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Potential winter distribution and stopovers of a long-distance migratory falcon: projected climate-induced changes

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Abstract The non-breeding ecology of the Sooty Falcon *(Falco concolor)* remains poorly understood despite its relevance for the conservation of this long-distance migratory species, which is undergoing population declines across its range. In this study, a georeferenced database of 535 non-breeding records from Africa and Madagascar was compiled to model climatic suitability across three phases of the annual cycle: post-breeding, wintering, and post-wintering. Current models indicate that post-breeding movements occur mainly through montane and sub-humid tropical regions of East Africa, whereas wintering areas are concentrated in Madagascar and, to a lesser extent, in the Mozambican and Malawian highlands. During the post-wintering (pre-breeding) phase, suitable habitats are largely confined to semi-humid zones in central Tanzania and eastern Zambia. Projections for 2050 and 2070 under warming scenarios suggest a progressive reduction and fragmentation of suitable areas, with climatic refugia persisting primarily in high-altitude and coastal environments. These findings highlight increasing climatic constraints on the species' migratory network. Conservation measures should prioritise the protection of humid montane and coastal ecosystems in Madagascar and East Africa, as well as key stopover areas that support migration. A coordinated flyway-level approach integrating climate adaptation and habitat management is recommended to ensure the long-term persistence of non-breeding populations.

Keywords: Sooty Falcon, *Falco concolor*, migration, winter distribution, species distribution models, climatic constraints

Összefoglalás A hamvas sólyom *(Falco concolor)* költésen kívüli ökológiája továbbra is kevéssé ismert, jóllehet ez döntő jelentőségű e hosszútávon vonuló, az elterjedési területének nagy részén csökkenő állományú faj megőrzése szempontjából. Jelen tanulmányban Afrika és Madagaszkár területéről származó 535, költési időszakon kívüli megfigyelést tartalmazó, georeferált adatbázis került összeállításra, annak érdekében, hogy az éghajlat követelményeket az éves ciklus három szakaszában modellezzék: a költés utáni, a telelő és a telelés utáni időszakban. A jelenlegi modellek azt jelzik, hogy a költés utáni mozgások elsősorban Kelet-Afrika hegyvidéki és enyhén nedves trópusi régióin keresztül zajlanak, míg a telelőterületek Madagaszkárra, kisebb mértékben pedig Mozambik és Malawi felföldjeire koncentrálódnak. A telelés utáni (költés előtti) szakaszban az alkalmas élőhelyek nagyrészt Tanzánia középső, mérsékelten nedves zónáira és Zambia keleti területeire korlátozódnak. A 2050-re és 2070-re vonatkozó, a felmelegedésen alapuló forgatókönyvek szerinti előrejelzések az alkalmas területek fokozatos csökkenését és feldarabolódását sugallják, miközben éghajlati refúgiumok elsősorban magashegységi és part menti környezetekben maradnak fenn. Az eredmények arra utalnak, hogy a faj vonulási hálózatát egyre erősebb éghajlati hatások érik. A természetvédelmi intézkedéseknek prioritásként kell kezelniük Madagaszkár és Kelet-Afrika nedves hegyvidéki és part menti ökoszisztémáinak védelmét, valamint azokat a kulcsfontosságú megállóhelyeket, amelyek a vonulást segítik. A hosszú távú fennmaradás biztosítása érdekében egy koordinált, vonulási útvonal szintű megközelítés ajánlott, amely ötvözi az éghajlathoz való alkalmazkodást és az élőhelykezelést a költésen kívüli populációk védelmében.

Kulcsszavak: hamvas sólyom, *Falco concolor*, vonulás, telelési elterjedés, elterjedési modellek, éghajlati korlátok

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Introduction

Wintering grounds are essential for migratory bird species, providing crucial resources such as food and shelter during the non-breeding season (Newton 2008). These habitats support the survival of individuals and ensure they are adequately prepared for the return migration and subsequent breeding period (Norris & Marra 2007, McKinlay *et al.* 2024). Any disruption to these habitats can have cascading effects on bird populations, influencing migration success and overall conservation condition of the species (Runge *et al.* 2015). Global warming poses a significant threat to the climatic stability of wintering habitats. Rising temperatures and shifting precipitation patterns may contribute to habitat degradation, reducing food availability and altering ecosystem dynamics (Jetz *et al.* 2007). As climate conditions change, suitable wintering habitats may shift geographically, forcing species to adapt or to relocate. However, not all species are able to adjust effectively, leading to increased mortality rates and reduced reproductive success (Gordo 2007, Studds *et al.* 2017). In addition to climate-related threats, human activities may also contribute to an accelerated loss of wintering habitats. Urban encroachment, deforestation, and agricultural development all contribute to habitat fragmentation and degradation, reducing the availability of suitable wintering areas (Wilcove & Wikelski 2008). When combined with the effects of global warming, these anthropogenic pressures place migratory species at increasing risk, potentially leading to long-term population declines (Fahrig 2003).

The Sooty Falcon *(Falco concolor)* is a medium-sized migratory raptor that breeds in arid regions of the Palearctic across north-eastern Africa, the Arabian Peninsula, and parts of the Persian Gulf (BirdLife International 2022, Leonardi *et al.* 2024). It typically nests on coastal small cliffs, uninhabited islands, and rocky desert landscapes with minimal vegetation (Booth 1961, Clapham 1964, Walter 1979). A peculiar feature of this species is its late breeding season, which coincides with the autumn migration of Eurasian passerines, offering an essential food source for nestlings (Moreau 1969, Mellone 2021). After the breeding season, Sooty Falcons undertake long-distance migrations to their wintering grounds (Javed *et al.* 2012, Al Jahdhami *et al.* 2020). Their primary destination is Madagascar, although some individuals also winter along the coastal regions of Mozambique and eastern South Africa (Mellone 2021). The main routes of adults, after leaving the breeding grounds of the Arabian Peninsula and crossing the Gulf of Aden, follow the Nile and Rift Valleys (Javed *et al.* 2012, Al Jahdhami *et al.* 2020). Tracking studies indicate that juveniles may take different routes than adults, showing greater variability in their migratory paths (Javed *et al.* 2012, Gschweng 2013). Additionally, some Sooty Falcons have been observed using alternative stopover sites in western Africa, likely influenced by prey availability and weather conditions (Buij 2011).

