Mammal Research (2026) 71:57
https://doi.org/10.1007/s13364-026-00878-6

RESEARCH

Snow loss and prey shift may threaten alpine stoats under climate change

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Received: 26 February 2026 / Accepted: 7 July 2026

Abstract
Climate change is profoundly affecting mountain ecosystems, yet its impacts on predator–prey relationships remain poorly understood. In this study, we investigated the effects of climate change on the stoat (*Mustela erminea*), a cold-adapted predator whose seasonal white coat relies on snow cover for camouflage, and its specialized prey, the snow vole (*Chionomys nivalis*), in the Italian Alps. Using occurrence records and an ensemble of Species Distribution Models, we projected current and future distributions under two climate scenarios to 2100. Snow cover duration and snow vole presence emerged as the most influential predictors of stoat distribution, together explaining over 64% of model variance. Our results forecast a projected contraction in stoat distribution, ranging from 15% (SD = 20) under SSP3-7.0 to 36% (SD = 19) under SSP5-8.5, whereas the snow vole is projected to expand its range under both scenarios, particularly in northern sectors of the Alps. Future projections also indicated a growing elevational mismatch between the species, with stoats shifting upward while snow voles showing a slight downward shift under both scenarios. Although further mechanistic studies are needed to clarify the processes underlying the projected decline, our findings suggest that reassessing the conservation status of the stoat at the Italian level may be warranted. We recommend the implementation of long-term monitoring programs and the use of innovative tools to improve stoat data collection. Conservation actions should prioritize high-elevation habitats and address broader anthropogenic pressures to support the persistence of stoats and other cold-adapted species in a warming alpine landscape.

Keywords Climate change · Alps · Mismatch · Camouflage · Predator–prey · Conservation

Communicated by Karol Zub

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Published online: 11 July 2026

Introduction

Climate change impacts mountain biodiversity through multiple ecological mechanisms, including phenological and range mismatches (Parmesan 2006; Chen et al. 2011; Vitasse et al. 2021). Cold-adapted species, highly specialized for high-elevation life, risk becoming decoupled from critical resources such as plant phenology or prey availability (Inouye 2020; Vitasse et al. 2021), as the timing of biological events no longer coincides with resource peaks due to rapid climatic shifts (Visser and Both 2005; Thackeray et al. 2016). Such disruptions might reduce individual fitness and can ultimately threaten population persistence (Visser and Both 2005; Both et al. 2006). For example, earlier green-up of alpine pastures shortens the period of high-quality forage, decreasing growth and survival in young ungulates such as bighorn sheep and alpine ibex (Pettorelli et al. 2007).

Species capable of tracking suitable conditions often shift their distributions upslope (Forero-Medina et al. 2011; Bellard et al. 2012). However, such shifts progressively reduce the extent of available habitat (Colwell et al. 2008; Dirnböck et al. 2011) and increase isolation among remaining patches (Jackson et al. 2015; Brambilla et al. 2017), creating small and fragmented "montane islands" (McDonald and Brown 1992). This dynamic may place high-elevation species on an "escalator to extinction" (Marris 2007; Urban 2018): already confined to mountaintops, they have little to no space for further upslope expansion, making them particularly vulnerable to local extinction (Wilson et al. 2007; Sekercioglu et al. 2008; Freeman et al. 2018).

Predator–prey dynamics are highly vulnerable to the effects of climate change, as predators rely on the timely and sufficient availability of prey (Vucic-Pestic et al. 2011; Öhlund et al. 2015; Bastille-Rousseau et al. 2018). Particularly, climate-driven shifts in prey distribution, abundance, or phenology can force predators to change their behaviour, move their ranges, or experience population declines (Durant et al. 2007; Gilg et al. 2009). Yet, despite growing concerns about the vulnerability of these ecological relationships, relatively few studies have explicitly examined how climate change may alter predator–prey interactions in mountain ecosystems (Aryal et al. 2016; Pedersen et al. 2017; Pintanel et al. 2021).

Since the late 19th century, the European Alps have warmed at nearly twice the Northern Hemisphere average (Auer et al. 2007), with projections indicating a dramatic intensification in the coming decades (Gobiet et al. 2014; Kotlarski et al. 2023). Due to their biogeographic position and exceptional ecological heterogeneity, the Italian Alps are considered particularly sensitive to climate change (Bravo et al. 2008; Viterbi et al. 2013). Signs of both phenological mismatches and elevational shifts have already been documented across several taxa (Vitasse et al. 2021), including mammals (e.g., Pettorelli et al. 2007; Schai-Braun et al. 2021; Simma et al. 2025). However, no study to date has explicitly focused on the effects of climate change on predator–prey interactions in the Alps.

Due to their high taxonomic diversity, central role in food webs, sensitivity to a wide range of threats, and rapid ecological responses, small carnivores are increasingly recognized as valuable sentinels of global environmental changes (Marneweck et al. 2022; Jachowski et al. 2024). Nevertheless, despite facing extinction risks comparable to those of large carnivores, they continue to receive disproportionately less conservation attention (Marneweck et al. 2021; Wright et al. 2022). Within this group, small mustelids (i.e., species of the genus *Mustela*) remain among the least studied carnivores worldwide, largely due to their small body size, elusive behaviour, and typically low population densities (Macdonald et al. 2017). As a result, growing concern surrounds their conservation status in the context of climate change (Valdez et al. 2025), with recent population declines reported in both North America (Jachowski et al. 2021; Cheeseman et al. 2024) and Europe (Coomber et al. 2021; Llorca et al. 2024).

In the Italian Alps, the stoat (*Mustela erminea;* Fig. 1) is the most common small mustelid, a seasonally moulting species confined to high elevations, often above the treeline (Boitani et al. 2003). Together with the least weasel (*Mustela nivalis*), it is considered a key specialist predator of small mammals, feeding on voles, mice, rabbits, and rats (King and Powell 2007). However, in the Italian Alps, the stoat shows a particularly strong association with the snow vole (*Chionomys nivalis;* Fig. 1), a large rodent restricted to rocky habitats (Bounous et al. 1995; Martinoli et al. 2001; Nappi 2002). At the same time, the stoat is itself preyed upon by several predators, particularly raptors and larger carnivores (Korpimäki et al. 1989; Boitani et al. 2003).

Fig. 1 A winter-coated stoat (*Mustela erminea*) preying on a snow vole (*Chionomys nivalis*) in the Alpi Marittime Protected Areas (photo: Edoardo Pelazza)

Despite its current classification as *Least Concern* at both the national and global level (Reid et al. 2016; Rondinini et al. 2022), growing evidence suggests that the species may be particularly vulnerable to climate change, as reduced snow cover increases camouflage mismatch during winter moulting, potentially exposing stoats to higher predation risk (Mills et al. 2018; Otte et al. 2024).

