

No hearts below the snow line: Snow loss and prey mismatch threaten alpine stoats under climate change

Marco Granata

`marco.granata@unito.it`

Università degli Studi di Torino

Margherita Cattaneo

Università degli Studi di Torino

Sonia Calderola

Parco Nazionale Gran Paradiso

Maria Chiara Deflorian

MUSE – Museo delle Scienze di Trento

Laura Martinelli

Ente di gestione delle Aree Protette delle Alpi Marittime

Luca Maurino

Ente di gestione delle Aree Protette delle Alpi Cozie

Mirko Di Febbraro

EnviXLab, Università degli Studi del Molise, Contrada Fonte Lappone

Sandro Bertolino

Università degli Studi di Torino

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Abstract

Climate change is profoundly affecting mountain ecosystems, yet its impacts on predator-prey dynamics 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 the high-emission RCP 8.5 IPCC scenario 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 severe 36% contraction in stoat range, primarily driven by a loss of snow cover and reduced spatial overlap with its prey. In contrast, the snow vole is expected to expand its range by 77%, particularly in northern sectors of the Alps. However, the stoat appears unable to track this expansion, suggesting a growing predator-prey mismatch. These findings indicate that despite its current *Least Concern* status in Italy, the stoat may warrant reclassification as *Vulnerable* under IUCN Criterion A3c. The study highlights the impacts of climate change on trophic interactions and moulting species in mountain ecosystems. 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.

Introduction

Climate change impacts mountain biodiversity primarily through 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 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 migration, 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 behavior, 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 animals (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 behavior, 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 glacial relict 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 rodents, 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). Despite its current classification as *Least Concern* at the national level (Rondinini et al. 2022), there is growing concern among experts regarding the conservation status of the stoat, especially in light of emerging evidence on its vulnerability to climate change (Mills et al. 2018; Otte et al. 2024).

Currently, Species Distribution Models (SDMs) are increasingly 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, despite growing evidence 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 short life cycle that enables rapid population responses, a strong dependence on snow cover due to its seasonal coat color change, and 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 mismatch and predator-prey decoupling, and (iii) quantifying expected elevational shifts and range contractions by the year 2100. We hypothesize that both abiotic and biotic factors will play a critical role in shaping the species' distribution, resulting in a significant upward shift and range reduction, with potential implications for its future 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). Elevation ranges from 47 to 4,809 m above sea level, culminating at Monte Bianco (Mont Blanc), Europe's highest peak. 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 (Pettorelli et al. 2007; Ferrari et al. 2023; La Morgia et al. 2023). 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). 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). The resulting dataset, which integrates all data sources, includes 956 records of stoat and 222 records of snow vole (Fig. 2). We then removed duplicate records falling within the same raster cell (i.e., 1 x 1 km; see below) of the environmental predictors. This process resulted in 569 stoat occurrences and 101 snow vole occurrences.

Table 1
Occurrence records of stoat and snow vole collected from institutional sources, open-access databases, citizen science contributions, and our field surveys conducted in the Alpi Marittime 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

Environmental predictors

Climate, geomorphology, land use, 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). Digital elevation model from the GMTED2010 database (Danielson and Gesch 2011) was used to derive slope and terrain roughness, which were also integrated into the models. Five land use 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). All variables were then clipped to the Italian alpine region (Roekaerts 2002) as raster layers with a 1 km spatial resolution. Furthermore, to investigate predator-prey interactions, we included the modeled 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., 2022). 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.

Table 2

Name, description, spatial resolution, and data source of all variables included in the SDMs, grouped into four categories: geomorphology, climate, land use, and biotic. The snow vole variable was included exclusively as a predictor for modeling the distribution of the stoat

Variable	Description	Resolution	Source
<i>Geomorphology</i>			
Elevation	Digital Elevation Model (DEM)	10 m ²	Worldclim: worldclim.org
Slope	Rate of change of elevation (from DEM)	10 m ²	Worldclim: worldclim.org
<i>Climate</i>			
Mean diurnal air temperature range (bio2)	Mean diurnal range of temperatures averaged over 1 year	1 km ²	CHELSA: chelsa-climate.org
Isothermality (bio3)	Ratio of diurnal variation to annual variation in temperatures	1 km ²	CHELSA: chelsa-climate.org
Temperature seasonality (bio04)	Annual temperature variation based on the standard deviation of monthly temperature averages.	1 km ²	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 ²	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 ²	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 ²	CHELSA: chelsa-climate.org
Snow cover days (scd)	Number of snow cover days throughout the year	1 km ²	CHELSA: chelsa-climate.org
<i>Land use</i>			
Urban areas	Euclidean distance from urban areas pixels	1 km ²	Chen et al. (2022)
Grasslands	Euclidean distance from grasslands pixels	1 km ²	Chen et al. (2022)
Croplands	Euclidean distance from croplands pixels	1 km ²	Chen et al. (2022)

