scale of *C. deserticola*, GLMs indicated a preference for structured shrublands (shrubs 2–4 m tall), steeper slopes, and an abundance of small-diameter trees. Overall, this work provides seasonal suitability maps, identifies habitat cores, and specifies the associated environmental conditions.

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Keywords: Algeria, Sylviidae, SDM, macro-habitat, micro-habitat, ecological niche.

Résumé

Les transformations induites par les changements globaux, qu'il s'agisse de modifications climatiques, de pressions anthropiques ou de changements d'occupation des sols, modifient profondément la structure, la composition et la répartition des habitats méditerranéens, avec des conséquences directes sur la distribution et la dynamique des populations d'oiseaux. Sur la rive sud du bassin méditerranéen, les connaissances restent limitées, notamment concernant l'identification précise des facteurs environnementaux structurant la répartition saisonnière et l'intégration conjointe des échelles macro- et micro-habitat. Cette thèse vise à fournir des éléments utiles pour orienter la gestion et la restauration des habitats méditerranéens en Algérie. Pour atteindre cet objectif, cette thèse a d'abord appliqué la modélisation de la distribution des espèces (SDM) à l'échelle du macrohabitat pour l'ensemble des fauvettes méditerranéennes présentes en Algérie, afin d'identifier les principaux déterminants environnementaux de leur distribution durant les saisons de reproduction et d'hivernage. Cette étape a été complétée par une analyse du chevauchement des niches écologiques entre espèces, permettant de caractériser leurs similarités et différences écologiques. Une SDM a ensuite été réalisée pour *Curruca sarda*, espèce endémique méditerranéenne, afin de localiser et de caractériser ses habitats favorables d'hivernage en Afrique du Nord. Enfin, pour *Curruca deserticola*, espèce endémique nord-africaine, l'étude a combiné une modélisation à l'échelle du macrohabitat avec une analyse du microhabitat issue de relevés de terrain, offrant ainsi une compréhension de ses exigences écologiques à travers différentes échelles spatiales. À l'échelle du macrohabitat, les SDM saisonniers intégrant des prédicteurs climatiques, d'indice de végétation, et d'occupation du sol ont montré que, durant la saison de reproduction, *C. melanocephala* présente une large distribution dans le nord de l'Algérie, tandis que *C. deserti* se limite aux steppes du sud-est. Les autres espèces se concentrent principalement dans la partie nord du pays. En hiver, *C. melanocephala* conserve une distribution étendue, alors que *C. deserticola* et *C. conspicillata* se regroupent dans les zones montagneuses de l'intérieur. L'analyse de chevauchement de niche révèle une similarité élevée entre *C. hortensis* et *C. iberiae*, ainsi qu'entre *C.* communis et C. *melanocephala* et un faible chevauchement entre *C. deserti* et *C. undata*, ainsi qu'entre *C. deserticola* et *C. undata*. Pour la Fauvette sarde (*C. sarda*), endémique méditerranéenne hivernant en Algérie, les cartes d'adéquation identifient deux noyaux principaux : l'Algérie (≈ 44 062 km^2) et la Tunisie (≈ 4 464 km^2), caractérisés par des températures favorables comprises entre 11 et 13 °C, des altitudes allant d'environ 1 024 à 1 300 m et une saisonnalité des précipitations comprise entre 32 et 41 %. Pour la Fauvette de l'Atlas (*C. deserticola*), endémique nord-africaine, les SDM situent l'adéquation maximale dans les massifs du nord-est algérien et du nord-ouest tunisien, définie par une altitude moyenne d'environ 1 250 m, un indice de végétation (EVI) intermédiaire (0,15–0,20) et des températures annuelles modérées (12–15 °C). À l'échelle micro-habitat de la Fauvette de l'Atlas, les GLM indiquent une préférence pour des fourrés structurés (arbustes de 2–4 m), des pentes marquées et une abondance d'arbres de petit diamètre. Dans l'ensemble, ce travail fournit des cartes d'adéquation saisonnière, identifie des noyaux d'habitat et précise les conditions environnementales associées.

Mots-clés : Algérie, Sylviidae, SDM, macro-habitat, micro-habitat, niche écologique.

ملخص

إن التحولات الناجمة عن التغيرات العالمية، سواء أكانت مرتبطة بالتغيرات المناخية أو الضغوطات البشرية أو تغير أنماط استخدام الأراضي، تؤثر بعمق على بنية وتكوين وتوزيع المواطن الطبيعية في منطقة حوض البحر الأبيض المتوسط،، مما يترتب عنه انعكاسات مباشرة على توزيع الطيور وحركية جماعاتها. وعلى الضفة الجنوبية لحوض البحر الأبيض المتوسط ، لا تزال المعارف محدودة، خاصة فيما يتعلق بالتحديد الدقيق للعوامل البيئية التي تتحكم في التوزيع الموسمي، وبالدمج المشترك بين الموئل واسع النطاق والموئل الدقيق. تهدف هذه الأطروحة إلى تقديم عناصر علمية مفيدة لتوجيه إدارة الموائل المتوسطية في الجزائر. و لتحقيق هذا الهدف، اعتمدت هذه الأطروحة أولاً على نمذجة توزيع الأنواع (SDM) على مقياس الموئل واسع النطاق لجميع أنواع الدخلات المتوسطية المتواجدة في الجزائر، بهدف تحديد المحددات البيئية الرئيسة التي تتحكم في توزيعها خلال موسمي التكاثر والشتاء. وقد استُكملت هذه المرحلة بتحليل درجة تداخل المجالات البيئية بين الأنواع، مما سمح بتوصيف أوجه التشابه والاختلاف في متطلباتها الإيكولوجية. بعد ذلك، أُنجزت نمذجة خاصة بدخلة مرمرة (*Curruca sarda*)، وهي نوع متوسطي متوطن، من أجل تحديد مواقع وأوصاف مواطنها الشتوية الملائمة في شمال إفريقيا. وأخيراً، تناولت الدراسة دخلة الأطلس (*Curruca deserticola*)، المتوطنة في شمال إفريقيا، عبر الجمع بين النمذجة على مقياس الموئل واسع النطاق والتحليل التفصيلي للموئل الدقيق بالاعتماد على البيانات الميدانية، مما أتاح فهماً أدق لمتطلباتها البيئية عبر مقاييس مكانية مختلفة. على مقياس الموئل واسع النطاق، أظهرت النماذج الموسمية المدمجة بمتغيرات مناخية، ومؤشر الغطاء النباتي (EVI)، واستعمالات الأراضي(LULC) أن *C. melanocephala* تتميز بانتشار واسع خلال فترة التكاثر في شمال الجزائر، بينما تقتصر *C. deserti* على السهوب جنوب شرق البلاد. أما الأنواع الأخرى فتتركز أساساً في الشمال. وفي فصل الشتاء، تحتفظ *C. melanocephala* بانتشار واسع، في حين تتجمع كل من *C. deserticola* و*C. conspicillata* في المناطق الجبلية الداخلية. وقد أبرز تحليل تداخل المجالات البيئية تشابهاً كبيراً بين بعض الأزواج *C. iberiae–C. hortensis* و *C. melanocephala–communis*، في مقابل تداخل ضعيف بين أزواج أخرى *C. undata–C. deserti*، *C. undata–deserticola* . بالنسبة لدخلة مرمرة (*C. sarda*) ، المتوطنة في البحر الأبيض المتوسط والشتوية في الجزائر، حددت خرائط الملاءمة نواتين رئيسيتين: الجزائر (≈ 44062 كم^2) وتونس (≈ 4464 كم^2)، تتصف بدرجات حرارة مناسبة بين 11 و 13 °م، وارتفاعات تتراوح بين 1024 و1300 م، وتباين مطري موسمي بين 32 و41%. أما دخلة الأطلس (*C. deserticola*)، المتوطنة في شمال إفريقيا، فقد أظهرت النماذج أن ملاءمتها القصوى تتمثل في مرتفعات الشمال الشرقي الجزائري والشمال الغربي التونسي، حيث يسود ارتفاع متوسط يقارب 1250 م، ومؤشر غطاء نباتي وسيط (0,15–0,20)، ودرجات حرارة سنوية معتدلة (12–15 °م). وعلى مقياس الموئل الدقيق، أبرزت النماذج الخطية العامة (GLM) تفضيلاً للشجيرات الكثيفة (2–4 م)، والانحدارات البارزة، وكثرة الأشجار ذات الأقطار الصغيرة. بصفة عامة، وفر هذا العمل خرائط ملاءمة موسمية، وحدّد نوى موئلية، وبيّن الظروف البيئية المرتبطة بها.

الكلمات المفتاحية: الجزائر، الهوازج (الدخل) ، نمذجة توزيع الأنواع (SDM)، الموئل واسع النطاق، الموئل الدقيق ، المجال البيئي.

Acknowledgments

I would like to begin by expressing my gratitude to Allah for granting me the faith, strength, and perseverance required to complete this thesis.

I extend my sincere thanks to my thesis supervisor, Dr. Mohcen MENAA from University of Cherif Messaadia of Souk Ahras for his guidance, insightful advice, and the trust he placed in me throughout this work.

My sincere thanks also go to my co-supervisor, Prof. Salah TELAILIA, for his valuable assistance, availability, and scientific support. I am deeply grateful to him for the kind attention he devoted to the progress of my research.

My sincere thanks go to Prof. Rachid ROUAG for the honour of chairing the examination board of my thesis. I also would like to express my gratitude to Prof. Mohamed Cherif MAAZI, Prof. Ali ELAFRI, and Dr. Raouf BOULAHBEL for kindly accepting to serve as members of this jury and for their thoughtful evaluation of my work.

I would also like to express my warmest thanks to Prof. Lamia BOUTABIA, for her encouragement and kind advice, as well as to Dr. Abdallah AOUADI and Kamel MEDERBAL for their valuable help with the statistical analyses.

Finally, I dedicate a special thought to my parents, for their encouragement, and to my husband, Omar, for his patience and support throughout this journey.

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GENERAL INTRODUCTION

General introduction

1. The Mediterranean Basin: a global biodiversity hotspot under strong pressures

The Mediterranean Basin is one of the 36 global biodiversity hotspots, encompassing areas that are both biologically rich and highly threatened. It covers more than 2 million km², from Portugal to Jordan and from Italy to Cape Verde, and ranks third worldwide in plant diversity (CEPF, 2019) (Figure 1). Hotspots are defined as regions that are exceptionally species-rich, ecologically unique, and often harbour a high number of narrowly distributed species (IPCC, 2022).

Figure 1. Boundaries of the Mediterranean Basin biodiversity hotspot (CEPF, 2017**)**

This diversity results from a mosaic of ecosystems shaped by millennia of interactions between humans and nature (Thirgood, 1981; Blondel & Aronson, 1995; Aurelle *et al.*, 2022). However, long-term human activities such as deforestation, overgrazing, and agriculture has profoundly transformed Mediterranean landscapes (Barbero *et al.*, 1990; Brooks *et al.*, 2002). Coastal urbanisation, pollution, recurrent fires, and the introduction of invasive alien species continue to alter biotic communities (Sala *et al.*, 2000).

In addition to these pressures, the region is experiencing marked climate warming, with rising temperatures and decreasing precipitation more pronounced than the global average, making it a climatic “hotspot” (Giorgi, 2006; Giorgi & Lionello, 2008). Although some species are adapted to natural disturbances such as fire (Pausas *et al.*, 2008), the intensity and rapidity of current climate change may exceed their adaptive capacities (Aurelle *et al.*, 2022).

2. Mediterranean ecosystems and Algerian forests

Mediterranean ecosystems are characterised by exceptional floristic diversity, estimated at 25 000 plant species, nearly 60% of which are endemic (Thompson, 2020), with concentrations in mountainous and insular areas (Guardiola & Sáez, 2023). Mediterranean forests cover about 25 million hectares and play a key role in hydrological regulation, carbon sequestration, and soil protection (FAO & Plan Bleu, 2018).

Algerian forests exhibit remarkable floristic and structural diversity. They are composed mainly of Aleppo pine (*Pinus halepensis*), holm oak (*Quercus rotundifolia*), zeen oak (*Quercus faginea*), and cork oak (*Quercus suber*), along with rarer species such as maritime pine (*Pinus pinaster*) and Barbary thuya (*Tetraclinis articulata*) (Haichour & Benabdeli, 2022). These forests are often characterised by discontinuous and degraded structures, with stands that are generally open, heterogeneous in age and height, combining trees with low maquis formations (Louni, 1994).

Forest area has experienced a historical decline (Haichour & Benabdeli, 2022) and today extends over approximately 4.1 million hectares, located mainly in the mountainous regions of the north. This includes 1.42 million hectares of forests, 2.41 million hectares of maquis, and 280 000 hectares of young plantations, representing only 1.76% of the national territory, an estimate confirmed by the official inventory of the General Directorate of Forests (DGF) in 2018 (United Nations, 2023). This geographical concentration increases their vulnerability to desertification, due to particularly strong anthropogenic and climatic pressures in the region (Meddour-Sahar & Bouisset, 2013), making the implementation of integrated strategies for conservation and sustainable management indispensable (MedECC, 2020; Hidalgo-Triana *et al.*, 2023).

3. Mediterranean birds: bioindicators, pressures, and spatial responses

Birds, due to their ecological sensitivity, wide distribution, and ease of detection, play a fundamental role as bioindicators of environmental and climatic changes. They respond rapidly to habitat modifications, so that their abundance or disappearance constitutes an early indicator of the condition and dynamics of natural environments (Mekonen, 2017; Fraixedas *et al.*, 2020; Aghababyan, 2024). They also provide key ecosystem services such as seed dispersal, biological control, and, for some species, pollination (Şekercioğlu *et al.*, 2004; Wenny *et al.*, 2011).

The Mediterranean avifauna comprises 534 species, 63 of which are endemic (CEPF, 2017). It can be grouped into three main assemblages: (1) northern or boreal species associated with forests, freshwater marshes, and rivers of the western Eurasian zone; (2) steppe species occupying the arid margins of the Mediterranean area; and (3) shrubland-dependent species, such as partridges (*Alectoris*) and warblers (Blondel *et al.*, 2010). Many migratory species cross the Mediterranean Basin to reach Africa from Europe, using major flyways such as the Bosphorus, the Rift Valley, Gibraltar, Sicily, the Balearic Islands, Corsica, Crete, Sardinia, and Cyprus (CEPF, 2017).

Nevertheless, this biodiversity faces multiple threats (Kannan & James, 2009), including climate warming, characterised by rising mean temperatures leading to range shifts and abundance declines, as well as land-use changes, which affect bird distribution at the global scale (Sanderson *et al.*, 2006; Simberloff, 2012). In the Mediterranean, these pressures are exacerbated by forest habitat fragmentation, hunting, and collisions with infrastructures (power lines, wind turbines) (Brotons *et al.*, 2004; Sirami *et al.*, 2008; BirdLife International, 2017).

Several species illustrate these impacts, such as the Bonelli's Eagle (*Aquila fasciata*), which is declining in southern Europe and North Africa due to the loss of nesting sites and collisions (Real *et al.*, 2001; Hernández-Matías *et al.*, 2015), or the Algerian Nuthatch (*Sitta ledanti*), endemic to Algeria and restricted to a few relict humid forests, threatened by fires, illegal logging, and habitat degradation, and listed as "Endangered" by the IUCN (2020) (Zemouri *et al.*, 2023). Fragmentation, often linked to urbanisation and fires, reduces bird diversity in holm oak woodlands (Sirami *et al.*, 2008). In Spain, in arid areas, only oak fragments larger than 100 ha still host strictly forest assemblages (Santos *et al.*, 2002). Losses of connectivity have also been observed in certain regions, such as the Guadalquivir Valley (Spain) and Apulia (Italy), although the restoration of ecological corridors can mitigate these effects (Hidalgo *et al.*, 2021).

Furthermore, climate warming is expected to alter ranges in the coming decades and drive shifts toward higher latitudes or elevations (Huntley *et al.*, 2008; Barbet-Massin & Jetz, 2015), with an increased risk for species with narrow climatic niches (Thuiller *et al.*, 2005; Slatyer *et al.*, 2013).

4. Habitat selection and multi-scale factors

Habitat selection by birds is considered a hierarchical and multi-scale process, following the theoretical framework of Johnson (1980), ranging from the choice of the distribution range to the fine-scale selection of localised resources. McGarigal *et al.* (2016) emphasise that organisms assess their environment at multiple spatial and temporal scales.

At broad scales, selection is influenced by landscape composition and configuration, habitat availability, the presence of ecotones, as well as climatic and topographic variables (Anderle *et al.*, 2022). For example, Lathouwers *et al.* (2023) showed that in the European Nightjar (*Caprimulgus europaeus*), landscape diversity determines broad-scale selection, whereas at a more local level, parameters such as the extent of grassland or shrubland become decisive. At these finer scales, Silveira (2025) highlights that birds respond not only to the proportion of vegetation, but also to heterogeneity in canopy height and density, which can provide both refuge areas and foraging sites.

Finally, several factors may interact simultaneously, and their combined influence, whether related to landscape configuration, climate, or habitat structure, can complicate the interpretation of habitat preferences (De Chazal & Rounsevell, 2009; Brambilla *et al.*, 2020).

5. Citizen science and species distribution modelling

The growing availability of large-scale data from citizen science, which engages volunteers alongside researchers in collecting ecological information, is profoundly transforming approaches in ecology and conservation (Mesaglio & Callaghan, 2021; Binley *et al.*, 2024). Platforms such as eBird (Cornell Lab of Ornithology), iNaturalist, and the Global Biodiversity Information Facility (GBIF) illustrate this dynamic by providing hundreds of millions of species occurrence records worldwide (Uyeda *et al.*, 2020; Waller *et al.*, 2021; Fink *et al.*, 2023), enabling documentation at spatial and temporal scales that were previously difficult to access (Chandler *et al.*, 2017; McKinley *et al.*, 2017). These data now represent an essential resource for species distribution models (SDMs), which combine occurrence data with environmental variables to predict the potential distribution of species in space and sometimes over time (Beery *et al.*, 2021; Wang L. *et al.*, 2024).

These approaches are now widely used around the world to analyse and anticipate bird distributions under environmental change (Bateman *et al.*, 2016; De Carvalho *et al.*, 2017; Williams *et al.*, 2017). In Europe, Barbet-Massin *et al.* (2012b) showed that climate, land use, and dispersal could reduce and shift the breeding ranges of many species, while other studies have highlighted spatial shifts related to climate warming (Huntley *et al.*, 2008; Langham *et al.*, 2015). More recently, the integration of citizen science data has enabled the development of models accounting for the full annual cycle of migratory birds (Fink *et al.*, 2020; Stevens *et al.*, 2023).

In North Africa, these methods have been applied in Morocco to predict the presence of forest birds in northwestern Africa (Tellería *et al.*, 2021), to model the distribution and abundance of the Houbara Bustard (*Chlamydotis undulata*) (Monnier-Corbel *et al.*, 2023), and to model the suitable range of the Barbary Partridge (*Alectoris barbara*) (El Fallah *et al.*, 2025). In Algeria, published applications remain limited, as illustrated by the study of Badis *et al.* (2024), which modelled the distribution of Levaillant's Woodpecker, using ecological niche models.

In this context, warblers of the Sylviidae family emerge as a particularly relevant group for the application of species distribution models. At the global scale, the family Sylviidae currently comprises about 32 species distributed mainly across Eurasia and Africa, with a particularly high diversity around the Mediterranean region (Gill *et al.*, 2026). These species exhibit a wide diversity of habitat preferences, a well-documented Mediterranean distribution, and marked sensitivity to landscape modifications related to vegetation structure and land use (Martin & Thibault, 1996; Voelker & Light, 2011; Moreno-Mosquera *et al.*, 2021, Moreno-Mosquera *et al.*, 2023). In Algeria, this group is represented by several species belonging mainly to the genera *Sylvia* and *Curruca*, following recent taxonomic revisions that separated many former *Sylvia* species into *Curruca* (Clements, 2021). The Algerian warbler community includes resident breeders, summer breeders, passage migrants, and wintering species, reflecting the country's position between Mediterranean, steppe, and Saharan biogeographical zones (Isenmann & Moali, 2000; Avibase, 2026). During the breeding season, this community includes species such as *Sylvia atricapilla*, *Curruca melanocephala*, *C. hortensis*, *C. iberiae*, *C. communis*, *C. conspicillata*, *C. undata*, *C. deserticola*, and *C. deserti*, while winter assemblages include resident taxa and wintering species such as *Curruca sarda*. Together, these characteristics justify the selection of Algerian warblers as a model group for investigating seasonal and spatial patterns of habitat use.

6. Objectives and structure of the thesis

This thesis aims to characterise the habitat and model the potential distribution of sylviid warblers in Algeria, considering two key phases of their annual cycle: the breeding and wintering periods, and integrating two levels of spatial analysis: macro-habitat (large-scale climatic and landscape factors) and micro-habitat (fine-scale variables measured in the field). The objective is to provide scientific knowledge applicable to the conservation and management of their habitats.

6.1. Specific objectives

- Identify the key environmental factors influencing species distribution at the macro-habitat scale, using species distribution models (SDMs) and a set of climatic, vegetation, and land-use variables.
- Model the regional potential distribution of species during the breeding and wintering periods, in order to detect suitable habitat areas and possible seasonal variations in their range.
- Assess the ecological niche overlap among co-occurring species and analyse degrees of similarity or differentiation, using recognised metrics (e.g., Schoener’s D index).
- To analyse local micro-habitat preferences of *Curruca deserticola* and identify microstructural predictors of presence.

6.2. Thesis organisation

This thesis, written in the form of articles, is structured into six parts that gradually lead the reader from the general context to the recommendations. The general introduction presents the scientific, ecological, and geographical framework of the study, outlines the methodological approach, and states the objectives. The chapter on general methodology describes the study area, the climatic, environmental, and biological data used, as well as the analytical methods at the macro- and micro-habitat scales, including modelling approaches and ecological niche analyses.

Chapter (II) analyses the potential distribution, the determining environmental factors, and niche overlap of Mediterranean warblers. Chapter (III) focuses on *Curruca sarda*, a migratory species wintering in North Africa, detailing its distribution and ecological preferences. Chapter (IV) addresses *Curruca deserticola*, an endemic species, characterising its macro- and micro-habitats. Each chapter includes the methodology employed and its own discussion of the results.

Following these three chapters, the general discussion places the results in a broader perspective, highlights the limitations of the adopted methodology, and identifies implications for habitat conservation and management. Finally, the general conclusion synthesises the major contributions of the work, provides conservation recommendations, and opens perspectives for future research.

This thesis is based on the following papers, which are included as corresponding chapters in the manuscript:

- Habitat suitability and niche overlap of Mediterranean warblers in Algeria
- Predicting suitable winter habitats of Marmora’s Warbler (*Curruca sarda)* in North Africa using species distribution models
- Breeding habitat suitability of the endemic Tristram's warbler *Curruca deserticola* in North Africa: a Micro- and Macro-scale approach

CHAPTER I

GENERAL METHODOLOGY

Chapter I
General methodology

This section presents the overall methodological approach adopted in this thesis. Specific details for each study (study sites, number of occurrence points, environmental variables used, etc.) are provided in the “Materials and Methods” section of the corresponding chapters to avoid redundancy.

1. Study area and geographical context

The primary geographical focus of this thesis is Algeria. However, some analyses published as part of this work also incorporate data from Tunisia. This geographical extension places the populations within a broader regional context, where habitats and climate are continuous across borders (Blondel *et al.*, 2010). Both countries are characterised by a Mediterranean climate, with hot, dry summers and mild, wet winters, and support typical forest ecosystems such as cork oak (*Quercus suber*), Aleppo pine (*Pinus halepensis*), and Atlas cedar (*Cedrus atlantica*) (Pswarayi-Riddihough, 2002).

2. Occurrence data and field survey

The occurrence data used in this study were retrieved from recognised databases, including GBIF (Global Biodiversity Information Facility), a global infrastructure established to enable the digital collection and dissemination of natural history specimen data (Lane & Edwards, 2007), as well as iNaturalist, an international social network–type platform (Matheson, 2014), and eBird, a platform that hosts an online community of bird observers (Sullivan *et al.*, 2009).

In addition, field surveys were conducted in regions of northeastern Algeria within the framework of Chapters III and IV. A protocol combining visual and auditory observations was applied at point counts spaced more than 200 m apart (Ralph *et al.*, 1995). Vegetation surveys were also carried out in plots around each point, and the GPS coordinates of all points were recorded.

3. Environmental variables

3.1. Macro-habitat scale

Nineteen bioclimatic variables for the 1970–2000 baseline, along with elevation data at 30 arc-seconds (~1 km), were obtained from WorldClim 2.1 (see: https://www.worldclim.org). These climatic normals are widely used in ecological modelling and GIS analyses, such as mapping the distribution of species and ecosystems, or assessing climate change impacts (Fick & Hijmans, 2017). Despite their temporal gap with some recent occurrence records, their use remains standard practice, cited in nearly one-third of SDM studies between 2013 and 2017 (Jarnevich & Young, 2019). More detailed information about the 19 variables is presented in table 1.

Table 1. WorldClim bioclimatic variables (BIO): description and measurement units

Source	Code	English name	Description	Spatial resolution	Unit
WorldClim	BIO1	Annual Mean Temperature	Mean annual temperature	30 arc-seconds (~1 km)	°C
	BIO2	Mean Diurnal Range	Mean of monthly (Tmax – Tmin)		°C
	BIO3	Isothermality	(BIO2 / BIO7) × 100		%
	BIO4	Temperature Seasonality	Standard deviation of temperature × 100		%
	BIO5	Max Temperature of Warmest Month	Monthly maximum value		°C
	BIO6	Min Temperature of Coldest Month	Monthly minimum value		°C
	BIO7	Temperature Annual Range	BIO5 – BIO6		°C
	BIO8	Mean Temperature of Wettest Quarter	Mean of the three wettest months		°C
	BIO9	Mean Temperature of Driest Quarter	Mean of the three driest months		°C
	BIO10	Mean Temperature of Warmest Quarter	Mean of the three warmest months		°C
	BIO11	Mean Temperature of Coldest Quarter	Mean of the three coldest months		°C
	BIO12	Annual Precipitation	Annual sum of precipitation		mm
	BIO13	Precipitation of Wettest Month	Monthly maximum value		mm
	BIO14	Precipitation of Driest Month	Monthly minimum value		mm
	BIO15	Precipitation Seasonality	coefficient of variation		%
	BIO16	Precipitation of	Sum of the three		mm

	Wettest Quarter	wettest months		
BIO17	Precipitation of Driest Quarter	Sum of the three driest months		mm
BIO18	Precipitation of Warmest Quarter	Sum of the three warmest months		mm
BIO19	Precipitation of Coldest Quarter	Sum of the three coldest months		mm

In addition, the Enhanced Vegetation Index (EVI), derived from the MODIS MOD09GA product for the period 2000–2023, as well as land-use/land-cover (LULC) data from the MODIS MCD12Q1 (Version 6.1) product for the period 2001–2024, based on the LC_Type4 classification, were extracted via Google Earth Engine. We used EVI and LULC following common practice in SDM studies that combine climatic, vegetation, and land-cover predictors (Wang L. *et al.*, 2024; Oliveira *et al.*, 2025). More detailed information on these variables is presented in Tables 2.

