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Hierarchical Habitat Selection for Reconstructing Past and Present Niches and Distributions of Data-Limited Species Under Climate Change

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ABSTRACT

Aim: Understanding ecological niche shifts is crucial for predicting future changes under climate change. Modelling past niche dynamics provides a baseline for gauging the severity and direction of ongoing shifts. However, reconstructing historical habitats for data-limited, range-restricted species is challenging, as sparse species records hinder robust inference. We introduce and apply a hierarchical modelling framework to reconstruct historical habitats, assess niche shifts over time, and estimate prediction uncertainty for data-limited species. We applied this framework to the Sierra Nevada Grey-crowned Rosy-Finch (*Leucosticte tephrocotis dawsoni*) to evaluate changes in breeding habitat suitability under climate change.

Location: Alpine regions of California, USA.

Methods: We applied a hierarchical habitat selection approach based on three orders. Available habitats of finer orders were selected based on insights from broader orders. For each covariate we defined a range of nested scales of effects and employed indicator variable selection and spike-and-slab priors for variable selection. Historical niche relationships (1954–1980) were used as priors alongside current survey and bioclimatic data to characterise present-day suitable habitats (2018–2022), estimate niche shifts, validate models and assess conservation implications.

Results: We found substantial habitat declines, with suitability contracting by 40%–64% across habitat selection orders and suitable breeding areas shifting upslope by approximately 280 m. Historically, suitable habitats were characterised by rugged, high-elevation terrain with persistent snow. Contemporary distributions show reduced topographic constraints but increased reliance on diminishing snow resources, suggesting potential niche expansion.

Main Conclusions: Our approach effectively identified key variables across habitat selection orders, revealing both niche contraction and expansion driven by reduced snow persistence, processes likely affecting many alpine species globally. This framework offers a robust tool for characterising habitat changes for data-limited species, with broad applicability for conservation planning. It also highlights the dynamic role of scale in species niches across space and time.

1 | Introduction

Climate change is shifting species distributions, often to higher altitudes or latitudes to track suitable habitats (Lenoir and Svenning 2015). Projections of future species distributions are essential for anticipatory management and conservation (Sofaer et al. 2019). Models of historical changes in niche and habitat suitability provide important complements to future distribution models, which are inherently uncertain (Santini et al. 2021). Modelling historical species distributions can provide baselines to compare to current distributions, revealing whether habitat loss or change has already occurred. Such comparisons are crucial for identifying trends in species resilience and adaptation or vulnerability (Franklin 2010).

However, reconstructing historical habitat suitability poses unique challenges: historical species records often are sparse, lack precise coordinates, and suffer from uneven sampling efforts (Moudrý et al. 2024). Species of greatest interest are often restricted in distribution and/or rare, limiting the availability of historical occurrences, and might not occupy all available suitable habitat (Amirkhiz et al. 2021). Thus, species records might not represent the full range of the species' niche, nor do absences necessarily mean that habitat is unsuitable (MacKenzie et al. 2002; McCune 2016). Small sample sizes also limit model complexity (Dormann et al. 2013), yet incorporating multiple variables remains critical for species with specialised habitat needs.

Previous solutions include reducing covariates based on expert knowledge of a species' niche, but such expertise is often unavailable for understudied taxa, especially where the Wallacean (where species occur), Prestonian (abundance and dynamics), and Hutchinsonian (ecological niche tolerances and requirements) shortfalls limit reliable expert elicitation (Hortal et al. 2015). Removing covariates to improve model transferability can also discard key niche dimensions, limiting understanding of habitat requirements (Guillera-Arroita et al. 2015). Other efforts to improve historical habitat model performance have focused on the impact of temporal mismatch between occurrence records and environmental variables, location inaccuracy, sampling bias, and observers' errors (Bracken et al. 2022; Naimi et al. 2014; Newbold 2010; Reside et al. 2011).

An efficient approach for modelling historical niches and distributions remains elusive (Hooten and Hobbs 2015). The application of hierarchical habitat selection theory (Johnson 1980) can boost predictive accuracy in data-limited settings by progressively narrowing available habitat from broader to finer spatial scales (Amirkhiz et al. 2021; McGarigal et al. 2016). At each habitat selection order, every habitat factor may have one or more optimal scales of effect and integrating these scales refines our grasp of species' niche requirements (Amirkhiz et al. 2023; Moraga et al. 2019). A drawback is that testing multiple scales for many habitat factors can inflate the candidate variable set (Jackson and Fahrig 2015), posing a challenge when data are limited. We explore the application of scales of effect within a hierarchical habitat selection framework to model historical species habitat suitability.

Alpine birds with small ranges and specialised needs often exhibit focused hierarchical habitat selection, targeting specific habitat features (Devictor et al. 2008; Razgour et al. 2011). This makes them ideal candidates to test the applicability of hierarchical habitat selection theory in species distribution modelling. Birds, as highly mobile species, perceive landscapes at multiple spatial scales, adjusting habitat selection based on information gathered at each level (Jedlikowski et al. 2016; Mayor et al. 2009). Moreover, climate change poses particular risks to alpine specialists, which are adapted to narrow conditions and often cannot shift higher in elevation, leaving them vulnerable to warming temperatures and habitat loss (Freeman et al. 2018; Neate-Clegg et al. 2021).

In this study, we built and evaluated a hierarchical approach to variable selection and modelling of historical distribution for the Sierra Nevada Rosy Finch (*Leucosticte tephrocotis dawsoni*, hereafter SNRF), an alpine-breeding songbird endemic to high elevations of California's Sierra Nevada and nearby mountains. Over the last century, these mountain ranges have undergone significant climatic shifts, warming faster than lower elevations, and experiencing declining snowpack and increasingly variable precipitation, with both extreme wet and dry years affecting snowmelt timing (Belmecheri et al. 2016; Rhoades et al. 2018). These changes can limit suitable habitats for high-elevation species, making it essential to understand their habitat preferences and trends in suitability and distribution to guide anticipatory conservation strategies (Peterson et al. 2011; J. A. Wiens and Bachelet 2010).