The conservation status of the Sooty Falcon is a growing concern, as the species is currently classified as 'Vulnerable' due to threats such as habitat modification, human disturbances, and predation by introduced, like rats (BirdLife International 2022, Leonardi *et al.* 2024). Climate change and alterations in prey availability may further challenge its survival, especially in its wintering grounds, where habitat degradation is accelerating (Gschweng 2013, McGrady *et al.* 2026). Global warming is expected to alter habitat availability and suitability, potentially affecting migratory routes and survival rates (Trouwborst 2012). These environmental changes may lead to range contractions, shifts, or habitat loss, posing significant challenges for the conservation of migratory raptors (Condro *et al.* 2022, Martínez-Ruiz *et al.* 2023).

This study aims to identify the potential wintering areas and main stopover sites of the Sooty Falcon during its long-distance migratory movements. To achieve this, the Maximum Entropy (MaxEnt) modelling approach is employed, a widely used method for species distribution modelling based on presence-only data (Phillips *et al.* 2006). By integrating occurrence records with environmental variables, MaxEnt allows for the prediction of suitable habitats for the species across its migratory range, providing robust insights into its spatial ecology (Elith *et al.* 2011). Furthermore, potential future changes in the Sooty Falcon's winter distribution and stopover sites are assessed under different climate change scenarios.

Methods

Current species data

An initial database of sightings was compiled for the first draft of the International Single Species Action Plan (ISSAP) for the Sooty Falcon through extensive data mining of academic, grey literature, and web-based databases (Gallo-Orsi *et al.* 2014). Sightings were categorised according to non-breeding stages: post-breeding (October), wintering (November–March), and post-wintering (April–May). The final version of the database was produced after removing duplicates, incomplete observations, and records questioned in the most recent 2022 updates, resulting in a total of 535 records, comprising post-breeding (n=151), wintering (n=303), and spring migration (n=81) records *(Supplementary Material, Figure 1)* (Leonardi *et al.* 2024).

Climatic and topographic predictors

To assess the current and future distribution of the Sooty Falcon, nineteen bioclimatic predictors were obtained from the WorldClim database (http://www.worldclim.org). These predictors are based on interpolated average monthly weather station data collected between 1970 and 2000, providing a baseline for current climatic conditions (Fick & Hijmans 2017).

To project future distributions, bioclimatic variables for the 2050s and 2070s were sourced using two global circulation models (GCMs) from the Coupled Model Intercomparison Project Phase 6 (CMIP6): (1) MIROC5 (Model for Interdisciplinary Research on Climate) and (2) CCSM4 (Community Climate System Model). Both models have demonstrated strong performance in ecological forecasting, particularly for vertebrates such as birds (Langham *et al.* 2015, Hu *et al.* 2020, Sierra-Morales *et al.* 2021). These projections were made under the RCP 6.0 scenario (Representative Concentration Pathway), which represents a stable and intermediate emissions pathway. This scenario assumes a temperature increase of approximately 3 °C above pre-industrial levels (Hof *et al.* 2018). Predictions generated by both GCMs were aggregated for each future time period. To complement the WorldClim dataset, a topographic variable – Terrain Roughness Index (TRI) – was incorporated from the ENVIREM dataset (Title & Bemmels 2018). TRI quantifies elevation differences, classifying terrain from nearly flat (0–80 m) to extremely rugged (959–4367 m) (Riley *et al.* 1999).

Raster layers were acquired at a 30 arc-second spatial resolution (approximately 1 km), and subsequently cropped and masked to a polygon delineating the known dispersal range of the Sooty Falcon across relevant countries (ca. 16,135,223 km^2) including Central African Republic, Chad, Democratic Republic of Congo, Djibouti, Eritrea, Ethiopia, Kenya, Madagascar, Malawi, Mauritius, Mozambique, Namibia, Rwanda, Somalia, South Africa, South Sudan, Sudan, Uganda, United Republic of Tanzania, Zambia, Zimbabwe (Gschweng 2013, Gallo-Orsi *et al.* 2014, Leonardi *et al.* 2024).

To minimize collinearity among predictors, a Variance Inflation Factor (VIF) analysis was applied to all 20 bioclimatic and topographic variables (Guisan *et al*. 2006, Franklin 2010, Dormann *et al.* 2013). Variables with a VIF value below 10 were retained through stepwise elimination, acknowledging that variables with VIF < 5 indicate low correlation and are acceptable for species distribution models (Dormann *et al.* 2013). The remaining variables were further assessed using Spearman's correlation coefficient, and only those with correlation values of $|r_s| \leq 0.7$ were kept. All analyses were conducted in R version 4.3.1 (R Core Team 2023). Following this process, six predictors were selected for post-breeding data (Bio1, Bio2, Bio3, Bio12, Bio18 and Bio19), six for the wintering data (Bio2, Bio3, Bio10, Bio16, Bio19 and TRI), and seven for the post-wintering data (Bio2, Bio4, Bio5, Bio12, Bio14, Bio18 and TRI) *(Supplementary Material, Tables 1–3)*.

Species distribution models

Species distribution models (SDMs) were developed using MaxEnt (version 3.4.1), a widely used algorithm that relies on presence-background data and performs well even with limited occurrence records (Phillips *et al.* 2006, Phillips & Dudík 2008, Duan *et al.* 2014). The model identifies the environmental conditions associated with species presence by contrasting them with randomly sampled background conditions, resulting in a spatial prediction map of habitat suitability (Zeng *et al.* 2015).

To estimate continuous suitability across the landscape, the *cloglog* (log-log) output transformation was selected. This transformation scales predicted values from 0 (lowest suitability) to 1 (highest suitability). Model settings followed MaxEnt defaults, with 10,000 background points and a convergence threshold set at 10^{-5}. To ensure model stability, the maximum number of iterations was increased from the default 500 to 5,000.

Model evaluation and tuning were guided by best practices for ecological forecasting. Data were partitioned into training (70%) and testing (30%) subsets, a method commonly recommended for projecting models under future climate scenarios (Phillips & Dudík 2008). To explore model complexity, combinations of regularization multipliers β (ranging from 0.5 to 5, in steps of 0.5) and feature classes (linear (L), quadratic (Q), hinge (H), product (P), and threshold (T)) were tested in four combinations of features: LQ, LQH, LQHP, and LQHPT (Warren & Seifert 2011).