Currently, Species Distribution Models (SDMs) are widely used to assess current and future species distributions under climate change scenarios, due to their ability to generate robust, large-scale inferences, often enhanced by citizen science data (Elith and Leathwick 2009; Guisan et al. 2017; Rathore and Sharma 2023). Several recent studies have applied SDMs to predict climate-driven range shifts in mustelid species (e.g., Dutta et al. 2022; Jamwal et al. 2022; Osinga et al. 2023). However, no study to date has explicitly integrated both abiotic and biotic predictors—such as snow cover and prey availability—into models for these species, although growing evidence suggests that the interplay between these factors can significantly influence species' responses to environmental change (Gorostiague et al. 2018; Penteriani et al. 2019; Li et al. 2024).

Despite being one of the first species used to model climate-driven extinction risk in mountain ecosystems (McDonald and Brown 1992), the stoat has never been explicitly proposed as a sentinel of climate change. Yet, several life-history traits highlight its potential for this role: a relatively short life cycle that enables rapid population responses, a strong dependence on snow cover due to its seasonal coat colour change, and a high trophic specialization on prey species that may themselves shift in distribution under changing climatic conditions. In this study, we aim to assess the vulnerability of the stoat in the Italian Alps by (i) modelling its current and projected future distribution under climate change scenarios, (ii) evaluating the influence of snow cover and snow vole suitability as proxies for camouflage and predator–prey mismatch, and (iii) quantifying expected elevational and distributional changes by the year 2100. We hypothesized that both abiotic and biotic factors play a critical role in shaping the species' distribution, which will result in a significant upward shift and range reduction in the future, with potential implications for its conservation status.

Materials and methods

Study area

The Italian Alps cover an area of 48,070 km², accounting for approximately 27.3% of the entire alpine region (Roekaerts 2002). Open areas, such as grasslands, rocky outcrops, and shrublands, cover nearly 40% of the landscape, supporting unique high-altitude ecosystems; in contrast, cultivated and urban areas account for only about 10% of the territory, playing a relatively minor role in overall land cover (ISPRA 2018). The remaining area is predominantly forested, with vegetation dominated by a limited number of tree species, such as silver fir (*Abies alba*), Norway spruce (*Picea abies*), larch (*Larix decidua*), beech (*Fagus sylvatica*), hazel (*Corylus avellana*), and ash (*Fraxinus excelsior;* Condé et al. 2002; ISPRA 2018).

The alpine region is a recognized biodiversity hotspot, hosting a wide array of plant and animal species uniquely adapted to high-altitude conditions (Condé et al. 2002; Nagy et al. 2003). Yet, these cold-adapted communities are increasingly threatened by climate change (Vitasse et al. 2021). In the Italian Alps, many species have already responded to warming through upward range shifts and phenological mismatches, including potential prey species of the stoat, such as the snow vole and more occasional prey (e.g., common and bank voles; Ferrari et al. 2023), and potential predators of the stoat, such as nocturnal raptors (Brambilla et al. 2020). Although this region benefits from relatively strong legal protection—encompassing four national and numerous regional parks—existing protected areas may be insufficient to buffer alpine biodiversity from the pace and scale of ongoing climate change (Brambilla et al. 2022; Alba and Chamberlain 2025).

Species occurrences

Geo-referenced records of stoats and snow voles were collected across the Italian Alps. Between April and December 2024, we gathered recent records (from 2000 to 2024) of the target species through a collaborative network that included regional administrations, parks, museums, and associations (Fig. 2; Table 1; see the full list of institutions in the Supporting Information, Table S1). Additional data came from open-source databases such as iNaturalist and GBIF, as well as from researchers, photographers, and hikers who submitted geo-referenced sightings directly to our project. To ensure species identification accuracy, we verified each record individually. Since the target species are quite easy to identify, records provided by experts, such as researchers and park rangers, were accepted without requiring photographic confirmation. Conversely, records with uncertain identification and/or spatial imprecision greater than 500 m were excluded. Lastly, we also incorporated data from our own fieldwork conducted in the Alpi Marittime Natural Park both in 2023 (Granata et al. 2025) and 2024 (see Supporting Information, Fig. S1). Small mustelids and their