Variable	Description	Resolution	Source
Barrens	Euclidean distance from barrens pixels	1 km ²	Chen et al. (2022)
Forests	Euclidean distance from forests pixels	1 km ²	Chen et al. (2022)
<i>Biotic</i>			
Snow vole suitability	Habitat suitability for the snow vole in the Italian Alps	1 km ²	This study (modelled data)

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 the worst-case scenario for climate and land use change. Specifically, we considered the SSP5-8.5 scenario from the Coupled Model Intercomparison Project Phase 6 (CMIP6; O'Neill et al. 2016; Karger et al. 2017; Chen et al. 2022), as this scenario reflects a plausible outcome under current global policy trajectories (Hausfather 2025) and provides a useful framework for assessing potential impacts (Sarofim 2024). These scenarios are based on General Circulation Models (GCMs), which simulate the dynamics of the atmosphere and ocean circulation. As GCMs are developed by different meteorological centers, variations among models can lead to differences in SDM projections (Buisson et al. 2010). To address this uncertainty, we used five different

GCMs under the RCP 8.5 scenario: 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)

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, longitude, and elevation. Following Aguirre-Gutiérrez et al. (2016), centroids were derived from binary maps for the present and 2100, and differences in their latitudinal, longitudinal, 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 use 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. S3).

Table 3
Environmental predictors and their percent contribution to the overall model for each species. Only variables with a contribution greater than 10% are shown (the complete list is available in Supporting Information, Fig. S2 and S3)

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

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 use variables had a more marginal influence on stoat habitat suitability (Supporting Information, Fig. S4). Modeled environmental suitability for both species across five GCMs is presented in Supporting Information, Fig. S2.

Model projections under future global change scenarios for 2100 predicted significant range shifts for both species (Fig. 4). The snow vole is expected to experience a net range change increase of + 76.77% (SD = 32.56), reflecting an overall gain in suitable habitat. 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 the southwestern and part of the central and eastern Italian Alps (Supporting Information, Fig. S5). Conversely, the stoat is expected to undergo a severe range contraction, with a net range change of -35.99% (SD = 19.16). 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 (southwestern Italian Alps) and much of the eastern Alps (Fig. 5). Projected changes in the distribution ranges of both species by 2100, modeled across five GCMs and using three alternative threshold criteria, are presented in Supporting Information, Figs. S6-S7.

Both species exhibited a northward shift in their range centroids by 2100. The snow vole centroid moved approximately 22 km northward, with minimal changes along the longitudinal and elevational axes. In contrast, the stoat centroid shifted about 15 km northward, 21 km westward, and 214 m upward (Fig. 6). The projected range of the stoat is expected to decrease from 8,698 km² ($\pm$ 4,961 SD) under current conditions to 5,722 km² ($\pm$ 3,425 SD) by 2100. In contrast, the snow vole is predicted to increase its range from 3,702 km² ($\pm$ 736 SD) to 6,474 km² ($\pm$ 1,255 SD). Focusing on predator-prey spatial dynamics, the range overlap between the two species is expected to decline by approximately 35%, from 1,739 km² at present to 1,145 km² by 2100.

Discussion

Through a collaborative network of institutions and the integration of validated citizen science data, we modelled the current and projected 2100 distributions of the stoat and the snow vole in the Italian Alps. Our results revealed a projected range contraction of approximately 36% for the stoat, accompanied by an average upward elevational shift of around 200 meters. These findings support the view that the species is effectively on an “elevator to extinction” (Marris 2007; Urban 2018), highlighting its vulnerability to ongoing climate change. 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 showed a 77% increase in suitable habitat, but a slight downward shift in mean elevation ($\sim$ 50 m), reflecting a different response to climate change. This spatial decoupling between predator and prey led to an estimated $\sim$ 35% spatial mismatch across the Italian Alps, potentially exacerbating the stoat’s vulnerability and weakening the functional link between these species, consistent with previous reports of climate-driven disruptions of predator-prey dynamics (Gilg et al. 2009; Aryal et al. 2016; Hamilton et al. 2017).