Table 2. Description of elevation, enhanced vegetation index, and land-use/land-cover variables used in this study

Sources	**Variable**	**Description**	**Spatial resolution**	**Unit**
Worldclim data	Elevation	The site's altitude above sea level	30 arc-seconds (~1km)	Metres (m)
MODIS MOD09GA	Enhanced Vegetation Index (EVI)	A vegetation index reflecting plant productivity and greenness	30 metres	Numeric value (0-1)
MODIS Land Cover Type (MCD12Q1)	Land Use and Land Cover (LULC)	0: Water Bodies - Area covered by permanent water (≥60%)	500 metres	Numeric values
		1: Evergreen Needleleaf - Dominated by evergreen conifers (>1m)		
		2: Evergreen Broadleaf - Dominated by evergreen broadleaf trees (>1m)		
		3: Deciduous Needleleaf - Dominated by deciduous needleleaf trees (>1m)		
		4: Deciduous Broadleaf - Dominated by deciduous broadleaf trees (>1m)		
		5: Annual Broadleaf - Herbaceous annuals, mainly broadleaf crops		
		6: Annual Grass - Herbaceous annuals, including cereal crops		
		7: Non-Vegetated - ≥60% barren land or permanent snow/ice		
		8: Urban - ≥30% impervious surfaces (buildings, asphalt)		

3.2. Micro-habitat scale

For the micro-habitat analysis, 29 environmental variables related to forest structure and vegetation were measured within circular plots of 18 m radius (Rondeux & Lecomte, 2005). In addition to these field measurements, two topographic variables, slope and aspect, were derived from the SRTM Digital Elevation Model (30 m resolution) downloaded from the USGS Earth Explorer platform.

To account for the circular nature of the aspect variable (where 0° and 360° both correspond to north), it was transformed into a linear variable using the following formula:

$$\text{linear aspect} = \cos[\pi \times (\text{aspect} - 30) / 180]$$

This transformation yields a variable ranging from –1 (representing the warmest slopes facing south-southwest) to +1 (the coldest slopes facing north-northeast) (Kane *et al.*, 2014).

The measured variables were as follows:

- Altitude (m)
- Mean trunk circumference (cm)
- Mean trunk diameter (cm)
- Diameter of the largest tree (dmax) > 40 cm
- Number of large trees (circumference > 150 cm)
- Number of medium trees (90–149 cm circumference)
- Number of small trees (40–89 cm circumference)
- Volume of deadwood (m^3)
- Maximum stand height (m)
- Mean stand height (m)
- Mean crown (canopy) height (m)
- Minimum crown (canopy) height (m)
- Canopy width (m)
- Tree cover 4–8 m (%)
- Tree cover 8–32 m (%)
- Shrub layer height (m)
- Shrub cover 0.5–2 m (%)
- Shrub cover 2–4 m (%)
- Shrub layer composition
- Herbaceous layer height (cm)
- Herb cover 0–12.5 cm (%)
- Herb cover 12.5–50 cm (%)
- Herbaceous layer composition

- Total vegetation cover (%)
- Forest development stage
- Percentage of Aleppo pine (%)
- Percentage of Holm oak (%)
- Presence of dead branches
- Stand health status

4. Data analysis

4.1. Occurrence and absence data processing

Occurrence data used in this thesis came from field surveys and open-access databases (GBIF, iNaturalist, and eBird). All geographic coordinates were checked, and records outside the study area or over water were removed. Temporal filters were applied to keep only data corresponding to the relevant biological season (breeding or wintering). To reduce spatial autocorrelation and sampling bias, occurrence points were filtered by keeping only one record within each 1 km grid cell (Aiello-Lammens *et al.*, 2015; Cerman *et al.*, 2022; Brambilla *et al.*, 2025). This distance was chosen because it corresponds to the resolution of the environmental variables used in the models (WorldClim bioclimatic data, EVI and land cover). Using the same spatial resolution ensures that each occurrence represents a single environmental pixel and avoids redundant information within the same cell (Planillo *et al.*, 2021). Moreover, several studies on bird species have shown that a 1 km filtering distance is commonly used as a practical balance between reducing the concentration of nearby records and keeping enough occurrences for accurate modelling (Aiello-Lammens *et al.*, 2015; Lindenmayer *et al.*, 2024).

Absence data were obtained exclusively from complete eBird checklists, ensuring that non-detections represented verified absences. These checklists were selected based on standardised sampling-effort criteria, including observation type, duration, and distance (Strimas-Mackey *et al.*, 2018). This approach avoided the use of pseudo-absences, which can introduce spatial or environmental bias (Lobo *et al.*, 2010; Barbet-Massin *et al.*, 2012a). Detailed filtering parameters and R functions used for data extraction and processing are described in the corresponding research articles (Chapters II–IV).

4.2. Processing of environmental variables for modelling

Environmental predictors included bioclimatic, topographic, vegetation, and land-use layers. All variables were resampled to a spatial resolution of 1 km to ensure consistency among datasets. Before modelling, multicollinearity among predictors was assessed using pairwise correlation tests and the variance inflation factor (VIF). Highly correlated variables were excluded to retain only independent predictors for model calibration.

This standardised procedure was applied across all analyses in the thesis to ensure methodological consistency. Detailed descriptions of variables, data sources, and modelling algorithms are provided in the individual chapters.

The combined use of Pearson's correlation test and the variance inflation factor (VIF) is commonly recommended to reduce redundancy among explanatory variables in species distribution models (Guirhem *et al.*, 2021; Tong *et al.*, 2023). In this context, Pearson's correlation coefficient is widely employed as a descriptive diagnostic of linear association during variable preselection, a practice well documented across SDM studies and methodological guides (Dormann *et al.*, 2012; De Marco & Nóbrega, 2018; Feng *et al.*, 2019; Mathur *et al.*, 2023)

4.3. Species distribution modelling and habitat suitability analysis

Habitat suitability was modelled using Species Distribution Models (SDMs) in R, applying two algorithms: Random Forest (RF) and Boosted Regression Trees (BRT)**;** both recognised for their strong predictive power and robustness in ecological modelling (Cutler *et al.*, 2007; Elith *et al.*, 2008; Naimi & Araújo, 2016). Model performance was assessed using three commonly applied evaluation metrics: the Area Under the Curve (AUC), the True Skill Statistic (TSS), and Cohen's Kappa coefficient, with higher values indicating greater model accuracy (Fernandes *et al.*, 2019). An ensemble model was then generated by weighting the predictions of individual models according to their TSS scores, following the approach recommended by Naimi & Araújo (2016). The resulting habitat suitability maps show predicted probabilities of occurrence ranging from 0 to 1, with higher values corresponding to the most suitable areas (Wang F. *et al.*, 2024; Wei *et al.*, 2024). Binary maps and graphical analyses were also produced to visualise the influence of environmental variables on the species' distribution.

The importance of environmental variables was assessed using two complementary approaches. The first was based on Pearson correlation, with low correlation indicating that the variable exerts a strong influence on the predictions (Thuiller *et al.*, 2009). The second approach used the AUC metric (Naimi & Araújo, 2016). Importance percentages for each variable were calculated from these two metrics using the *getVarImp* function in the *sdm* package in R, with higher values indicating a more decisive role in species distribution (Naimi & Araújo, 2016).

In Chapter III, in addition to these approaches, an explanatory regression analysis was carried out to identify the most influential predictors of habitat suitability. A Generalised Linear Model (GLM) with a binomial link function was used, initially including all explanatory variables. A backward selection procedure guided by the Akaike Information Criterion (AIC) was then applied, iteratively removing non-significant variables until the final model with the lowest AIC value was obtained (Reineking & Schröder, 2006; Faraway, 2016).

In chapter II, some species were excluded from the wintering analysis. *Curruca deserti* was removed because of the low number of available records (five occurrence points), which was insufficient for reliable modelling (Papeş & Gaubert, 2007). *Curruca melnocephala* was also excluded due to its low predictive performance, with AUC and TSS values of 0.60 and 0.33, respectively. Following Zhang *et al.* (2015), AUC values below 0.7 and TSS values below 0.4 were considered to indicate poor model performance. In addition, certain species were not included in the analysis because they are long-distance migrants that do not overwinter in Algeria; therefore, their occurrence data do not represent actual wintering distributions within the study area.

4.4. Analysis of ecological niche overlap

The ecological niches of the species analysed in Chapter II were characterised using presence data (Broennimann *et al.*, 2012). Environmental predictors, including the 19 WorldClim bioclimatic variables (BIO1–BIO19), elevation (ELV), the Enhanced Vegetation Index (EVI), and land-use/land-cover (LULC), were subjected to a Principal Component Analysis (PCA) to reduce dimensionality and summarise the main environmental gradients. The first two principal components together explained 74.1% of the total variance (45.1% for PC1 and 29.0% for PC2), representing gradients mainly associated with temperature and seasonality (PC1) and with precipitation and elevation (PC2). Niche overlap among species was then quantified using Schoener's D index, calculated with the *ecospat* package, ranging from 0 (completely distinct niches) to 1 (identical niches), thereby measuring the degree of ecological similarity between species pairs (Rödder & Engler, 2011)

4.5. Micro-habitat analysis

Micro-habitat variables influencing the presence of *Curruca deserticola* (Chapter IV) were analysed using a binomial Generalised Linear Model (GLM) with a logit link function**.** After removing non-informative variables and controlling for collinearity (VIF < 5; correlation < 0.8), 12 predictors were retained. A stepwise variable selection procedure was applied using the *My.stepwise* package (ISC Company, 2017), and the final model was chosen based on the lowest AIC value. Model performance was assessed using the Hosmer–Lemeshow test and AUC, while predicted probabilities ≥ 0.7 were considered indicative of favourable micro-habitat conditions (Van Proosdij *et al.*, 2016).

4.6. Software used for the analyses

All data processing, variable preparation, modelling, and statistical analyses were performed in R (R Core Team, 2023), using specialised packages such as *raster, usdm, sdm, tidysdm, auk,* and *ggplot2* for visualisation.

A summary diagram of the main analytical steps conducted in each chapter is presented in the figure below.

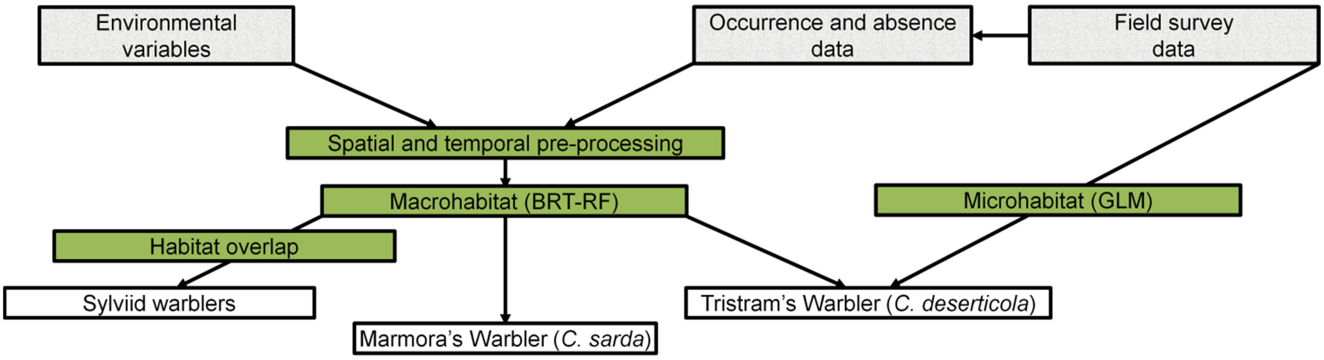

Figure 2. Summary diagram of the general methodology and analyses carried out in this thesis

CHAPTER II

HABITAT SUITABILITY AND NICHE OVERLAP OF MEDITERRANEAN WARBLERS IN ALGERIA

This manuscript has been submitted and is currently under review in the journal Bird Study
(ISSN: 0006-3657, E-ISSN: 1944-6705).

Habitat suitability and niche overlap of Mediterranean warblers in Algeria

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Abstract

The Mediterranean Basin, and particularly North Africa, is a major biogeographic crossroads for avian biodiversity due to the heterogeneity of its habitats and its role for numerous migratory species. Mediterranean warblers exhibit diverse seasonal strategies, with some species resident and others breeding or wintering in the region. This study models their distribution in Algeria using species distribution models (SDMs) that integrate climatic variables, the Enhanced Vegetation Index (EVI), and land-cover/land-use (LULC), explicitly distinguishing the breeding and wintering periods. Niche overlap among species in the breeding season was quantified using ecospat. The multi-species SDMs reveal suitability cores concentrated in northern Algeria. Niche overlap analysis (Schoener's D) highlights strong similarities for certain pairs, notably *C. hortensis – C. iberiae* (D = 0.79), and *C. communis – C. melanocephala* (D = 0.71). Conversely, very low values (≤ 0.10) indicate marked niche differentiation, as in *C. deserti – C. undata* (D = 0.00), and *C. deserticola – C. undata* (D = 0.00). These results underscore the importance of climate, vegetation productivity, and landscape structure in shaping species distributions, and provide operational foundations for spatial conservation prioritisation in Mediterranean landscapes.

Keywords: Mediterranean warblers, species distribution models, niche overlap, conservation, Algeria

1. Introduction

Sylviid warblers form a group of small insectivorous passerines widely distributed across Europe, Africa, and Asia. Their biogeographical range is primarily centred on the Mediterranean Basin, where nearly 70% of the species are found (Voelker & Light, 2011). In Europe, these birds have been extensively studied, particularly regarding their migratory phenology (Fransson, 1995; Askeyev *et al.*, 2009), breeding ecology (Mason, 1976), community structure (Cody & Walter, 1976; Martin & Thibault, 1996), competitive interactions (Papanikolas *et al.*, 2021), and the molecular aspects of their evolution (Blondel *et al.*, 1996).

The Mediterranean Basin, and particularly North Africa, represents a key region for avian biodiversity due to its habitat diversity and its role for many migratory species (Blondel & Aronson, 1999; Valavanidis & Vlachogianni, 2011). The region hosts a broad assemblage of warblers, including residents, breeding migrants, and winter visitors (Isenmann & Moali, 2000; Shirihai *et al.*, 2001). These species exploit habitats ranging from sclerophyll forests and maquis to agricultural landscapes, hedgerows, and shrublands, reflecting their high ecological flexibility (Mason, 1976; Martin & Thibault, 1996). This diversity of habitats raises the question of habitat selection and niche positioning for each species within a regional context (Soberón & Peterson, 2005).

Among North African countries, Algeria is of particular interest due to the diversity of ecosystems it encompasses (Quézel & Médail, 2003). It hosts a varied assemblage of warblers, including resident species (*Curruca deserticola*, *C. melanocephala*, *C. undata*), migratory breeders (*C. communis*, *C. iberiae*, *C. hortensis*), and winter visitors such as *C. sarda* (Isenmann & Moali, 2000).

However, despite the biogeographical importance of North Africa for Palearctic migratory birds (Moreau, 1972), the spatial and seasonal dynamics of warblers in this region remain poorly studied (Toffa *et al.*, 2022). While several studies have addressed their ecology in certain areas of the Mediterranean Basin (Martin & Thibault, 1996; Shirihai *et al.*, 2001; Laube *et al.*, 2015), their ecological niche dynamics in North Africa remain insufficiently understood.

In this context, the present study aims to address these gaps by analysing the ecological niche of warblers in Algeria through a species distribution modelling (SDM) approach, integrating climatic variables, the Enhanced Vegetation Index (EVI), and Land Use and Land Cover (LULC) data, while taking into account breeding and wintering periods. In addition, it evaluates the ecological niche overlap to better understand their patterns of spatial coexistence.

2. Materials and Methods

2.1. Study area and species distribution data

This study focused on Algeria, considering two key periods in the annual cycle of the species: the breeding season and the wintering season. For the breeding phase, nine species were selected based on their confirmed breeding status in the country, as documented by Isenmann & Moali (2000). These include *Sylvia atricapilla* (Eurasian Blackcap), *Curruca conspicillata* (Spectacled Warbler), *Curruca communis* (Common Whitethroat), *Curruca melanocephala* (Sardinian Warbler), *Curruca deserti* (Desert Warbler), *Curruca undata* (Dartford Warbler), *Curruca iberiae* (Western Subalpine Warbler), *Curruca hortensis* (Western Orphean Warbler), and *Curruca deserticola* (Tristram's Warbler).

In the wintering season, only five species were considered: C. deserticola, C. sarda, C. conspicillata, *C. undata* and *S. atricapilla*, while *C. iberiae*, *C. hortensis*, and *C. communis* were excluded from this phase because they are considered long distance migrants and do not overwinter in Algeria (Isenmann & Moali, 2000; Shirihai *et al.*, 2001).

2.2. Occurrence data processing

Presence data were collected from three databases: GBIF (Global Biodiversity Information Facility), eBird (Cornell Lab of Ornithology), and iNaturalist. These records span from the 1970s to 2025.

Geographical coordinates were checked to exclude points located at sea or outside the study area. A temporal filter was then applied to retain only occurrences corresponding to the relevant biological periods (breeding or wintering, depending on the study objective). Finally, a spatial filtering procedure was implemented using the *thin_by_dist()* function from the tidysdm package in R (Leonardi *et al.*, 2024), imposing a minimum distance of one kilometre between retained points, for both presences and absences (Veloz, 2009; Fourcade *et al.*, 2014), in order to limit spatial autocorrelation (Mammola *et al.*, 2018).

The absence data used in this study were obtained from complete checklists in the eBird database, extracted through a query targeting the study area and the species of interest. These checklists were selected based on sampling effort criteria, including an observation protocol of the "stationary" or "traveling" type, a minimum duration of 2 hours, and a maximum distance of 4 kilometres, using the *auk* package in R (Strimas-Mackey *et al.*, 2018). Filters were applied to isolate complete checklists, and the *auk_zerofill()* function was then used to generate explicit absences (zeros), converting the data into a presence–absence format.

This study does not rely on the use of pseudo absences (randomly generated points). Although this approach is widespread in the literature, it presents several limitations: the actual absence of the species is not guaranteed, and environmental or spatial biases may be introduced (Lobo *et al.*, 2010; Barbet-Massin *et al.*, 2012). To avoid these limitations, only verified absences were retained (Johnston *et al.*, 2018).

After final filtering, the number of occurrences (presences/absences) per species are as follows: in wintering, *Curruca deserticola*: 22/96, *C. conspicillata*: 31/130, *C. sarda*: 14/370, *C. undata*: 32/240, *Sylvia atricapilla*: 68/194; in breeding, *C. melanocephala*: 293/1000, *C. deserticola*: 32/188, *C. deserti*: 17/99, *C. conspicillata*: 52/281, *C. hortensis*: 39/113, *C. iberiae*: 39/106, *C. undata*: 17/92, *S. atricapilla*: 195/453, *C. communis*: 82/327.

2.3. Processing of environmental variables for modelling

Nineteen bioclimatic variables, together with altitude data at a spatial resolution of 30 arc-seconds (approximately 1 km), were retrieved from the WorldClim database (https://www.worldclim.org/data/bioclim.html). In addition, the Enhanced Vegetation Index (EVI) and Land Use and Land Cover (LULC) data, based on the LC_Type4 classification, were downloaded via Google Earth Engine.

All environmental variable rasters were resampled to a resolution of approximately 1 km using the bilinear method with the *resample()* function from the raster package in R (Hijmans *et al.*, 2013), in order to harmonise the resolution and spatial extent across all variables. To select the variables to be included in the models, correlations among the 22 initial variables were first assessed using Pearson's correlation test, followed by the variance inflation factor (VIF) calculated with the *vifstep()* function from the *usdm* package. Highly correlated variables and those with high VIF values were excluded from the analysis (Naimi *et al.*, 2014). After checking for collinearity, four variables were retained for the breeding season: annual mean temperature (BIO1), annual precipitation (BIO12), elevation (ELV), and the Enhanced Vegetation Index (EVI). For the wintering season, six variables were selected: BIO1 (Annual Mean Temperature), BIO8 (mean temperature of the wettest quarter), BIO15 (precipitation seasonality), LULC (land use and land cover), ELV, and EVI. Selection was based on a Pearson correlation threshold below 0.8 and a VIF below 10 (Kutner *et al.*, 2005; Dormann *et al.*, 2013).

2.4. Species distribution modelling and habitat suitability analysis

Habitat suitability was estimated using species distribution models (SDMs) implemented in R with the *sdm* package (Naimi & Araújo, 2016), employing two complementary algorithms: Random Forest (RF) and Boosted Regression Trees (BRT). Model performance was evaluated using three metrics: AUC, TSS, and the Kappa coefficient. AUC values range from 0 to 1, while TSS and Kappa values range from –1 to 1, with higher values indicating better predictive performance (Fernandes *et al.*, 2019). An ensemble model was then generated by averaging the predictions of the different models, weighted according to their TSS scores.

The resulting maps represent continuous habitat suitability, with values ranging from 0 to 1. Values close to 0 indicate a low probability of species presence, whereas values close to 1 indicate a high probability (Wang *et al.*, 2024; Wei *et al.*, 2024). Habitat suitability maps and response curves illustrating the effect of predictors on habitat suitability were all produced using the sdm package in R (Naimi & Araújo, 2016).

2.5. Analysis of ecological niche overlap

The ecological niche of the species was characterised using the *ecospat* package (Broennimann *et al.*, 2012), based on presence data. Environmental variables were first extracted at the geographical coordinates of the occurrences, including the 19 bioclimatic variables from WorldClim (BIO1 to BIO19), elevation (ELV), the Enhanced Vegetation Index (EVI), and land use and land cover (LULC).

A Principal Component Analysis (PCA) was then applied to the 22 environmental variables in order to reduce dimensionality while retaining the main ecological information (Jolliffe & Cadima, 2016). The first two components were retained for subsequent analyses (Broennimann *et al.*, 2012).

Ecological niche overlap was assessed for each species pair using the *ecospat.niche.overlap()* function, which calculates Schoener's D index, ranging from 0 to 1. This index can be refined according to the categories proposed by Rödder & Engler (2011), in which values between 0.6 and 0.8 indicate high overlap, and values above 0.8 indicate very high overlap.

3. Results

3.1. Model evaluation during breeding season

The species distribution models (SDMs) developed for the nine warbler species during the breeding season showed good predictive performance. The ensemble models achieved AUC values ranging from 0.84 to 0.975 and TSS values between 0.585 and 0.88. The best performances were recorded for *C. melanocephala* (AUC = 0.975; TSS = 0.88), *C. hortensis* (AUC = 0.93; TSS = 0.825), and *C. undata* (AUC = 0.915; TSS = 0.81). In contrast, relatively lower predictive scores were obtained for *C. conspicillata* and *S. atricapilla* (Table 1).

Table 1. Ensemble model performance for the nine warbler species during the breeding season

Species	**AUC**	**TSS**
Curruca melanocephala	0.975	0.880
Curruca deserticola	0.895	0.74
Curruca deserti	0.845	0.680
Curruca conspicillata	0.840	0.595
Curruca hortensis	0.930	0.825
Curruca iberiae	0.885	0.705
Curruca undata	0.915	0.810
Sylvia atricapilla	0.845	0.585
Curruca communis	0.870	0.655

3.2. Habitat suitability maps during breeding season

The SDM models generated habitat suitability maps for the nine warbler species studied. *C. melanocephala* shows the widest predicted distribution, with suitable habitats forming a broad continuous band across northern Algeria. In contrast, *C. deserti* occupies more limited suitable areas, associated with steppe zones and the northern edge of the Sahara. Two other species, *C. communis* and *S. atricapilla*, showed an intermediate distribution, with relatively continuous suitable habitats in the northeast, for example around Guelma, Jijel, and Skikda. A third group, consisting of *C. hortensis*, *C. iberiae*, and *C. undata*, displayed an affinity for areas in the northeast and central north, particularly in the Bibans and Kabylia. Finally, *C. deserticola* highlighted a concentration of favourable areas primarily in the mountainous regions of northeastern and northwestern Algeria and *C. conspicillata* was characterised by a fragmented distribution, with suitable habitats in the northeast as well as in certain regions of the central west (Figure 1).