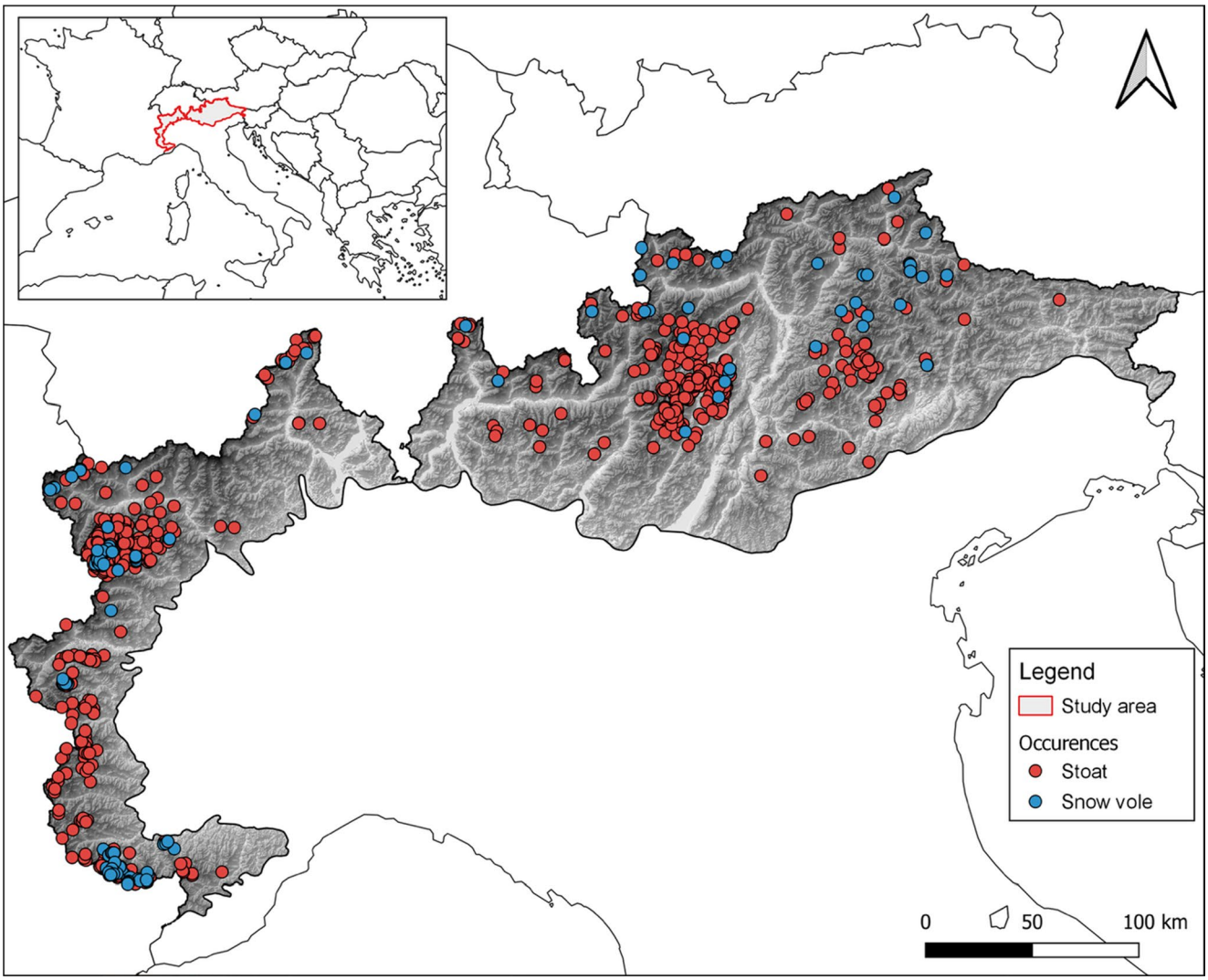

Fig. 2 Our study area, the Italian Alps, showing the hillshade derived from the digital elevation model used for modelling. Recent occurrences of stoats (red dots) and snow voles (blue dots) from 2000 to 2024 are overlaid. These data were compiled from a collaborative network of institutions, open-source databases, citizen science contributions, and field surveys conducted in 2023 and 2024. The top-left inset map illustrates the location of the study area within Europe

Table 1 Occurrence records of stoat and snow vole collected from institutional sources, open-access databases, citizen science contributions (2000–2024), and our field surveys conducted in the Alpi Maritime Natural Park during 2023–2024

Source	Number of occurrences	
	Stoat	Snow vole
Regional administrations	84	0
National parks	279	92
Regional parks	178	10
Museums	220	41
Associations	47	7
Open-source databases	91	28
Citizen science contributions	33	0
2023 fieldwork	15	10
2024 fieldwork	9	35

prey, including snow voles, were monitored with baited external cameras (bait: salmon oil), unbaited Alpine Mostelas, i.e., enclosed camera traps for alpine small mustelid monitoring (Salvador et al. 2022), and live-trapping sessions, including Sherman traps for small mammals and wooden traps for stoats. The resulting dataset, which integrates all data sources, includes 956 records of stoat and 222 records of snow vole (Fig. 2), with most observations concentrated in the last decade (Fig. S2). We then removed duplicate records falling within the same raster cell (i.e., 1 × 1 km; see below) of the environmental predictors. This process resulted in 569 stoat occurrences and 101 snow vole occurrences.

Environmental predictors

Climate, geomorphology, land cover, and biotic variables were included in the SDMs, as these factors significantly influence the habitat preferences of the target species (Janeau and Aulagnier 1997; Martinoli et al. 2001; King and Powell 2007; Amori et al. 2008). From the CHELSA database (Karger et al. 2017), we extracted all 19 bioclimatic variables at 1 km resolution, along with the annual number of snow cover days, given the critical role of snow for stoat survival during winter (Mills et al. 2018; Otte et al. 2024). These predictors represent climatological normals, i.e., monthly and seasonal statistics averaged over a representative 30-year period (1981–2010), and were used to characterize the species' environmental niche across the study area, allowing us to capture average environmental conditions while minimizing short-term climatic variability. A mean-elevation Digital Elevation Model from the GMTED2010 database (30 arc-second resolution; Danielson and Gesch 2011) was used to derive slope and terrain roughness, which were also integrated into the models. Five land cover categories, rasterized at 1 km resolution, were included from Chen et al. (2022): forests, grasslands, croplands, urban areas, and barrens (i.e., sparsely vegetated habitats such as rock screes).

We converted categorical variables into continuous predictors by calculating, for each pixel, the minimum Euclidean distance to the nearest pixel of the focal category (e.g., distance to forests, distance to urban areas, etc.; Jamwal et al. 2022). No minimum patch-size threshold was applied prior to distance calculations, allowing even small or fragmented habitat patches to contribute to the models. Land use predictors had the same 1 km spatial resolution as the other environmental variables, thereby avoiding additional resampling procedures. All variables were then clipped to the Italian alpine region (Roekaerts 2002) as raster layers with a 1 km spatial resolution. Although this resolution exceeds the mean home range size of both species (King and Powell 2007), it is appropriate for capturing broad-scale environmental heterogeneity and regional distribution patterns across the Italian Alps. Furthermore, to investigate predator–prey interactions, we included the modelled distribution of the snow vole as a predictor variable in the stoat distribution model. For each species separately, the 28 initial predictors underwent a variable selection procedure as implemented in the *SDMtune* R package (Vignali et al. 2020). In brief, the variable selection algorithm first ranks variables by importance (after training a preliminary model) and checks for high correlations among them, using a Pearson correlation coefficient of 0.7 as the threshold (Zuur 2007). When correlated variables are detected, it applies a leave one out jackknife test and discards the one whose exclusion has the smallest impact on model performance (Vignali et al., 2020). We applied the procedure repeatedly for each modelling algorithm used in the final SDMs and assessed model performance using the same metrics and cross-validation scheme (see below). The variable importance values obtained from the selection procedure for each algorithm were then merged by calculating a weighted average, with predictive performance scores as weights, to generate a final ranked list of predictors. The retained predictors for both species are shown in Table 2.

Species distribution models

Based on species occurrences, we used the selected variables to predict species distributions through an ensemble forecasting approach implemented in the *biomod2* R package (Thuiller et al. 2016). We employed three modelling algorithms: Boosted Regression Tree (BRT), Random Forest (RF), and Maxent. For each species, 10,000 background points were generated across the study area, distributed according to the density of occurrence data (i.e., more points are concentrated in areas with higher record density), thereby mitigating potential sampling bias (Syfert et al. 2013; Roy-Dufresne et al. 2019). SDMs predictive performance was quantified relying on a block cross-validation approach (Roberts et al. 2017), that is, splitting data into four geographically non-overlapping bins of equal occurrence number, corresponding to each corner of the entire geographical space.

To assess the predictive performance, we calculated the area under the receiver operating characteristic curve (AUC; Hanley and McNeil 1982) and the Boyce index (Boyce et al. 2002). AUC values close to 1 indicate excellent model performance, while a value of 0.5 corresponds to random prediction (Hanley and McNeil 1982). Models with AUC > 0.7 are generally considered reliable (Swets 1988). The Boyce index ranges from − 1 and + 1: positive values indicate good agreement between predictions and observed occurrences; values near zero suggest no improvement over random; and negative values indicate counter-predictions (Boyce et al. 2002; Hirzel et al. 2006). To exclude poorly calibrated models, we only retained projections from models with AUC values ≥ 0.7 for subsequent analyses. Model averaging was then carried out by weighing each projection according to its AUC value and calculating their average (Marmion et al. 2009).