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 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 (King and Powell 2007).

Our models identified areas with approximately 250 annual snow cover days as optimal for stoat habitat suitability. Beyond this threshold, suitability declined sharply, likely reflecting the transition to environments dominated by glaciers or permanent snow, which likely offer limited resources and prey availability. While this suggests a strong dependence on seasonal snow cover in the Alps, it could be

argued that stoats may persist even in 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. Moreover, if stoats were able to persist under entirely or partially snow-free conditions in this region, they would likely already occupy lower elevations, where typical prey items such as rabbits, rats, or water voles—among the most common components of their European diet (King and Powell 2007)—are more abundant. Yet, their absence from these areas further reinforces the importance of snow cover in shaping their distribution.

We also found a strong positive response to snow vole suitability, highlighting the tight ecological association between the two species. To our knowledge, this represents one of the few successful examples of joint modelling of a specialist predator and its primary prey at a broad spatial scale. A comparable example is provided by Aryal et al. (2016) who modelled the distributions of the snow leopard (*Panthera uncia*) and the blue sheep (*Pseudois nayaur*) in the Himalayas. Similarly to the snow leopard-blue sheep relationship, the stoat is considered a specialist predator of the snow vole in the Italian Alps, where this rodent consistently emerges as the most frequently consumed prey item in both the Western (Bounous et al. 1995) and Central Alps (Martinoli et al. 2001). Nevertheless, stoat diets in these regions also include other small mammals—such as 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 both bank voles and wood mice 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.

The stoat usually exhibits a marked preference for larger prey (King and Powell 2007), 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*)—in central and northern Europe (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). Similarly, in the Italian Alps the snow vole is more than 30–50% larger than both bank vole and wood mice, making it a more energetically profitable resource (Martinoli et al. 2001; Amori et al. 2008). Thus, while stoats exhibit dietary plasticity that may allow them to exploit alternative prey in the absence of snow voles, the availability of larger rodent species likely remains essential for supporting viable stoat populations, particularly in energetically demanding high-elevation environments.

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 scree 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, 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 ('petricolic species'; 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).

It may seem surprising that the snow vole appears essential for stoat persistence, given the relatively low overlap between their predicted current distributions. However, this discrepancy likely reflects a data bias affecting the predicted snow vole distribution, as indicated by the lower predictive performance of its models. While the stoat is more frequently spotted and reported by hikers and photographers, the snow vole is cryptic and rarely detected. In our study, while most stoat records originated from citizen science platforms, the majority of snow vole occurrences came from targeted live-trapping studies. This sampling bias likely results in an underrepresentation of snow vole occurrences at higher altitudes and an overrepresentation at lower elevations, where small mammal surveys are more frequently conducted. Supporting the hypothesis of snow vole underrepresentation, snow voles have been detected wherever stoats have been studied across the Italian Alps: Aosta Valley (Bounous et al. 1995), Adamello-Brenta (Martinoli et al. 2001), Maritime Alps (Granata et al. 2025), and Cottian Alps (among the data used for this paper).

We strengthened our methodological framework by using an ensemble approach based on three algorithms and by repeating analyses across five independent GCMs. Nonetheless, one may question the reliance on the most pessimistic IPCC pathway (RCP 8.5, broadly equivalent to SSP5-8.5), which assumes continuously rising CO₂ emissions and substantial global warming by 2100 (IPCC 2014, 2023). Although recent analyses suggest that such high-emission trajectories have become less likely (Hausfather and Peters 2020; Huard et al. 2022), they cannot be excluded under current policies and in the absence of stronger mitigations (IPCC 2023; Hausfather 2025). Importantly, high-end scenarios remain valuable for exploring low-probability but high-impact outcomes and for stress-testing ecological models under extreme conditions (IPCC 2023; Sarofim 2024). Adopting a precautionary approach, we therefore used RCP 8.5 to estimate the most severe potential consequences of climate change for the snow vole and the stoat and to quantify the maximum plausible shifts in their distribution.