Model performance was assessed using the "block" cross-validation method (k=4) implemented in the *ENMeval* package in R (Muscarella *et al.* 2014). The best-performing model was selected based on Akaike's Information Criterion corrected for small sample sizes (AICc, Akaike 1974, Hurvich & Tsai 1989) *(Table 1)*, and then used to project species distributions under future climate scenarios for the years 2050 and 2070.

Model evaluation

To evaluate model performance, we used the area under the curve (AUC) metric. AUC values range from 0.5 (no better than random prediction) to 1.0 (maximum predictive performance). The optimal model was selected based on the highest AUC values. To assess model overfitting, we calculated the difference between training and testing AUC ($AUC_{DIFF} = AUC_{TRAIN} - AUC_{TEST}$). Values close to zero indicate minimal overfitting, reflecting a more generalizable model (Muscarella *et al.* 2014).

We also computed the True Skill Statistic (TSS) and the continuous Boyce Index (CBI) as secondary evaluation metrics (Allouche *et al.* 2006, Hirzel *et al.* 2006). TSS values range from -1 to +1, where +1 indicates perfect performance, 0 reflects random prediction, and values ≥ 0.5 suggest good model reliability (Allouche *et al.* 2006). CBI values also range from -1 to +1. Positive values indicate agreement between predicted climate suitability and observed presences, values near zero imply performance similar to a random model, and negative values suggest poor suitability predictions in areas with many observed occurrences (Hirzel *et al.* 2006).

We assessed the importance of each environmental variable within the ensemble model using the *getVarImp* function, ranking variables by their AUC test scores. To illustrate the relationship between key environmental predictors and the probability of species presence, we generated Partial Dependence Plots (PDPs) for the three most influential variables.

When projecting models across different spatial or temporal contexts, extrapolation of predictor variables can introduce significant error – particularly in correlative species distribution models (SDMs) (Elith *et al.* 2011). To mitigate this, we applied a multivariate environmental similarity surface (MESS) analysis to identify areas where predictor variables fall outside the calibration range (Elith *et al.* 2011).

Results

Species distribution model

Across all non-breeding stages, the best candidate models show strong performance in terms of AUC and CBI, yet relatively lower TSS values and consistent spatial autocorrelation highlight the importance of accounting for spatial structure in model evaluation *(Table 1)*. The post-breeding model demonstrates good predictive performance, with AUC and CBI values both >0.8, and a low omission rate (<0.2), although the MOR value of 0.360 suggests some residual spatial autocorrelation. During the wintering stage, the model performs very well, with high AUC and CBI values (>0.8), but a slightly higher omission rate of 0.220 suggests possible underprediction in certain regions *(Table 1)*. In the spring migration stage, the model reaches its highest accuracy, with AUC and pROC values around or above 0.9, although the high spatial autocorrelation (MOR=0.456) may signal overfitting to spatial patterns *(Table 1)*.

Table 1. Comparative performance metrics of best-fit species distribution models (ΔAICc = 0.0), including Regularisation Multiplier (RM), Feature Classes (FC: L = Linear, Q = Quadratic, P = Product, H = Hinge), and validation statistics: Area Under the Curve (AUC), Continuous Boyce Index (CBI), True Skill Statistic (TSS), Mean Overlap Ratio (MOR), Omission Rate at 10% training threshold (OM10), and partial ROC (pROC) averaged across bootstrap replicates

1. táblázat A legjobban illeszkedő elterjedési modellek összehasonlító teljesítménymutatói (ΔAICc = 0,0), beleértve a regularizációs szorzót (RM), a változótípusokat (FC: L = lineáris, Q = kvadratikus, P = szorzat, H = töréspontos), és az érvényességi statisztikákat: a görbe alatti területet (AUC), a folytonos Boyce-indexet (CBI), a True Skill-statisztikát (TSS), az átlagos átfedési arányt (MOR), a 10%-os tanulási küszöb melletti kihagyási arányt (OM10), és a részleges ROC-értéket (pROC), amelyeket bootstrap ismétlések átlagaként számoltak

	RM	FC	AUC	CBI	TSS	MOR	OM10	pROC
Post-breeding	0.5	LQ	0.810	0.829	0.512	0.360	0.181	0.82
Wintering	0.5	LQPH	0.858	0.851	0.488	0.365	0.220	0.88
Spring migration	0.5	LQPH	0.880	0.821	0.431	0.456	0.183	0.92

Predicted current distribution

Under current climatic conditions, areas of highest suitability during the post-breeding period are concentrated in the Ethiopian Highlands, eastern part of Democratic Republic of the Congo, south Uganda, west Kenya, and parts of northern Tanzania. Additional suitable zones extend into the southern part of the Rift Valley and central Madagascar *(Figure 1)*.

During wintering, suitability shifts southwards and becomes more restricted. The most suitable areas occur in eastern Zambia, Malawi, the central Mozambican highlands, and Madagascar, particularly along the eastern escarpment *(Figure 1)*.

In the post-wintering period, suitability markedly decreases across the subcontinent, with only limited patches of favourable conditions persisting in central Tanzania, south Malawi, and eastern Zambia. Smaller suitable areas are also present in northern Mozambique and the eastern margins of Madagascar *(Figure 1)*.

Predicted future distribution

Future scenarios project a general decline and spatial shift in climatic suitability across all phases *(Figure 1)*. During the post-breeding period, models predict a southward extension and fragmentation of suitable areas. By 2050, suitability diminishes across most of Tanzania and Uganda, and also in the southern part of the Rift Valley, persisting only in the Ethiopian and Kenyan highlands, as well in eastern Madagascar. By 2070, suitable zones become restricted to high-elevation and humid montane regions.

For the wintering period, projections indicate a substantial loss in suitable habitat, particularly within continental southern Africa. By mid-century, suitability will persist only in the Mozambican and Malawian highlands and Madagascar, while by 2070, the latter will emerges as the main climate refugium.

During the post-wintering period, both 2050 and 2070 projections reveal a further reduction and isolation of suitable areas. Limited patches will persist in central Tanzania and the eastern escarpment, while most regions of Zambia, Malawi, but Mozambique will become unsuitable. By 2070, only small high-altitude remnants will remain.

Environmental predictors

Sooty Falcon predicted occurrence during the post-breeding season increased with temperature seasonality (Bio3), reaching its highest values under moderate to high variability *(Figure 2)*. Suitability in relation to annual precipitation (Bio12) peaked at intermediate levels, while precipitation of the warmest quarter (Bio18) showed a consistent positive trend towards wetter conditions *(Figure 2)*. These patterns indicate a preference for areas with pronounced temperature fluctuations and humid warm periods.