The SNRF breeds in rugged, sparsely vegetated landscapes above treeline (MacDougall-Shackleton et al. 2020; Twining 1940). During the summer breeding season, it forages on highly visible insects immobilised on late-lying snowfields; melting snow also provides a consistent water source and seeds at margins (Epanchin et al. 2010; Stanek 2009). SNRF nests on cliffs and rocky outcrops, which offer protection from predators. Despite its specialised ecology, this subspecies remains understudied because of its remote breeding grounds (Beedy et al. 2013). These data gaps hinder conservation efforts, preventing an accurate depiction of species distribution. This is especially crucial in the context of climate change, as it can alter snow accumulation and melt, potentially reducing the availability of summer foraging habitats.

To address data limitations in historical habitat modelling, we applied hierarchical habitat selection theory (Johnson 1980). We iteratively limited available habitat and used indicator variable selection (Kuo and Mallick 1998) and spike-and-slab priors (Ročková and George 2018) to identify influential covariates at their optimal scales while managing collinearity. We assumed that specific habitat factors at each order of habitat selection shape the species niche, and that if their requirements are not met at that order, the species continues to consider them in finer orders. We also assumed that each habitat factor operates at a specific spatial scale where its influence on habitat suitability is most pronounced, referred to as its optimum scale of effect. We applied our approach to model the historical distribution of SNRF by relating relative abundance to environmental variables at fine temporal and spatial resolutions. Further, we collected and employed a set of contemporary records to evaluate model accuracy and compare past and current niches and distribution of SN Rosy-Finch. We asked the following questions: (1) What are the main environmental factors shaping SNRF niche at each hierarchical habitat selection order? (2) Have breeding habitat suitability and niches of SNRF changed between the historical period (1954–1980) and the present (2018–2022)? (3) Does the species distribution derived from the model calibrated with present-day records match the projection of the historical model under current bioclimatic conditions?

2 | Methods

2.1 | Study Area

The study area is located within California's Sierra Nevada and White Mountains, featuring steep gradients and diverse high-elevation ecosystems (Figure 1). Above treeline, alpine habitats support SNRF breeding. Rugged terrain includes exposed granitic peaks and U-shaped valleys (Graham and O'Green 2016). The climate is cold, windy, and snow-covered well into summer (Björk and Molau 2007). Coarse-textured, glacial soils sustain specialised alpine flora and fauna (Beedy et al. 2013).

2.2 | Count Data

We compiled historical SNRF records from museum specimens (Vertnet, http://www.vertnet.org; Arctos, https://arctos.database.museum) and publications (Johnson 1975; Taylor 1923; Twining 1938, 1940) for June–July within the study area. We manually transcribed publication-derived occurrence records and georeferenced them from locality descriptions (e.g., named peaks, passes, lakes) in Google Earth Pro. (Google LLC 2023). To reduce positional uncertainties, we followed Frey et al. (2013) by assigning each record to a precision category (H: <30 m, I: 30–500 m, J: 500–1000 m, K: >1000 m), retaining only the first three classes. This filtering restricted the historical dataset to observations from 1954 to 1980.

Current data were gathered via point counts conducted at fixed stations along line transects (Ralph et al. 1995) between late May and early August 2018–2022. We established 18 line transects (2 km each) in a priori–selected survey areas with both reported historical and recent SNRF detections and practical access. Two observers surveyed between 06:00 and 13:00 under favourable weather, recording all finches seen or heard at fixed stations spaced every 250 m along each transect (8 stations per transect).

2.3 | Predictor Covariates and Scales of Effect

We incorporated two core SNRF habitat components in our models: cliffs for nesting and late-summer snowfields for foraging (Epanchin et al. 2010; Grinnell 1913), using a suite of raster layers for terrain, soil, snowpack, and climate. Cliffs were identified via ruggedness (Vector Ruggedness Measure) and landform indices, while snowpack was represented by monthly Snow Water Equivalent data (1950–1980 and 2011–2020). Additional covariates included bioclimatic variables, soil bulk density, and