Another potential limitation of our study concerns the source and consistency of occurrence data. Records were gathered from a network of institutions and citizen science platforms, introducing variability in both data quality and survey efforts across the study area. On one hand, these efforts were

unevenly distributed, depending on institutional engagement and the availability of existing records. On the other hand, citizen science played a crucial role in filling important spatial gaps. In recent years, such platforms have become increasingly important for species distribution modeling (Feldman et al. 2021), especially in the absence of standardized, high-quality datasets (Van Eupen et al. 2021). However, citizen science data come with challenges, including spatial and temporal biases—such as oversampling in easily accessible areas (Geldmann et al. 2016)—and the risk of species misidentification, which can lead to false positives (Dickinson et al. 2010; Aceves-Bueno et al. 2017). To address this issue, we manually verified species identifications for records from iNaturalist, GBIF, and opportunistic sources by reviewing associated photos or videos, thereby improving the reliability of our data.

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 a previous study (Granata et al. 2025), we demonstrated that the “Alpine Mostela”—an enclosed camera trap specifically adapted from the original Mostela model for mountain small mustelids (Salvador et al. 2022)—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, the stoat’s easy recognizability and its recent selection as the official mascot for the upcoming Milano–Cortina 2026 Winter Games make it an ideal flagship species for citizen science initiatives. Such initiatives could raise public awareness and strengthen conservation efforts, as exemplified by the case of the three-banded armadillo (*Tolypeutes tricinctus*), mascot of the 2014 FIFA World Cup in Brazil (Melo et al. 2014), even if the species did not significantly benefit from the initiative, due to a lack of political commitment and follow-through by event organizers (Bernard and Melo 2019).

From a conservation perspective, the projected ~ 40% decline of the stoat in Italy represents a significant finding, particularly given its current classification as *Least Concern* (Rondinini et al. 2022). Based on our projections, the stoat would qualify as *Vulnerable* at the Italian level under IUCN criterion A3c, which applies to population reductions within the next 100 years, based on declines in area of occupancy (AOO), extent of occurrence (EOO), and/or habitat quality (IUCN 2022). 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, we argue that future research on stoats should move beyond assessing the direct impacts of climate change alone and adopt a more integrative approach that also addresses indirect and interacting pressures. These include: (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 indicate that climate change is likely to disrupt key predator-prey dynamics in high-elevation ecosystems, as exemplified by the projected sharp decline of the stoat driven by the combined effects of snow cover loss and spatial mismatch with its primary prey, the snow vole. 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 and as a potential flagship species for alpine biodiversity conservation. 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.

Declarations

Competing interests

The authors declare no competing financial interests

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Author Contribution

Marco Granata*: Conceptualization, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing; Margherita Cattaneo*: Data curation, Formal analysis, Writing – original draft, Writing – review & editing; Sonia Calderola : Data curation; Maria Chiara Deflorian: Data curation; Laura Martinelli: Data curation; Luca Maurino: Data curation; Mirko Di Febbraro: Conceptualization, Methodology, Software, Writing – review & editing; Sandro Bertolino: Conceptualization, Supervision, Project administration, Writing – review & editing. *These authors contributed equally to this work.

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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