Suitability was highest under moderate mean diurnal temperature range (Bio2) and declined sharply with increasing mean temperature of the warmest quarter (Bio10) in the wintering period *(Figure 2)*. The relationship with precipitation of the wettest quarter (Bio16) was non-linear, rising under intermediate to high precipitation *(Figure 2)*. Overall, wintering distribution appears constrained by excessive heat but favoured in humid environments.

Predicted values were generally low across climatic gradients during post-wintering, with suitability decreasing along with changes in mean diurnal temperature range (Bio02) and annual precipitation (Bio12), if precipitation of the driest month (Bio14) peaked at moderate values *(Figure 2)*. These indicators suggest a preference for dry and thermally stable conditions at the end of the annual cycle.

Discussion

Following the breeding season, Sooty Falcons depart from their breeding grounds and migrate to their wintering areas via a variety of dispersal and migratory routes (Javed *et al.* 2012, Al Jahdhami *et al.* 2020, McGrady *et al.* 2026). Although the details of these movements remain incompletely understood – owing to sightings recorded across many

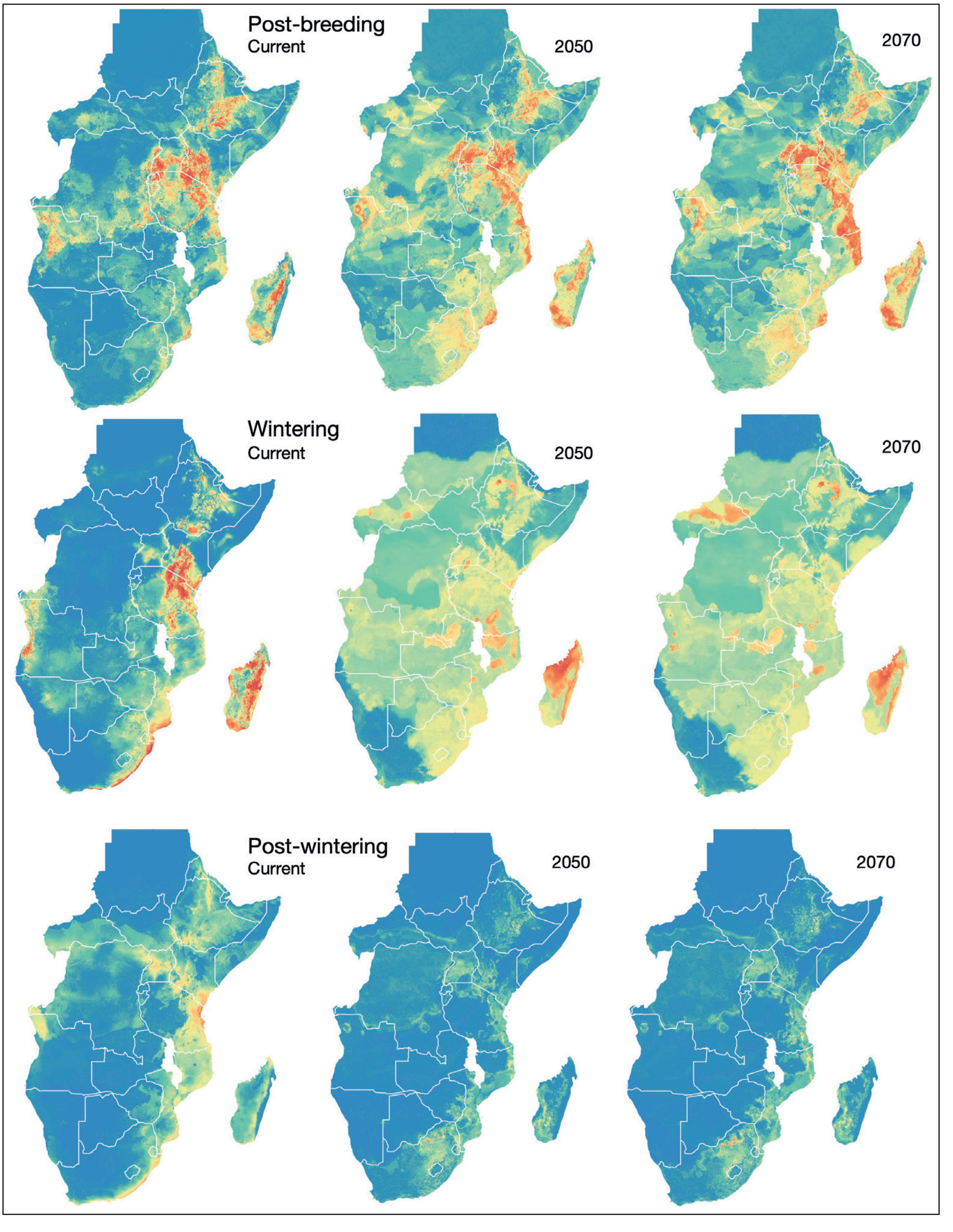

Figure 1. Predicted current and future distribution of Sooty Falcon during the non-breeding period, segmented into three phases: (1) post-breeding migration, (2) wintering distribution, and (3) post-wintering migration. The intensity of red colour indicates higher habitat suitability

1. ábra A hamvas sólyom költésen kívüli időszakra előre jelzett jelenlegi és jövőbeni elterjedése, három fázisra bontva: (1) költés utáni vonulás, (2) telelő elterjedés, és (3) telelés utáni vonulás. A piros szín intenzitása az élőhely alkalmasságának mértékét jelzi