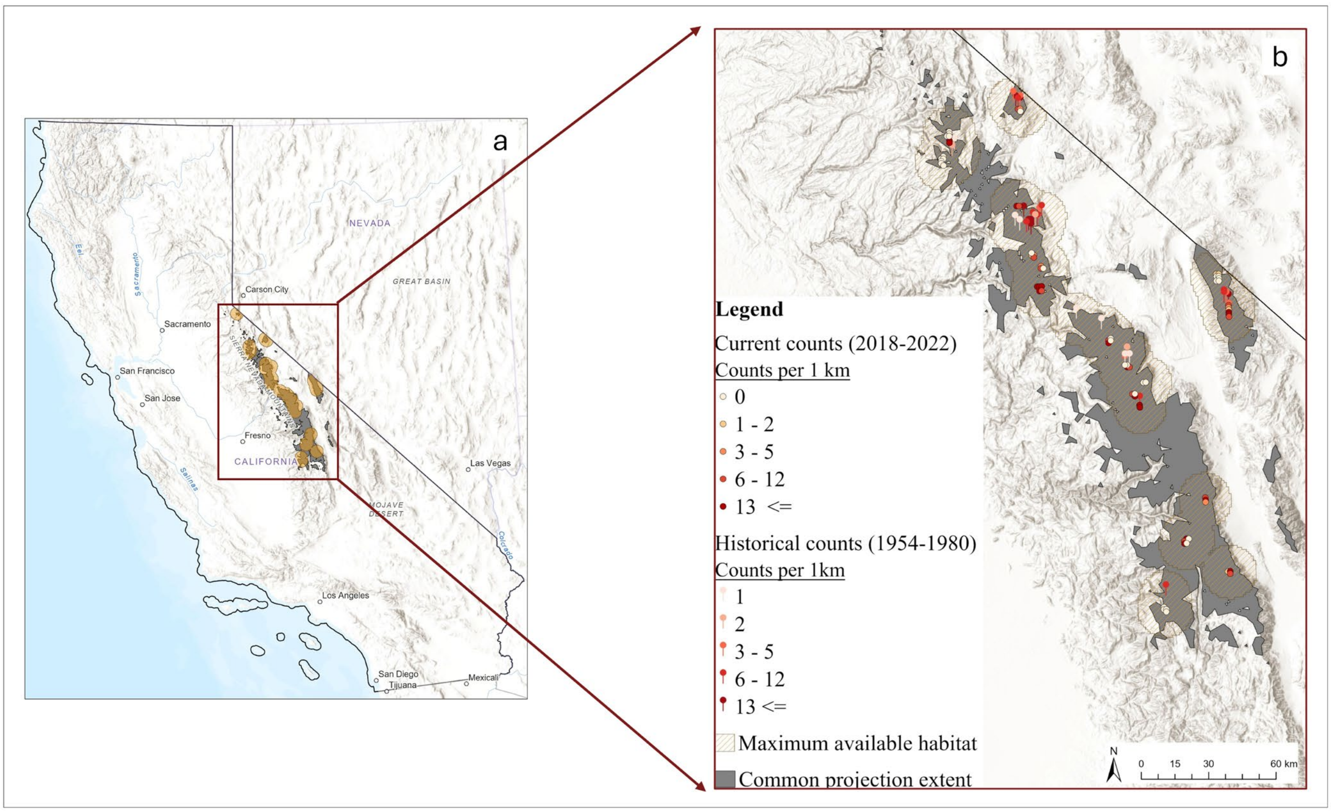

FIGURE 1 | Study area and species counts in the Sierra Nevada and White Mountains, California, USA. (a) Location of study area. (b) Historical (1954–1980) and current (2018–2022; including cells with recorded zeros), Sierra Nevada Rosy Finch counts aggregated in 1 km cells. Overlays show the maximum available habitat (species range order; union of historical and current envelopes) and the common projection extent used for prediction maps (elevations ≥ 3000 m). The base map is the World Hillshade Map (Esri 2023).

indices related to water accumulation and solar exposure. See Tables S1 and S2 for full details on thresholds, spatial resolutions, data sources, and the complete list of bioclimatic variables.

2.4 | Modelling Approach

Based on the framework outlined by Johnson (1980) and Meyer and Thuiller (2006), we structured our analysis into three hierarchical levels of habitat selection: Order 0 (Species range order, representing geographic ranges), Order 1 (Population order, representing regions containing populations within the geographic range), and Order 2 (Individual order, representing home ranges within those regions). At each level, available habitat was defined using information from the preceding, broader scale. For Order 0, we applied kernel density estimation of observation points at a 1 km spatial resolution to delineate the maximum available habitat for SNRF (Fleming and Calabrese 2017, figure 2).

Every habitat factor may have one or more optimal scales at which it influences habitat selection and species distribution (Amirkhiz et al. 2023; Moraga et al. 2019). To determine the optimal scale of variables for SN Rosy-Finch, we defined a range of candidate nested scales with radii from 150 m to 2 km, including intermediate values of 250 m, 350 m, 450 m, 850 m, and 1 km. For each of these nested circular scales, we calculated the proportion of, and the mean topographic distance to, categorical variables, and the mean of continuous variables, except for SWE, which had a spatial resolution greater than 2 km. We prepared the predictor variables using ArcGIS Pro 3.3.1 (Esri 2023) and the R package terra (Hijmans 2023).

Information on breeding season home range sizes for rosy-finches in North America is limited, but available estimates suggest that breeding SNRF individuals may forage up to 0.8 km or more from their nests (Twining 1940), consistent with our observations in the study area. Given this and considering the spatial accuracy of our historical records, we selected a 1 km grain size. We then aggregated all counts within each cell and considered cells without observations as zero across the available habitat grid in each time frame. Because survey effort could vary across space and time, these zeros indicate non-detections rather than verified absences (Kéry and Royle 2016; MacKenzie et al. 2002). We therefore interpret predicted values as indices of relative abundance/suitability (Drake and Richards 2018; Franklin 2010). This process resulted in 34 unique cells with ≥ 1 count in the historical dataset and 42 cells with ≥ 1 count in the current dataset. The current surveys also visited 35 cells with zero counts (Figure 1).

For the species range order (Order 0), we defined available habitat as the union of the historical and current kernel density envelopes to maximize environmental coverage given uneven sampling across eras (Figures 1 and 2). For Order 1 and Order 2, available habitat was further refined by restricting cells based on the response curves of the most influential predictors, identified through the variable selection process at the previous level. Cells located in areas estimated to be unsuitable were removed. This hierarchical approach aimed to progressively refine predictions, moving from broader to finer habitat selection orders by removing unsuitable habitat at each level before advancing to the next. We assumed that at each hierarchical order, specific habitat requirements shape the SNRF niche. If these broader-scale requirements are met, finer-scale selection focuses on