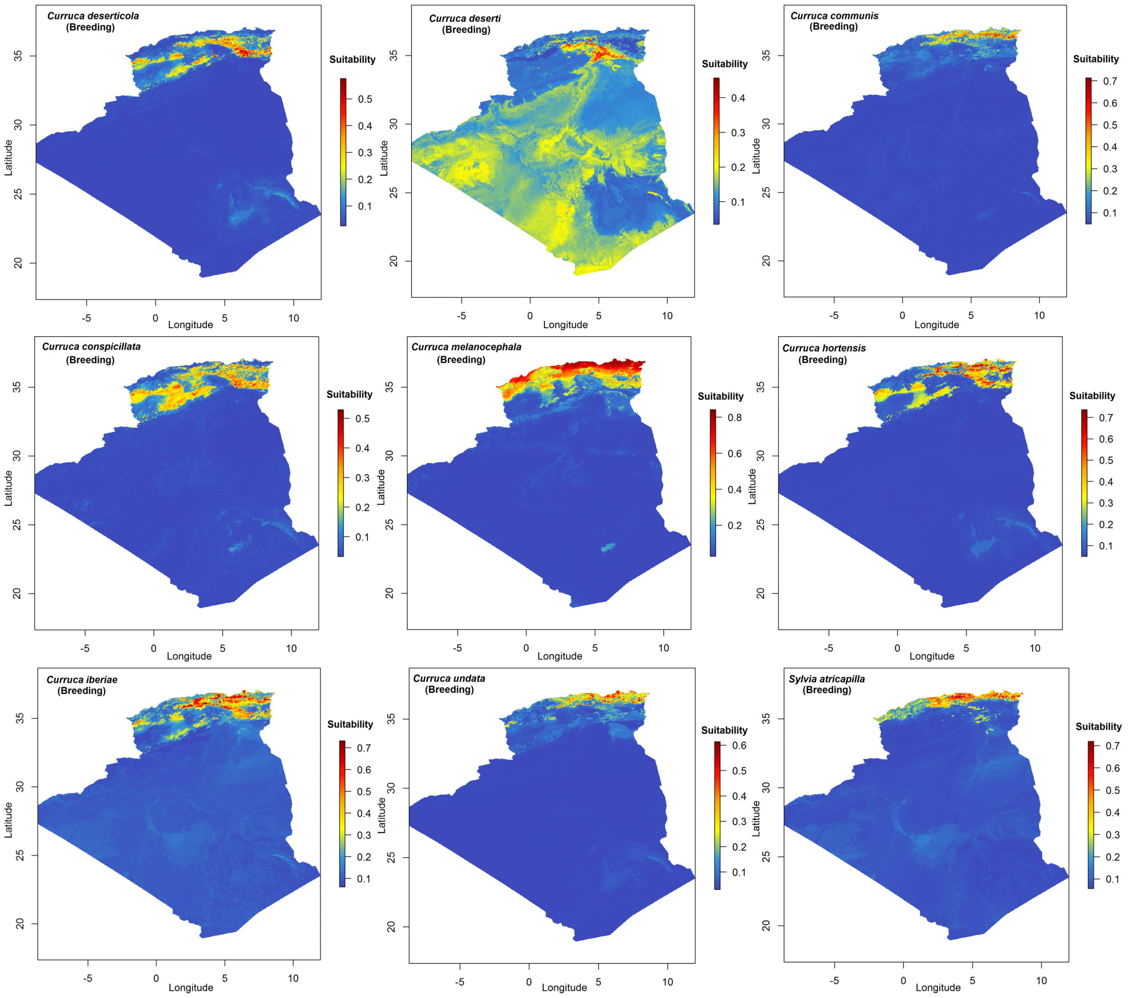

Figure 1. Habitat suitability maps of species during breeding season in Algeria

3.3. Response curves from SDMs during breeding season

The analysis of response curves highlighted the relationships between environmental variables and the distribution of warbler species. Several species showed an affinity for annual mean temperatures between 11 °C and 15 °C, including *C. conspicillata*, *C. hortensis*, *C. undata*, and *C. iberiae*. In contrast, *S. atricapilla* and *C. deserti* preferred higher temperatures, between 15 °C and 20 °C. *Curruca melanocephala* displayed a suitability peak around 17 °C, while *C. communis* reached its maximum around 15 °C (Figure 2).

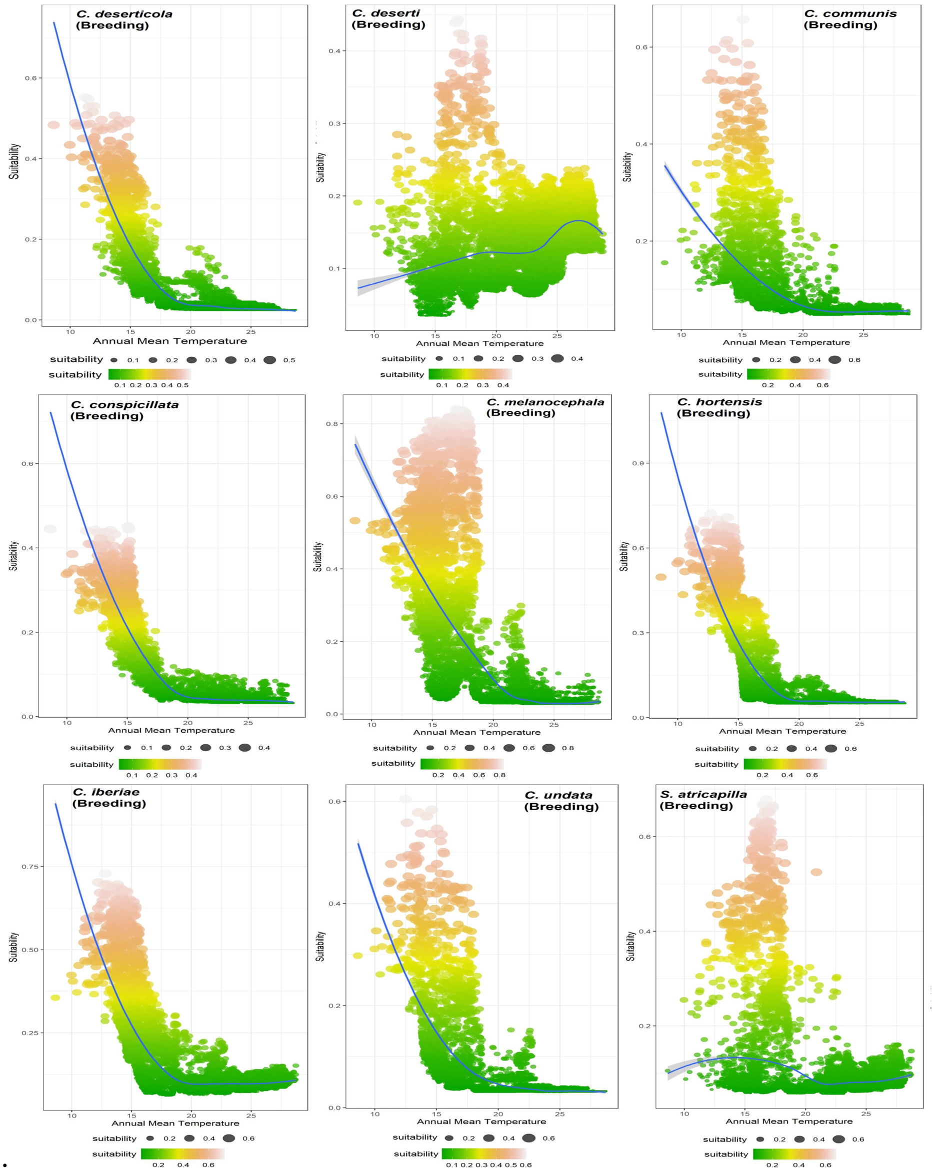

Figure 2. Response curves of species suitability with annual mean temperature during the breeding season

Regarding elevation, maximum responses were observed between 1 000 and 1 700 m for *C. deserticola, C. conspicillata, C. hortensis*, and *C. iberiae*. *Curruca communis* exhibited a marked preference between 500 and 1 000 m. Other species also displayed affinities for mid-altitudes, notably *C. undata*, between 600 and 1 250 m. Conversely, *S. atricapilla* and *C. deserti* favoured lower elevations, respectively between 250 and 750 m and between 500 and 750 m. Finally, *C. melanocephala* was also well represented in low-altitude habitats (Figure 3).

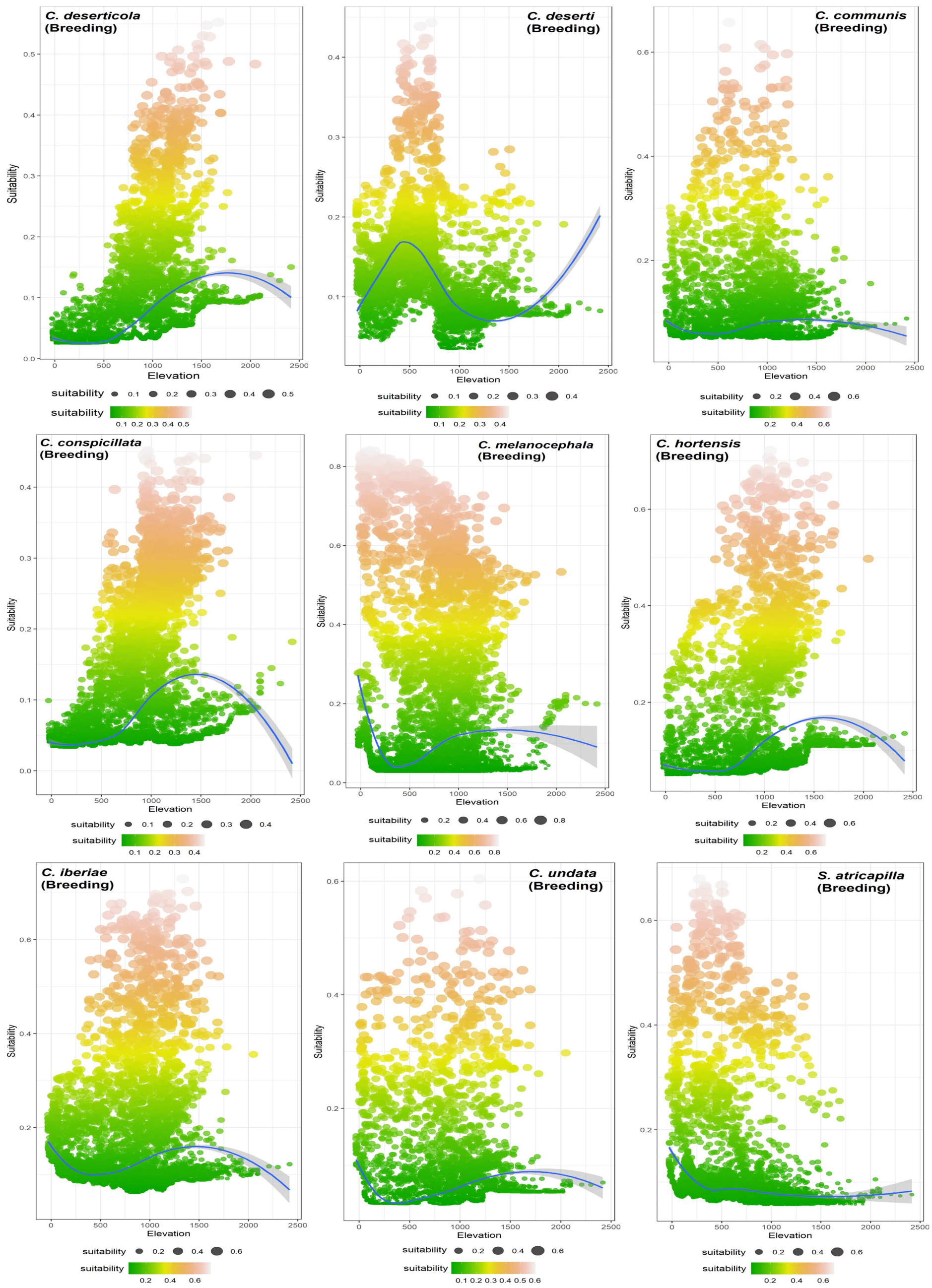

Figure 3. Response curves of species suitability with elevation during the breeding season

In terms of vegetation, represented by the EVI, the curves indicated that *C. communis*, *C. hortensis*, *C. iberiae*, *C. undata*, and *S. atricapilla* exhibited maximum suitability for values between 0.30 and 0.45. *C. conspicillata* and *C. deserticola* reached their peaks between 0.15 – 0.20. *Curruca deserti* was distinct in its preference for low values, between 0.10 and 0.15. Finally, *C. melanocephala* demonstrated a broad tolerance, with suitability gradually increasing from 0.15 to a maximum around 0.35–0.40 (Figure 4).

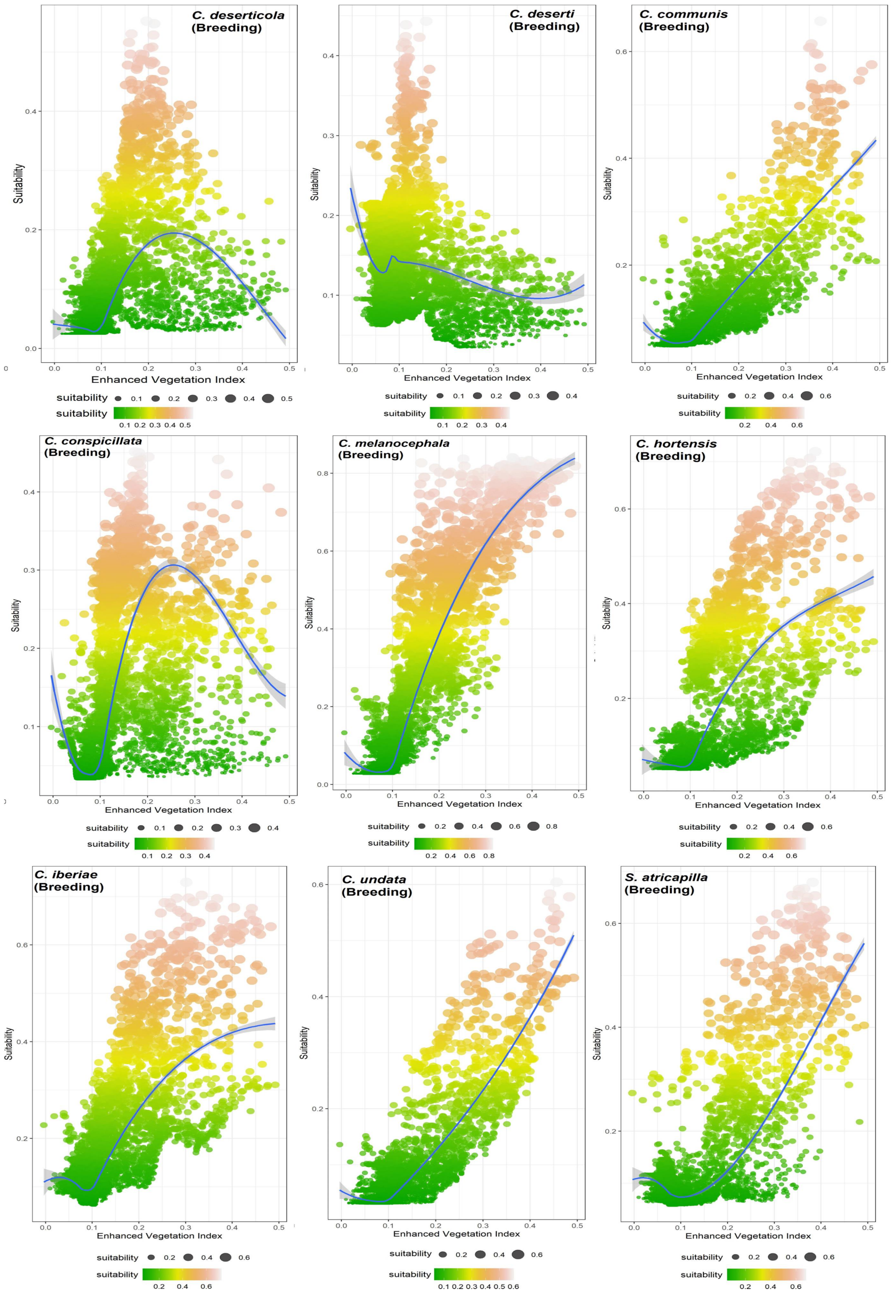

Figure 4. Response curves of species suitability with EVI during the breeding season

3.4. Model evaluation during wintering season

During the wintering season, the species distribution models generally showed good performance. The ensemble models achieved AUC values ranging from 0.88 to 0.98 and TSS scores from 0.74 to 0.94. The best predictions were obtained for *C. sarda* (AUC = 0.98; TSS = 0.945), *S. atricapilla* (AUC = 0.93; TSS = 0.78). Intermediate performances were observed for *C. deserticola* (AUC = 0.895; TSS = 0.725), *C. conspicillata* (AUC = 0.885; TSS = 0.74), and *C. undata* (AUC = 0.90; TSS = 0.745).

3.5. Habitat suitability maps during wintering season

The SDM models produced habitat suitability maps for the warbler species during the wintering season in Algeria. *C. sarda* showed a much more restricted wintering range, concentrated in the northeastern region, particularly around Batna. *C. deserticola* was characterised by suitable habitats located in the mountainous range of the east, especially in the Aurès (Batna, Khenchela), complemented by isolated patches in the southeast. *C. conspicillata* displayed an almost continuous band of suitable habitats stretching from west to east through the mountainous and inland areas of the north, while being less present along the coast. *Curruca undata* showed a preference for winter habitats in marked areas of northern Algeria, notably in the Aurès (Batna, Khenchela), as well as in a few fragmented areas in the northwest of the country. Similarly, *S. atricapilla* was mainly concentrated in the north-central and northeastern regions, with more limited areas of suitable habitat (Figure 5).

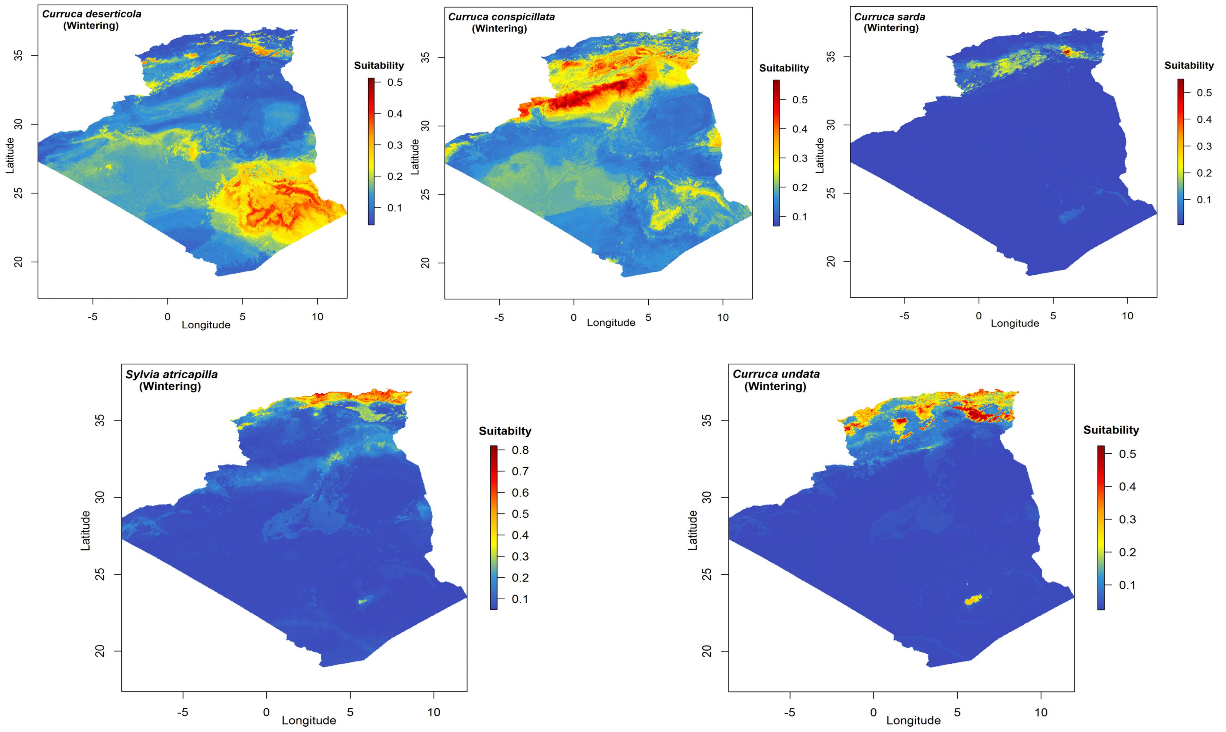

Figure 5. Habitat suitability maps of species during wintering season in Algeria

3.6. Response curves from SDMs during wintering season

The analysis of response curves during the wintering season revealed variations in the environmental preferences of warbler species. Regarding annual mean temperature, *C. sarda* showed a suitability peak around 12.5 °C, while *S. atricapilla* displayed a broader thermal range, with high suitability between 12.5 °C and 17.5 °C. *C. conspicillata* and *C. undata* exhibited maximum suitability within a range of 15 °C to 20 °C. Finally, *C. deserticola* showed a clear preference for higher temperatures, between 20 °C (Figure 6).

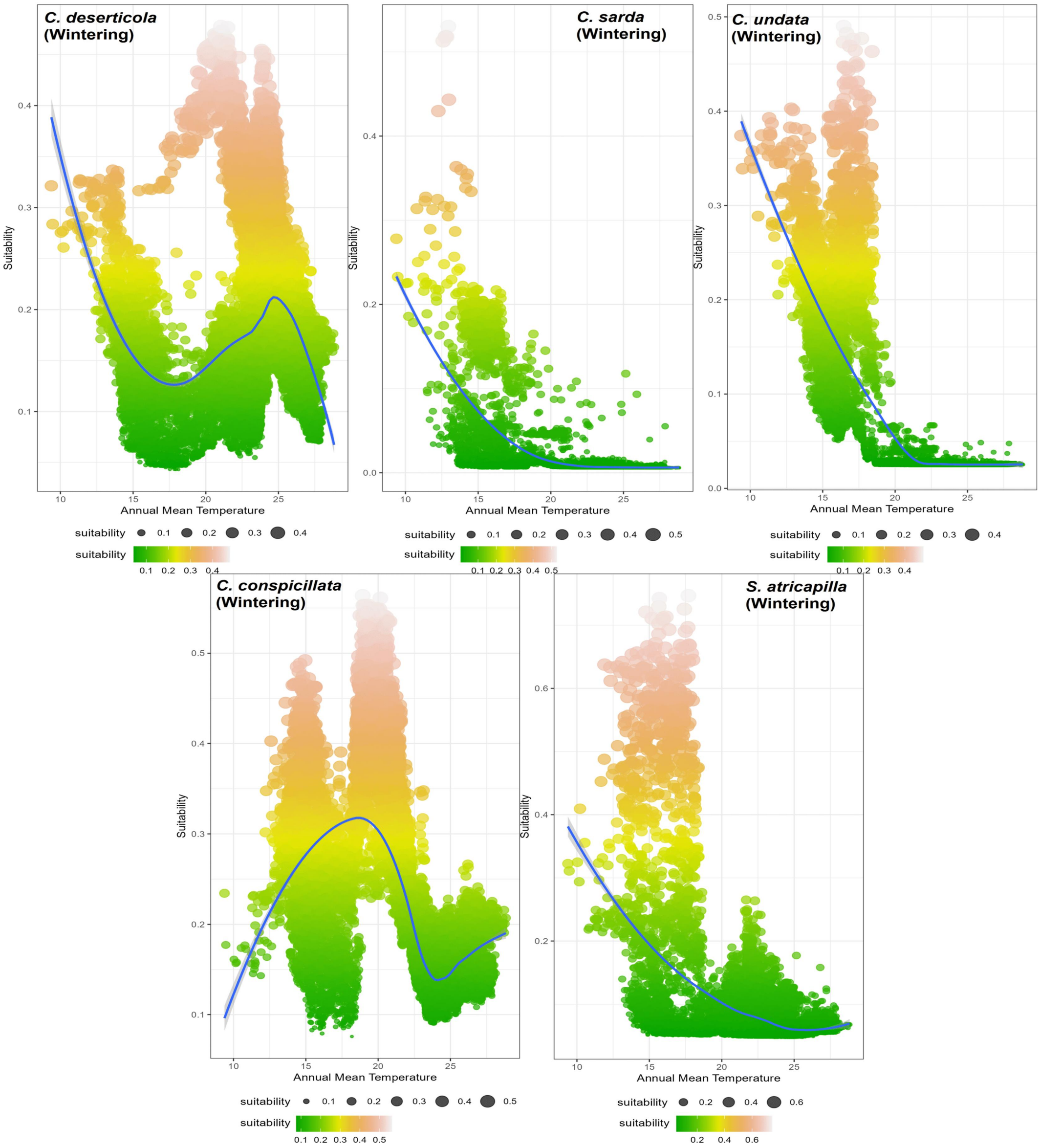

Figure 6. Response curves of species suitability with annual mean temperature during the wintering season

For elevation, *C. conspicillata* reached a clear peak around 750 m, while *C. sarda* and *C. deserticola* showed maximum suitability around 1 000 m and 1 500 m, *C. undata*, and *S. atricapilla* favoured lower altitudes, with marked suitability between 0 and 500 m (Figure 7).

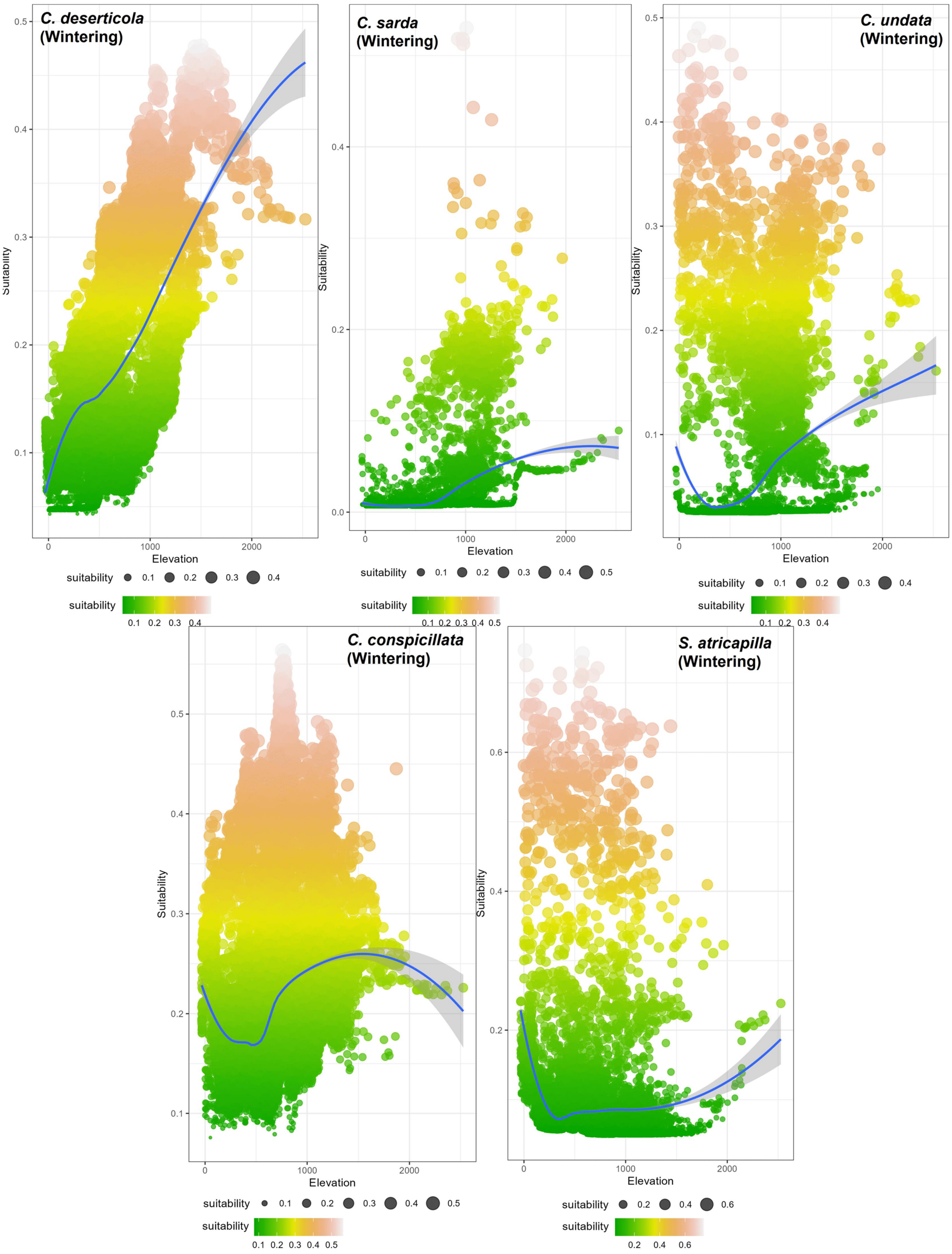

Figure 7. Response curves of species suitability with elevation during the wintering season

Regarding the Enhanced Vegetation Index (EVI), the curves revealed distinct species preferences. *C. deserticola* and *C. conspicillata* showed maximum suitability for low EVI values, between 0.05 and 0.1. *C. undata* exhibited a double peak, around 0.1 and 0.4. *S. atricapilla* reached a maximum around 0.2. Finally, *C. sarda* showed an optimal response for EVI values between 0.1 and 0.15 (Figure 8).