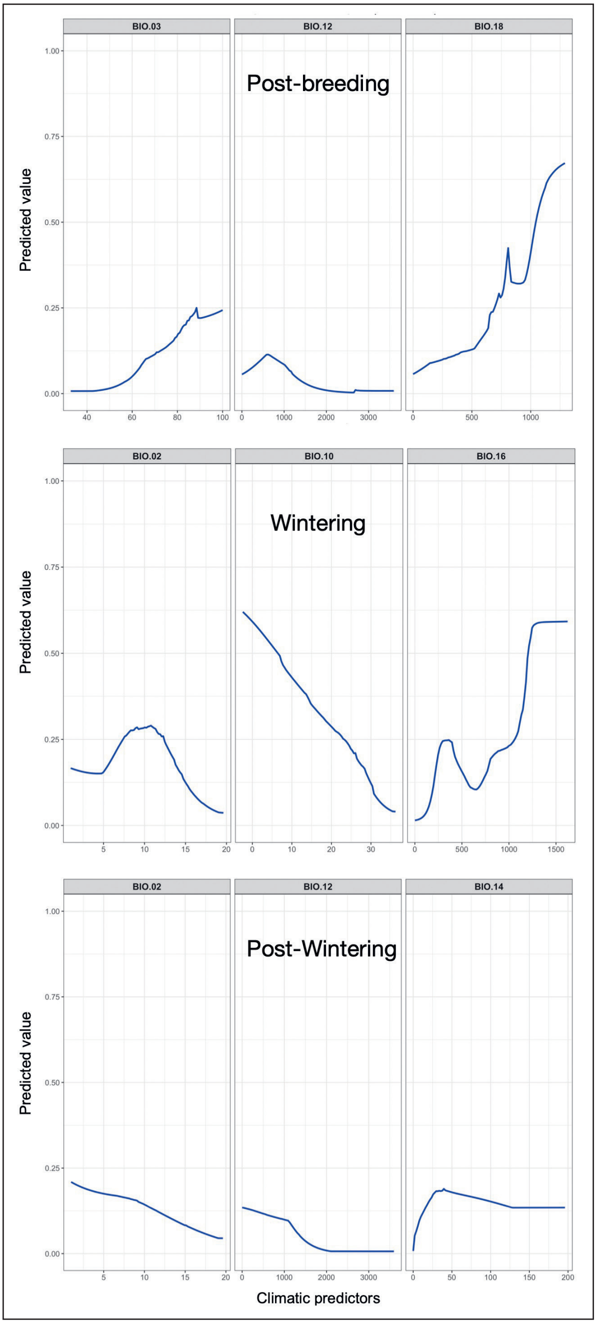

Figure 2. Response curves for main predictors used in the current distribution model for the Sooty Falcon in the non-breeding areas (Bio2 = Mean Diurnal Range, Bio3 = Isothermality, Bio10 = Mean Temperature of Warmest Quarter, Bio12 = Annual Precipitation, Bio14 = Precipitation of Driest Month, Bio16 = Precipitation of Wettest Quarter, Bio18 = Precipitation of Warmest Quarter)

2. ábra A hamvas sólyom jelenlegi elterjedési modelljében használt fő prediktorok válaszgörbéi (Bio2 = átlagos napi hőmérséklet-ingás, Bio3 = izotermalitás, Bio10 = átlagos hőmérséklet a legmelegebb negyedévben, Bio12 = éves csapadékmennyiség, Bio14 = csapadékmennyiség a legszárazabb hónapban, Bio16 = csapadékmennyiség a legcsapadékosabb hónapban, Bio18 = csapadékmennyiség a legmelegebb negyedévben) countries – it is well established that most individuals migrate to Madagascar (Leonardi *et al.* 2024). During the post-breeding journey, migrants traverse regions characterised by montane and sub-humid tropical climates, with moderate temperatures and relatively high precipitation, particularly during the warm season *(Figures 1, 2)*. The combination of high elevation and abundant rainfall likely provides favourable conditions for post-breeding activities, including access to food resources and suitable habitat structure.

Sooty Falcons begin arriving in Madagascar in late October, with the last individuals departing in early May, most birds staying on the island from November to April, coinciding with the austral summer rainy season, and are absent during austral winter (Gschweng 2013). Their wintering distribution has traditionally been associated with the coastal lowlands of western Madagascar and the dry, open inland areas of the southeast (Zefania 2001, Gschweng 2013) *(Figure 1)*. However, more recent data suggest a stronger association with the island's drier western side (Zefania 2001, Javed *et al.* 2012, Gschweng 2013, Al Jahdhami *et al.* 2020). Within these areas, Sooty Falcons utilise a variety of habitats, including savannas, marshes, rice paddies, wooded grasslands, and brush mosaics near cultivated land (Rand 1936, Javed *et al.* 2012, Orta *et al.* 2018). The species is also known to perch on powerlines while hunting insects (Boedts 2010), on aerials and towers in towns, and low anthills in more open areas (Rand 1936). These regions experience tropical savanna and humid subtropical climates, characterised by warm temperatures and a pronounced wet season *(Figure 2)*. The concentration of suitable conditions in these environments suggests a preference for relatively warm and humid climate by birds during the wintering period, likely reflecting resource availability and reduced climatic stress. Similar conditions sustain smaller wintering populations along the coasts of Mozambique and South Africa (Gschweng 2013, Leonardi *et al.* 2024) *(Figure 1)*.

The post-wintering migration towards the breeding grounds appears to be confined to more restricted areas *(Figure 1)*. These zones correspond mainly to semi-humid tropical regions transitioning into drier savanna and woodland systems *(Figure 2)*. The overall reduction in suitability indicates a contraction of optimal climatic conditions following the wintering phase, possibly linked to the onset of the dry season and foretelling declining resource availability in the future.

Both model projections for short (2050), as well long term (2070) suggest a progressive decline and spatial shift in climatic suitability across all non-breeding phases of the lifecycle of Sooty Falcons *(Figure 1)*. The most pronounced changes are expected during the post-breeding and wintering periods, with suitable areas becoming increasingly fragmented and likely displaced towards higher elevations and more humid regions *(Figure 1)*. By mid-century, climatic suitability is projected to decrease across much of continental East Africa, persisting mainly in the Ethiopian and Kenyan highlands and, to a lesser extent, in Madagascar. By 2070, these areas are predicted to serve as the main climatic refugia, reflecting the growing importance of montane and coastal environments under warming and drying scenarios *(Figure 1)*. During the wintering phase, models forecast a substantial reduction in suitable habitats within southern and central Africa, accompanied by a shift towards Madagascar and limited coastal areas of Mozambique and Tanzania *(Figure 1)*. This trend highlights the increasing influence of aridification across the continental interior and suggests that wintering populations may be forced to use the humid or insular regions which will still maintaining stable precipitation regimes. Suitability during the post-wintering (pre-breeding) period is predicted to contract even further, likely reducing the available habitats to isolated fragments of montane and sub-humid enclaves in central Tanzania and along the eastern escarpment of Madagascar *(Figure 1)*. Such reductions likely reflect the combined effects of rising temperatures, reduced humidity, and the seasonal advance of the dry period across eastern and southern Africa. Overall, these projections point to an increasing dependence on high-altitude and coastal refugia, which may play a critical role in maintaining the species' non-breeding populations under future climate change scenarios.