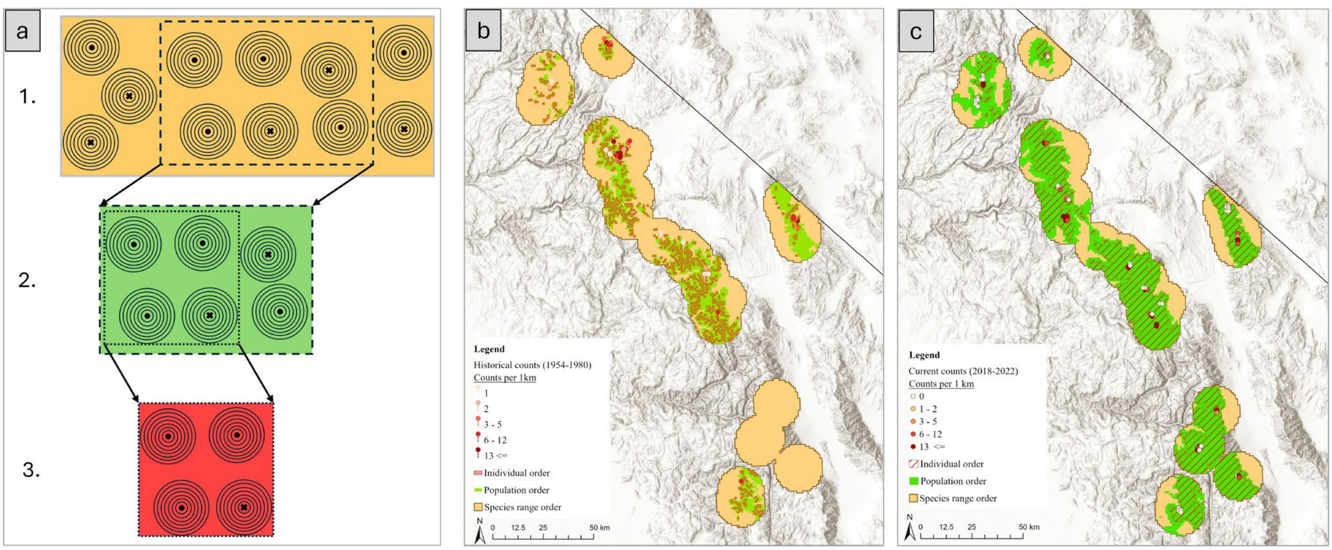

FIGURE 2 | Hierarchical habitat selection framework, scales of effect, and available habitat by era. (a) Schematic: (1) Species range order defines the broad geographic range; light-brown rectangle is the maximum available habitat (union of historical and current kernel density estimation envelopes). (2) Population order (green rectangle) represents regions containing local populations within the species-range envelope. (3) Individual order (red rectangle) depicts finer-scale home ranges within those population regions. Available habitat is progressively restricted at each order using response curve thresholds from the preceding order (nested dashed boxes). Concentric rings illustrate the candidate radii (150, 250, 350, 450, 850, 1000, 2000 m) used for scales of effect selection. Symbols indicate conceptual cells with observed counts (black dots) and zero-count cells (×). (b) Historical era (1954–1980): Counts aggregated to 1 km cells. Light-brown polygons: Maximum available habitat (species range order); green: Population order available habitat; red hatched: Individual order available habitat. (c) Current era (2018–2022): Counts aggregated to 1 km cells, including surveyed zero cells (0). Polygons are the same as in panel (b).

localized features, such as food availability or nesting sites (Johnson 1980).

We restricted model fitting to the order-specific available habitat. For map creation and cross-order comparison, we then projected predictions on a common geography: areas ≥ 3000 m elevation (Figure 1). Exploratory projections indicated that areas < 3000 m were consistently unsuitable across orders. We chose this extent because SWE raster layers were at a coarser resolution (4 km) than our 1 km response grain, which can smooth or misplace fine-scale snow patterns in mountains and cause omission error due to scale mismatch (Araújo and Guisan 2006; Livneh et al. 2015; Lundquist et al. 2019). In addition, historical bioclimatic surfaces are statistically downscaled, and early-period estimates inherit greater uncertainty from sparse station networks (Wang et al. 2016). Projecting on this common geography helps identify candidate microrefugia even where coarse predictors imply broader unsuitability, while we interpret fine-order suitability as conditional on broader-order requirements (Johnson 1980; Ashcroft 2010; Dobrowski 2011).

To estimate the relative abundance of SNRF y_i at each hierarchical level, in R package brms (Bürkner 2017), we developed Bayesian negative binomial models. Negative Binomial distribution NB was chosen due to its ability to handle overdispersion (i.e., when variance exceeds the mean), which we expected given the species clustered distribution. By addressing overdispersion, the negative binomial model prevents underfitting that could occur with simpler models such as Poisson regression (Kéry and Royle 2016). Also, negative binomial distribution inherently accommodates a higher frequency of zeros compared to the Poisson distribution without needing a separate zero-inflation component (White and Bennetts 1996). Our exploratory analyses and model diagnostics showed that negative binomial models provided a good fit to the data and performed better in predicting relative abundance than zero-inflated models. Exploratory analyses also indicated that, of the candidate random effects (year and mountain range), only mountain range improved predictive performance. Therefore, we avoided adding unnecessary complexity into our models:

$$y_i \sim \mathrm{NB}(\mu_i, \phi)$$

where y_i is the observed count in cell i ($i = 1, \ldots, N$), μ_i is the mean abundance, and ϕ is the overdispersion parameter.

We used a log link for μ_i:

$$log(\mu_i) = \alpha + \delta_{r(i)} + \sum_{k=1}^{K} \beta_k x_{ik}$$

where α is an intercept, $\delta_{r(i)}$ is a random intercept for each mountain range r, β_k are their regression coefficients, x_{ik} are the selected habitat predictors at their selected scales of effect. We assigned weakly informative priors to these parameters, including a gamma prior on ϕ to favour reasonable levels of overdispersion, and a half-Cauchy prior on the random effect variance σ^2_δ. Mountain range (Sierra Nevada, Sweetwater Mountains, White Mountains) was included as a random effect in the models to account for variation among ranges not captured by other predictors.

We performed variable selection in two steps for each habitat selection order using an indicator variable selection approach (Kuo and Mallick 1998) and spike-and-slab priors (Ročková and George 2018). Indicator variable selection provides Posterior Inclusion Probabilities (PIPs) for variable selection, but without a clear threshold, it can be challenging to determine the most important variables (Barbieri and Berger 2004). On the other hand, spike-and-slab priors are effective at shrinking coefficients but may fail to shrink some variables fully to zero, resulting in small nonzero estimates for less important variables (Ročková and George 2018). By combining these methods, indicator variable selection helps prioritise variables through inclusion probabilities, while spike-and-slab priors handle variable shrinkage, allowing for a more robust and precise selection process.