Models were projected to the year 2100 under two future climate change scenarios, specifically SSP3-7.0 and SSP5-8.5, from the Coupled Model Intercomparison Project Phase 6 (CMIP6; O'Neill et al. 2016; Karger et al. 2017; Chen et al. 2022). SSP5-8.5 represents a high-emission trajectory commonly used to assess severe climate

Table 2 Name, description, spatial resolution, and data source of all variables included in the SDMs, grouped into four categories: geomorphology, climate, land cover, and biotic

Variable	Description	Resolution	Source
Geomorphology			
Elevation	Digital Elevation Model (DEM)	10 m	Worlclim: worldclim.org
Slope	Rate of change of elevation (from DEM)	10 m	Worlclim: worldclim.org
Climate			
Mean diurnal air temperature range (bio2)	Mean diurnal range of temperatures averaged over 1 year	1 km	CHELSA: chelsa-climate.org
Isothermality (bio3)	Ratio of diurnal variation to annual variation in temperatures	1 km	CHELSA: chelsa-climate.org
Temperature seasonality (bio04)	Annual temperature variation based on the standard deviation of monthly temperature averages.	1 km	CHELSA: chelsa-climate.org
Precipitation seasonality (bio15)	The Coefficient of Variation is the standard deviation of the monthly precipitation estimates expressed as a percentage of the mean of those estimates (i.e. the annual mean)	1 km	CHELSA: chelsa-climate.org
Mean monthly precipitation amount of the warmest quarter (bio19)	The warmest quarter of the year is determined (to the nearest month)	1 km	CHELSA: chelsa-climate.org
Mean monthly precipitation amount of the coldest quarter (bio19)	The coldest quarter of the year is determined (to the nearest month)	1 km	CHELSA: chelsa-climate.org
Snow cover days (scd)	Number of snow cover days throughout the year	1 km	CHELSA: chelsa-climate.org
Land use			
Urban areas	Euclidean distance from urban areas pixels	1 km	Chen et al. (2022)
Grasslands	Euclidean distance from grasslands pixels	1 km	Chen et al. (2022)
Croplands	Euclidean distance from croplands pixels	1 km	Chen et al. (2022)
Barrens	Euclidean distance from barrens pixels	1 km	Chen et al. (2022)
Forests	Euclidean distance from forests pixels	1 km	Chen et al. (2022)
Biotic			
Snow vole suitability	Habitat suitability for the snow vole in the Italian Alps	1 km	This study (modelled data)

The snow vole variable was included exclusively as a predictor for modelling the distribution of the stoat

change impacts, whereas SSP3-7.0 reflects an intermediate-to-high emission pathway under weaker mitigation policies (IPCC 2023; Hausfather 2025). As these scenarios are based on different General Circulation Models (GCMs), variation among models can lead to differences in SDM projections (Buisson et al. 2010). To address this uncertainty, we used five different GCMs under both scenarios: GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL (Krasting et al. 2018; Tang et al. 2019; Yukimoto et al. 2019; Mauritsen et al. 2019; Boucher et al. 2020). Future projections of stoat suitability incorporated GCM-matched future projections of snow vole suitability as a dynamic biotic predictor.

Current and future model projections were binarized using three thresholding approaches: 'equalize sensitivity and specificity', 'maximize sensitivity and specificity', and 'minimum training presence' (Di Febbraro et al. 2019). At the end of this process, we obtained range maps depicting the current and projected future distribution of the target species. From binary maps, we calculated the current and future range extension for both species, as well as their spatial overlap under present environmental conditions and in 2100. Also, we quantified range shifts by examining the movement of range centroids along latitude and elevation. Following Aguirre-Gutiérrez et al. (2016), centroids were derived from binary maps for the

present and 2100, and differences in their latitudinal and altitudinal positions were calculated.

Results

The SDM for snow vole achieved good predictive performances, with a mean AUC = 0.82 (SD = 0.064) and a mean Boyce index of 0.68 (SD = 0.24). The primary drivers of snow vole habitat suitability were land cover variables, notably the distance from barrens, followed by distance from grasslands and urban areas; the most influential climatic variable was the annual number of snow cover days (Table 3). Specifically, habitat suitability increased with proximity to barrens and grasslands and with greater distance from urban areas, but it decreased with higher numbers of snow cover days (Fig. 3). All other predictors individually contributed less than 10% to model performance (Supporting Information, Fig. S4).

The SDM for stoat exhibited a fair predictive performance, with a mean AUC = 0.77 (SD = 0.074) and a mean Boyce index of 0.88 (SD = 0.10). The two most important predictors of stoat distribution were snow cover days and the snow vole suitability, which together explained over 64% of the overall model (Table 3). Stoat habitat suitability followed a hump-shaped response to snow cover days, peaking at approximately 250 days, and increased with the probability of snow vole occurrence (Fig. 3). Other climatic and land cover variables had a more marginal influence on stoat habitat suitability (Supporting Information, Fig. S5).

Modeled environmental suitability for both species across two future scenarios and five GCMs is presented in Supporting Information, Fig. S3. Overall, despite variability in the magnitude of projected changes, the different GCMs consistently predicted similar trends for both the stoat and the snow vole.

Future projections to 2100 predicted range shifts for both species, although the magnitude of change varied among scenarios and GCMs (Fig. 4; Table 4). Across all GCMs and thresholding approaches, the snow vole is projected to experience a net range expansion under both climate scenarios, with a mean increase of +109.65% (SD = 23.67) under SSP3-7.0 and +76.77% (SD = 32.56) under SSP5-8.5 (Table 4). This expansion is primarily northward, with minor habitat gains at lower elevations in regions such as the Aosta Valley (northwestern Italian Alps). However, the snow vole is projected to disappear from parts of the southwestern, central, and eastern Italian Alps (Supporting Information, Fig. S6). Conversely, the stoat is projected to undergo a substantial range contraction under both scenarios, with a mean net range change of -15.36% (SD = 20.22) under SSP3-7.0 and -35.99% (SD = 19.16) under SSP5-8.5 (Table 4). Moderate range expansions are anticipated only in isolated patches of the Dolomites (eastern Italian Alps) and the highest parts of the Aosta Valley, whereas strong contractions are predicted in the Maritime and Cottian Alps and across much of the eastern Alps (Fig. 5). Projected distribution changes across all GCMs and thresholding criteria are presented in Supporting Information, Fig. S7-S8.