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Figures



Figure 1

Figure 1

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

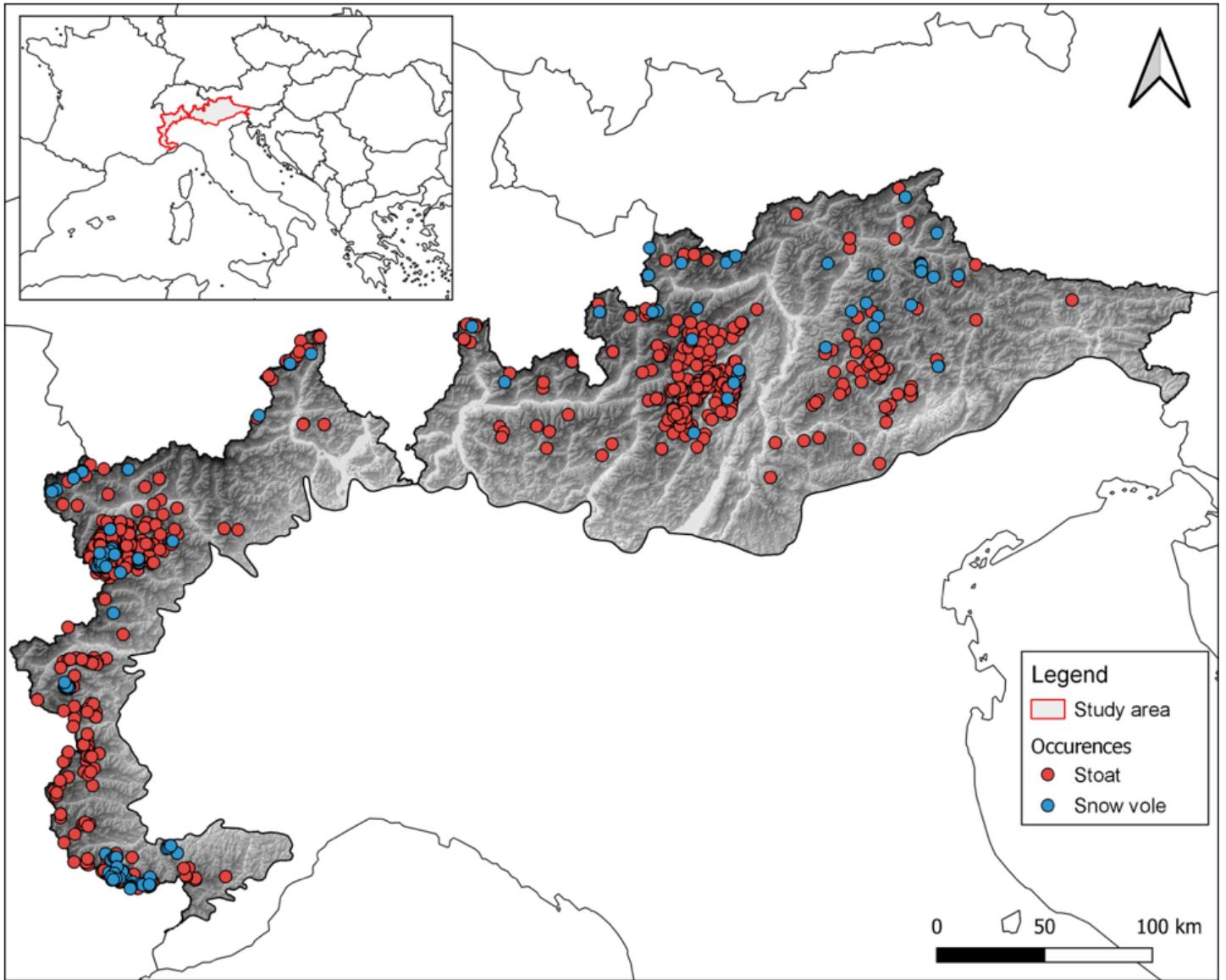


Figure 2

Figure 2