We chose indicator variable selection because it allows scale and variable selection to be performed together (Stuber and Gruber 2020). We incorporated all combinations of scales of effects and abundance covariates. For each candidate covariate, we applied both linear and quadratic transformations across all scales of effect. Indicator variables were introduced for each candidate predictor in our negative binomial models (George and McCulloch 1993):

$$log(\mu_i) = \alpha + \delta_{r(i)} + \sum_{k=1}^{K} \beta_k x_{ik} \delta_k$$

where δ_k is a Bernoulli indicator variable that toggles predictor k on ($\delta_k = 1$) or off ($\delta_k = 0$). To allow the Markov Chain Monte Carlo (MCMC) sampler to explore different subsets of predictors, we assigned each δ_k a Bernoulli (0.5) prior:

$$\delta_k \sim \text{Bernoulli}\,(0.5), \qquad k = 1, \ldots, K$$

This implies no a priori preference for including or excluding any given predictor, and probability is fixed at 0.5.

During MCMC sampling, each δ_k fluctuates between 0 and 1. The posterior inclusion probability for predictor k is then the empirical mean of δ_k across MCMC draws:

$$\hat{P}(\delta_k = 1) = \frac{1}{T} \sum_{t=1}^{T} {\delta_k}^{(t)}$$

where T is the total number of MCMC iterations and ${\delta_k}^{(t)}$ is the value of the indicator variable δ_k in iteration t. Predictors with high posterior inclusion probabilities are considered strongly supported by the data, while those near zero are less likely to be important.

We coded this model in the R package Nimble, version 0.9.1 (de Valpine et al. 2017). We defined a custom negative binomial distribution to accommodate the $NB(\mu_i, \phi)$ parametrization.

We included variables with PIP > 0 that are not highly correlated ($p < 0.8$) in negative binomial models with spike and slab priors in the R package brms (Bürkner 2017). This two-step approach was designed to consider all candidate variables but ultimately removes collinear predictors, thereby retaining only the most relevant predictors and enhancing interpretability and avoiding identifiability issues in the final set of predictors.

We evaluated model goodness of fit via posterior predictive checking (Conn et al. 2018). We compared the chi-squared discrepancy measure (Gelman et al. 1996), $\hat{c}$ (the amount of over dispersion), and Bayesian p-value (global lack of fit, Kéry and Royle 2016). We also calculated Root Mean Square Error (RMSE) and Mean Absolute Error (MAE) for zero and non-zero counts to evaluate accuracy of model predictions on unsuitable and suitable habitats (Potts and Elith 2006).

We projected the best historical model of each habitat selection order to the same common geography (≥ 3000 m elevation) to create the historical habitat suitability map for each order. Although we did not account for the detection process for both historical and current datasets, we mitigated potential spatial biases by aggregating count data into the same spatial units across the two time periods and focusing on areas that were surveyed during both periods (Moritz et al. 2008; Tingley and Beissinger 2009). Additionally, the SNRF is highly detectable during the breeding season due to its conspicuous breeding behaviours and vocalisations, and it exclusively inhabits high alpine zones above the treeline, where it is often the sole breeding passerine species (Beedy et al. 2013; Johnson 2020). This unique use of its habitat increases detectability and reduces the likelihood of misidentification. Previous studies have demonstrated that meaningful insights into changes in relative abundance and habitat suitability over time can still be obtained for such species, even when detection probabilities cannot be directly estimated (Tingley and Beissinger 2009).

Given these considerations, we produced two current habitat suitability maps for each habitat selection order. The first map was generated by projecting the historical model onto the current period using contemporary bioclimatic and SWE data, providing a historical-parameter baseline for current conditions. The second map was produced by updating the historical model with current data and then projecting this updated model. We used the posterior distributions from the historical models as priors and updated them with the current dataset (hereafter "updated current model"). We evaluated the influence of informative priors by conducting prior predictive checks to assess the appropriateness of the priors and followed up with a prior sensitivity analysis to compare model performance under both informative and weakly informative priors (Gabry et al. 2019; Figure 3).

To test if our current models reflect true potential use of habitat, rather than an unassessed extrapolation into novel environmental space (Mesgaran et al. 2014), we examined whether relative SNRF abundance differs between historical and current data under equivalent environmental conditions by performing a comparable-environment analysis. We defined environmentally comparable conditions based on shared suitable habitats recognised by models (response curves) of each habitat selection order. To classify prediction maps, the percentile of predicted relative abundance values was used to define thresholds for unsuitable habitats (Jarnevich et al. 2021). A classification sensitivity analysis was performed to evaluate how various habitat classifications responded to changes in percentile thresholds. This analysis allowed us to identify the most stable percentile threshold, minimising the sensitivity of the suitability categories to changes in thresholds. We then classified prediction raster layers into six bins of relative abundance (predicted expected count) at 1 km: unsuitable, marginal (≤ 1), low (1–2), moderate (2–5), high (5–12), and optimal (≥ 12). These bins are used for relative comparisons across eras and orders and are not biological density thresholds. We summarised class areas both across the common geography and within the comparable environment mask to reduce extrapolation risk. To assess whether there was a significant shift in elevation between the historical and current distributions, we performed a paired t-test on the category-level mean elevations.