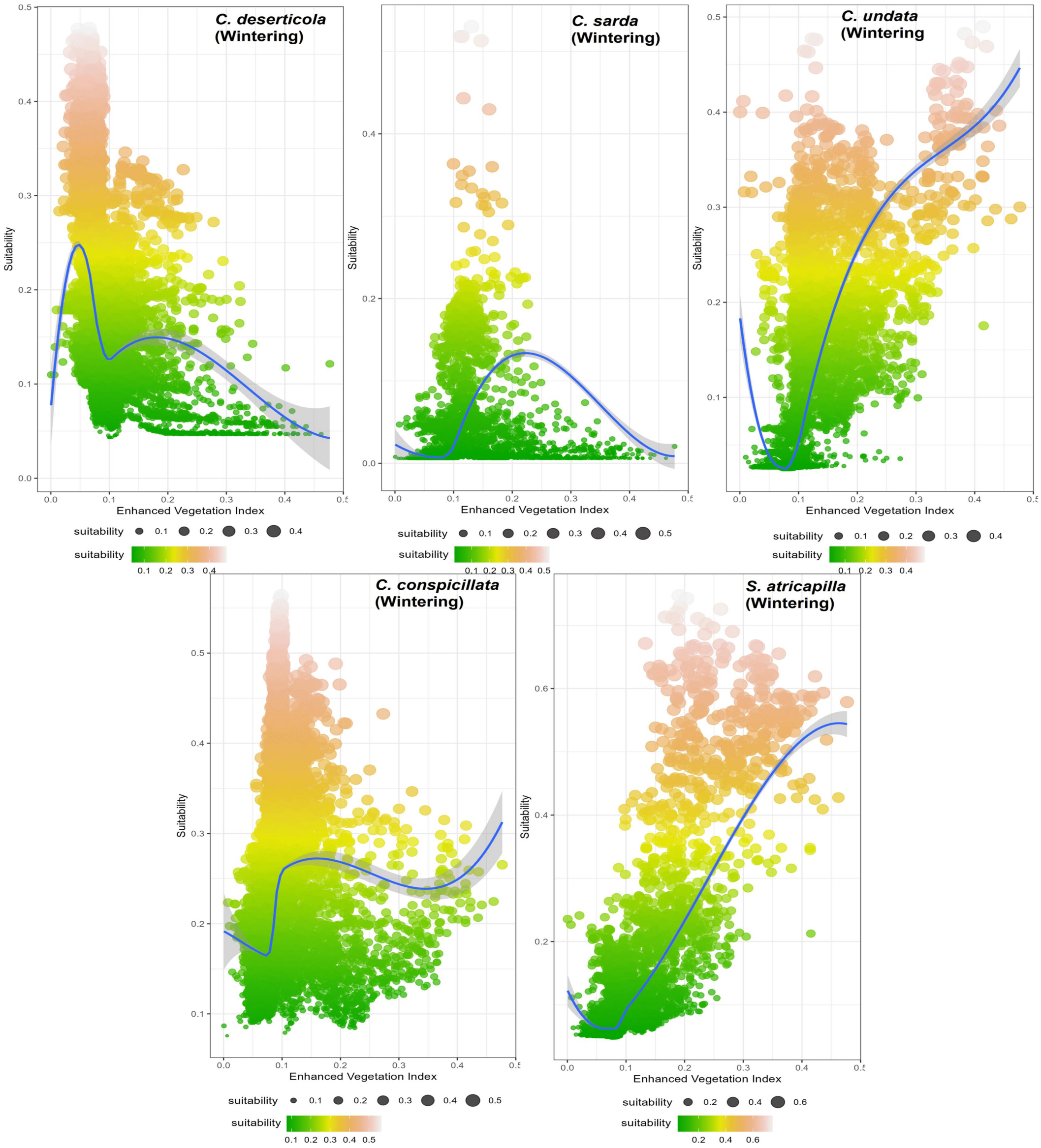

Figure 8. Response curves of species suitability with EVI during the wintering season

3.7. Ecological niche overlap in breeding season

The analysis of niche overlap based on Schoener's D index revealed a clear gradient of ecological similarity among the studied species. High D values (≥ 0.60) indicate substantial sharing of environmental conditions, as observed between *C. hortensis* and *C. iberiae* (D = 0.79) or between *C. communis* and *C. melanocephala* (D = 0.71). In contrast, very low values (≤ 0.10) indicate marked niche differentiation, reflecting distinct environmental preferences, as in the case of *C. deserti* and *C. undata* (D = 0.00) or *C. deserticola* and *C. undata* (D = 0.00) (Figure 9).

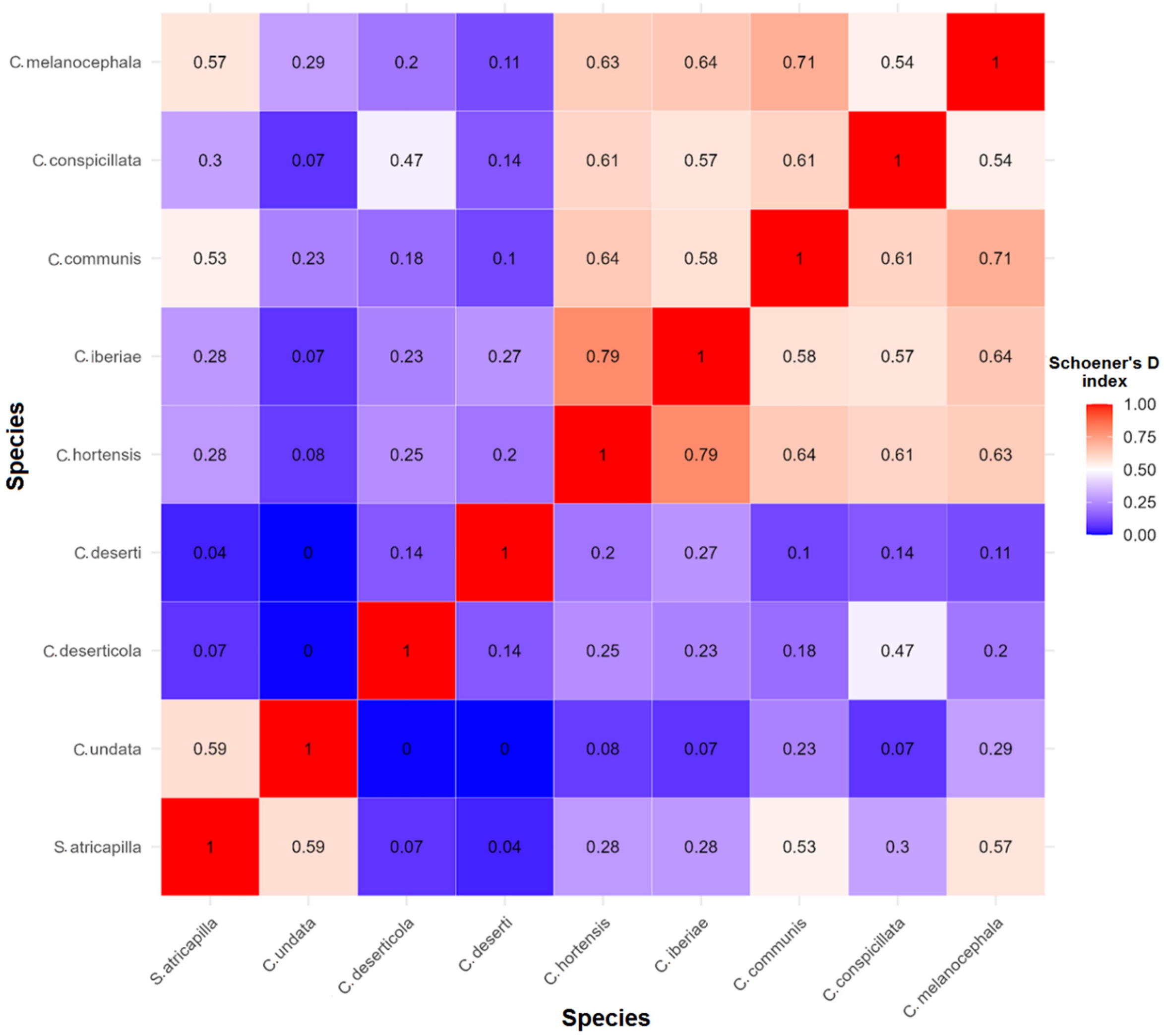

Figure 9. Pairwise overlap of the ecological niches of the studied warbler species during the breeding season, measured using Schoener's D index. Colours range from blue (D = 0, no overlap) to red (D = 1, maximum overlap), with intermediate shades indicating increasing levels of ecological similarity

4. Discussion

Suitability maps from the species distribution models (SDM) for the breeding period show a distribution that is generally consistent with biogeographical and ecological knowledge. Most of the studied species exhibit suitable areas concentrated in northern Algeria, particularly in coastal and sublittoral zones. More specialised species, such as *Curruca deserticola*, display restricted and localised distributions, often associated with arid or semi-arid habitats (Cramp, 1992; Isenmann & Moali, 2000; Shirihai *et al.*, 2001).

Suitability curves during the breeding period indicate that most of the studied species prefer average thermal ranges between 11 °C and 20 °C, in accordance with Mediterranean climate conditions (Peel *et al.*, 2007). These results are consistent with those reported in Spain for *S. atricapilla*, *C. hortensis*, *C. melanocephala*, *C. undata*, and *C. communis* (Seoane *et al.*, 2006; Herrando *et al.*, 2019), and reflect a synchronisation with peaks in invertebrate abundance during the breeding season (Sokolov, 2006; Leech & Crick, 2007).

The altitudinal preferences observed in the studied warblers reflect a close relationship between thermal constraints and vertical distribution, a phenomenon widely documented in passerines (Körner, 2007; Sundqvist *et al.*, 2013). Species associated with cooler temperatures (11–15 °C) are mainly found at medium and high altitudes, such as *C. deserticola* (≈ 1700 m), *C. conspicillata*, *C. hortensis*, and *C. iberiae* (1000–1500 m), as well as *C. undata* (600–1250 m). In contrast, species preferring warmer temperatures (15–20 °C) mainly occupy low altitudes, such as *S. atricapilla* (250–750 m), and *C. melanocephala*, which is well represented in lowlands. *C. communis*, with a thermal optimum around 15 °C, shows an intermediate distribution (500–1000 m). These patterns are consistent with those described for other passerines, where altitudinal segregation helps reduce interspecific competition and reflects specific ecological adaptations (Able & Noon, 1976; Araneda *et al.*, 2018). Studies conducted in various biogeographical contexts confirm that some species clearly favour high altitudes for breeding, while others concentrate on intermediate altitudes. For example, in the White-browed Tit-warbler (*Leptopoecile sophiae*), nests are mostly located between 4,300 and 4,500 m, showing a strong affinity for very high elevations (Lu *et al.*, 2009). Conversely, surveys carried out in the Korean mountains (Jirisan National Park) reveal a “bell-shaped” distribution for the richness and density of breeding species, with a maximum at mid-altitudes, reflecting a compromise between the availability of diverse habitats and environmental conditions (Kim *et al.*, 2018).

The EVI values for *C. communis*, *C. hortensis*, *C. iberiae*, *C. undata*, and *S. atricapilla* show maximum suitability between 0.30 and 0.45, typical of semi-open habitats with moderately dense vegetation (Wang *et al.*, 2022). In contrast, *C. deserticola* and *C. deserti* prefer EVI values close to 0.10–0.20, characteristic of arid or semi-desert habitats (Sedighifar *et al.*, 2019).

According to several studies, *C. conspicillata* inhabits open areas with sparse xerophytic shrubs (Cramp, 1992). *S. atricapilla* favours heterogeneous shrub formations such as edges, maquis, or open forests (Cody & Walter, 1976). *C. communis* occurs in open or semi-open habitats with low vegetation such as shrublands, bramble patches, or agricultural hedgerows (Cramp, 1992; Meichtry-Stier *et al.*, 2013; Szymański & Antczak, 2013). *C. iberiae* is a specialist of open shrub habitats (Blondel, 1965). *C. undata* is typical of dry heathlands dominated by gorse (*Ulex*) and avoids intensively farmed areas (van den Berg *et al.*, 2001). *C. melanocephala* occupies a wide range of Mediterranean habitats, including maquis, garrigue, dry coastal areas, and semi-urban or cultivated landscapes, while avoiding closed forests (Bibby, 1978; Cramp, 1992; Blondel & Aronson, 1999; Shirihai *et al.*, 2001). Finally, *C. deserti* occurs in sandy areas with shrubby vegetation (Isenmann & Moali, 2000).

The analysis of ecological niche overlap using Schoener's index (D) shows that certain species, such as *C. hortensis, C. iberiae, C. communis*, and *C. melanocephala*, share similar niches ($D \geq 0.63$), indicating the use of comparable macro-environmental conditions (climate, EVI, altitude, vegetation cover) (Broennimann *et al.*, 2012). These results are consistent with ecological descriptions available in the literature, which report the co-occurrence of these species in semi-open Mediterranean habitats with shrub-dominated structure (Cody & Walter, 1976; Cramp, 1992; Isenmann & Moali, 2000). In contrast, very low D values (≤ 0.04) between *C. deserticola* vs. *C. undata*, *C. deserti* vs. *C. undata*, and *S. atricapilla* vs. *C. deserti* reflect divergent ecological preferences. *C. deserticola* and *C. deserti* are confined to open steppes, whereas *C. undata* inhabits dense Mediterranean heathlands, and *S. atricapilla* occupies wooded habitats with dense shrub layers (Bibby, 1978; Cramp, 1992; Isenmann & Moali, 2000).

During the winter period, some species show a marked preference for areas with higher temperatures, which helps reduce the energetic costs of thermoregulation and increases winter survival (Carrascal *et al.*, 2016). The species *C. undata* and *C. conspicillata* show a tendency to move to higher altitudes during the breeding season and to descend in winter, a pattern corresponding to altitudinal migration, which is well documented in birds (Hsiung *et al.*, 2018; Vander Pluym & Mason, 2024). This type of migration allows them to take advantage of thermal, trophic, and vegetation cover conditions that are more favourable for breeding, while avoiding the harsh climatic conditions of high plateaus in winter (Carrascal *et al.*, 2012).

Finally, the lower EVI values recorded in winter should not be interpreted as a selection of poor habitats, but rather reflect Mediterranean phenology, characterised by a decrease in chlorophyll activity during the cold season (Pettorelli *et al.*, 2005).

Although species distribution models (SDMs) are powerful tools for understanding and predicting relationships between species and their environment, their results must be interpreted with caution. Many SDMs rely solely on environmental variables and overlook important ecological processes such as species interactions, dispersal limits, or population dynamics (Dormann *et al.*, 2013). Predictions can be unreliable when the number of records is low, particularly when fewer than 30 occurrences are available (Wisz *et al.*, 2008). Georeferencing errors and sampling biases also reduce model accuracy, and a coarser spatial resolution does not correct this issue (Gábor *et al.*, 2022). Even advanced tools such as MaxEnt may produce biased results if data are poorly distributed or inaccurately georeferenced (Syfert *et al.*, 2013). The choice of pseudo-absences, their number, spatial location, and distance from presences strongly influences prediction quality (Barbet-Massin *et al.*, 2012).

The accuracy of an SDM depends on several factors, such as the type and number of data (presence/absence or presence/pseudo-absence), the selection of environmental variables, the spatial and temporal scale, and the algorithm used (Liu *et al.*, 2019; Arenas-Castro *et al.*, 2022). Data quality, including sampling biases and the availability of absence data, also plays a crucial role (Beale & Lennon, 2012; Thuiller *et al.*, 2019). The choice of variables and algorithms can strongly affect the results, making it difficult to identify the best model for a given species (Elith *et al.*, 2006; Feng *et al.*, 2019). Catalano *et al.* (2023) showed that model selection directly influences the accuracy and consistency of prediction maps. The lack of true absence data complicates calibration (Boyce *et al.*, 2002; Engler *et al.*, 2004), while randomly generated pseudo-absences can distort the estimated distribution and produce misleading performance metrics such as AUC (Zaniewski *et al.*, 2002; Buisson *et al.*, 2010; Lobo *et al.*, 2010; Konowalik & Nosol, 2021). To minimise these biases, we used absence data from eBird, which better reflects environmental constraints (Lobo *et al.*, 2010; Johnston *et al.*, 2021; Arenas-Castro *et al.*, 2022), as well as land-use/land-cover (LULC) variables, which improve accuracy by more faithfully representing habitat preferences (Bradley & Fleishman, 2008).

5. Conclusion

This study provides a new contribution to the understanding of the distribution and ecological preferences of Mediterranean warblers in North Africa, by applying species distribution models (SDMs) that explicitly consider two key phases of the annual cycle, breeding and wintering, and by quantifying ecological niche overlap. The approach provides insights to guide conservation strategies in a context of climate change and landscape transformation.

The results highlighted that high-suitability areas for Mediterranean warblers are mostly concentrated in northern Algeria, where moderate temperatures, intermediate to high elevations, and medium to high vegetation productivity overlap. The analysis of niche overlap identified species pairs that are ecologically close and share similar habitats, as well as others with clearly differentiated preferences, underlining the importance of considering interspecific interactions in conservation planning.

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CHAPTER III

PREDICTING SUITABLE WINTER HABITATS OF MARMORA'S WARBLER (*Curruca sarda)* IN NORTH AFRICA USING SPECIES DISTRIBUTION MODELS

This manuscript has been published in the **Journal of Ornithology**
(ISSN: 2193-7192, E-ISSN: 2193-7206)
https://doi.org/10.1007/s10336-025-02300-5

Predicting suitable winter habitats of Marmora's Warbler (*Curruca sarda)* in North Africa using species distribution models

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Abstract

Understanding the complex patterns of habitat use by animal species and unravelling the processes that control these patterns are fundamental goals in the field of ecology. In cases where data on the wintering range of bird species are limited, species distribution models (SDMs) become essential tools for predicting distributions. This study investigates the winter habitat suitability of Marmora's warbler (*Curruca sarda* Temminck, 1820), an endemic Mediterranean bird, for which research on habitat preferences during the wintering period is particularly limited in North Africa, especially in parts of northern Algeria and Tunisia. Initially, 96 occurrence records, ranging from 1970 to 2022, were extracted from biodiversity database platforms and local surveys. After filtering for spatial bias and removing duplicate records, 51 points were retained for modelling. Additionally, 1 085 absence points were generated using eBird sampling event data, applying strict filters to ensure reliable presence-absence data for robust modelling. Advanced modelling techniques, including Boosted Regression Trees (BRT) and Random Forest (RF), were employed, with Random Forest achieving the highest performance metrics, including an AUC of 0.956 and a true skill statistic (TSS) of 0.78. Habitat suitability maps highlight Algeria (44 062 km^2) and Tunisia (4 464 km^2) as critical wintering areas. These models identified key environmental predictors influencing habitat suitability, with annual mean temperature (11–13°C), elevation (1 024–1 300 m asl), and precipitation seasonality (32–41%) emerging as the most significant factors. These findings provide essential insights for conservation planning, emphasising the need to address habitat fragmentation and climatic variability to ensure the survival of this species.

Key words: Habitat, SDMs, Biodiversity, Birds, Conservation, Marmora's Warbler

1. Introduction

Understanding the intricate patterns of habitat utilisation among animal species and unravelling the underlying processes governing these patterns represent fundamental objectives in ecology (Deppe & Rotenberry, 2008). The idea behind adaptive habitat selection involves a structured decision-making process, where costs and benefits change with scale (Mayor *et al.*, 2009). Migratory passerine birds, despite their small physical stature, traverse some of the most considerable distances of any animal species during their annual migration cycle (Alerstam *et al.*, 2003). For instance, several studies have shown that climatic conditions significantly influence the presence and abundance of bird species in Mediterranean ecosystems (Sanz, 2002; Crick *et al.*, 2003; Rodríguez & Bustamante, 2003;

Jiguet *et al.*, 2007; Regos *et al.*, 2015). According to Newton (2008), ecological processes in breeding and wintering grounds strongly influence habitat occupancy and the seasonal abundance of migratory birds. However, most research has focused on the breeding season, leaving a significant gap in understanding species in the wintering period (Faaborg *et al.*, 2010).

Several studies have shown that wintering habitats play a pivotal role in determining the survival and population trends of migratory birds. Research on the Wood Thrush *Hylocichla mustelina* highlighted that the loss and fragmentation of wintering habitats are primary factors driving its decline (Taylor & Stutchbury 2016). Similarly, Ockendon *et al.* (2012) demonstrated that bioclimatic zones and wintering habitat types were critical determinants of population trends in British-breeding Afro-Palaearctic migrant birds, potentially influencing constraints on arrival time advancement. Another example is the common whitethroat *Curruca communis* which winters in the Sahel, studies showed that increased rainfall in this region since the 1980s has contributed to stabilizing or even increasing its numbers in British breeding grounds, highlighting the critical role of climatic factors in wintering areas (Baillie *et al.*, 2010). These findings emphasise the importance of considering wintering habitats and climatic conditions when studying migratory bird populations and their long-term viability.

The spatial distribution of endemic species and the factors influencing it at multiple scales are pivotal in biodiversity conservation (Moukrim *et al.*, 2017). Their heightened vulnerability to climate change and habitat degradation places these species among the highest priorities for conservation efforts (Feng *et al.*, 2020). The Marmora's warbler *Curruca sarda* is an endemic species of the Mediterranean that has an insular distribution, its habitat spans Sarda, Corsica, and the Balearic Islands, excluding Minorca and a few smaller islands along western Italy in the Tyrrhenian Sea (Nespoli *et al.*, 2021). During the breeding season, *C. sarda* inhabits low and consistent Mediterranean scrubland, often degraded and uniform, including garrigue with *Cistus* species and maquis dominated by plants such as *Juniperus*, *Quercus*, *Erica*, *Calycotome*, *Chamaerops*, *Genista*, *Pistacia*, and *Arbutus* (Aymí & Gargallo, 2021; Shirihai *et al.*, 2001). While primarily resident, a small number of adults and first-winter individuals migrate to Sicily and North Africa, where observations of wintering individuals extend from November to March, covering northeastern Algeria, and Tunisia, reaching the north Saharan oases, and northwest Libya (Shirihai *et al.*, 2001). Studies on *C. sarda* during its wintering period have been conspicuously restricted, with notable exceptions such as the study conducted by Lovaty in 2013 in Corsica. Particularly, there is a notable lack of studies addressing the migration behaviour of this species in North Africa.

The modelling of habitat suitability and species' distribution has become progressively vital within ecology (Brambilla & Ficetola, 2012). Understanding the patterns and processes that govern species distribution is imperative to address the pervasive decline of biodiversity. This knowledge forms a crucial foundation for effective conservation planning, as mentioned by Guisan *et al.* (2013). Species Distribution Models (SDMs) play a pivotal role as the primary basis for evaluating the conservation status of many species (Cardoso *et al.*, 2012). In recent times, numerous studies have utilised SDMs to estimate the potential distribution of species in the context of current environmental conditions (Jarnevich *et al.*, 2018). SDMs are predictive tools that establish connections between observed occurrences and environmental predictors through the application of statistical models or theoretically derived response curves (Guisan & Thuiller, 2005).

According to Guisan and Thuiller (2005), the employment of these models was widespread in the field of conserving rare or endangered species, as well as for other species. This approach links species occurrence with environmental variables to produce a map representing the relative habitat suitability (Guisan & Zimmerman, 2000; Moudrý *et al.*, 2023). Over the past two decades, the utilisation of SDMs has significantly increased with the application of advanced modelling techniques such as Boosted Regression Trees (BRT) and Random Forest (RF). BRT models are characterised by their flexibility and robustness in handling nonlinear relationships, managing collinearity, and quantifying the relative importance of predictors (Elith *et al.*, 2008). Additionally, RF models have demonstrated superior prediction accuracy compared to standard decision trees in SDMs and other applications (Gislason *et al.*, 2006; Prasad *et al.*, 2006). These tools are particularly valuable for studying dynamic environments where species distributions are influenced by complex interactions among environmental factors.

Due to a lack of research on the habitat preferences and distribution of *C. sarda* during its wintering period, particularly in North Africa, our research aims to address this gap. Using Species Distribution Models (SDMs), we seek to delineate the habitat preferences of this species during the winter season and model its distribution in the North African region. This study seeks to provide essential insights to inform specific conservation strategies, underscoring the significance of understanding the ecological requirements of the wintering *C. sarda* in a region where knowledge is currently limited.

2. Materials and methods

2.1. Study area and species occurrence data

The study focused within the North African region, particularly Algeria, Tunisia (Figure 1), due to the availability of biodiversity occurrence data, Libya was excluded because of its limited sample size, with only one recorded presence. Both Tunisia and Algeria harbour various forests ecosystems, including cork oaks, Aleppo pines, and Atlas cedars, predominantly located in the northern mountainous regions (Pswarayi-Riddihough, 2002). In Algeria, forests are primarily concentrated in the Kabylie region, the Aurès Mountains, and northeastern Numidia (Djema & Messaoudene, 2009), while in Tunisia, they are predominantly found in the northern mountainous areas, such as the Kroumirie Mountains and the Medjerda Valley (Daly-Hassen & Ben Mansoura, 2005). The climate in both countries is characterised by hot, dry summers and mild, wet winters. Tunisia's highest peak, Jebel ech Chambi, rises to 1 544 m above sea level, while the Atlas Mountains in Algeria reach up to 2 308 m asl, making them the highest in the country.