Both species exhibited a northward shift in their range centroids by 2100 under both climate scenarios. Under SSP3-7.0, the snow vole centroid moved approximately 22 km northward, accompanied by a slight downward elevational shift, whereas under SSP5-8.5 the northward displacement was similar, with only a minor elevational change (Table 5). In contrast, under SSP3-7.0 the stoat centroid moved approximately 16 km northward and 144 m upward, whereas under SSP5-8.5 the shift reached approximately 15 km northward and 214 m upward (Table 5). Under SSP3-7.0, the projected range of the stoat decreased from 8,698 km² (SD = 4,961) under current conditions to 7,305 km² (SD = 3,664) by 2100, while the snow vole increased from 3,702 km² (SD = 736) to 7,678 km² (SD = 1,018). Under SSP5-8.5, the stoat range further declined to 5,722 km² (SD = 3,425), whereas the snow vole reached 6,474 km² (SD = 1,255). Focusing on predator–prey spatial dynamics, the overlap between the two species was projected to increase under both scenarios, from 2,704 km² (SD = 1,338) at present to 4,628 km² (SD = 1,926) under SSP3-7.0 and 3,544 km² (SD = 1,829) under SSP5-8.5 by 2100.

Table 3 Environmental predictors and their percent contribution to the overall model for each species

Variable	Percent contribution
Snow vole	
Barrens	32.7
Grasslands	15.0
Urban areas	11.8
Snow cover days	11.2
Stoat	
Snow cover days	38.8
Snow vole suitability	25.7

Only variables with a contribution greater than 10% are shown (the complete list is available in Supporting Information, Fig. S4 and S5)

Discussion

Through a collaborative network of institutions and the integration of validated citizen science data, we modelled the current and projected distributions to 2100 of the stoat and the snow vole in the Italian Alps. Our results revealed a projected range contraction for the stoat under both future climate scenarios, ranging from approximately 15% under SSP3-7.0 to 36% under SSP5-8.5, accompanied by a marked upward elevation shift in distribution, from 144 to 214 m respectively. Although

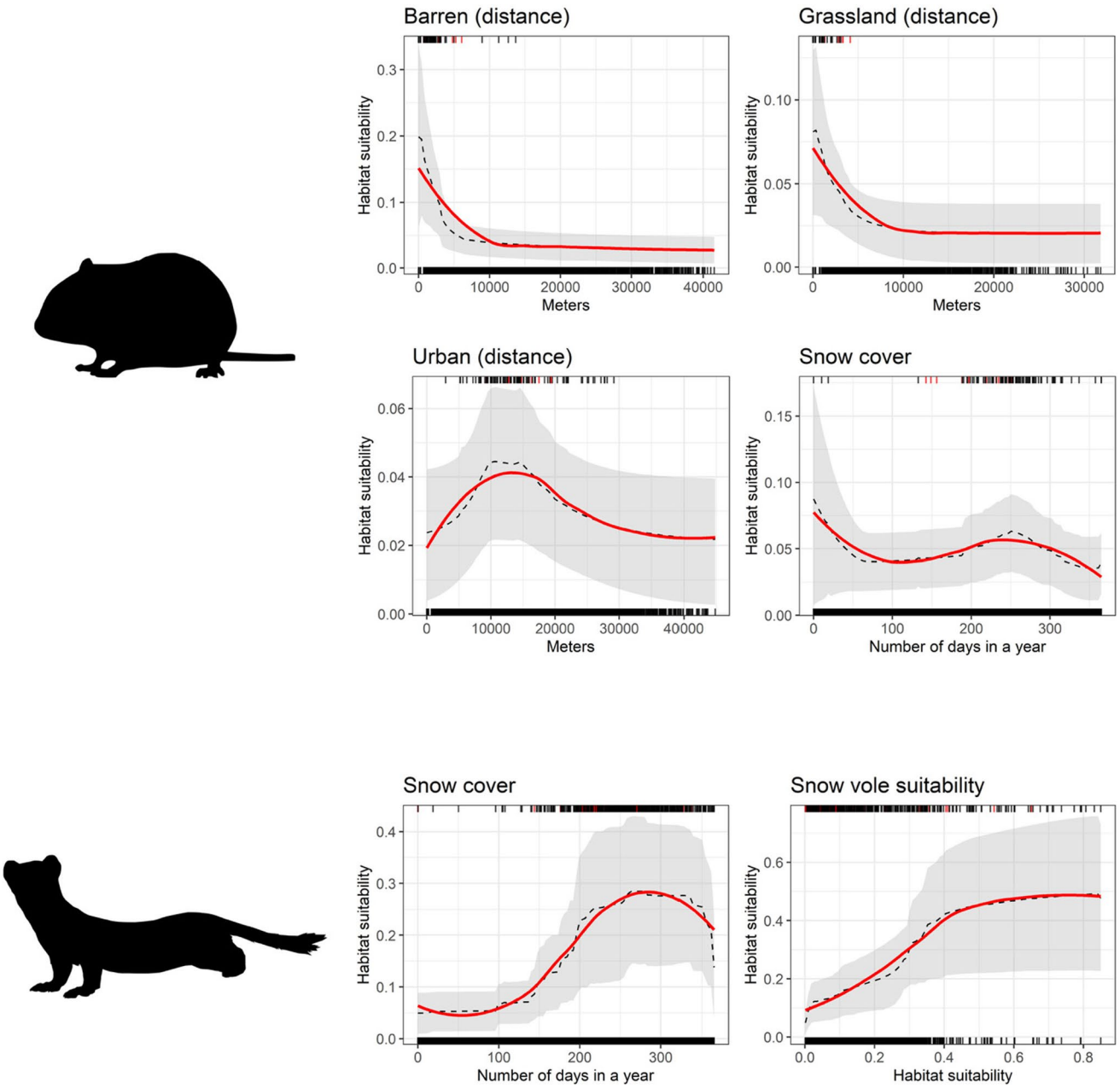

Fig. 3 Response curves showing the relationship between habitat suitability and environmental variables with >10% contribution in the ensemble models for the snow vole (top) and the stoat (bottom). The dashed line indicates the actual response curve produced by the ensemble model, while the solid red line represents a post-hoc loess smoothing applied for visualization purposes. The grey ribbon represents the 95% confidence interval around mean predicted suitability values of the selected models. Rug plots along the x-axes show the distribution of presence records (top) and pseudo-absence points (bottom), with early records (2000–2002) highlighted in red to show their relative position along the environmental gradients

uncertainty among projections was substantial (SD=20.22 and 19.16 respectively), all model combinations and thresholding approaches across GCMs consistently indicated a negative trend for stoats. This predicted decline is consistent with recent trends observed in small mustelids (Jachowski et al. 2021; Coomber et al. 2021; Cheeseman et al. 2024), and reflects similar elevational shifts reported for other alpine mammals (Schai-Braun et al. 2021; La Morgia et al. 2023; Simma et al. 2025). In contrast, the snow vole was projected to increase its suitable habitat under both scenarios, although projections were larger under SSP3-7.0 than under SSP5-8.5, and showed a slight downward shift in mean elevation (100 and 50 m respectively), reflecting a different response to climate change. Unexpectedly, we projected an increase in overlap between the two species under both scenarios, likely driven by the marked expansion of suitable habitat for the snow vole