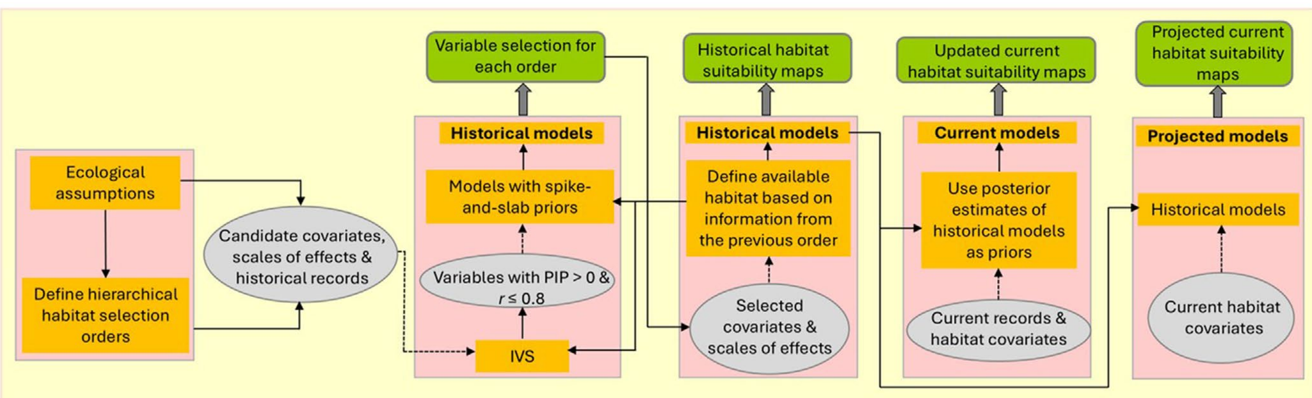

FIGURE 3 | A conceptual diagram of the modelling framework and data analysis approach used in this study. Oval grey circles are input data and dashed lines show where they were used. Pink rectangles include modelling approaches and solid lines show how they are connected. Green rounded rectangles represent modelling outcomes and thick grey arrows show the processes through which they are achieved. PIP: Posterior Inclusion Probability. IVS: Indicator Variable Selection. Scale of effect selection: For each candidate covariate, values were computed at nested radii (150, 250, 350, 450, 850, 1000, 2000 m); IVS and spike-and-slab priors operated on covariate and scale combinations, and the selected covariates at their optimal scales fed the models.

3 | Results

3.1 | Goodness of Fit

All three historical models fit adequately based on Bayesian *p*-values, with the species range and individual order models showing values near 0.5, indicating no lack of fit. The population order model had a higher *p*-value, suggesting a slight overestimation of variance. In the updated current models, the species range order again had a *p*-value near 0.5, while the population and individual orders had higher values, pointing to potential overestimation at finer scales. Across the historical models, RMSE and MAE were low for zero counts (i.e., absences), but higher for non-zero counts, reflecting robust identification of unsuitable habitats but less precision where the species was present (Data S1).

The prior sensitivity analysis demonstrated that using informative priors derived from historical models, compared to weakly informative priors, led to narrower credible intervals (CIs) for most variables and better convergence of the updated current models. The signs of the estimated coefficients remained consistent with those in the historical models, suggesting that the informative priors did not bias the results but rather refined the estimates (See Data S1 for coefficient plots of updated current models with weakly informative priors and Figure 4 for coefficient plots of updated current models with informative priors).

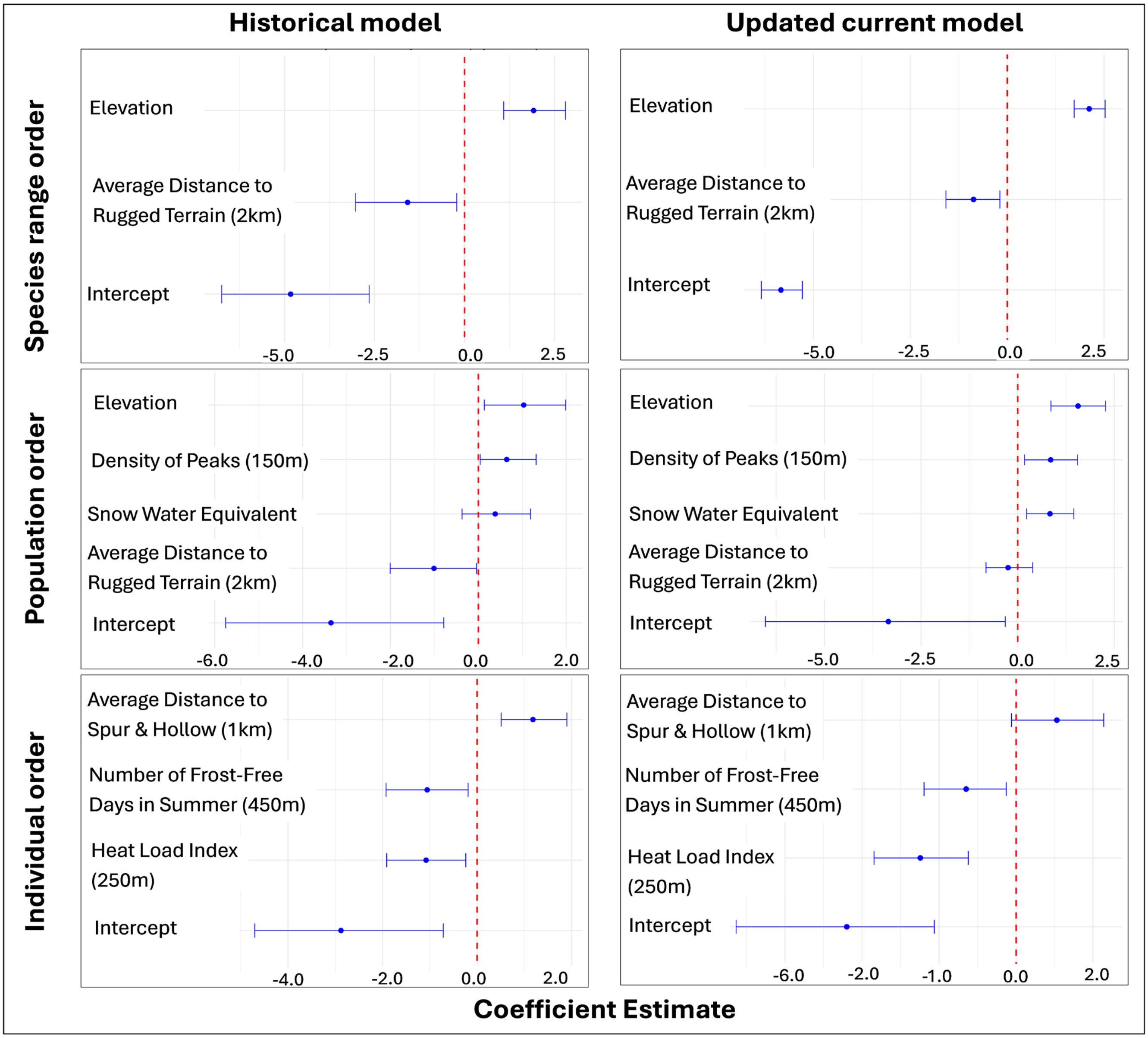

FIGURE 4 | Coefficient plots of selected covariates for historical and updated current models of habitat selection orders. The updated models were generated using contemporary data and the posterior estimates of historical models as priors. Blue dots represent the mean of the posterior distributions, and blue bars show the 95% credible intervals. The red dashed line represents zero; if a credible interval crosses this line, it indicates uncertainty in the effect of that covariate. Numbers in parentheses are selected scales of effect for each covariate. See Data S1 for the inclusion probability of top ranked variables of each habitat selection order.