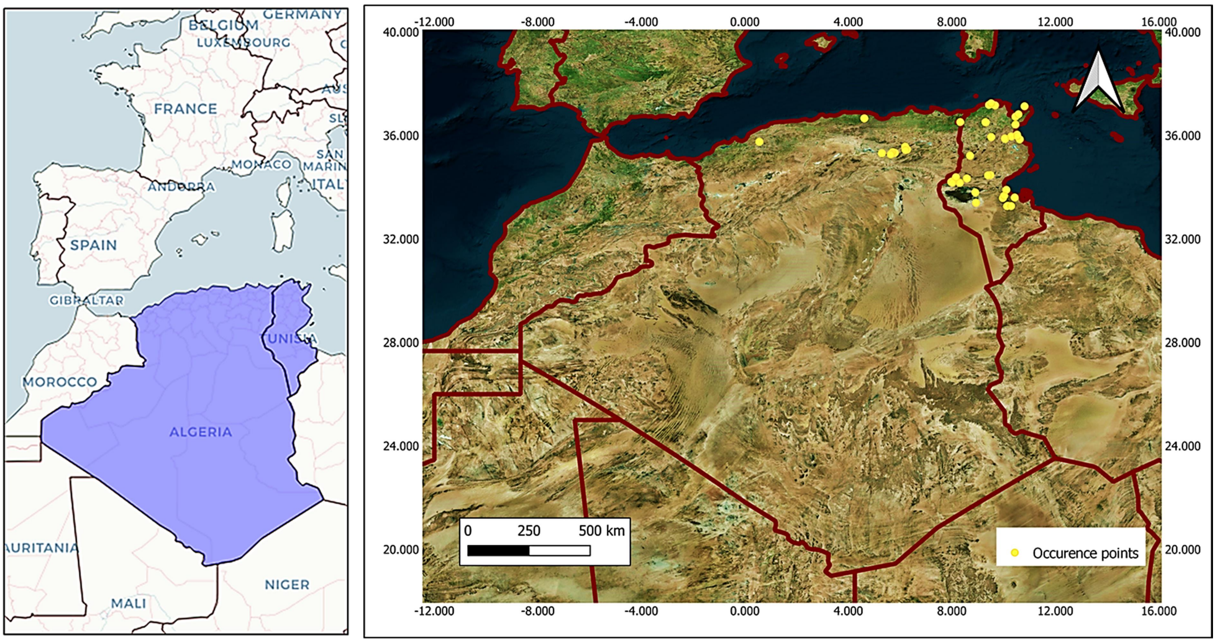

Figure 1. Location map showing the spatial distribution of *Curruca sarda* observation records within the study area

Field surveys were conducted at six sites in the Batna region of northeastern Algeria to confirm the presence of *C. sarda* and gain a deeper understanding of its habitat. Additionally, several historical sites documented by Isenmann and Moali (2000) were also surveyed, and information on the distribution of the species was gathered from nature enthusiasts and local associations. To enhance and expand our database, occurrence records of *C. sarda* were gathered from multiple sources to ensure comprehensive coverage. Data were extracted from the Global Biodiversity Information Facility (GBIF) database (GBIF.org, 3 December 2024, GBIF Occurrence Download, DOI: 10.15468/dl.a935wd) and the eBird Basic Dataset (https://ebird.org/data/download), encompassing a wider geographical range that included Algeria and Tunisia. A total of 96 georeferenced occurrences spanning from 1970 to 2022 and corresponding to the wintering season, were extracted. Additionally, supplementary occurrence points were obtained from literature records reported by El Bouhissi *et al.* (2023). Subsequently, occurrences outside the study area and erroneous records were excluded. Then, the thin_by*_dist()* function from the R package tidysdm (Leonardi *et al.*, 2023) was applied with a 1 km distance threshold to remove duplicate records and points within the same pixel, in order to avoid spatial autocorrelation (Mammola *et al.*, 2018) and sampling bias (Phillips *et al.*, 2009; Eckert *et al.*, 2023). As a result, the dataset was reduced to 51 retained points, which we used for the species distribution modelling. Furthermore, to generate absence points, both the eBird Basic Dataset (EBD) and the sampling event data corresponding to our species and study area were obtained through a request in eBird. Using the package auk implemented in R (Strimas-Mackey *et al.*, 2018), we applied filters to select only complete checklists with a duration of at least 2 hours, an effort distance of a maximum of 4 km, and "stationary" or "traveling" survey protocol. Furthermore, the function *auk_zerofill()* was applied for zero-filling, transforming the data into presence-absence format. Subsequently, the processed data was collapsed into a unified structure using *collapse_zerofill()*, converting it into a data frame. In total, 1 085 absence points were initially retained, from which 421 were included in the final dataset after applying spatial thinning.

2.2. Environmental variables

We retrieved 19 bioclimatic variables, along with elevation data, at a spatial resolution of 30 arc-seconds (~1 km). Additionally, we generated raster data for the Enhanced Vegetation Index (EVI) for the period from 1 January 1970, to 31 December 2000, and calculated the median EVI values for this time. We also obtained land use and land cover (LULC) from the MODIS dataset (Moderate Resolution Imaging Spectroradiometer-MCD12Q1), specifically using the LC_Type4 class table, which includes nine distinct classes (Table 1). All raster's were then adjusted to (~1 km) by a bilinear method using the *resample()* function from the package raster (Hijmans *et al.*, 2013) to match the resolution and extent of the variables. For the variable selection process, the 22 variables were assessed for collinearity with the function *vifstep()* from the R package usdm (Naimi *et al.*, 2014), using variance inflation factors (VIF). Variables with VIF values exceeding a threshold of 10 and a correlation coefficient (r) of 0.80 were considered to exhibit high collinearity and were excluded from the analysis (see Figure S1) in supplementary material). The retained variables included Elevation, EVI, Annual mean temperature, Mean temperature of wettest quarter, Precipitation seasonality, and LULC (Table 1).

Table 1. Description of the retained environmental variables used in species distribution modelling

Sources	**Variable**	**Description**	**Spatial resolution**	**Unit**
Worldclim data	BIO1 = Annual Mean Temperature	The average air temperature for the entire year	30 arc-seconds (~1km)	°C
	BIO8 = Mean Temperature of Wettest Quarter	The average temperature during the wettest quarter of the year	30 arc-seconds (~1km)	°C
	BIO15 = Precipitation Seasonality	Seasonal variation in precipitation (coefficient of variation)	30 arc-seconds (~1km)	Index (0-1)
	Elevation	The site's altitude above sea level	30 arc-seconds (~1km)	Meters (m)
Landsat Collection 2 Tier 1 Level 2	Enhanced Vegetation Index (EVI)	A vegetation index measuring plant density and health	30 meters	Numeric value (0-1)
MODIS Land Cover Type (MCD12Q1)	Land Use and Land Cover	0: Water Bodies - Area covered by permanent water (≥60%)	500 meters	Numeric values
		1: Evergreen Needleleaf - Dominated by evergreen conifers (>1m)		
		2: Evergreen Broadleaf - Dominated by evergreen broadleaf trees (>1m)		
		3: Deciduous Needleleaf - Dominated by deciduous needleleaf trees (>1m)		
		4: Deciduous Broadleaf - Dominated by deciduous broadleaf		

	trees (>1m)	
	5: Annual Broadleaf - Herbaceous annuals, mainly broadleaf crops	
	6: Annual Grass - Herbaceous annuals, including cereal crops	
	7: Non-Vegetated - ≥60% barren land or permanent snow/ice	
	8: Urban - ≥30% impervious surfaces (buildings, asphalt)	

The VIF values for the retained variables ranged from 1.4758 (LULC) to 5.2014 (Annual mean temperature), suggesting that all variables were suitable for inclusion in the final model (see Figure S2).

2.3. Habitat suitability modelling

Boosted Regression Trees (BRT) and Random Forest (RF) were chosen to model the habitat suitability of the species. The dataset was divided into 30% for testing and 70% for training, ensuring a robust model performance evaluation. Subsequently, the predictive accuracy of the models was assessed using, True Skill Statistics (TSS) (Allouche *et al.*, 2006), Cohen's kappa (Cohen, 1960), and Area Under the Curve (AUC) (Lobo *et al.*, 2008). The two first metrics (TSS and kappa) range from -1 to 1, and the AUC ranges from 0 to 1, where a trend toward 1 in kappa, TSS, and AUC values suggests a robust predictive model. A final ensemble model was created using a weighted averaging approach based on TSS. However, it is important to note that assessment metrics, such as AUC, TSS, and Kappa have limitations and are influenced by the nature and quality of data. For instance, when sample prevalence is low or species distributions are small, these metrics may be less reliable. Additionally, presence-only or pseudo-absence data can introduce biases, making accurate evaluation dependent on the availability of high-quality presence-absence data (Leroy *et al.*, 2018).

The habitat suitability map and binary map for Marmora's warbler were generated using the ggplot2 package (Wickham, 2011). Subsequently, an analysis was conducted to estimate variable importance within the habitat suitability model. To determine the key factors affecting habitat suitability in our study area, we used a generalised linear model (GLM) with a binomial link function. Initially, we included all potential explanatory variables in the model to evaluate their effects. Next, we applied a backward selection method, where we systematically removed the least significant variables one at a time. This process was guided by the Akaike Information Criterion (AIC) and Bayesian (BIC) information criteria (Reineking, 2006; Faraway, 2016), which helps identify the best-fitting model. After each removal, we reassessed the model until only the most significant variables remained, resulting in a model with the lowest AIC value. The SDM modelling, graphics, and statistical analyses were carried out using R software 4.2.2 (R Core Team, 2023).

2.4. Models assessment

The area under the curve (AUC) and true skill statistic (TSS) of the models ranged from 0.553 to 0.956 and from -0.004 to 0.78, respectively. The ensemble model showed an AUC value of 0.728 and a TSS of 0.343. Additionally, the kappa statistic ranged from -0.001 to 0.57, with an average of 0.207. Random Forest (RF) outperforms Boosted Regression Tree (BRT) across all evaluation metrics, achieving higher AUC (0.79 vs. 0.76), COR (0.44 vs. 0.37), and TSS (0.52 vs. 0.49), while also exhibiting lower deviance (0.5 vs. 0.55). This indicates that RF provides more accurate and reliable predictions compared to BRT in this context. The comparison of SDMs (Table 2) highlights distinct performance patterns across methods and replication techniques. For Boosted Regression Tree, bootstrap outperforms subsampling with higher AUC, TSS, and Kappa values, indicating better accuracy. Random Forest shows the highest AUC values, especially with bootstrap (AUC 0.956, TSS 0.78), while subsampling is less effective. The Ensemble model achieves balanced, intermediate results (AUC: 0.728, TSS: 0.343). Overall, bootstrap consistently improves performance, particularly for Random Forest and Boosted Regression Tree, making it the preferred replication method for SDMs.

Table 2. Performance metrics of species distribution models (SDMs) using different methods and replication techniques

Method	Replication	AUC	Deviance	TSS	Kappa
Boosted Regression Tree	Subsampling	0.553	0.65	0.132	0.053
	Subsampling	0.697	0.606	0.43	0.217
	Subsampling	0.641	0.623	0.141	0.056
	Bootstrap	0.803	0.581	0.44	0.225
	Bootstrap	0.654	0.673	0.404	0.21
	Bootstrap	0.786	0.55	0.308	0.138
Random forest	Subsampling	0.599	0.766	-0.004	-0.001
	Subsampling	0.653	0.695	0.141	0.056
	Subsampling	0.696	0.623	0.173	0.073
	Bootstrap	0.956	0.358	0.78	0.57
	Bootstrap	0.783	0.58	0.507	0.282
	Bootstrap	0.916	0.37	0.667	0.426
Ensemble model		0.728	0.59	0.343	0.192

3. Results

3.1. Climatic and environmental variables in occurrence regions

The average annual precipitation in regions where the species occurred was 352.60 mm, accompanied by an average elevation of 438.13 m asl, as depicted in Figure 2. Vegetation cover was generally sparse, with an average value of 0.12. Annual temperatures and those of the wettest quarter were 17.67 °C and 12.78 °C, respectively. The Land Use and Land Cover (LULC) index averages 4.72; precipitation seasonality is moderate, with an average of 50.26, and precipitation during the wettest quarter averages 140.09 mm.

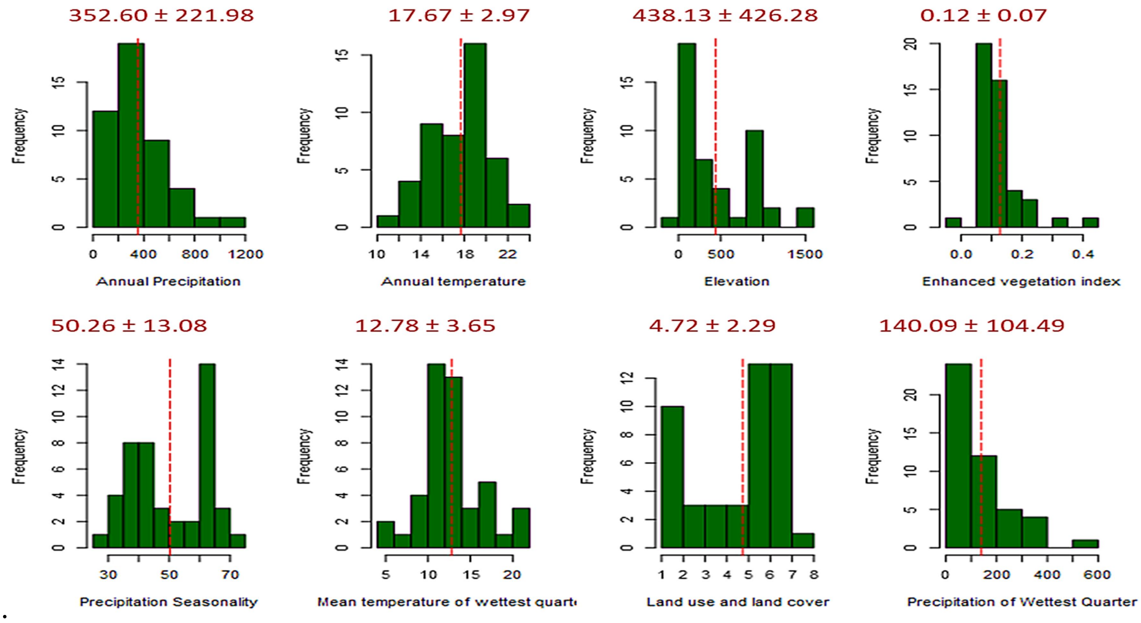

Figure 2. Histograms illustrating the comparative analysis of environmental data metrics

3.2. Habitat suitability

The habitat suitability map (Figure 3) highlighted highly suitable areas for *C. sarda*, predominantly concentrated in northeastern Algeria, particularly in the mountainous regions of Batna and the adjacent lowland areas of Biskra, Khenchela, and Tébessa. Additional patches of suitability were observed in central regions such as Laghouat, Tiaret, and Djelfa, as well as in western regions like Tlemcen and Sidi Bel Abbès. In Tunisia, high suitability areas were primarily located in the central-eastern region, with some patches in the south. Across North Africa, the analysis identified approximately 48 526 km² of suitable habitat, with 44 062 km² in Algeria and 4 464 km² in Tunisia (Figure 4).

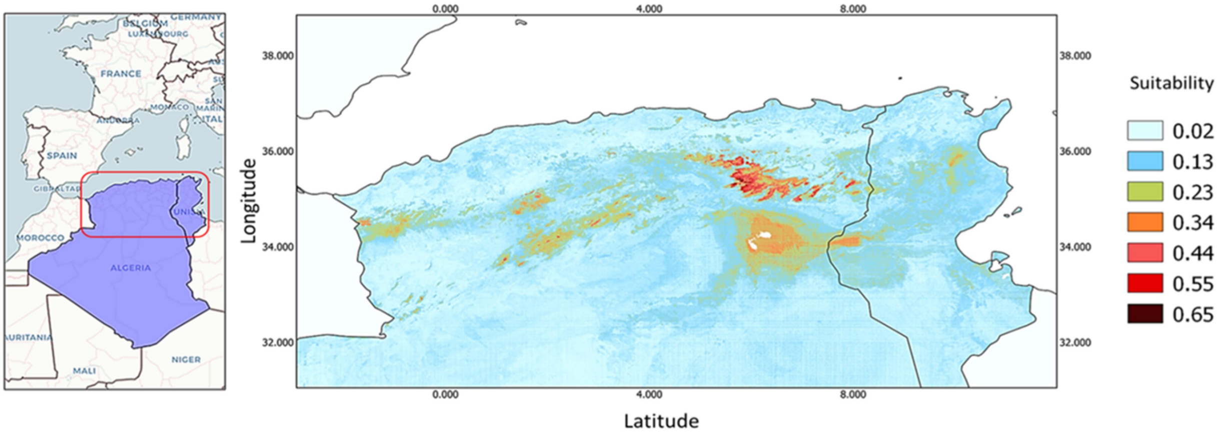

Figure 3. Habitat suitability map for *C. sarda* in North Africa

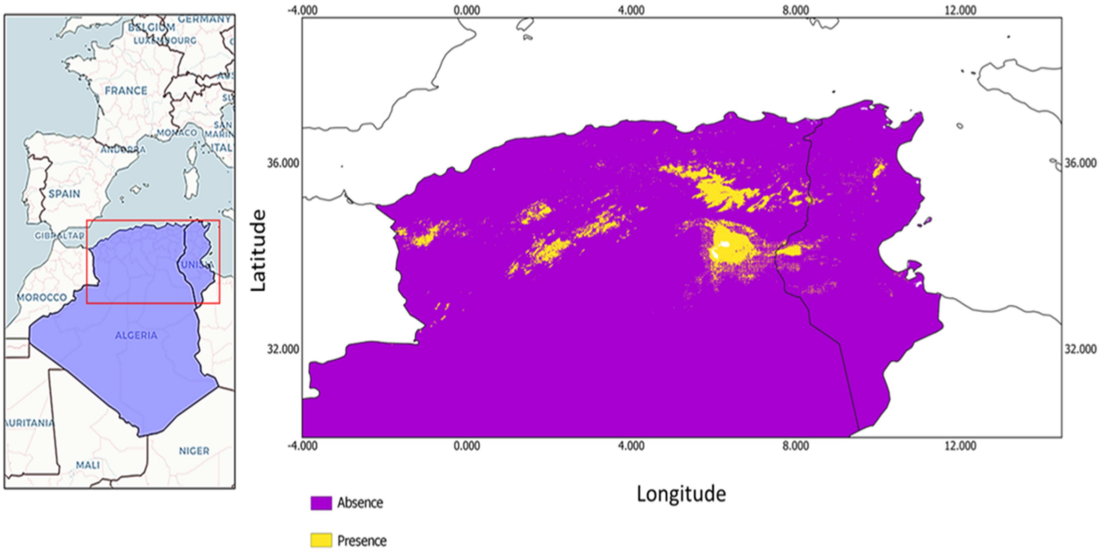

Figure 4. Binary habitat suitability map for *C. sarda* in North Africa

Distinct ranges characterised the ecological niche of *C. sarda* across multiple environmental variables (Figure 5). The species showed preference for LULC types, particularly evergreen needleleaf vegetation (ENV) associated with Enhanced Vegetation Index (EVI) values between 0.09 and 0.15, and for evergreen broadleaf vegetation (EBV) with 0.09 EVI values (Figure 5A). The suitable habitat was defined by annual precipitation ranging from 404.5 mm to 484.4 mm, with precipitation during the wettest quarter falling between 115.95 mm and 158.6 mm (Figure 5B). The species' optimal ecological niche corresponded to areas with annual mean temperatures ranging from 11.15°C to 13.25°C and precipitation seasonality between 32.25% and 40.82%, indicating moderate seasonal precipitation variation (Figure 5C). Additionally, *C. sarda* demonstrated optimal habitat conditions at elevations between 1 023.8 m asl and 1 300 m asl, where the mean temperature during the wettest quarter ranges from 6°C to 10.5°C (Figure 5D), and also some preference in area below 500 m asl and with moderate temperature.

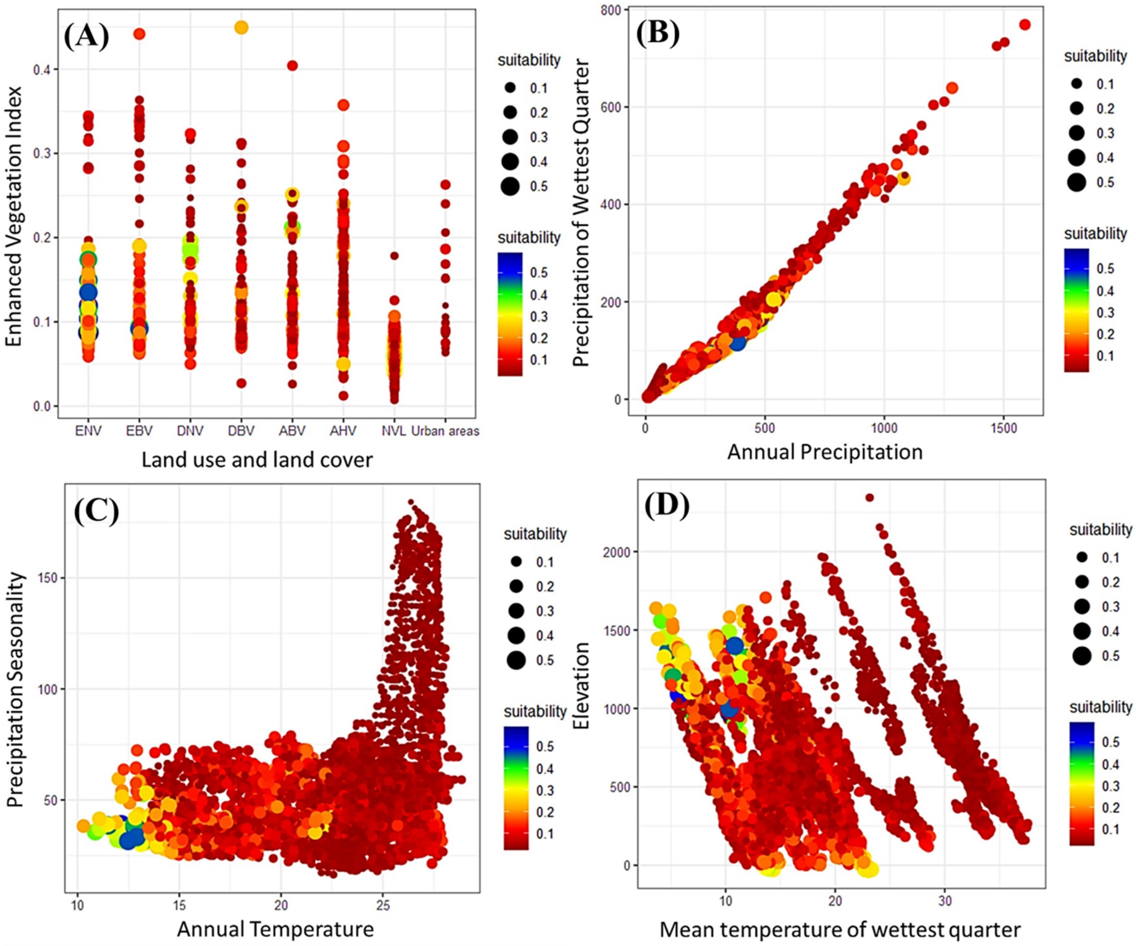

Figure 5. N-dimensional hypervolume plots illustrating influential ecological variables. In (A), ENV evergreen needleleaf vegetation, EBV evergreen broadleaf vegetation, DNV deciduous needleleaf vegetation, DBV deciduous broadleaf vegetation, ABV annual broadleaf vegetation, AHV annual herbaceous vegetation, NVL non-vegetated land

3.3. Variable importance

Annual Mean Temperature emerged as the most influential predictor of *C. sarda* distribution, contributing 40.6% according to the Pearson correlation metric, though its importance was notably lower (14.2%) using the AUC metric. Elevation and Precipitation Seasonality showed substantial influence, with Pearson correlations of 18.3% and 17.9% respectively, although their AUC importance values were lower. LULC and EVI showed moderate importance across both metrics, while Mean Temperature of Wettest Quarter had the lowest contribution to the model with both metrics showing values below 6% (Table 3).

Table 3. Summary of relative variable importance based on Pearson correlation and AUC metrics.

Variables	Importance (Pearson correlation Metric %)	Importance (AUC Metric %)
Elevation	18.3	13.2
Enhanced Vegetation Index (EVI)	9.5	9.8
Annual Mean Temperature	40.6	14.2
Mean Temperature of Wettest Quarter	4.6	5.4
Precipitation Seasonality	17.9	5.9
Land Use and Land Cover (LULC)	15.7	7.8

Habitat suitability demonstrated clear patterns across various environmental variables (Figure 6). Suitability peaked around 20°C for annual mean temperature but declined at higher values. Similarly, the optimal suitability for the mean temperature of the wettest quarter was observed at 15°C, with a decline at extreme values. Elevation exhibited the highest suitability below 500 m asl, with a sharp decrease between 1 000 and 1 500 m asl. Annual precipitation reaches its optimum between 200 and 400 mm, with suitability decreasing significantly above 400 mm. For precipitation seasonality, areas with low variability (<40) showed higher suitability, which decreased as seasonality increases. Likewise, precipitation of the wettest quarter showed peak suitability at 100 mm, while lower and higher levels reduced suitability. The EVI indicated the highest suitability within the range of 0.04 to 0.2 levels, with declines at very low (<0.04) or high (>0.2) values. Finally, LULC showed variability in habitat suitability across classes. Evergreen needleleaf vegetation (ENV), evergreen broadleaf vegetation (EBV), and non-vegetated lands (NVL), exhibit higher suitability. Suitability was lower in other land cover types including deciduous vegetation (DNV-DBV) and declined further in remaining classes, excluding urban areas.