The identification of key wintering and stopover areas provides essential insights for the long-term conservation of the Sooty Falcon. The species relies on a limited network of climatically suitable habitats distributed mainly across Madagascar, the Mozambican and Malawian highlands, and selected East African escarpments (Gschweng 2013, Al Jahdhami *et al.* 2020, Leonardi *et al.* 2024). Many of these regions are subject to increasing anthropogenic pressure, including agricultural expansion, deforestation, and infrastructure development, which may further reduce habitat availability. Equally important are the stopover areas used during post-breeding and pre-breeding movements, particularly in eastern Africa and along the Mozambique Channel, where individuals depend on favourable environmental conditions to rest and refuel in a short but critical period of their lifecycle (Javed *et al.* 2012, McGrady *et al.* 2026). Protecting these transit habitats, often overlooked in conservation planning, is critical for maintaining the connectivity of the migratory network and ensuring successful annual cycles. Integrated conservation strategies should therefore adopt a flyway-level approach, combining the protection of breeding, stopover, and wintering sites with the mitigation of threats arising from land-use change and climate variability.

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References

Akaike, H. 1974. A new look at the statistical model identification. – IEEE Transactions on Automatic Control 19(6): 716–723. DOI: 10.1109/TAC.1974.1100705

Al Jahdhami, M. H., Karelus, D. L., Al Fazari, W. A., Réné de Roland, L.-A., Razafimanjato, G., McGrady, M. J. & Oli, M. K. 2020. Movement patterns of Sooty Falcons *Falco concolor* tracked via satellite across their annual cycle. – Bird Study 67(4): 505–552. DOI: 10.1080/00063657.2021.1950123

Allouche, O., Tsoar, A. & Kadmon, R. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). – Journal of Applied Ecology 43(6): 1223–1232. DOI: 10.1111/j.1365-2664.2006.01214.x

BirdLife International 2021. *Falco concolor*. – The IUCN Red List of Threatened Species 2021: e.T22696446A180387681. Accessed on 11/07/2024

Boedts, B. 2010. Observations du Faucon concolore *Falco concolor* dans les environs d'Antananarivo, Madagascar [Observations of Sooty Falcon *Falco concolor* around Antananarivo, Madagascar]. – Bulletin of the African Bird Club 17(2): 220–224. (in French with English Summary)

Booth, B. D. M. 1961. Breeding of the Sooty Falcon in the Libyan desert. – Ibis 103(1): 129–130. DOI: 10.1111/j.1474-919X.1961.tb02425

Buij, R. 2011. Sightings of Sooty Falcon *Falco concolor* in the far north of Cameroon. – Bulletin of the African Bird Club 18(2): 211–214.

Clapham, C. S. 1964. The Birds of the Dahlac Archipelago. – Ibis 106(3): 376–388. DOI: 10.1111/j.1474-919X.1964.tb03717.x

Condro, A. A., Syartinilia, S., Higuchi, H., Mulyani, Y. A., Raffiudin, R., Rusniarsyah, L., Setiawan, Y. & Prasetyo, L. B. 2022. Climate change leads to range contraction for Japanese population of the Oriental Honey-Buzzards: implications for future conservation strategies. – Global Ecology and Conservation 34(2): e02044. DOI: 10.1016/j.gecco.2022.e02044

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D. & Lautenbach, S. 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. – Ecography 36(1): 27–46. DOI: 10.1111/j.1600-0587.2012.07348.x

Duan, R. Y., Kong, X. Q., Huang, M. Y., Fan, W. Y. & Wang, Z. G. 2014. The predictive performance and stability of six species distribution models. – PLoS One 9(11): e112764. DOI: 10.1371/journal.pone.0112764

Elith, J., Phillips, S. J., Hastie, T., Dudık, M., Chee, Y. E. & Yates, C. J. 2011. A statistical explanation of MaxEnt for ecologists. – Diversity and Distribution 17(1): 43–57. DOI: 10.1111/j.1472-4642.2010.00725.x

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. – Annual Review of Ecology, Evolution, and Systematics 34(1): 487–515. DOI: 10.1146/annurev.ecolsys.34.011802.132419

Fick, S. E. & Hijmans, R. J. 2017. WorldClim 2: New 1 km spatial resolution climate surfaces for global land areas. – International Journal of Climatology 37(12): 4302–4315. DOI: 10.1002/joc.5086

Franklin, J. 2010. Mapping Species Distributions: Spatial Inference and prediction. – Cambridge University Press, Cambridge

Gallo-Orsi, U., Williams, N. P., Javed, S. & McGrady, M. 2014. Draft International Single Species Action Plan for the Sooty Falcon *Falco concolor*. – CMS Raptors MOU. Unpublished Report

Gordo, O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. – Climate Research 35(1–2): 37–58. DOI: 10.3354/cr00713

Gschweng, M. 2013. Sooty Falcon, *Falco concolor*. – In: Safford, R. & Hawkins, F. (eds.) The Birds of Africa, Vol. 8: The Malagasy Region. – Christopher Helm, London, pp. 231–233.

Guisan, A., Lehmann, A., Ferrier, S., Austin, M., Overton, J. M. C., Aspinall, R. & Hastie, T. 2006. Making better biogeographical predictions of species' distributions. – Journal of Applied Ecology 43(3): 386–392. DOI: 10.1111/j.1365-2664.2006.01164.x

Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C. & Guisan, A. 2006. Evaluating the ability of habitat suitability models to predict species presences. – Ecological Modelling 199(2): 142–152. DOI: 10.1016/j.ecolmodel.2006.05.017

Hof, C., Voskamp, A., Biber, M. F., Böhning-Gaese, K., Engelhardt, E. K., Niamir, A., Willis, S. G. & Hickler, T. 2018. Bioenergy cropland expansion may offset positive effects of climate change mitigation for global vertebrate diversity. – Proceedings of the National Academy of Sciences 115(52): 13294–13299. DOI: 10.1073/pnas.1807745115