3.2 | Prediction Maps Classification

The classification sensitivity analysis showed that unsuitable and marginal habitat classes were most sensitive to changes in percentile thresholds, generally showing linear relationships. Other categories showed little to no sensitivity except in some high thresholds. Consequently, the 50th percentile was a reasonable threshold for map classification because it marked a point where the sensitivity of several classes (e.g., Moderate Suitability, High Suitability) remained relatively stable in both models. Additionally, it balanced the trade-offs between unsuitable and suitable areas across the models, making it appropriate for comparing the historical and updated current models for different habitat suitability classes (Data S1).

3.3 | Species Range Order

The historical model identified elevation (positive) and average topographic distance to rugged terrain at the 2 km scale (negative) as the main predictors of SNRF relative abundance (Figure 4). Response curves indicated that areas below 3000 m elevation and more than 600 m from rugged terrain were unsuitable. The updated current model confirmed that areas below 3000 m remain unsuitable, but the threshold for unsuitable distance to rugged terrain has increased from 600 to 1500 m (Figure 5). We excluded cells outside these ranges from the available habitat dataset for model fitting in the subsequent population order model.

Low to high habitat suitability categories have all declined in predicted area since 1950 (Figures 6 and 7a). The modelled mean elevation of suitable habitats has shifted upward by approximately 47.8 m (95% CI: 12.4–83.2; $p < 0.05$). Both models predicted species presence across Sierra Nevada, White Mountains, and Sweetwater Mountains, with the latter offering the least suitable habitat, likely due to lower available elevations (max: 3552 m) and prevalence of cliff nesting habitat. Mount Shasta also emerged as high-quality habitat, and additional low-quality habitats were identified on the east sides of the Inyo Mountains, Glass Mountain, and other smaller peaks in both time periods. Within the comparable environment (3000–4000 m elevation and 0–2000 m distance to rugged terrain), the share of suitable classes (low–high) increased from historical to current, while unsuitable declined (Figure 7b). We did not produce a projected-current map for this order because the historical model retained only static topographic predictors; with no bioclimatic covariates, a projection to current conditions would be numerically identical to the historical map.

3.4 | Population Order

Historically, key predictors at this order were elevation, average distance to rugged terrain within a 2 km radius, and frequency of peaks at a fine scale (150 m; Figure 4). Response curves revealed that areas below 3250–3500 m elevation, with fewer than one peak and over 600 m from rugged terrain, were generally unsuitable (Figure 5). Snow Water Equivalent (SWE) had a positive but uncertain effect (Figure 4).

In the updated current model, proximity to rugged terrain remained important with a positive effect, but the effect was uncertain compared to the historical model. SWE showed a consistently positive effect (Figure 4). The highest suitability areas featured fewer peaks, suggesting a potential shift in niche preferences. Thresholds for elevation and rugged terrain distance remained similar (Figure 5).

Both the current and projected prediction maps (the latter based on historical data and recent SWE layers from 2011 to 2021) showed declines in habitat suitability across most suitability classes (low to optimal), with slightly greater declines in the updated current model. In contrast, both models predicted considerable increases in the area of marginal habitat. Declines in habitat suitability were most pronounced in the northern Sierra Nevada (Figures 6 and 7a). The updated current model indicated a 283-m upward shift in mean suitable-habitat elevation (95% CI: 145.1–420.9; $p < 0.05$). Within the comparable environment (SWE < 150 mm), results showed redistribution of habitat suitability with a higher share in high and optimal categories alongside a larger share in unsuitable and marginal categories (Figure 7b).

3.5 | Individual Order

At this finest order, the historical model indicated that suitable habitats were characterised by an average topographic distance of more than 40 m to spurs and hollows within a 1 km radius, lower heat load index (HLI) within a 250 m radius, and fewer than 50–55 frost-free summer days within a 450 m radius. In contrast, the updated current model suggested that suitable habitats are farther from hollows (greater than 60 m) and have a higher number of summer frost-free days (greater than 70–75; Figures 4 and 5). Similar to the population order, both the current and projected prediction maps showed a decrease in the area of low to optimal habitat suitability classes and an increase in the area of marginal habitats (Figures 6 and 7a). The modelled mean elevation of suitable habitats has shifted upward by approximately 62 m, though this shift was not statistically significant (95% CI: 3–128 m, $p \approx 0.059$). Within the comparable environment (distance to spurs and hollows: 0–55 m, HLI: 0.70–0.95, and 60–90 frost-free summer days), the share in higher quality classes (moderate–optimal) decreased and marginal increased (Figure 7b).

4 | Discussion

Our approach revealed declines in modelled suitable SNRF breeding habitat over the past 68 years at the species range order ($-40\% \pm 21.8\%$), population order ($-64.3\% \pm 9.9\%$), and individual orders ($-64.1\% \pm 21\%$). Larger declines in the finer-scale orders reflect trends of declining persistence of snow into the summer months. Our present habitat suitability models, based on current field observations, largely validated the forward projection of the historical model to the present, with some exceptions. This increases confidence in the effectiveness of this approach for reconstructing historical distributions of a data-limited, range-restricted species and provides