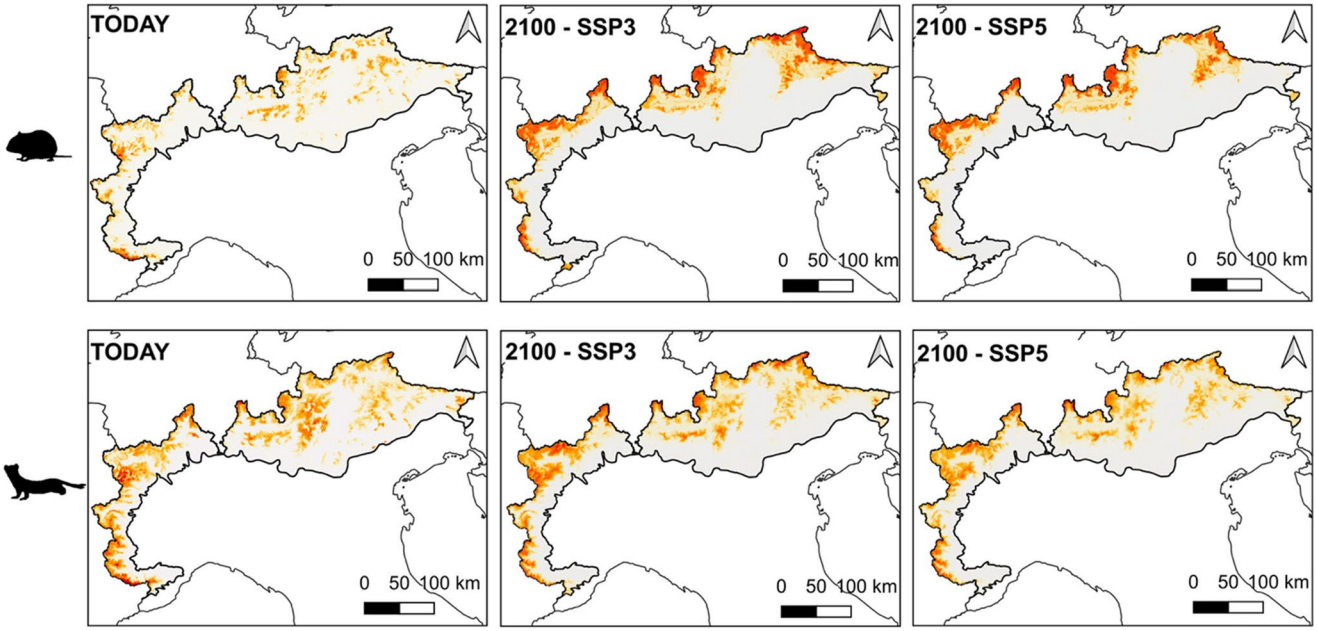

Fig. 4 Modelled current and projected future environmental suitability for the snow vole (top) and the stoat (bottom) in the Italian Alps under present-day conditions and future climate scenarios for 2100 (SSP3-7.0 and SSP5-8.5). Suitability is represented using a sequential colour scale ranging from white (low suitability) through yellow and orange to red (high suitability)

despite the concurrent contraction and upward shift of the stoat distribution. However, this pattern should be interpreted cautiously given the potential sampling bias affecting snow vole projections, as discussed below.

The number of snow cover days emerged as the most important variable shaping stoat distribution in the Italian Alps. As described for other moulting species (Imperio et al. 2013; Zimova et al. 2014, 2022; Mills et al. 2018), reductions in snow cover can severely affect small mustelids by increasing the risk of seasonal camouflage mismatch (Mills et al. 2018; Atmeh et al. 2018; Otte et al. 2024). This phenomenon, driven by climate-induced shortening of the snow season, occurs when stoats in their white pelage are exposed against snow-free backgrounds, making them highly visible to visually oriented predators, particularly raptors (Korpimäki et al. 1989), and consequently more vulnerable to predation (Otte et al. 2024). Snow cover is also critical for stoat foraging ecology, as they depend on subnivean access to prey during winter, often exploiting the tunnels and burrow systems of rodents that remain active beneath the snowpack, as well as for their own thermoregulation, with temperatures beneath the snow remaining close to 0 °C compared to much colder external conditions (King and Powell 2007). Habitat suitability declined beyond 250 annual snow-cover days, likely reflecting the transition toward glacier-dominated environments with reduced prey availability. While our results suggest a strong dependence of alpine stoats on seasonal snow cover, stoats may persist even in largely snow-free environments, as observed in England, where non-moulting or partially moulting populations have been documented (MacPherson 2024). However, no such populations are currently known in the Italian Alps, suggesting that local stoat populations may lack the phenotypic plasticity or genetic adaptations required to cope with reduced snow cover. This could reflect the peripheral position of our study area within the species' range, as populations occurring at range margins are often smaller, more isolated, and therefore potentially constrained in their evolutionary potential under rapidly changing environmental conditions (Bridle and Vines 2007).

Table 4 Projected range net change (RNC) for the stoat and the snow vole under SSP3-7.0 and SSP5-8.5 scenarios by 2100

Species	Scenario	Mean RNC (%)	SD	Min (%)	Max (%)
Snow vole	SSP3-7.0	- 15.3	20.2	- 41.8	+9.4
	SSP5-8.5	- 36.0	19.2	- 61.3	- 8.7
Stoat	SSP3-7.0	+109.6	23.7	+74.1	+142.5
	SSP5-8.5	+76.8	32.5	+31.6	+128.4

Standard deviation (SD), minimum, and maximum values summarize variability among projections

Table 5 Projected elevation and latitude shifts (mean ± SD) for the stoat and the snow vole under SSP3-7.0 and SSP5-8.5 scenarios by 2100

Species	Scenario	Elevation (m)	SD	Latitude (km)	SD
Snow vole	SSP3-7.0	- 109.7	64.4	21.6	4.1
	SSP5-8.5	- 47.4	87.5	22.2	6.2
Stoat	SSP3-7.0	+ 143.7	69.7	15.7	5.3
	SSP5-8.5	+ 213.6	87.1	15.3	6.0