Hu, R., Gu, Y., Luo, M., Lu, Z., Wei, M. & Zhong, J. 2020. Shifts in bird ranges and conservation priorities in China under climate change. – PLoS One 15: e0240225. DOI: 10.1371/journal.pone.0240225

Hurvich, C. M. & Tsai, C. L. 1989. Regression and time-series model selection in small sample sizes. – Biometrika 76(2): 297–307. DOI: 10.2307/2336663

Javed, S., Douglas, D. C., Khan, S., Shah, J. N. & Al Hammadi, A. A. 2012. First description of autumn migration of Sooty Falcon *Falco concolor* from the United Arab Emirates to Madagascar using satellite telemetry. – Bird Conservation International 22(1): 106–119. DOI: 10.1017/S0959270911000189

Jetz, W., Wilcove, D. S. & Dobson, A. P. 2007. Projected impacts of climate and land-use change on the global diversity of birds. – PLoS Biology 5(6): e157. DOI: 10.1371/journal.pbio.0050157

Langham, G. M., Schuetz, J. G., Distler, T., Soykan, C. U. & Wilsey, C. 2015. Conservation status of North American birds in the face of future climate change. – PLoS One 10: e0135350. DOI: 10.1371/journal.pone.0135350

Leonardi, G., Lopes, L., Gallo-Orsi, U., Javed, S. & McGrady, M. 2024. International Single Species Action Plan for the Sooty Falcon 2024–2036. – CMS Raptors MOU, Abu Dhabi, United Arab Emirates

Martínez-Ruiz, M., Dykstra, C. R., Booms, T. L. & Henderson, M. T. 2023. Conservation letter: effects of global climate change on raptors. – Journal of Raptor Research 57(1): 92–105. DOI: 10.3356/JRR-22-75

McGrady, M., Whelan, R., Porej, D., Cowie, W., Schmidt, M., Ramalho, O. & Alghrair, M. 2026. Migration stopover behaviour of Sooty Falcons *(Falco concolor)* during their southward journey. – Ornis Hungarica 34(1): 76–89. DOI: 10.2478/orhu-2026-0007

McKinlay, S. E., Morganti, M., Mazzoleni, A., Labate, A., Sorrenti, M. & Rubolini, D. 2023. Non-breeding ranging behaviour, habitat use and pre-breeding migratory movements of Fieldfares *(Turdus pilaris)* wintering in southern Europe. – Journal of Ornithology 165(2): 123–136. DOI: 10.1007/s10336-023-02136-x

Moreau, R. E. 1969. The Sooty Falcon *Falco concolor* Temminck. – Bulletin of the British Ornithologists' Club 89(3): 62–67.

Mellone, U. 2021. Sooty Falcon, *Falco concolor*. – In: Panuccio, M., Mellone, U. & Agostini, A. (eds.) Migration Strategies of Birds of Prey in Western Palearctic. – CRC Press, Boca Raton, Florida, pp. 235–237.

Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M. & Anderson, R. P. 2014. ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. – Methods in Ecology and Evolution 5(11): 1198–1205. DOI: 10.1111/2041-210X.12261

Newton, I. 2008. The Migration Ecology of Birds. – Academic Press, London, UK

Norris, D. R. & Marra, P. P. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. – Condor 109(3): 535–547. DOI: 10.1093/condor/109.3.535

Orta, J, Kirwan, G. M., Boesman, P., Marks, J. S. & Sharpe, C. J. 2018. Sooty Falcon *(Falco concolor)*. – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & de Juana, E. (eds.) Handbook of the Birds of the World Alive. – Barcelona www.hbw.com/node/53229. Accessed on 16/04/2023

Phillips, S. J., Anderson, R. P. & Schapire, R. E. 2006. Maximum entropy modeling of species geographical distributions. – Ecological Modelling 190(3–4): 231–259. DOI: 10.1016/j.ecolmodel.2005.03.026

Phillips, S. J. & Dudík, M. 2008. Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. – Ecography 31(2): 161–175. DOI: 10.1111/j.0906-7590.2008.5203.x

R Core Team 2023. R: A Language and Environment for Statistical Computing. – R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org/

Rand, A. L. 1936. The distribution and habits of Madagascar birds. – Bulletin of the American Museum of Natural History 72: 143–499.

Riley, S. J., DeGloria, S. D. & Elliot, R. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. – Intermountain Journal of Science 5(1–4): 23–27.

Runge, C. A., Martin, T. G., Possingham, H. P., Willis, S. G. & Fuller, R. A. 2015. Conserving mobile species. – Frontiers in Ecology and the Environment 12(7): 395–402. DOI: 10.1890/130237

Sierra-Morales, P., Rojas-Soto, O., Ríos-Muñoz, C. A., Ochoa-Ochoa, L. M., Flores-Rodríguez, P. & Almazán-Núñez, R. C. 2021. Climate change projections suggest severe decreases in the geographic ranges of bird species restricted to Mexican humid mountain forests. – Global Ecology and Conservation 30: e01794. DOI: 10.1016/j.gecco.2021.e01794

Studds, C. E., Kyser, T. K. & Marra, P. P. 2008. Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. – Proceedings of the National Academy of Sciences of the United States of America 105(8): 2929–2933. DOI: 10.1073/pnas.0710732105

Title, P. O. & Bemmels, J. B. 2018. ENVIREM: An expanded set of bio-climatic and topographic variables increases flexibility and improves performance of ecological niche modeling. – Ecography 41(2): 291–307. DOI: 10.1111/ecog.02880

Trouwborst, A. 2012. Transboundary wildlife conservation in a changing climate: Adaptation of the Bonn Convention on migratory species and its daughter instruments to climate change. – Diversity 4(3): 258–300. DOI: 10.3390/d4030258

Walter, H. 1979. The Sooty Falcon *(Falco concolor)* in Oman: Results of a breeding survey, 1978. – Journal of Oman Studies 5: 9–59.

Warren, D. L. & Seifert, S. N. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. – Ecological Applications 21(2): 335–342. DOI: 10.1890/10-1171.1

Wilcove, D. S. & Wikelski, M. 2008. Going, going, gone: Is animal migration disappearing. – PLoS Biology 6(7): e188. DOI: 10.1371/journal.pbio.0060188

Zefania, S. 2001. Observation of Sooty and Eleonora's Falcons in Madagascar. – In: Leshem, Y., Froneman, A., Mundy, P. & Shamir, H. (eds.) Wings over Africa. – International Seminar on Bird Migration: Research, Conservation, Education and Flight Safety. – International Center for the Study of Bird Migration, Tel Aviv, pp. 151–159.