Our study area, the Italian Alps, showing the hillshade derived from the digital elevation model used for modeling. 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

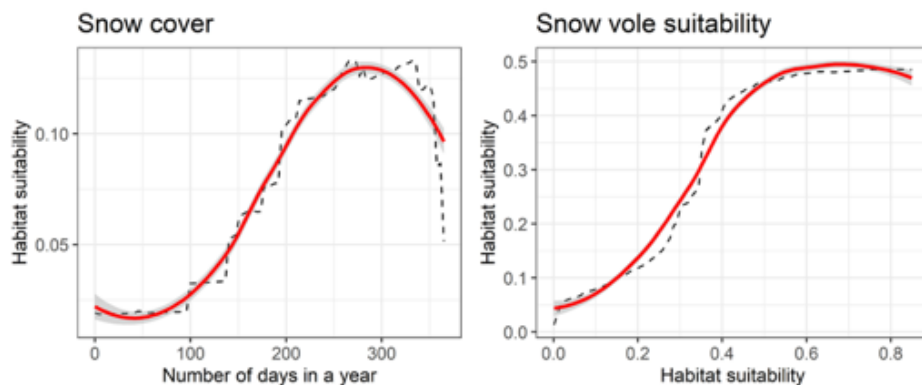
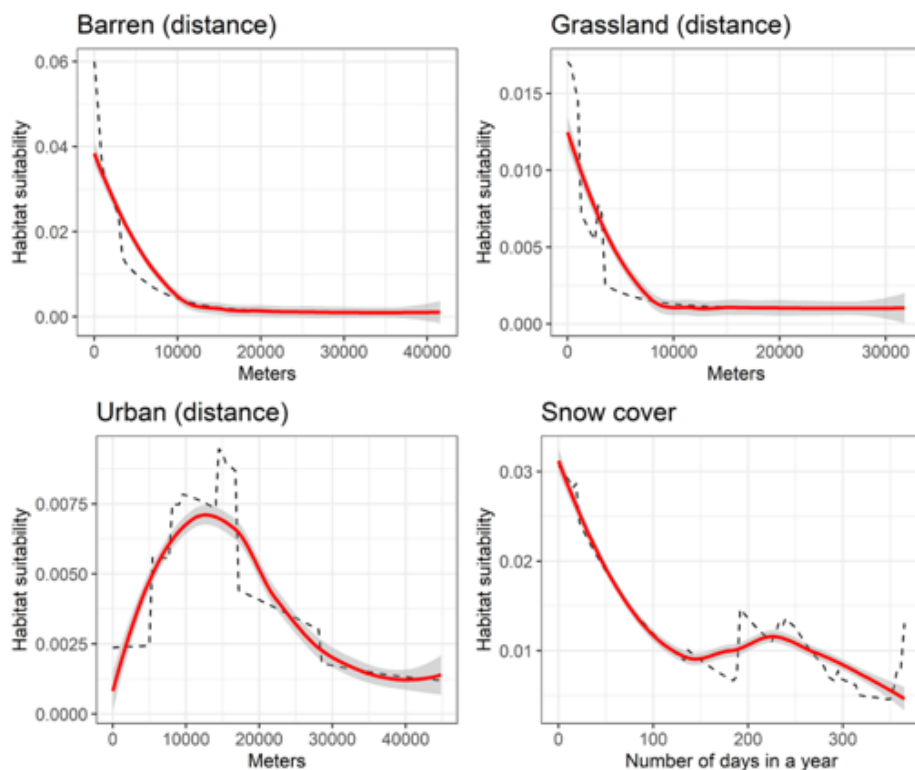