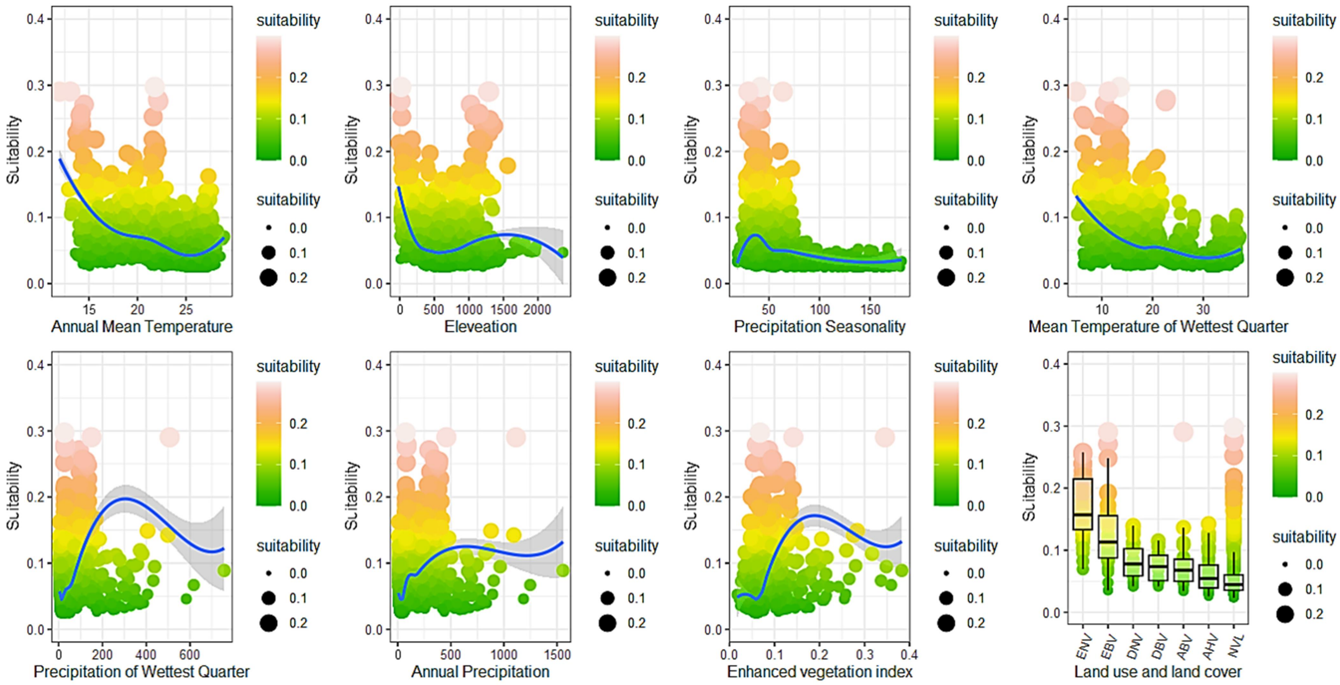

Figure 6. Response curves illustrating the relationship between environmental predictor variables and the modelled habitat suitability probability

3.4. Environmental suitability probability

The generalised linear model (GLM) results (Table 4; Figure 7) revealed that land cover types, climate variables, and elevation significantly influenced habitat suitability for *C. sarda*. Using annual broadleaf vegetation as the baseline, evergreen broadleaf vegetation is positively associated with suitability, while annual herbaceous vegetation shows a significant negative effect. Other land cover categories, including evergreen and deciduous needleleaf vegetation, non-vegetated land, and urban areas, do not significantly differ from the baseline. Among the climatic variables, only annual mean temperature has a significant negative effect. Elevation was positively associated with suitability, while other variables such as precipitation seasonality, mean temperature of the wettest quarter, and EVI show no significant effects.

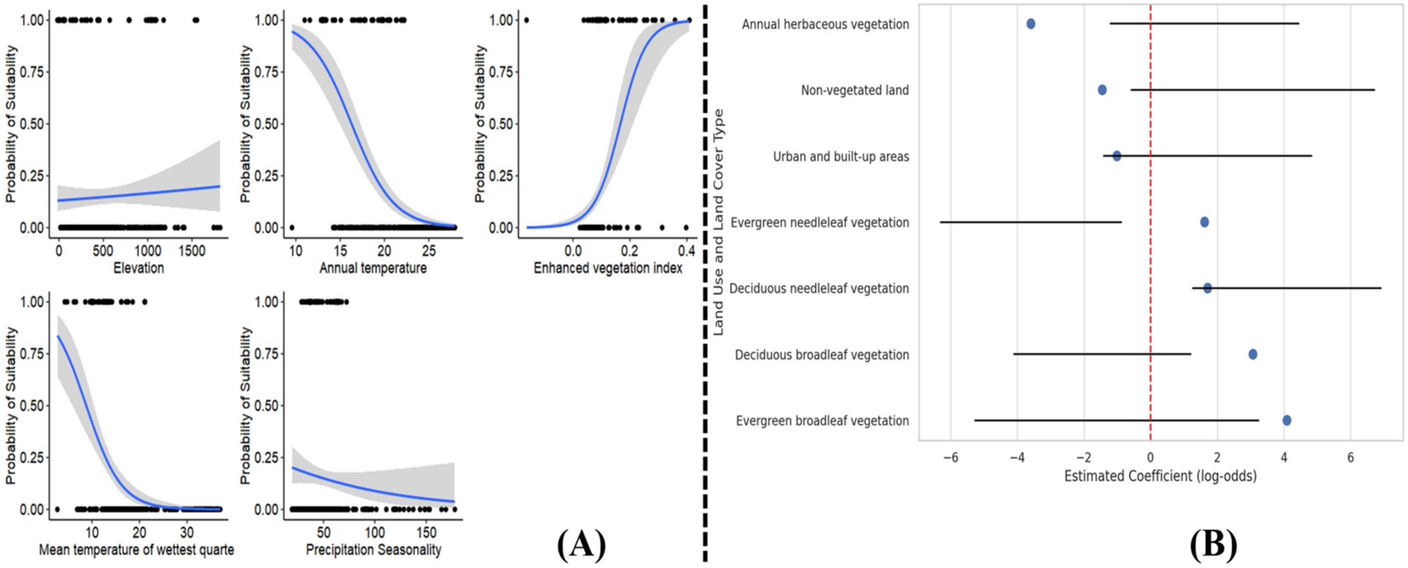

Figure 7. Binomial GLM results showing: (A) response curves for numerical predictors and (B) a forest plot for land use and land cover categories. In (B), positive coefficients (right of the red dashed line) indicate increased habitat suitability, while negative coefficients indicate reduced suitability

Table 4. Generalised Linear Model (GLM) results of habitat suitability for *C. sarda*, with annual broadleaf vegetation as the Baseline of LULC factor

		Estimate	**Std.error**	**Z value**	**P value**
Land use and land cover	(Intercept)	25.26	5.38	4.69	<0.001 ***
	Evergreen needleleaf vegetation	1.62	1.44	-1.13	0.26
	Deciduous broadleaf vegetation	3.07	1.86	-1.65	0.1
	Deciduous needleleaf vegetation	1.71	1.59	-1.08	0.28
	Annual herbaceous vegetation	-3.59	1.38	-2.59	0.01*
	Evergreen broadleaf vegetation	4.09	1.44	-2.84	0.004**
	Non-vegetated land	-1.45	1.35	-1.08	0.28
	Urban and built-up areas	-1.01	2.17	-0.47	0.64
Climatic variables	Mean temperature of wettest quarter	0.02	0.09	0.22	0.83
	Annual mean temperature	-1.15	0.24	-4.77	<0.001 ***
	Precipitation seasonality	-0.01	0.03	0.18	0.85
Topography and vegetation index	Enhanced Vegetation Index (EVI)	2.07	4.72	0.44	0.66
	Elevation	0.01	0.002	-4.68	<0.001 ***

*: Significant at $p < 0.05$; **: Significant at $p < 0.01$; ***: Significant at $p < 0.001$

4. Discussion

The current study focuses on projecting the wintering habitat distributions of Marmora's warbler *C. sarda*, a migratory bird inhabiting the North African region. In this research, we employed SDM as a tool to predict and analyse the distribution of this avian species during winter.

The presence and abundance of birds in a given environment are closely linked to climatic conditions, which affect their movements and migrations (Correia, 2014). This influence primarily manifests indirectly by altering resources and habitat structure (Newton, 1998). The variability in Species Distribution Model (SDM) outcomes is driven by multiple parameters, which in turn underscores the critical importance of careful modelling choices (Gaul *et al.*, 2020; Lambert & Virgili, 2023). Additionally, as emphasised by Guisan *et al.* (2013), the predictive effectiveness of SDMs significantly depends on the quality and relevance of input data, including both presence and absence records. For *C. sarda*, which has a restricted distribution during winter in North Africa, using thinned presence-absence data proved to be a more effective approach in our modelling efforts compared to presence-pseudo-absence or random absence data. Through the application of SDM, we were able to identify and emphasise crucial variables that play a pivotal role in shaping species' distribution. Moreover, this approach allowed us to delineate suitable habitats for the species in an area that had not been studied previously. Our findings produced a suitability map that aligns with the historical presence regions identified by Isenmann and Moali (2000), further supporting the distribution map compiled by BirdLife. This includes northeastern areas such as Tébessa, western regions like Tlemcen and Sidi Bel Abbès, and central lowland areas including Laghouat, Tiaret, and Djelfa.

In this study, Annual Mean Temperature (Bio1) emerged as the most significant factor among the bioclimatic variables tested, with importance exceeding 40% according to the Pearson correlation method. This was confirmed in Figures. 6 and 7, which showed habitat suitability characterised by temperatures ranging approximately from 13°C to 22.5°C, with the probability of species presence nearing 100% at a temperature of around 9°C .

According to Meehan *et al.* (2004) and Evans *et al.* (2006), temperature is a limiting factor during the winter period because of its impact on individual energy, resulting from increased physiological costs associated with low winter temperatures. This constraint appeared to prevail over other biotic processes that could also influence distributions. These results were consistent with previous research emphasising temperature as the primary determinant for avian species establishment, often overshadowing the role of precipitation (Gordo, 2007). Moreover, temperature conditions at wintering sites strongly influence bird survival, as Woodworth *et al.* (2017) found that immigration rates and individual survival were notably higher during warm years, likely due to increased food availability compared to cold winters.

Our results indicated a marked preference for elevations below 500 m asl and a progressive decline in habitat suitability with increasing elevation. These findings aligned with previous studies showing that elevation influenced microclimatic conditions, notably through decreasing temperatures and increasing wind exposure at higher elevations, which can affect resource availability and elevate energetic costs for birds (Rahbek, 1997; McCain, 2009; Acharya *et al.*, 2011). Such factors make high altitude areas less favourable by limiting insect availability and placing greater physiological demands on individuals.

The negative effect of higher elevations was further supported by Rahbek (1997), who documented a significant decline in bird populations between 1 000 and 1 500 m asl, attributed to physiological constraints associated with low temperatures and reduced prey biomass. Lower elevation sites, while providing more favourable temperatures, were often associated with higher levels of anthropogenic activities, such as agriculture and overgrazing, which may reduce their suitability for the species. These findings highlight the necessity of integrating habitat conservation efforts with sustainable land-use practices, as previously emphasised by Seoane *et al.* (2013).

The third most important factor following temperature and elevation was precipitation seasonality (Bio15), contributing 17.9% according to Pearson correlation analysis. This parameter plays a fundamental role in the wintering of migratory passerines, directly influencing the availability of food resources and the quality of habitats. In tropical and subtropical regions, precipitation concentrated over a short period leads to a significant increase, which is crucial for insectivorous species such as passerines (Saino *et al.*, 2004; Zurell *et al.*, 2018). However, irregular variations in precipitation patterns, exacerbated by climate change, can desynchronise resource abundance with migration and wintering seasons, which may compromise the physical condition and reproductive success of individuals (Both & Visser, 2001; Saino *et al.*, 2004). These observations highlighted the critical dependence of migratory passerines, such as *C. sarda*, on seasonal climatic cycles, emphasising the significance of customised conservation strategies to reduce their vulnerability to climatic disruptions. In this context, a Bio15 suitability value ranging between 25 and 50 indicated a moderate variability in annual precipitation (Figure 6). In Batna, Algeria, the region where *C. sarda* was observed exhibits a semi-arid climate characterised by adapted vegetation dominated by xerophytic species such as *Artemisia herba-alba*, *Stipa tenacissima*, and *Juniperus phoenicea.* These plants, well adapted to water stress, play a vital role in maintaining the region's ecological stability by providing critical microhabitats and food resources for local fauna. Furthermore, as highlighted by Gordo (2007), seasonal variations in precipitation significantly influence the life cycles of migratory birds, which rely on the availability of resources during critical phases of their annual cycle.

Significant fluctuations in abiotic factors and productivity between seasons play a crucial role in shaping the dynamic patterns of species distribution and diversity throughout the year in temperate ecosystems (Seoane *et al.*, 2013). According to Gordon (2000), Studds and Marra (2007), and Macías-Duarte *et al.* (2009), precipitation exerts a profound influence on the structural composition of herbaceous and woody vegetation, which in turn cascades down to impact seed and food production crucial for avian species, particularly arthropods, which serve as their primary dietary source.

The analysis of the habitat suitability map showed a highly suitable habitat for *C. sarda* in the southwestern region of Tunisia and the northeastern expanse of the Algerian Sahara; these regions represent the Mediterranean arid zone (Floret, 1981; Le Houérou, 2004). The prospected site of Batna (Djbel Metlili) is characterised by a semi-arid to arid climate. This type of climate typically hosts xerophytic plant species belonging to several families such as Asteraceae, Poaceae, Lamiaceae, Fabaceae, Brassicaceae, and Chenopodiaceae (Kawada *et al.*, 2012; Beghami, 2013; Gamoun, 2014; Gamoun *et al.*, 2018; Neji *et al.*, 2018).

Kawada *et al.* (2012) observed that species like *Stipa tenacissima* and *Rosmarinus officinalis* dominated more than 20% and 10%, respectively, of the 17 surveyed sites in semi-arid regions. They also noted the presence of other dominant species, such as *Retama raetam*, *Artemisia campestris*, and *Artemisia herba-alba*. In the northern part of the Mediterranean basin, *C. sarda* is often found in a low and degraded maquis, characterised by a certain uniformity and including species belonging to genera such as *Juniperus*, *Quercus*, *Erica*, *Calicotome*, *Chamaerops*, *Genista*, *Pistacia*, *Arbutus*, *Myrtus*, and *Daphne*. It preferred vegetation heights that are always lower than 2 m, usually less than 1 m, and avoids trees except when they are widely dispersed (Lunn, 1985; Shirihai *et al.*, 2001; Coreau & Martin, 2007; Lovaty, 2013). The vegetation encountered on the visited site was characterised by the presence of *Artemisia herba-alba*, *Stipa tenacissima*, *Juniperus phoenicea*, and other species with low dominance. This observation suggested that these plant species may have a direct or indirect effect on the establishment of the *C. sarda* species in semi-arid to arid regions of North Africa.

The Enhanced Vegetation Index (EVI), while having a moderate impact in our models, remains a critical indicator for assessing habitat quality. An EVI suitability range between 0.04 and 0.1, corresponding to sparse but persistent vegetation cover, appeared optimal for *C. sarda*. According to Gamoun *et al.* (2018), these conditions are characteristic of semi-arid regions where the vegetation cover is sufficient to provide shelter and food resources without being overly dense, which could impede bird mobility.

The probability of species presence during wintering varies across LULC classes (Figure 7). However, the analysis indicated that the most suitable habitats were primarily found in evergreen needleleaf vegetation and evergreen broadleaf vegetation. These classes provided favourable conditions for the species during its wintering period by offering an abundance of food resources (e.g., invertebrates and seeds) and stable microclimates, which supported the energetic needs of birds during this critical phase (Betts *et al.*, 2007). Interestingly, non-vegetated areas, also exhibited notable suitability (Figure 6). Although these habitats were generally considered suboptimal due to the lack of dense vegetation and diverse food resources, they may provide specific advantages associated with unique microhabitats or opportunities for wintering birds. For instance, bare soils and rocky areas may harbour specialized insects or served as safe resting sites, allowing the species to exploit these marginal environments despite their ecological constraints (McKinney, 2006). These results highlighted the species' ability to adapt to a wide range of habitats during its wintering period, while emphasising the critical importance of natural and semi-natural habitats for its survival. The conservation and management of these habitats should be prioritised to ensure the availability of adequate resources and refuges during the winter season.

Laube *et al.* (2015) suggested that species within the genus *Curruca* travel much greater distances than would be optimal, likely due to environmental and ecological constraints. *C. sarda* travels an average distance of 400 km between its breeding and wintering grounds, with the maximum distance reaching 2 400 km (Doswald *et al.*, 2009). This migration pattern was likely due to other factors than, such as biotic interactions, the availability of resting sites, and unsuitable stopover sites rather than only reaching wintering ground with similar climates and land cover to breeding ground (Laube *et al.*, 2015). Therefore, the integration of both biotic and abiotic factors was essential to gain a comprehensive understanding of the factors behind the complexity of migration patterns (Leach *et al.*, 2016). In contrast to long distance migrants, short distance warblers like *C. balearica*, *C. deserticola*, or *C. sarda* are indeed facing a more severe negative impact from climatic change due to the reduced overlap between their present and potential future ranges (Doswald *et al.*, 2009). In addition, Simulation of current and future migration distances carried out by Doswald *et al.* (2009) predicts a potential increase for most species, with trans-Saharan migrants showing a greater increase compared to resident, short-distance, or partial migrants. This finding highlights the potential impact of climate change on the migratory patterns of birds, particularly those undertaking long-distance journeys across ecological barriers like the Sahara desert.

Both land use changes and ongoing climate change are expected to significantly impact the distribution of *C. sarda* (Doswald *et al.*, 2009; Jetz *et al.*, 2007; Laube *et al.*, 2015). Climate change, through alterations in temperature and precipitation patterns, which are key factors in determining wintering habitats, had the potential to substantially affect habitat quality and availability (Zurell *et al.*, 2018; IPCC, 2019). Warming trends, for instance, may cause appropriate habitat zones to move further north, but they may also cause habitat loss in already suitable places because of increased aridity (Riordan & Rundel, 2014). However, by destroying habitats and dividing landscapes necessary for migratory and wintering, land use change like deforestation, agriculture, and urbanisation can make these effects worse, especially for birds such as *C. sarda*, which are particularly affected due to their reliance on specific habitat structures (Riordan & Rundel, 2014).

The accuracy of species distribution model outputs depends on several factors, such as the number and nature of data points (presence/absence or presence/pseudo-absence), the selection of relevant environmental variables, spatial and temporal scale and algorithm choice (Liu *et al.*, 2019; Arenas-Castro *et al.*, 2022). Furthermore, data quality, including sampling bias and the availability of absence data, directly affects the robustness of predictions (Beale & Lennon, 2012; Thuiller *et al.*, 2019). The choice of environmental variables and modelling algorithms can significantly influence results, making it difficult to identify the most suitable model for a given species or context (Elith *et al.*, 2006; Feng *et al.*, 2019). Catalano *et al.* (2023) confirmed that model selection directly impacts the accuracy and consistency of prediction maps, highlighting the importance of rigorous calibration and methodological choices tailored to the study's objectives. The lack of reliable data for model calibration, especially in the absence of true absence data, can lead to prediction errors and reduce their relevance for species conservation and management (Boyce *et al.*, 2002; Engler *et al.*, 2004). Pseudo-absences, which can be randomly generated, may misrepresent species distributions and distort model calibration and evaluation metrics such as AUC, leading to a false impression of high performance (Zaniewski *et al.*, 2002; Buisson *et al.*, 2010; Lobo *et al.*, 2010; Konowalik & Nosol, 2021). To mitigate these biases, we used absence data from eBird, which better represents environmental constraints and enhances model accuracy (Lobo *et al.*, 2010; Johnston *et al.*, 2021; Arenas-Castro *et al.*, 2022). In addition, including LULC as a predictor improved the model's accuracy by better capturing habitat preferences and reflecting the influence of land cover on species distribution, leading to a more precise identification of suitable habitats (Bradley & Fleishman, 2008). Thus, ensuring robust methodological choices is essential, as they directly influence SDM predictions and subsequent ecological inferences, in our case, the presence of observation clusters in eastern Tunisia outside the predicted range suggests potential limitations in the model's ability to capture localised habitat preferences or microclimatic conditions, these discrepancies may reflect differences in temporal resolution between occurrence data and environmental layers (Filz *et al.*, 2013). The current modelled distribution in Algeria remains largely hypothetical due to limited sampling effort and ground validation, owing to the country's vast size (Beddek, 2017). Although the model predicts suitable habitats, the lack of extensive field surveys in these areas requires cautious interpretation of the results (Mederbal *et al.*, 2024). Beyond methodological considerations, SDMs could be useful instruments for forecasting a species' probable range and directing conservation initiatives. SDMs facilitate the identification of habitats that have not yet been thoroughly investigated by pinpointing high-suitability locations, providing a foundation for focused field research (Phillips *et al.*, 2006; Elith *et al.*, 2011). For instance, areas like the northeast of the Algerian Sahara and the southwest of Tunisia seemed to be possible habitats for *C. sarda*, offering a framework for prioritizing prospecting activities. By pinpointing underrepresented regions, these models also close data gaps in biodiversity, which is crucial for improving distribution maps and conservation tactics (Guisan *et al.*, 2017; Yates *et al.*, 2018). Additionally, SDMs offered insight into possible distribution patterns under various environmental conditions, addressing sample biases and emphasising the significance of combining biotic and abiotic elements to enhance conservation planning.

5. Conclusion

Species distribution models (SDMs) have become a fundamental method in modern biogeography, linking species occurrence data to spatial environmental information (Engler *et al.*, 2017). Despite their utility, they have drawbacks such as a tendency to overestimate species richness in species-poor areas and underestimate it in species-diverse areas (Calabrese *et al.*, 2014; Zurell *et al.*, 2016). Nevertheless, they remain a powerful tool for understanding past, current, and future species distributions (Engler *et al.*, 2017). Our models confirmed the critical importance of temperature, altitude, and precipitation seasonality, on the species' establishment. Habitat suitability maps highlighted key wintering areas, primarily located in the southwestern region of Tunisia and the northeastern expanse of Algeria. These results provided crucial insights into the ecological requirements of *C. sarda* and revealed the strong association between the species' presence and semi-arid climatic conditions.

These findings carried significant implications for conservation. SDMs can assist in identifying and protecting critical habitats and guiding reserve selection by prioritising high-conservation-value areas. The identification of priority habitats offers actionable guidance for conservation efforts, including the establishment of protected areas, habitat restoration, and targeted monitoring programs (Guisan *et al.*, 2013). Furthermore, the generated maps and datasets provide valuable tools for environmental managers, enabling them to inform policy decisions and optimise targeted conservation strategies effectively. Future research should focus on refining the understanding of interactions between *C. sarda* and its environment, including the role of vegetation structure and potential biotic interactions. Moreover, extensive fieldwork in suitable areas is recommended to gather detailed data on the species' presence, population size and habitat use. Additionally, longitudinal studies are crucial for assessing how habitat suitability may evolve under future climate scenarios. In addition, engaging local communities in conservation efforts is also crucial for fostering stewardship of these vital habitats. Overall, a proactive approach which aims to prevent threats before they occur, instead of reacting to their consequences once the damage is done (Drechsler *et al.*, 2011) is necessary to conserve *C. sarda* in a changing environment, such as integrating climate scenarios into conservation planning (Hole *et al.*, 2009), to ensure effective protection of suitable habitats.

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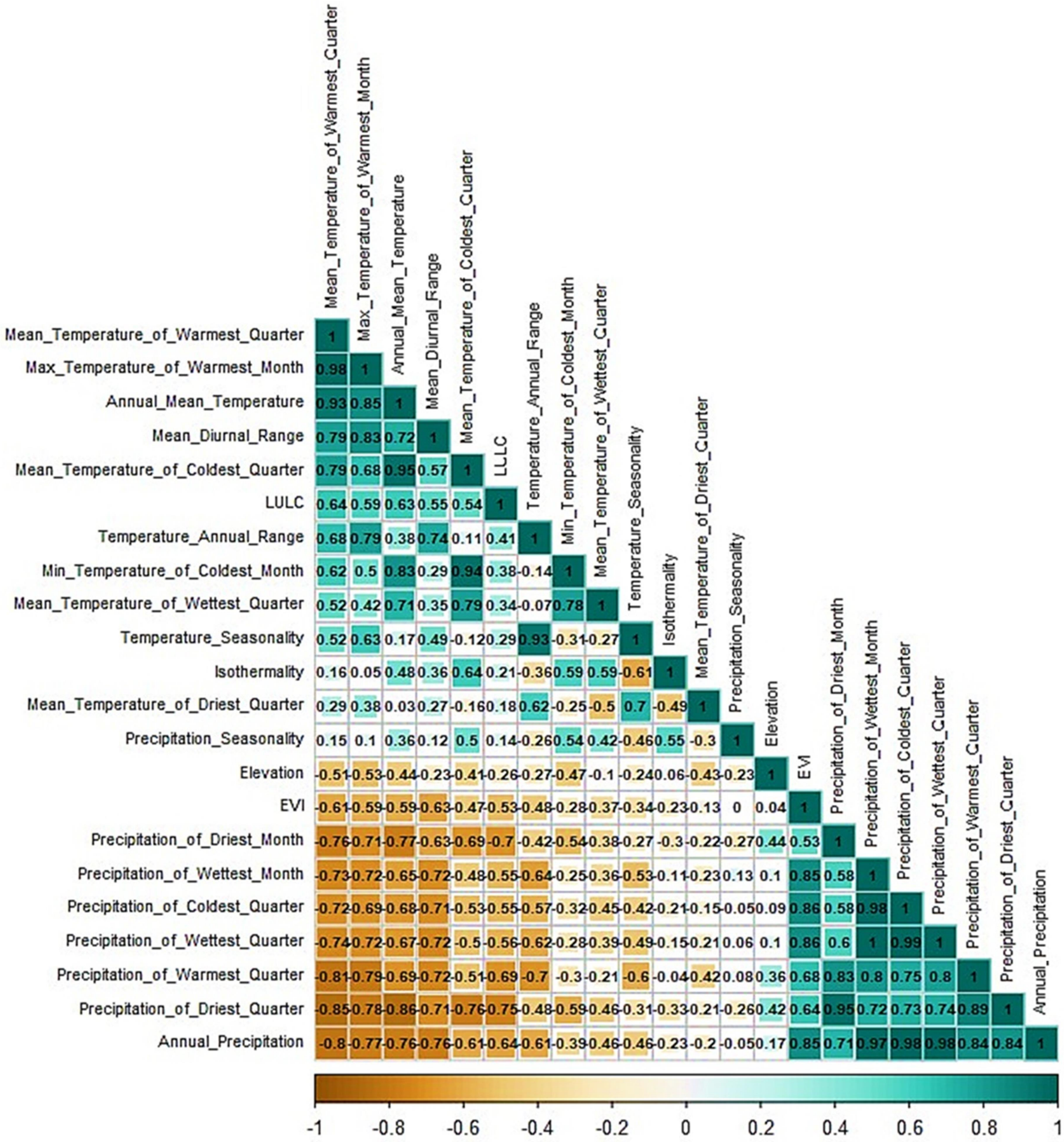
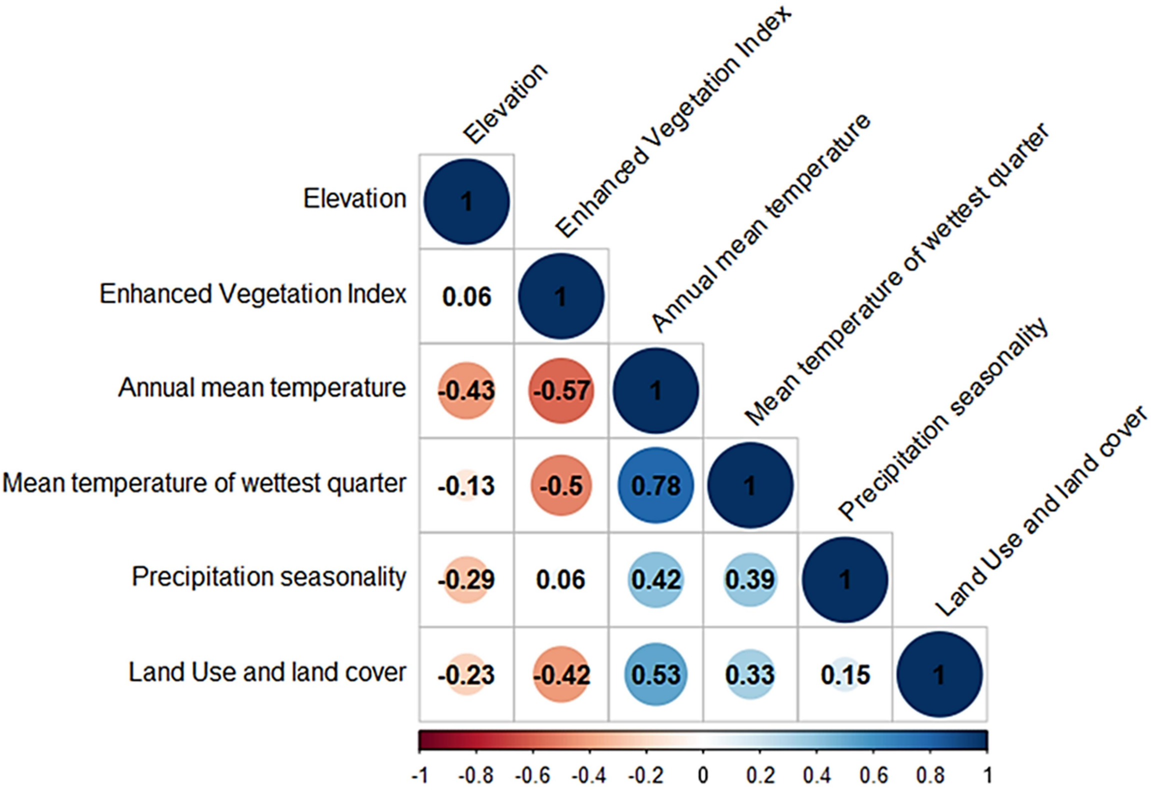
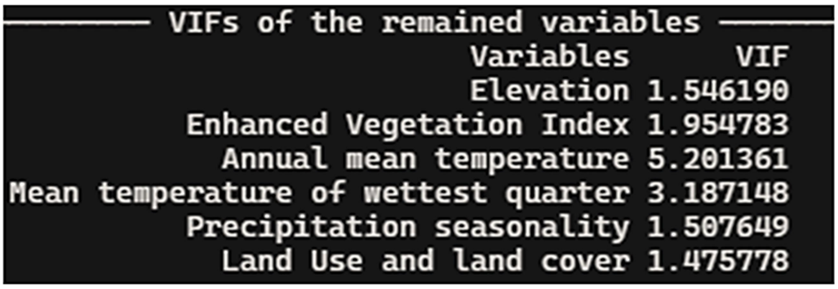
7. Supplementary figures