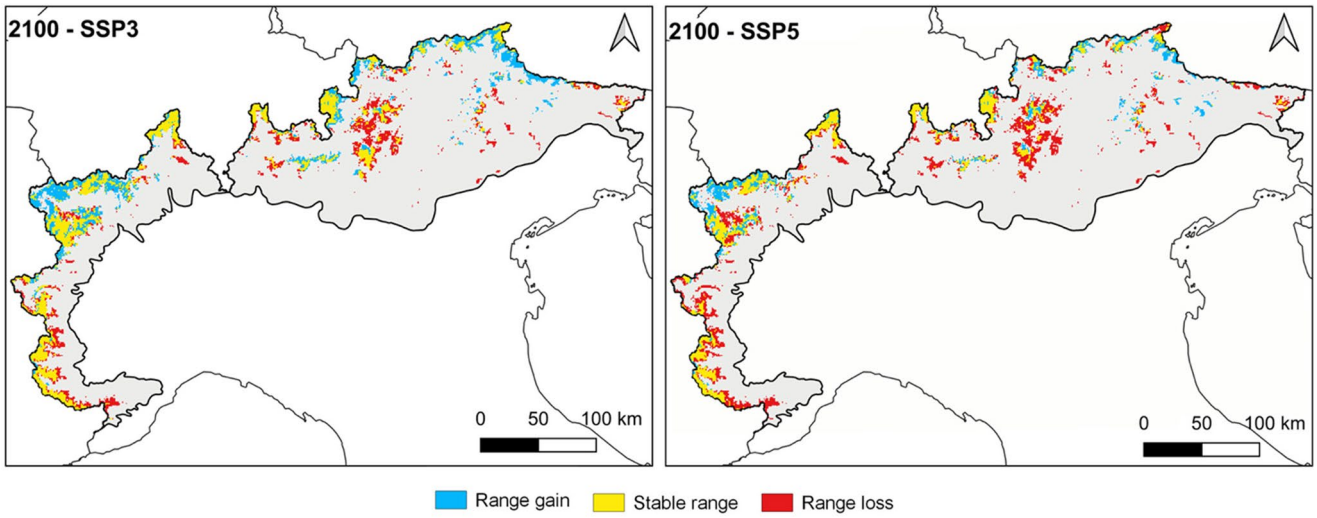

Fig. 5 Projected changes in the distribution range of the stoat in the Italian Alps by 2100 under the SSP3-7.0 and SSP5-8.5 scenarios. Areas of projected range gain are shown in blue, stable range in yellow, and range loss in red. Predictions were generated using the MPI-ESM1-2-HR global circulation model and the 'maximize sensitivity and specificity' binarization threshold

We also found a strong positive response to snow vole suitability, highlighting the tight ecological association between the two species. In the Italian Alps, the snow vole consistently represents the main prey of the stoat in both the western (Bounous et al. 1995) and central Alps (Martinoli et al. 2001). Nevertheless, stoat diets also include other small mammals, such as the bank vole (*Clethrionomys glareolus*), wood mice (*Apodemus* spp.), and the garden dormouse (*Eliomys quercinus*), as well as fruit, particularly during late summer (Bounous et al. 1995; Martinoli et al. 2001). With several small mammals currently expanding to higher elevations in the Italian Alps (Ferrari et al. 2023), there is potential for these species to partially substitute snow voles in the stoat's diet. However, the snow vole is more than 30–50% larger than both the bank vole and wood mice, making it a more energetically profitable resource (Martinoli et al. 2001; Amori et al. 2008). This interpretation is consistent with observations from central and northern Europe, where stoats usually exhibit a marked preference for large prey, including rabbits (*Oryctolagus cuniculus*; McDonald et al. 2000), rats (*Rattus* spp.; Sleeman 1992), and larger vole species—namely the Eurasian water vole *Arvicola amphibius* (synonyms *Arvicola terrestris*; Erlinge 1981; Delattre 1983). For example, while bank voles have been reported as the main prey for stoats in Norway, this occurred alongside the presence of tundra voles (*Microtus oeconomus*), a significantly larger species, that likely plays an important role in meeting the stoat's high energetic demands (Piontek et al. 2015). Thus, while stoats exhibit dietary plasticity, the availability of large rodent species likely remains essential for supporting viable stoat populations, particularly in energetically demanding high-elevation environments. Notably, apart from the snow vole, no other rodent species occurring in the Italian Alps appears to combine comparable body size, habitat association, and local abundance (Amori et al. 2008).

Snow vole habitat suitability declined with increasing distance from barrens and grasslands, confirming that its distribution is primarily shaped by land cover, particularly the presence of rock screes and alpine prairies, rather than by climate or geomorphology factors (Nappi 2002; Bertolino et al. 2023). These rugged, high-altitude habitats provide the structural complexity, thermal buffering, and concealment opportunities that are essential for survival, foraging, and predator avoidance (Janeau and Aulagnier 1997; Amori et al. 2008). More broadly, our findings are consistent with the species' known ecological preferences in the Italian Alps, as it is closely associated with scree slopes and alpine grasslands above the treeline (Amori et al. 2008; Bertolino et al. 2023). Responses to urban areas and snow cover were less straightforward: suitability peaked at ~10 km from urban areas and at very low snow cover days. The apparent optimum distance of 10 km from urban areas likely reflects the distribution of suitable habitats, typically located at a similar distance from alpine settlements. Despite its name, the snow vole is more strongly tied to rock screes (Janeau and Aulagnier 1997), and can occur at much lower altitudes (Nappi 2002), even at sea level in the Mediterranean region (Janeau and Aulagnier 1997; Amori et al. 2008). While snow cover offers important winter protection, excessively long snow periods may restrict resource availability, ultimately limiting habitat suitability (Amori et al. 2008; Bertolino et al. 2023). Nevertheless, projected snow vole distributions should be interpreted cautiously. While the stoat is frequently reported

through citizen science platforms, the snow vole is rarely detected, with most records originating from live-trapping surveys. This may have led to an underrepresentation of occurrences at higher elevations, where sampling effort remains limited. Consistent with this interpretation, snow voles have been recorded wherever stoats have been studied across the Italian Alps, particularly at high elevations (Bounous et al. 1995; Martinoli et al. 2001; Granata et al. 2025).

Other potential limitations of our study concern both the occurrence dataset and the modelling framework adopted. Our analyses relied on presence-only records collected through institutions and citizen science platforms, resulting in uneven spatial and temporal sampling effort across the study area. Although these data substantially improved coverage in remote environments, where standardized monitoring is often lacking, opportunistic records may still introduce spatial biases toward more accessible areas and cannot fully account for variation in detection probability or survey effort (Feldman et al. 2021). These limitations are particularly relevant for the snow vole, for which the comparatively small sample size likely increased uncertainty in both current and future projections and may have reduced the ability of the models to fully capture the species' environmental niche. In particular, the projected increase in its suitability should be interpreted cautiously and would benefit from further field validation, especially in light of recent elevational trends (Ferrari et al. 2023). Consequently, stoat projections may also be optimistic, particularly with respect to future suitability and range overlap. In addition, as snow vole suitability was first modelled using environmental predictors largely shared with the stoat model and subsequently included as a biotic predictor for the stoat itself, part of the observed prey effect may reflect overlapping environmental information rather than an exclusively biotic relationship. Although this approach is ecologically justified by the strong trophic association between the two species in the Italian Alps (Martinoli et al. 2001), the exact magnitude of their projected range changes remains sensitive to this source of uncertainty. Nevertheless, sensitivity analyses excluding the snow vole predictor still projected substantial contractions in stoat distribution, suggesting that snow cover loss was the primary driver of the projected decline, while the prey variable likely amplified the magnitude of the response.