Zeng, Q., Zhang, Y., Sun, G., Duo, H., Wen, L. & Lei, G. 2015. Using species distribution model to estimate the wintering population size of the endangered scaly-sided Merganser in China. – PLoS One 10(2): e0117307. DOI: 10.1371/journal.pone.0117307

Supplementary information

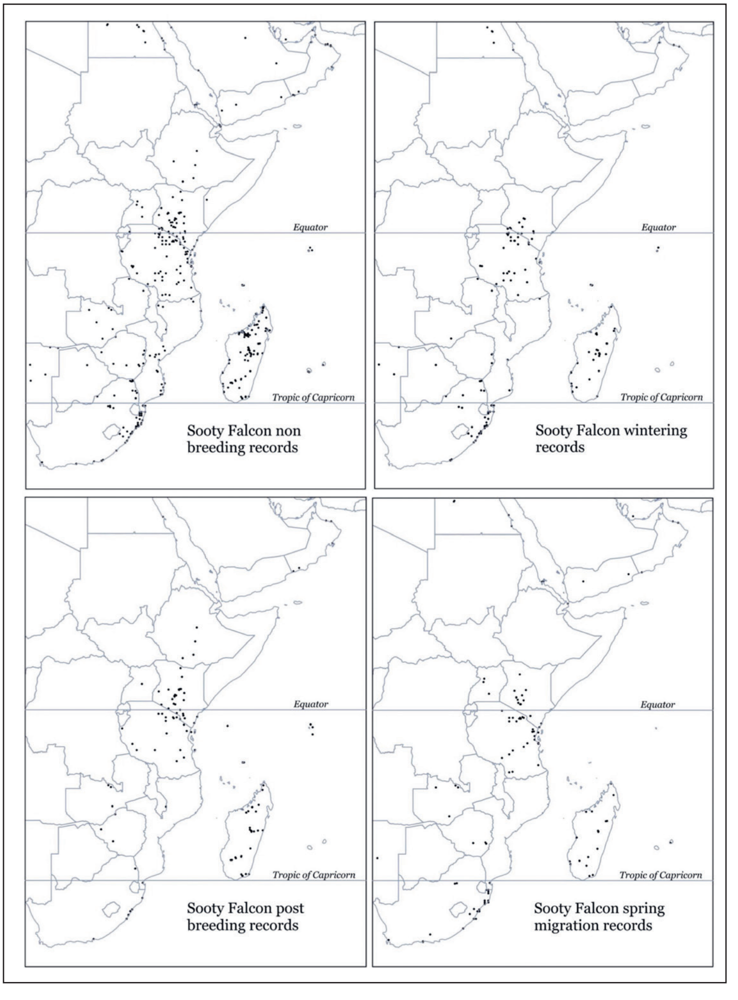

Figure 1. Geographic coverage of records in the Sooty Falcon non-breeding database after removal of duplicates, incomplete observations, and records flagged in the 2022 updates (total n=535). Records were categorised into three seasonal periods: post-breeding (n=151), spring migration (n=81), and wintering (n=303)

1. ábra A hamvas sólyom költési időszakon túli adatainak földrajzi lefedettsége a duplikációk, a hiányos megfigyelések és a 2022-es frissítések során megjelölt adatok eltávolítása után (összesen n=535). Az adatokat három szezonális időszakba soroltuk: költés utáni időszak (n=151), tavaszi vonulás (n=81) és telelés (n=303)

Table 1. Selection of bioclimatic variables for multi-collinearity through stepwise elimination based on Variance Inflation Factor (VIF) analysis, conducted within the framework of predictive modeling using post-breeding distribution data

1. táblázat A bioklimatikus változók kiválasztása a multikollinearitás szempontjából a VIF-elemzésen (Variance Inflation Factor) alapuló, a költés utáni adatok felhasználásával prediktív modellezés keretében végzett fokozatos kizárás útján

Climatic and topographic predictor	**Code**	**VIF**
WorldClim		
Annual mean temeperature	Bio1	1.443
Mean Diurnal Range (Mean of monthly: max temp-min temp)	Bio2	1.175
Isothermality (×100)	Bio3	1.523
Annual Precipitation	Bio12	2.777
Precipitation of Warmest Quarter	Bio18	2.855
Precipitation of Coldest Quarter	Bio19	1.789
ENVIREM		
Terrain roughness index	TRI	1.183

Table 2. Selection of bioclimatic variables for multi-collinearity through stepwise elimination based on Variance Inflation Factor (VIF) analysis, conducted within the framework of predictive modeling using wintering distribution data

2. táblázat A bioklimatikus változók kiválasztása a multikollinearitás szempontjából a VIF-elemzésen (Variance Inflation Factor) alapuló, a téli adatok felhasználásával prediktív modellezés keretében végzett fokozatos kizárás útján

Climatic and topographic predictor	**Code**	**VIF**
WorldClim		
Mean Diurnal Range (Mean of monthly: max temp-min temp)	Bio2	1.241
Isothermality (×100)	Bio3	1.083
Mean Temperature of Warmest Quarter	Bio10	1.317
Precipitation of Wettest Quarter	Bio16	1.078
Precipitation of Coldest Quarter	Bio19	1.622
ENVIREM		
Terrain roughness index	TRI	1.456

Table 3. Selection of bioclimatic variables for multi-collinearity through stepwise elimination based on Variance Inflation Factor (VIF) analysis, conducted within the framework of predictive modeling using post-wintering distribution data

3. táblázat A bioklimatikus változók kiválasztása a multikollinearitás szempontjából a VIF-elemzésen (Variance Inflation Factor) alapuló, a telelési időszak utáni adatok felhasználásával prediktív modellezés keretében végzett fokozatos kizárás útján

Climatic and topographic predictor	**Code**	**VIF**
WorldClim		
Mean Diurnal Range (Mean of monthly: max temp-min temp)	Bio2	1.794
Temperature seasonality (standard deviation ×100)	Bio4	1.335
Precipitation Seasonality	Bio5	1.652
Annual Precipitation	Bio12	2.049
Precipitation of Driest Month	Bio14	1.865
Precipitation of Warmest Quarter	Bio18	1.927
ENVIREM		
Terrain roughness index	TRI	1.899