Figure 3

Figure 3

Response curves showing the relationship between habitat suitability and environmental variables with over 10% contribution in the ensemble model, for the snow vole (top) and the stoat (bottom). Response curves were smoothed using a loess function

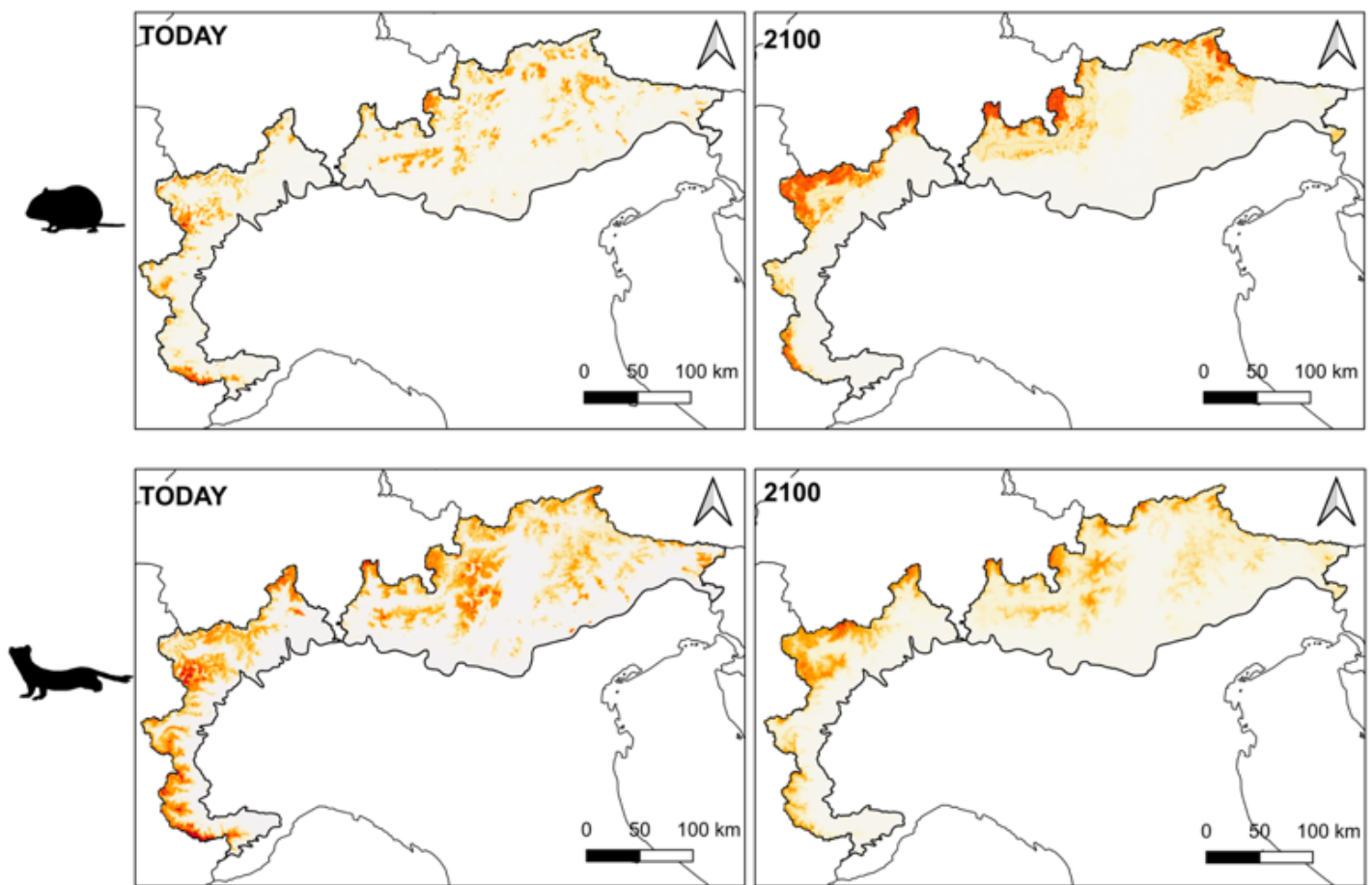


Figure 4

Figure 4

Modelled current and future environmental suitability for the snow vole (top) and the stoat (bottom) in the Italian Alps. Suitability is represented using a sequential color scale ranging from white (low suitability) through yellow and orange to red (high suitability)