Despite these limitations, we consider our study an important step toward improving conservation knowledge for the stoat in the Alps. Further research is nonetheless needed to assess climate change impacts at local scales and to develop targeted conservation strategies. In particular, long-term standardized monitoring programs will be essential to move beyond opportunistic presence-only datasets and improve our understanding of population trends and ecological responses over time. In a previous study (Granata et al. 2025), we demonstrated that the Alpine Mostela, an enclosed camera trap for alpine small mustelids, proved the most effective method for monitoring stoats and other elusive alpine species, and it is a promising candidate for long-term monitoring programs in high-altitude environments. Moreover, given its easy recognizability and recent adoption as a mascot species for the Milano–Cortina 2026 Winter Games, the stoat could also serve as an effective flagship species for citizen science initiatives aimed at improving long-term monitoring and public awareness of climate change impacts on alpine biodiversity. In this context, our study also highlights the value of citizen science data for monitoring elusive alpine mammals, although their long-term utility will depend on more coordinated sampling efforts involving local stakeholders, such as protected areas and mountain huts.

From a conservation perspective, the projected ~ 40% decline of the stoat in Italy under SSP5-8.5 represents a significant finding, particularly given its current classification as *Least Concern* (Rondinini et al. 2022). Although the more moderate SSP3-7.0 scenario projected a less pronounced contraction, current climatic trends in the Alps suggest that SSP5-8.5 may provide a particularly informative framework for evaluating potential long-term conservation risks of alpine stoat populations (Auer et al. 2007; Kotlarski et al. 2023). Under this scenario, our projections suggest that the species could meet the threshold for classification as *Vulnerable* at the national level under IUCN criterion A3c, based on the projected decline in habitat quality (IUCN 2024). Although climate change is often perceived as the primary driver of biodiversity loss (Caro et al. 2022), it more frequently acts as an amplifier of existing threats rather than as a standalone factor (Mantyka-Pringle et al. 2012; Williams et al. 2022). Accordingly, in the context of existing threats, our research contributes to a more comprehensive understanding of factors influencing conservation such as: (i) the growing overlap and potential conflict over suitable snow-covered habitats due to the upslope expansion of ski pistes and resorts (Rixen and Rolando 2013; Brambilla et al. 2016); (ii) the abandonment of traditional agro-silvo-pastoral practices, which has already resulted in the loss of high-altitude grasslands essential for a wide range of taxa, including insects (Tocco et al. 2013) and birds (Laiolo et al. 2004); (iii) the limited capacity of existing alpine protected areas to safeguard future climate refugia for cold-adapted species (Brambilla et al. 2022; Alba and Chamberlain 2025); and (iv) the use of illegal rodenticides at high elevations (Lestrade et al. 2021), which pose a serious threat to small mustelids (e.g., for stoats: McDonald et al. 1998; Elmeros et al. 2011).

In conclusion, our results suggest that snow cover loss and shifts in predator–prey spatial overlap may represent

important mechanisms through which climate change could alter predator–prey dynamics in alpine ecosystems. These findings underscore the importance of co-modelling interacting species under future climate scenarios. Moving beyond single-species approaches is essential to more accurately predict biodiversity responses and to inform conservation strategies in rapidly changing mountain environments. Moreover, our findings highlight the stoat's value as a sentinel species for detecting climate change impacts. Due to its strong dependence on seasonal snow cover, tight trophic association with cold-adapted prey, and rapid ecological responses, the species may provide an early and measurable indication of broader ecosystem changes occurring in high-elevation environments (Hazen et al. 2024). Given the significant range contraction projected under future climate scenarios, we recommend reassessing the stoat's conservation status at the national level. Prioritising its protection could not only support the conservation of this vulnerable predator but also strengthen broader efforts to monitor and preserve high-altitude ecological communities increasingly threatened by climate change.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13364-026-00878-6.

Acknowledgements We are grateful to Riccardo Alba and Enrico Caprio (Università di Torino), Thamara Benazzoli (Museo Civico di Storia Naturale di Pordenone), Radames Bionda (Aree Protette dell'Ossola), Marco Cazzola and Cristina Movalli (Parco Nazionale della Val Grande), Luca Dorigo (Museo Friulano di Storia Naturale), Roberto Facchini and Daniele Stellin (Parco Naturale Monte Avic), Umberto Fattori and Andrea Cadamuro (Regione autonoma Friuli Venezia Giulia), Eva Ladurner and Petra Kranebitter (Museo di Scienze Naturali dell'Alto Adige), Paolo Pedrini (MUSE – Museo delle Scienze di Trento), Andrea Mosini (Cooperativa Valgrande), Marco Rastelli (Parco del Monviso), Roberto Sindaco (Istituto per le Piante da Legno e l'Ambiente), Giulia Tessa (Museo Civico di Storia Naturale di Morbegno), Santa Tutino and Ornella Cerise (Museo Regionale di Scienze Naturali della Valle d'Aosta Efisio Noussan), Enrico Vettorazzo and Mauro Bon (Parco Nazionale Dolomiti Bellunesi), the park rangers of the Alpi Marittime and Alpi Cozie Protected Areas, and the Gran Paradiso National Park Surveillance Corps (who collected field data in the territories under their jurisdiction), as well as the wildlife photographers Andrea Belingheri and Emilio Ricci, for their valuable contributions. We also sincerely thank all individuals and institutions who provided data and support throughout this project. Special thanks go to the rest of the Ermlin Team: Nadia Rocco, Michela Bagnasco, and Filippo Di Paolo.

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Funding Open access funding provided by Università degli Studi di Torino within the CRUI-CARE Agreement. Fieldwork in the Alpi Marittime Natural Park was funded by the Unione Buddhista Italiana (UBI) through a grant awarded to Marco Granata.

Data availability Open-access data used in this study are publicly available from iNaturalist (https://www.inaturalist.org/) and GBIF (https://www.gbif.org/). Additional data collected in collaboration with protected areas and other institutions are not publicly available but can be provided by the corresponding author upon reasonable request, subject to the data-sharing agreements of the relevant institutions.

Declarations

Ethical approval Not applicable.

Clinical trial number Not applicable.

Competing interests The authors declare no competing interests.

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