	Mean_Temperature_of_Warmest_Quarter	Max_Temperature_of_Warmest_Month	Annual_Mean_Temperature	Mean_Diurnal_Range	Mean_Temperature_of_Coldest_Quarter	LULC	Temperature_Annual_Range	Min_Temperature_of_Coldest_Month	Mean_Temperature_of_Wettest_Quarter	Temperature_Seasonality	Isothermality	Mean_Temperature_of_Driest_Quarter	Precipitation_Seasonality	Elevation	EVI	Precipitation_of_Driest_Month	Precipitation_of_Wettest_Month	Precipitation_of_Coldest_Quarter	Precipitation_of_Wettest_Quarter	Precipitation_of_Warmest_Quarter	Precipitation_of_Driest_Quarter	Annual_Precipitation
Mean_Temperature_of_Warmest_Quarter	1																					
Max_Temperature_of_Warmest_Month	0.98	1																				
Annual_Mean_Temperature	0.93	0.85	1																			
Mean_Diurnal_Range	0.79	0.83	0.72	1																		
Mean_Temperature_of_Coldest_Quarter	0.79	0.68	0.95	0.57	1																	
LULC	0.64	0.59	0.63	0.55	0.54	1																
Temperature_Annual_Range	0.68	0.79	0.38	0.74	0.11	0.41	1															
Min_Temperature_of_Coldest_Month	0.62	0.5	0.83	0.29	0.94	0.38	-0.14	1														
Mean_Temperature_of_Wettest_Quarter	0.52	0.42	0.71	0.35	0.79	0.34	-0.07	0.78	1													
Temperature_Seasonality	0.52	0.63	0.17	0.49	-0.12	0.29	0.93	-0.31	-0.27	1												
Isothermality	0.16	0.05	0.48	0.36	0.64	0.21	-0.36	0.59	0.59	-0.61	1											
Mean_Temperature_of_Driest_Quarter	0.29	0.38	0.03	0.27	-0.16	0.18	0.62	-0.25	-0.5	0.7	-0.49	1										
Precipitation_Seasonality	0.15	0.1	0.36	0.12	0.5	0.14	-0.26	0.54	0.42	-0.46	0.55	-0.3	1									
Elevation	-0.51	-0.53	-0.44	-0.23	-0.41	-0.26	-0.27	-0.47	-0.1	-0.24	0.06	-0.43	-0.23	1								
EVI	-0.61	-0.59	-0.59	-0.63	-0.47	-0.53	-0.48	-0.28	-0.37	-0.34	-0.23	-0.13	0	0.04	1							
Precipitation_of_Driest_Month	-0.76	-0.71	-0.77	-0.63	-0.69	-0.7	-0.42	-0.54	-0.38	-0.27	-0.3	-0.22	-0.27	0.44	0.53	1						
Precipitation_of_Wettest_Month	-0.73	-0.72	-0.65	-0.72	-0.48	-0.55	-0.64	-0.25	-0.36	-0.53	-0.11	-0.23	0.13	0.1	0.85	0.58	1					
Precipitation_of_Coldest_Quarter	-0.72	-0.69	-0.68	-0.71	-0.53	-0.55	-0.57	-0.32	-0.45	-0.42	-0.21	-0.15	-0.05	0.09	0.86	0.58	0.98	1				
Precipitation_of_Wettest_Quarter	-0.74	-0.72	-0.67	-0.72	-0.5	-0.56	-0.62	-0.28	-0.39	-0.49	-0.15	-0.21	0.06	0.1	0.86	0.6	1	0.99	1			
Precipitation_of_Warmest_Quarter	-0.81	-0.79	-0.69	-0.72	-0.51	-0.69	-0.7	-0.3	-0.21	-0.6	-0.04	0.42	0.08	0.36	0.68	0.83	0.8	0.75	0.8	1		
Precipitation_of_Driest_Quarter	-0.85	-0.78	-0.86	-0.71	-0.76	-0.75	-0.48	-0.59	-0.46	-0.31	-0.33	-0.21	-0.26	0.42	0.64	0.95	0.72	0.73	0.74	0.89	1	
Annual_Precipitation	-0.8	-0.77	-0.76	-0.76	-0.61	-0.64	-0.61	-0.39	-0.46	-0.46	-0.23	-0.2	-0.05	0.17	0.85	0.71	0.97	0.98	0.98	0.84	0.84	1

Figure S1. Correlation plot for the 22 environmental variables considered during the initial stages of the SDM.