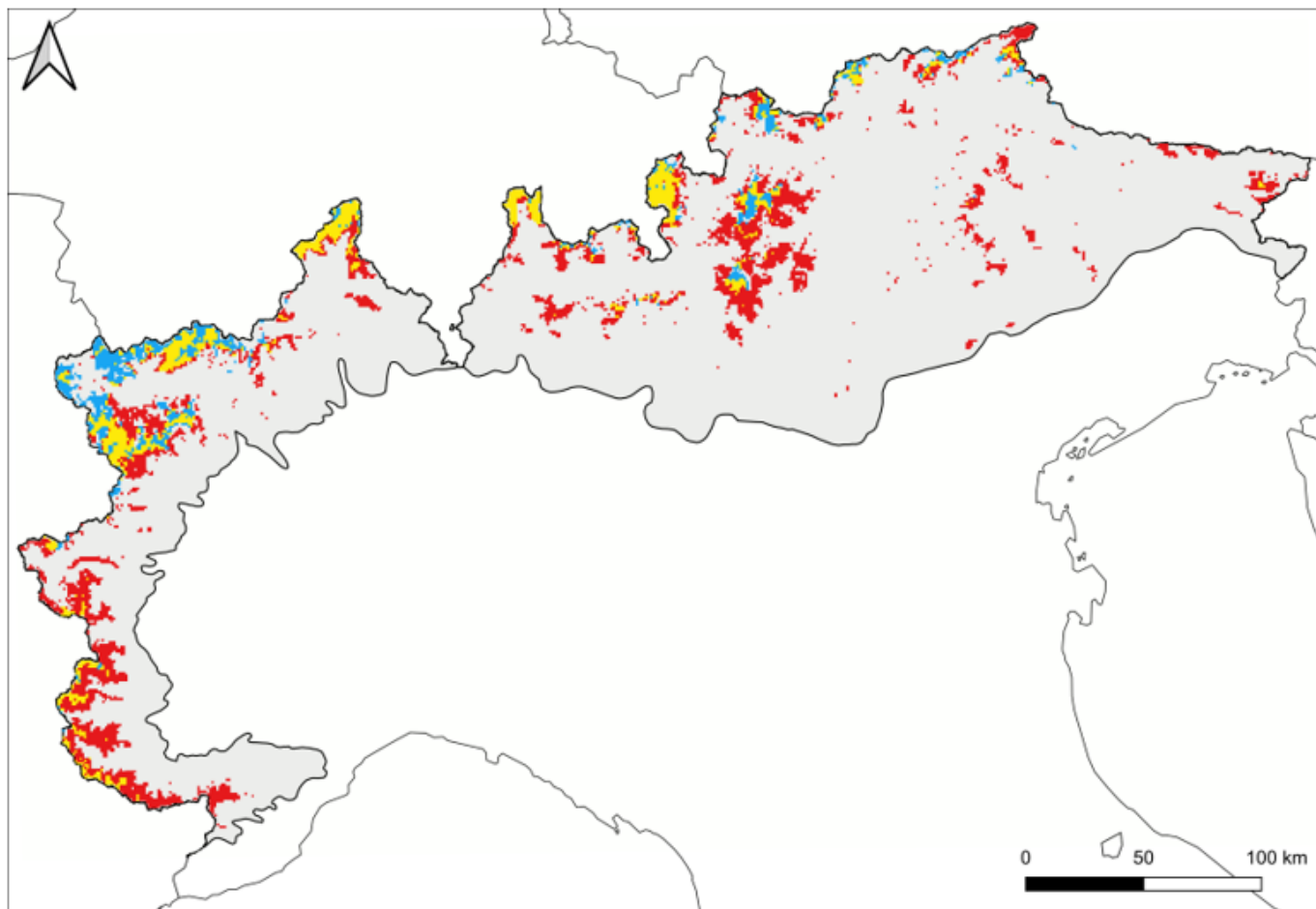


Figure 5

Figure 5

Projected changes in the distribution range of the stoat by 2100 under land use and climate change scenarios, based on RCP 8.5. Areas of projected range gain are shown in blue, stable range in yellow, and range loss in red. Predictions were generated using the IPSL-CM6A-LR global circulation model and the 'maximize specificity and sensibility' binarization threshold

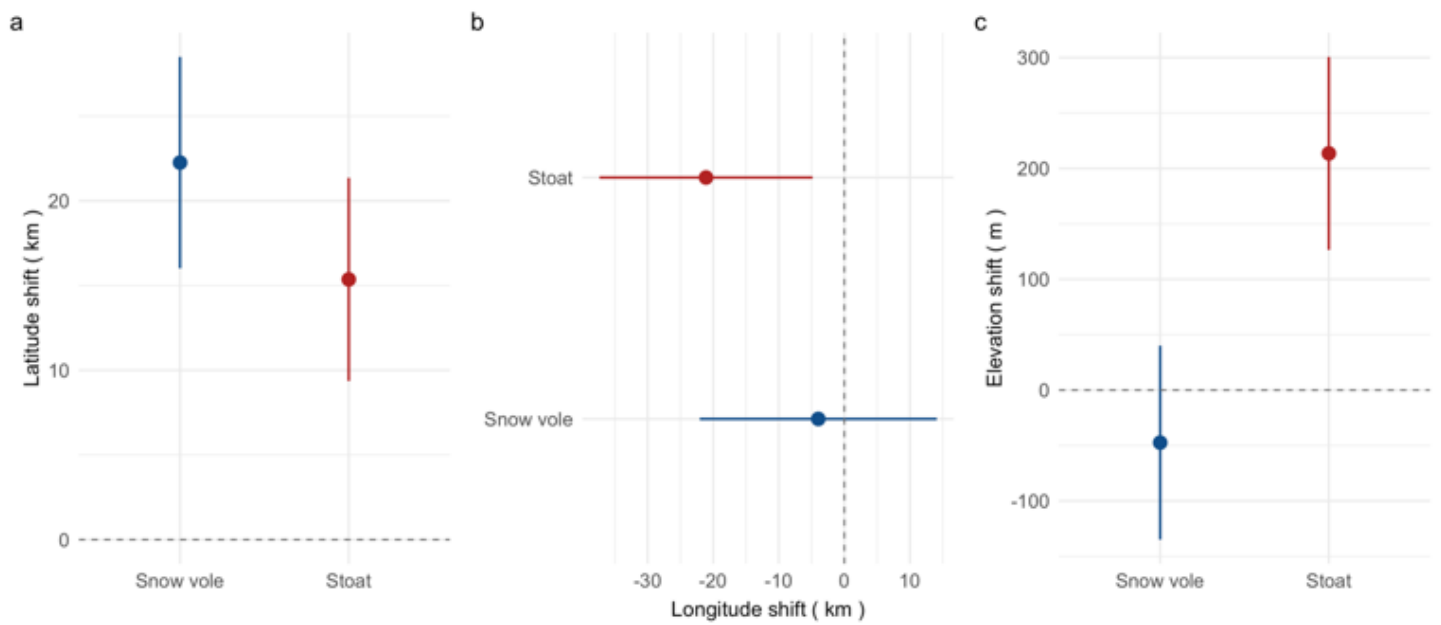


Figure 6

Figure 6

Latitudinal (a), longitudinal (b), and elevational (c) shifts (mean $\pm$ SD) of the stoat and the snow vole range centroids between the present day and 2100 in the Italian Alps

Supplementary Files

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