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──────── VIFs of the remained variables ────────
                            Variables      VIF
                            Elevation 1.546190
             Enhanced Vegetation Index 1.954783
               Annual mean temperature 5.201361
Mean temperature of wettest quarter 3.187148
             Precipitation seasonality 1.507649
               Land Use and land cover 1.475778
```

Figure S2. Pearson correlation analysis and VIF (Variance Inflation Factor) assessment of environmental variables

CHAPTER IV

BREEDING HABITAT SUITABILITY OF THE ENDEMIC TRISTRAM'S WARBLER *Curruca deserticola* IN NORTH AFRICA: A MICRO- AND MACRO-SCALE APPROACH

This manuscript has been published in the journal **Ostrich**

(ISSN: 0030-6525, E-ISSN: 1727-947X)

Breeding habitat suitability of the endemic Tristram's warbler *Curruca deserticola* in North Africa: a Micro- and Macro-scale approach

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Abstract

The Tristram's Warbler *Curruca deserticola*, an understudied North African endemic, remains poorly understood in terms of its ecological niche and habitat preferences. This study offers a comprehensive multi-scale habitat assessment combining macroecological SDMs (Random Forest and BRT) across Algeria and Tunisia with fine-scale microhabitat analysis at occupied sites. The species' distribution was concentrated in mountainous regions of northeastern Algeria and northwestern Tunisia, highlighting its reliance on structurally heterogeneous shrublands. Elevation emerged as the most influential factor, with optimal suitability at ~1 250 metres, while intermediate EVI values (0.15–0.2) and moderate annual temperatures (12–14 °C) further defined suitable habitats. The integration of both spatial scales highlights the species' strong association with structurally heterogeneous shrublands in moderately elevated, semi-arid zones. Microhabitat modelling (GLMs) highlighted preferences for abundant small trees, moderate shrub cover (2–4 m), and steeper slopes. These findings demonstrate the species' vulnerability to habitat fragmentation and climate change, reinforcing the need for scale-integrated conservation strategies focused on structurally heterogeneous highland habitats.

Keywords: Habitat suitability, endemic species, multiscale analysis, species distribution model

1. Introduction

Northern Africa hosts remarkable biodiversity due to its strategic geographical position between the Mediterranean, Atlantic, and Saharo-Arabian biogeographical zones, along with diverse climatic influences Draper *et al.* (2007). The exceptional biodiversity of this region, isolated from Europe by the Mediterranean Sea and from tropical Africa by the Sahara Desert, has been a key focus of avian taxonomy and endemism studies, emphasising its critical role in global biodiversity research (Isenmann & Thévenot, 2018). The region constitutes a significant hotspots of endemism, harbouring many species that are considered either threatened on an international scale or have disappeared from other parts of the world (Garrido *et al.*, 2021). Isenmann and Thévenot (2020) identified 17 endemic bird species in North Africa, including *Curruca deserticola*, which is characterised by two distinct subspecies: *C. deserticola maroccana*, found in Morocco and northwestern Algeria, and *C. deserticola deserticola,* occurring in the rest of Algeria and Tunisia (Shirihai *et al.*, 2001; Aymí & Gargallo, 2021).

The ongoing fragmentation of natural ecosystems has significantly reduced the quality and size of habitats available for many plant and animal species of high ecological value (Haddad *et al.*, 2015). Endemic species are often prioritized in conservation efforts due to their heightened vulnerability (Bonn *et al.*, 2002). Understanding their distribution patterns and ecological drivers across spatial scales represents a fundamental focus in conservation biogeography, given their exceptional susceptibility to both climate change and habitat degradation (Feng *et al.*, 2020). Multi-scale habitat modelling provides more robust ecological inferences by explicitly accounting for hierarchical habitat selection processes across complementary spatial and temporal scales (Wiens, 1989; Levin, 1992). The strength of the relationship between specific bird species and their individual habitats varies significantly among different species (Wiens, 1989). Some species are restricted to a single biotope, while others are more generalized and inhabit a broader variety of them (Futuyma & Moreno, 1988). Particularly for specialist species, comprehensive assessment of habitat selection must incorporate multiple spatial scales and critical biological periods (Berlusconi *et al.,* 2022). A multi-scale perspective is essential, as habitat selection depends on scale-specific responses to environmental features (Mayor *et al.,* 2009). Ignoring these scale dependencies may lead to misleading conclusions regarding habitat species relationships (McGarigal *et al.,* 2016).

Although Mediterranean warblers have been extensively studied across multiple ecological dimensions including microhabitat selection (Moreno-Mosquera *et al.,* 2024), broad-scale distribution patterns, historical biogeography (Voelker & Light, 2011), and migratory strategies (Ponti *et al.*, 2018), the Tristram's warbler *C. deserticola* remains comparatively understudied. While basic distribution data exist for Tristram's warbler *C. deserticola* (Isenmann & Moali 2000; Aymí & Gargallo, 2021), critical knowledge gaps persist regarding both its current potential distribution and specific breeding habitat requirements. Notably, only one study (Doswald *et al.*, 2009) has examined climate change impacts on Mediterranean warbler species' (including *C. deserticola*) breeding and non-breeding ranges (North Africa and Europe), thus finding that range-restricted species with narrow and overlapping seasonal distributions like *C. deserticola* are particularly vulnerable to climate warming. Given these gaps, it is crucial to improve our understanding of Tristram's warbler's habitat distribution and selection patterns to Inform conservation strategies, particularly for this range-restricted and thermally sensitive species. The objective of this study is to assess the habitat suitability and ecological preferences of *C. deserticola* across Northern Africa using a dual-scale approach. At the macro scale, we applied species distribution modelling (SDM), which has become a fundamental tool in ecology and conservation (Zurell *et al.*, 2020), using Random

Forest and BRT algorithms to identify suitable habitats. At the micro scale, we examined field-collected data using Generalised Linear Models (GLM) to determine which local habitat variables best explain the presence of the species.

2. Materials and methods

2.1. Study area

The study was conducted in North Africa, specifically in Algeria and Tunisia, which host diverse forest habitats that serve as key refuges for forest-dependent bird species (Bouchenak *et al.*, 2024). Key areas such as the Djurdjura and Akfadou forests (Algeria) and the Kroumirie and Mogod mountains (Tunisia) support endemic species, including the endangered Algerian Nuthatch *Sitta ledanti* and Levaillant's Woodpecker *Picus vaillantii* (Isenmann & Moali, 2000; Isenmann & Thévenot, 2018). However, forest ecosystem threats may negatively impact avian diversity and distribution (Mariano-Neto & Santos, 2023). Within this context, SDMs were performed at the regional scale using occurrence data from both countries. Additionally, field surveys were carried out in El Merahna (36°11′16.8″N, 8°13′29.9″E) and El Hedada (36°8′57.9″N, 8°17′40.4″E), two forest sites located in the Souk Ahras region, northeastern Algeria, to further investigate habitat features at the local scale (Figure 1).

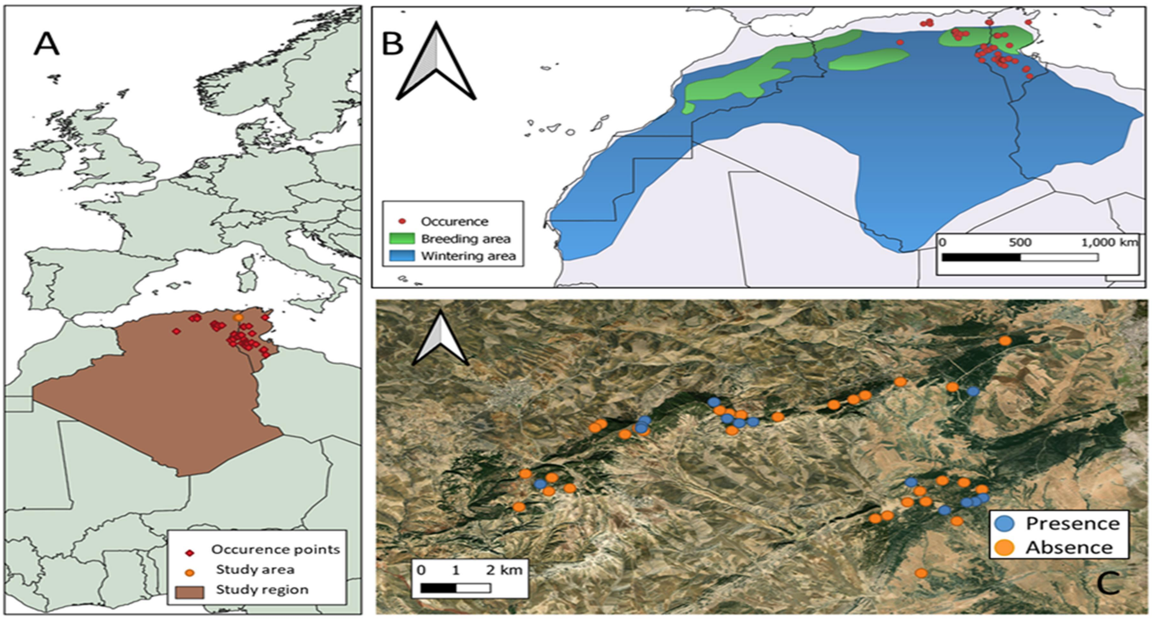

Figure 1. Geographical location of the study area: A) Occurrence records of *Curruca deserticola* across Algeria and Tunisia used for SDM; B) Historical range of breeding and wintering range obtained from Handbook of the Birds of the World; C) Local-scale field survey sites in Souk Ahras province (Merahna and El Hedada)

2.2. Data occurrence and environmental variables

The data used for species distribution modelling were primarily obtained from open-access biodiversity databases. Occurrence records were downloaded, filtered, and processed from the Global Biodiversity Information Facility (GBIF; accessed 12 March 2025, Occurrence Download: https://doi.org/10.15468/dl.8vpyaw) and the eBird Basic Dataset (eBird; https://ebird.org/data/download). We retained only records from Tunisia and Algeria, as the literature identifies two subspecies: one in Morocco, and another found in Tunisia and Algeria (Aymí & Gargallo, 2021). To avoid potential bias in the distribution model, Moroccan records were excluded. After gathering the presence and absence data, we filtered the dataset to retain only records corresponding to the breeding season, defined here as March to June.

After filtering, 156 presence records (1970–2024) were retained. Absence data were generated using the *auk_zerofill()* function from the auk R package, based on complete eBird checklists with at least 2 hours of effort, over 4 km, and using "stationary" or "travelling" protocols (Strimas-Mackey *et al.*, 2018).

Spatial thinning was applied using the thin_by_dist() function from the tidysdm R package (Leonardi *et al.*, 2023), with a 1 km minimum distance to reduce sampling bias and spatial autocorrelation (Mammola *et al.,* 2018), resulting in 37 presence and 195 absence points. Nineteen bioclimatic variables, as well as elevation data, were obtained from the WorldClim 2.1 database at a spatial resolution of 30 arc-seconds (~1 km^2) (Fick & Hijmans, 2017). In addition, the Enhanced Vegetation Index (EVI) was used as an environmental predictor for the macro-scale study. All predictors were resampled to the same spatial resolution using the *resample()* function from the R package raster (Hijmans *et al.*, 2013), to ensure consistent resolution and alignment. Before modelling, pairwise correlations between variables were assessed using Pearson's correlation coefficient and the Variance Inflation Factor (VIF). Variables showing high correlation ($r > 0.7$ or $VIF > 5$) were excluded to reduce multicollinearity and improve model reliability. The final predictors were Annual Mean Temperature, Annual Precipitation, EVI, and Elevation.

2.3. Microhabitat characterisation and field sampling

The two study sites, El Merahna and El Hedada (Souk Ahras), located at approximately 900 m elevation, are dominated by Aleppo pine and were selected to investigate microhabitat preferences. The vegetation includes *Quercus ilex*, *Pistacia lentiscus*, *Cistus* spp., and other typical Mediterranean shrubs. Twelve environmental variables related to forest structure, vegetation, and topography were measured within 18 m radius plots (Rondeux and Lecomte 2005), spaced at least 500 m apart. Aspect was transformed into a linear variable to account for its circular nature, with values ranging from -1 (SSW) to 1 (NNE), and was used in all analyses (Table 1).

Table 1. Environmental variables measured at the micro-habitat scale

Variable code	**Description**	**Mean ± SD**
Slope	Slope (degrees)	10.68 ± 6.3
NLT	Number of large trees (circumference >150 cm at 1.30 m height)	1.02 ± 2.82
NMT	Number of medium trees (circumference 90–149 cm at 1.30 m height)	26.07 ± 27.41
NST	Number of small trees (circumference 40–89 cm at 1.30 m height)	66.44 ± 21.94
CW	Canopy width (m)	2.87 ± 0.68
TC	Tree cover (%)	9.8 ± 10.74
Linear Aspect	Linear Aspect (Slope orientation)	0.17 ± 0.63
SC_0.5_2m	Shrub cover between 0.5 and 2 metres height (%)	50.22 ± 23.28
SC 2 4m	Shrub cover between 2 and 4 metres height (%)	7.33 ± 10.69
TVC	Total vegetation cover (%)	71.67 ± 15.52
HLH	Height of herbaceous layer (m)	43.87 ± 31.29
HC_0_0.125m	Herbaceous cover between 0 and 0.125 metres (%)	26.93 ± 30.6

2.4. Species distribution modelling (SDM)

To identify suitable habitats, we applied two machine learning algorithms, namely Random Forest (RF) and Boosted Regression Trees (BRT), due to their strength in modelling nonlinear relationships and complex interactions among predictors (Cutler *et al.*, 2007; Elith *et al.,* 2008). The dataset was randomly split into training (70%) and testing (30%) subsets for model evaluation. Performance was assessed using AUC, TSS, and Cohen's Kappa, AUC values range between 0 and 1, whereas TSS and Kappa range from -1 to 1. In all cases, higher values reflect better predictive performance (Fernandes *et al.*, 2019). An ensemble model was then created by averaging model outputs weighted by TSS scores. Habitat suitability maps, binary presence–absence maps, variable importance plots, N-dimensional hypervolume representations of ecological variables, and response curves illustrating the effect of predictors on suitability were generated using the sdm package in R (Naimi & Araújo, 2016).

2.5. Microhabitat statistical analysis

To evaluate the influence of habitat variables on the presence/absence of *C. deserticola*, generalised linear model (GLM) with binomial distribution and a logit link function was fitted using the *glm()* function in R. Variable selection was conducted using a stepwise procedure implemented via the *My.stepwise.glm()* function Implemented in the R package My.stepwise (Company ISC, 2017), which allows automatic inclusion and exclusion of variables based on predefined significance thresholds (sle = sls = 0.25).

Model assumptions were checked using residual diagnostics, and multicollinearity among predictors was assessed using variance inflation factors (VIFs), with all retained variables showing VIF values under 5, indicating negligible collinearity. The final model was selected based on the lowest AIC value. Performance was evaluated using the Hosmer–Lemeshow test and AUC of the ROC curve. Microhabitat suitability was defined by retaining predicted cases with logistic probability ≥ 0.7, representing high-confidence presence. All analyses were conducted in R version 4.4.1 (R Core Team, 2023).

3. Results

3.1. Model assessment

Across the 12 model runs, AUC values ranged from 0.731 to 0.933, indicating good to excellent discrimination ability. TSS values varied from 0.442 to 0.785, with the best models showing high sensitivity and specificity. The highest-performing model (ID = 4) achieved AUC = 0.933, TSS = 0.785, sensitivity = 1.000, and specificity = 0.937, with a Kappa value of 0.850 (Table 2).

Table 2. Evaluation metrics of the SDM models

Model ID	AUC	TSS	Sensitivity	Specificity	Kappa
1	0.816	0.589	0.917	0.672	0.369
2	0.747	0.663	0.750	0.913	0.622
3	0.731	0.442	0.667	0.776	0.341
4	0.933	0.785	1.000	0.937	0.850
5	0.889	0.746	0.923	0.812	0.570
6	0.800	0.667	0.667	1.000	0.757
7	0.774	0.589	0.917	0.672	0.369
8	0.747	0.512	0.667	0.741	0.352
9	0.747	0.465	0.500	0.965	0.536
10	0.904	0.738	0.917	0.922	0.733
11	0.893	0.762	0.923	0.833	0.594
12	0.872	0.628	0.722	0.906	0.616
Mean model performance	0.829	0.621	0.804	0.837	0.538

3.2. Habitat suitability and potential distribution

The suitability map (Figure 2) highlights that the most suitable areas for *C. deserticola* are mainly concentrated in the mountainous and highland regions of northeastern and northwestern Algeria, as well as parts of northwestern Tunisia. High suitability zones (values > 0.6, shown in red) are particularly prominent in areas corresponding to the Aurès and Tellian Atlas ranges, encompassing regions such as Tébessa, Oum El Bouaghi, Khenchela, and parts of western Algeria like Tiaret and Tlemcen. Based on this suitability distribution, the binary habitat map (Figure 3) delineates predicted suitable (coded 1) and unsuitable (coded 0) areas. These predicted habitats cover a total surface of approximately 47 348.382 km² in Algeria and 4 191.564 km² in Tunisia, indicating that the core suitable range is concentrated within Algerian territory.

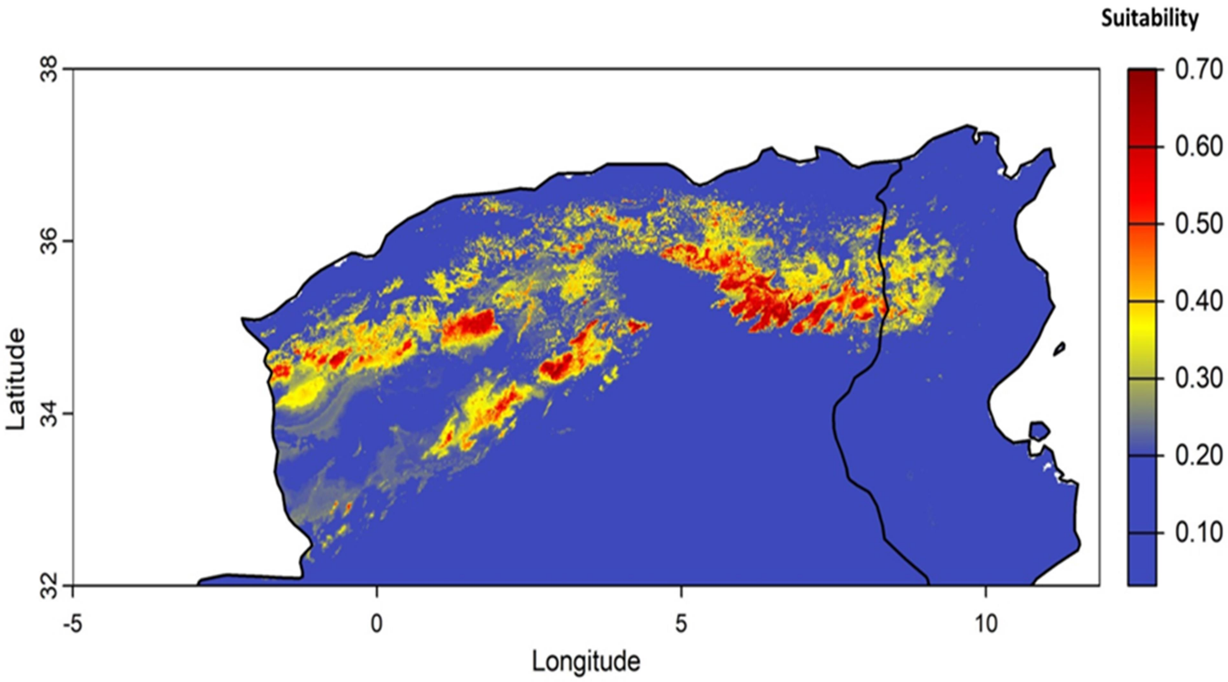

Figure 2. Habitat suitability map for *C. deserticola* in North Africa

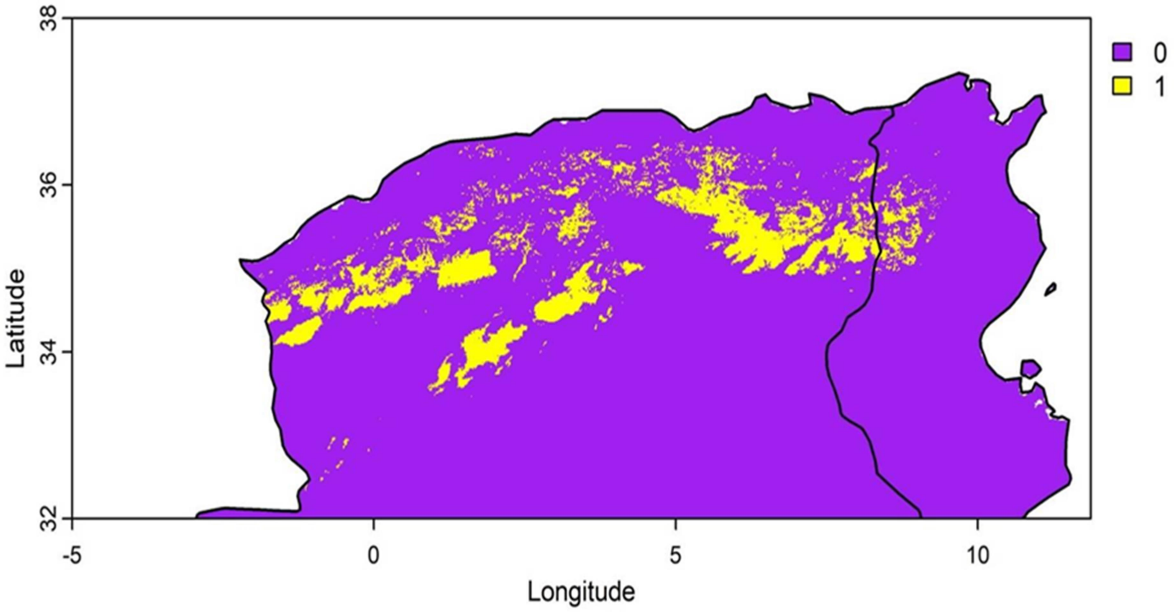

Figure 3. Binary habitat suitability map of *C. deserticola* in North Africa. Areas predicted as suitable habitat (coded 1, shown in yellow) and unsuitable habitat (coded 0, shown in purple)

3.3. Variable importance

Variable importance (Table 3) revealed that elevation was the most influential predictor in the distribution model of *C. deserticola*, showing the highest contribution across both evaluation metrics: 41.4% based on the Pearson correlation metric and 24.2% based on the AUC metric. The Enhanced Vegetation Index (EVI) ranked second, contributing 14.9% according to the correlation metric and 9.2% based on the AUC metric.. Annual Mean Temperature also contributed notably, with values of 17.7% and 7.5% across the two metrics, respectively. Lastly, Annual Precipitation showed the lowest importance scores (7.3% and 5.2%), suggesting that although it contributes to the suitability model, its influence remains comparatively weaker.

Table 3. Relative importance (%) of environmental predictors for the distribution of *C. deserticola* based on Pearson correlation and AUC metrics

Variables	Importance (Pearson correlation Metric %)	Importance (AUC Metric %)
Elevation	41.4	24.2
Enhanced Vegetation Index (EVI)	14.9	9.2
Annual Mean Temperature	17.7	7.5
Annual Precipitation	7.3	5.2

3.4. Relationship between environmental factors and habitat suitability

Following the patterns observed in the response curves, suitability was highest at Annual Mean Temperatures between 12 and 14 °C, with a marked decline above 15 °C. Annual precipitation showed a positive effect on suitability, ranging from approximately 250 mm to 500 mm, Elevation had a strong positive relationship with suitability where it reached its peak at 1 250 metres, Enhanced Vegetation Index (EVI) showed the highest suitability for values ranging from 0.15 to 0.2, while Precipitation Seasonality was generally associated with a decline in suitability. Finally, The Mean Temperature of the Warmest Quarter showed the highest suitability values, exceeding 0.5 between 22 °C and 23 °C (Figure 4).

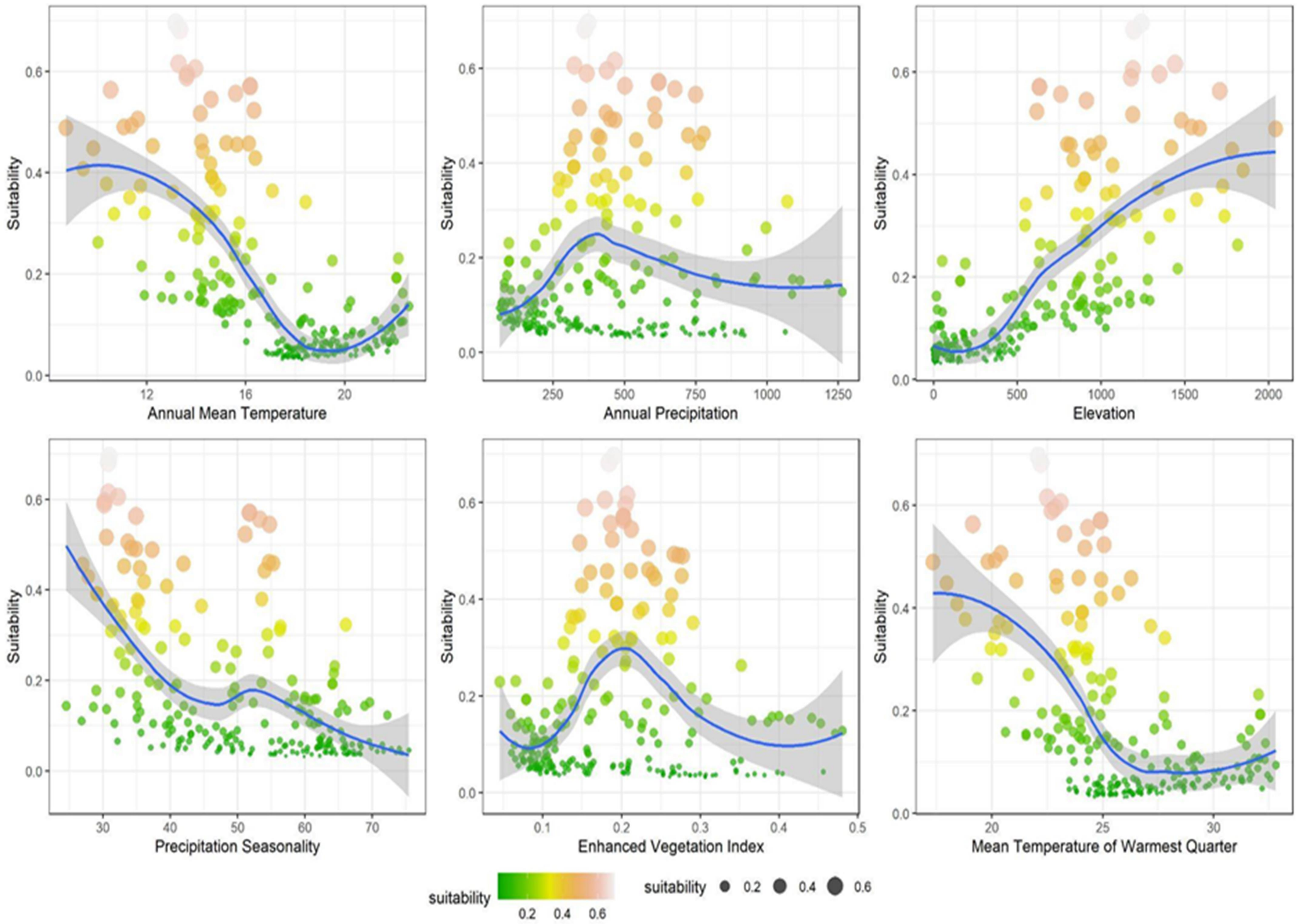

Figure 4. Response curves illustrating how environmental variables influence the predicted habitat suitability for *C. deserticola*.

3.5. Environmental niche characterisation

Figure 5A shows that the highest habitat suitability for *Curruca deserticola* occurs in areas with mean temperatures during the warmest quarter ranging from 20 to 22.5 °C, combined with low precipitation seasonality (30–40%). Figure 5B indicates a clear preference for sites with Enhanced Vegetation Index (EVI) values between 0.15 and 0.2, and annual precipitation ranging from 250 to 650 mm. Figure 5C reveals that the species tends to favour areas with annual mean temperatures between 11 and 14 °C, typically found at elevations of 1 250 to 1 500 metres above sea level.

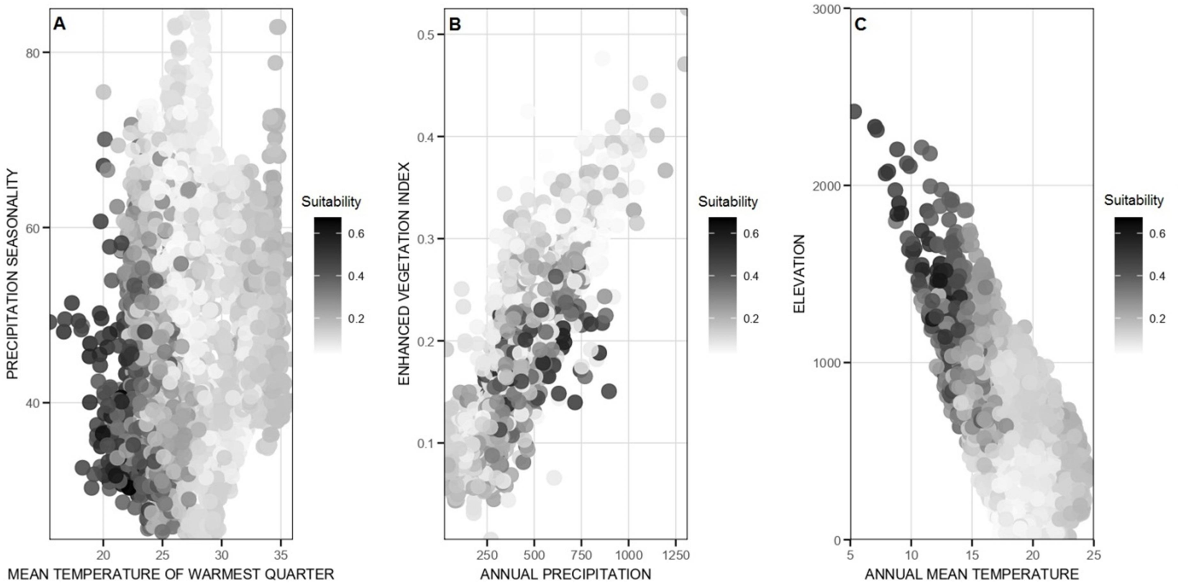

Figure 5. N-dimensional hypervolume niche plots illustrating the response of *C. deserticola* to pairs of environmental variables

3.6. Microhabitat selection

The final model showed good fit (Hosmer–Lemeshow $p = 0.42$) and strong discrimination (AUC = 0.816). The model included five predictors, with small trees and slope having significant positive effects. Shrub cover was marginally significant, while canopy width and aspect were not (Table 4).

Table 4. Summary of the logistic regression model (GLM) explaining the presence of *C. deserticola* based on five micro-habitat variables

Variable	Odds Ratio	Std. Error	z-value	p-value
Intercept		3.64176	-2.777	0.00549 **
N_SmallTrees	1.064	0.02857	2.298	0.02155 *
ShrubCover_2_4m	1.163	0.03627	1.676	0.09377.
Slope	1.082	0.07802	2.148	0.03171 *
Canopy_Width	1.064	0.63708	1.377	0.16864
Linear Aspect	1.307	0.65000	0.413	0.67993

**: $p < 0.01$, *: $p < 0.05$

Microhabitat conditions associated with high predicted presence (≥ 0.7) were characterised by a mean density of 123 small trees, a shrub cover between 2 and 4 metres in height reaching 22.7%, a slope inclination of 14.9°, a canopy width of 3.0 metres, and a linear aspect value of 0.04. The corresponding 95% confidence intervals for these variables are provided in Table 5.

Table 5. Micro-habitat conditions associated with high predicted presence (≥ 0.7).

Variable	Mean	95% CI
Small Trees	123	[117–129]
Shrub Cover 2–4m	22.70%	[20.0–25.4]
Slope	14.9°	[13.3–16.5]
Canopy Width	3.0 m	[2.7–3.2]
Linear Aspect	0.04	[-0.10–0.18]

4. Discussion

The present study provides a comprehensive multi-scale analysis of the habitat suitability of the Tristram's Warbler (*Curruca deserticola*) in Northern Africa. By integrating both macroecological modelling (SDM using Random Forest and BRT) and microhabitat analysis (GLM based on field-collected data), thus providing insights into the species' habitat selection and spatial distribution of *C. deserticola*. These findings are particularly relevant for the conservation of this North African endemic species, whose ecological requirements remain understudied. SDM identified elevation (41.4% contribution), EVI (14.9%), and annual mean temperature (17.7%) as the dominant macro-scale drivers, while microhabitat analysis highlighted small trees (p = 0.021) and slope (p = 0.032) as critical local predictors. The potential distribution of Tristram's Warbler, derived from species distribution modelling (SDM), aligns with its historical range as described by Isenmann and Moali (2000), and Aymí and Gargallo (2021).

Our results confirm that *C. deserticola* is primarily associated with highland environments, which aligns with the concept of realised niche as defined by Hirzel and Le Lay (2008). The positive association between suitability and elevation, with optimal values around 1 250 m, suggests that higher elevations provide favourable conditions for the species, as elevation has previously been identified as an important predictor of avian species distributions (Snell Taylor *et al.,* 2020). Likely due to reduced disturbance and the presence of specific vegetation types in these areas (White & Bennett 2015; Yousefi *et al.*, 2023), as Aymí and Gargallo (2021) report that *C. deserticola* breeds in dry montane scrublands between 1 000 and 2 500 metres, particularly in habitats dominated by dense juniper thickets and open holm oak woodlands.

These elevation preferences appear to be tightly linked to temperature gradients, as elevation not only defines vegetation structure but also regulates thermal conditions (Wang *et al.*, 2020; Wang *et al.*, 2022). Annual Mean Temperature was also identified as a key predictor in our model, with the highest habitat suitability for *C. deserticola* observed between 12 °C and 14 °C, and a marked decline beyond 15 °C. This thermal range corresponds to semi-arid regions where *C. deserticola* is typically found (Biederman *et al.*, 2018). While specific physiological studies on *Curruca deserticola* are lacking, Brotons *et al.* (2018) noted that its climatic niche differs from that of other *Curruca* species, such as *C. cantillans* and *C. melanocephala*, which reach their highest abundances in the warmer southern Mediterranean, particularly in open shrubland habitats. This pattern aligns with observations by Blondel and Aronson (1999), who noted that Mediterranean *Curruca* species exhibit distinct habitat preferences influenced by temperature gradients and vegetation structure.

In addition to elevation and temperature, the Enhanced Vegetation Index (EVI) was also identified as a significant predictor of habitat suitability. The association of *Curruca deserticola* with intermediate values of vegetation greenness (EVI: 0.15–0.2) suggests a preference for semi-open shrublands characterised by a mix of sparse and denser vegetative patches (Wang *et al.*, 2022). As Blondel (1965) noted, Mediterranean warblers such as *C. deserticola* exhibit a remarkable ecological expansion into dry habitats. Several species within *Curruca* species, such as *Curruca cantillans* and *C. melanocephala*, occupy structurally heterogeneous habitats characterised by variation in vegetation height, shrub density, and canopy cover, which together offer a mosaic of microhabitats for nesting, foraging, and shelter (Brotons *et al.*, 2018).

Although annual precipitation was the least influential predictor in our model, it showed an effect on habitat suitability, particularly within the 250–500 mm range, corresponding to semi-arid zones characterised by open, dry, and structurally heterogeneous shrublands (FAO, 2000). Although precipitation may not directly determine the presence of *C. deserticola*, it plays a critical indirect role by regulating vegetation productivity and food availability especially during the breeding season and in the low to mid-elevation zones where the species occurs (Wang *et al.*, 2022). Enhanced vegetative growth linked to seasonal rainfall can increase the abundance of invertebrate prey (Brotons *et al.*, 2018), directly benefiting insectivorous warblers such as *C. deserticola*. In Mediterranean landscapes, such rainfall-driven productivity influences bird habitat selection and distribution patterns, including those of frugivorous and insectivorous passerines (Tellería *et al.*, 2005).

In addition to macro-ecological factors, microhabitat analysis revealed that the presence of *C. deserticola* was positively associated with the number of small trees, while many studies emphasise the ecological importance of large-diameter trees, Dondina *et al.* (2015) highlighted the ecological importance of small trees, showing that *Sitta europaea* and *Cyanistes caeruleus* have positive associations with trees in this diameter range.

Shrub cover between 2 and 4 metres also appeared as a favourable feature, although its effect was marginally significant. Catfolis *et al.* (2023) reported that dense shrub layers and diverse young tree structures play a crucial role in providing resources and habitat for a wide range of bird species, according to Melin *et al.* (2018), diversity along edges is largely driven by the density of vegetation below 4 metres. Furthermore, Krebs *el al.* (2019) highlighted that the understorey vegetation structure and its relationship with forest canopies and site conditions are important determinants of wildlife habitat quality.

Slope had a significant positive effect on the presence of the species, likely due to its influence on vegetation structure, site productivity and secondary biotic interactions (Kebede *et al.,* 2013). Additionally, Kellner (2018) found that slope, alongside elevation and aspect, significantly influenced the local abundance of bird species. In contrast, canopy width and aspect were not significant, suggesting that relatively canopy conditions align with the species' habitat preferences.

Although species distribution models (SDMs) represent a powerful tool for understanding and predicting species environment relationships, several limitations must be considered when interpreting their outputs. A key challenge is that SDMs often rely solely on environmental variables and ignore important ecological processes, such as species interactions, dispersal limitations, or demographic dynamics (Dormann *et al.,* 2012), Small sample sizes, can lead to unstable and inaccurate predictions, regardless of the algorithm used (Wisz *et al.*, 2008).

Moreover, spatial biases and positional errors in occurrence data can reduce model reliability, and these issues are not resolved by using coarser spatial resolutions (Gábor *et al.,* 2022). Even advanced methods like MaxEnt can produce biased results if the input data are unevenly distributed or poorly georeferenced (Syfert *et al.,* 2013). Finally, the generation of pseudo-absences plays a critical role in model accuracy, as their number, location, and distance from presence points can affect predictions (Barbet-Massin *et al.*, 2012).

Despite methodological limitations, multi-scale approaches are essential in habitat selection studies, as ecological processes are inherently scale-dependent, and overlooking spatial or temporal scales can mislead interpretations of species environment relationships (Wiens, 1989; McGarigal *et al.*, 2016). At large scales, broad climatic and topographic variables may define the potential distribution, while at finer scales, structural habitat components and biotic interactions become more influential (Mayor *et al.*, 2009).

This study provides the first comprehensive multi-scale assessment of the habitat suitability of the Tristram's Warbler *Curruca deserticola* across Northern Africa, integrating both macroecological and microhabitat perspectives. Our findings highlight the species' strong association with highland environments characterised by moderate temperatures, intermediate vegetation greenness, and structurally heterogeneous shrublands. Such specific habitat preferences suggest that *C. deserticola* may be particularly vulnerable to ongoing habitat alterations, including those driven by climate change, as species with narrow ecological niches and limited distributions are often more susceptible to environmental changes (Jacobsen *et al.*, 2020). These insights are crucial for informing conservation planning and habitat management strategies for this endemic species, emphasising the need for targeted actions to preserve its specialised habitats (Skolnik *et al.*, 2012). Future research integrating physiological tolerance studies and long-term monitoring would further enhance our understanding of the ecological requirements and resilience of *C. deserticola* in a changing environment.

5. References

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GENERAL
DISCUSSION

General discussion

The results obtained in this thesis show that the distribution of Mediterranean warblers mainly depends on a combination of climatic, topographic, and vegetation structure factors. The relative importance of these factors varies according to species and season. In particular, the analyses consistently identified temperature, elevation, and vegetation heterogeneity as the most influential predictors of species occurrence, confirming that habitat selection in Sylviid warblers results from their interaction, as previously observed in other Mediterranean ecosystems (Blondel & Aronson, 1999; Brotons *et al.*, 2018)

From a methodological point of view, this thesis uses large-scale species distribution models (SDMs) and small-scale microhabitat analyses. SDMs identify climatically suitable areas, while local analyses describe the ecological conditions that determine species presence (Soberón & Peterson, 2005; Elith *et al.*, 2011; Guisan *et al.*, 2017). This multi-scale approach is particularly valuable as it links broad climatic factors with local habitat characteristics.

From an ecological point of view, the seasonal analyses highlight different adaptation strategies. During the breeding season, warblers prefer areas with moderate temperatures, which favour reproductive success (Sokolov, 2006; Leech & Crick, 2007). In winter, they move to warmer and more stable areas to reduce their energy requirements (Carrascal *et al.*, 2016). This alternation between breeding and wintering habitats illustrates a clear seasonal partitioning of ecological niches (Laube *et al.*, 2015).

The Mediterranean region is recognised as one of the world's major biodiversity hotspots, but also as one of the most vulnerable to climate change (IPCC, 2022). Climate projections indicate an average increase in temperature, a decrease in annual precipitation, and more frequent drought events, coupled with greater interannual variability (Giorgi & Lionello, 2008). These changes profoundly affect habitat availability and quality, as well as bird phenology and reproductive success (Andreasson *et al.*, 2020). In this context, Sylviid warblers are particularly concerned. Huntley *et al.* (2008) projected that these changes may lead to contractions or shifts in their ranges across Europe. A study on several Mediterranean warbler species revealed that breeding sites are shifting northward for most species due to climate change (Doswald *et al.*, 2009). However, sensitivity to climate change varies according to ecological specialisation: specialist species, dependent on particular vegetation structures or climatic conditions, show reduced tolerance to environmental variation and suffer more severe declines than generalists, which can exploit a broader range of habitats (Jiguet *et al.*, 2007).

To effectively protect species and their habitats, SDMs are valuable tools for guiding the development of tailored conservation strategies. Among these strategies, the concept of dynamic reserves has been explicitly recognised as a means to facilitate range shifts in response to environmental change. This approach involves using temporal corridors that connect populations in space and time (Rose & Burton, 2009). Bengtsson *et al.* (2003) developed the concept of "temporary conservation areas," designed to provide periodic protection to fixed sites that can be shifted across space and time to track relevant spatio-temporal dynamics. Another approach consists of restoring and creating scattered favourable habitats that serve as refuges and feeding areas for species (Broughton *et al.*, 2025). For example, the Common Whitethroat (*Curruca communis*) is listed as a vulnerable species in Switzerland due to population declines linked to the loss of hedgerows and shrubs in agricultural landscapes (BirdLife Suisse, 2023). A conservation programme led by BirdLife Suisse was implemented based on the planting of hedgerows, the creation of flowering fallows and herbaceous strips, to provide a network of "stepping stones" enabling birds to move, feed, and breed in a fragmented landscape (BirdLife Suisse, 2023).

SDMs can also support conservation planning by identifying priority areas for biodiversity. In Catalonia (Spain), SDMs helped identify key habitats for four threatened birds and guided the management of an agricultural area (Brotons *et al.*, 2004). In Madagascar, SDMs developed for numerous taxonomic groups (mammals, birds, reptiles, amphibians, freshwater fish, invertebrates, plants) helped define priority conservation areas (Kremen *et al.*, 2008).

GENERAL CONCLUSION

General conclusion

This thesis provides a new contribution to the understanding of the distribution and ecological preferences of Mediterranean warblers in North Africa, through a multi-scale approach ranging from macro-habitat to micro-habitat, and by considering two key phases of their annual cycle: breeding and wintering. By combining data from citizen-science platforms, field observations, and spatial analyses (SDMs, niche analyses, GLMs), it delivers robust insights to guide conservation strategies in a context of climate change and landscape transformation.

At the regional scale, Chapter II highlighted that high-suitability areas for Mediterranean warblers are mostly concentrated in northern Algeria, where moderate temperatures, intermediate to high elevations, and medium to high vegetation productivity overlap. The analysis of niche overlap identified species pairs that are ecologically close and share similar habitats, as well as others with clearly differentiated preferences, underlining the importance of considering interspecific interactions in conservation planning.

For the Marmora's Warbler (*Curruca sarda*), Chapter III revealed that its suitable wintering habitats in North Africa are mainly concentrated in north-eastern Algeria and parts of Tunisia, covering an estimated area of 48 526 km². Annual mean temperature, elevation, and precipitation seasonality emerged as the main determinants, with a marked affinity for semi-arid zones with evergreen vegetation.

For Tristram's Warbler (*Curruca deserticola*), an endemic species, Chapter 4 identified favourable breeding habitats covering about 51 500 km², mainly in mountainous regions. Altitude (optimum around 1 250 m), EVI (0.15–0.20), and annual temperature (12–14 °C) were identified as key macro-habitat factors, while locally, small tree density, intermediate shrub cover, and moderate slope were determinants. These findings illustrate the importance of vertical structural diversity and heterogeneous landscapes.

These results demonstrate that the distribution of Sylviid warblers in North Africa results from a combination of climatic, topographic, and structural factors, which vary by species and season.

Perspectives and recommendations

- Conduct standardised surveys in predicted habitat cores to refine model accuracy and confirm species presence.
- Develop long-term multi-scale monitoring to detect distributional shifts linked to climate or land-use changes.
- Preserve Mediterranean mosaics (maquis, garrigue, edges, open woodlands) and ecological corridors, while limiting fragmentation.
- Adapt forest management to maintain vertical heterogeneity and avoid homogenising interventions.

In conclusion, this work demonstrates that the combination of spatial data, ecological analyses, and field knowledge provides a solid foundation for developing effective conservation strategies tailored to the specific requirements of Mediterranean species.

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