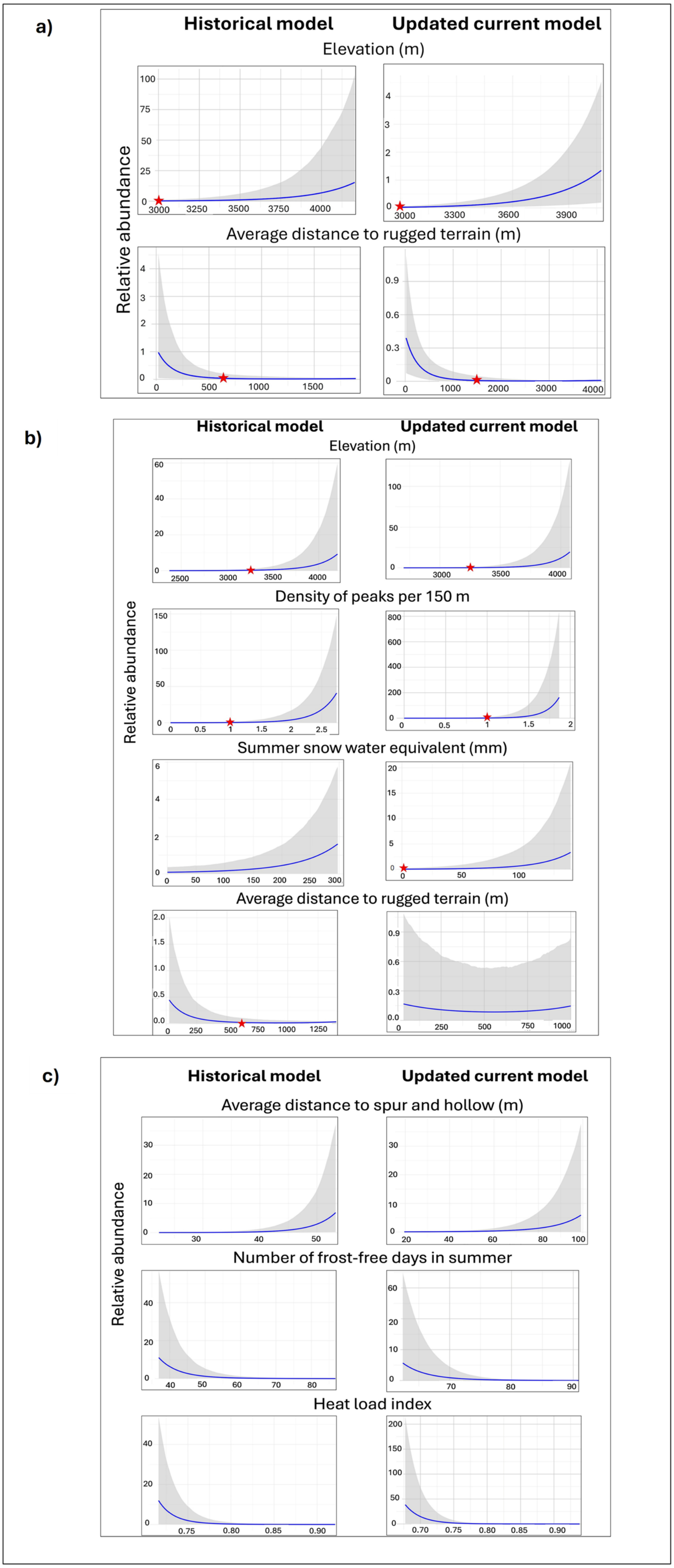

FIGURE 5 | Legend on next page.

FIGURE 5 | Response curves of selected covariates for historical and updated current species range (a), population (b) and individual (c) habitat selection order models. The updated models were generated using contemporary data and the posterior estimates of historical models as priors. Blue lines represent the mean predicted relative abundance, grey shaded areas indicate the 95% credible intervals, and red star markers on the x-axis indicate the thresholds defining unsuitable conditions used to restrict the available habitat for the next habitat-selection order. Relative abundance represents the expected count of individuals in relation to each environmental factor while holding other variables constant. See Figure 4 for scales of effects.

a retrospective test of temporal transferability, a prerequisite for projecting current relationships to future conditions (Yates et al. 2018).

4.1 | Historical Niche

By considering species range order and defining the maximum available habitat, we estimated the full fundamental niche (Yates et al. 2018). Historically, at this broadest order, higher elevation and closer distance to rugged terrains were the main limiting factors, likely reducing interspecific competition and predation risk (Freeman et al. 2019; Jankowski et al. 2013). SNRF foraging grounds are located near their nesting sites in steep cliffs. Although rosy-finches can transport large quantities of seeds, foraging closer to nests enables more efficient feeding of nestlings (MacDougall-Shackleton et al. 2020). The selected scale of effect by models for distance to rugged terrain was 2 km. This indicates that although foraging activities might be influenced by habitat characteristics at a relatively broad scale, high-quality foraging habitats are more constrained to the vicinity of nesting sites.

At the population order, our model indicated that elevation and distance to rugged terrain continued to influence habitat selection, with preference for areas containing at least one to two peaks within 150 m. These microtopographic features are associated with the availability of steep, rocky crevice nesting sites that provide protection from predators and harsh weather (R. Johnson 2020; Martin and Wiebe 2004).

At the individual order, newly selected variables by models implied that limiting factors were met at previous orders. SNRF was modelled to prefer areas adjacent to, but not within topographic spurs and hollows. While spurs and hollows can retain moisture and provide seeds and insects, they could also host denser vegetation cover—a feature selected against by another rosy-finch species (Bernier et al. 2023) and might also have a more rugged and uneven surface with little soil or vegetation to support seeds or insects (Bennie et al. 2006). Areas adjacent to productive spurs and hollows might combine resource availability with higher visibility and mobility (Lima et al. 1987).

At the individual order, modelled habitat also indicated that SNRF prefers cooler areas with less direct solar radiation (lower heat load index) at a fine scale of effect (250 m). Microclimatic conditions become more influential at finer scales, affecting immediate habitat suitability. Lower heat load index could enhance snowpack persistence (Marks and Dozier 1992) and help both adults and chicks avoid heat stress during summer (Abramsky et al. 1996; O'Connor et al. 2024). Our historical model also indicated a preference for areas where frost persists longer into summer which generates longer-lying snowpack that provides the high-quality foraging habitat (MacDougall-Shackleton et al. 2020). These findings are consistent with a previous study indicating the importance of precipitation as snow and the mean temperature of the warmest month for habitat suitability and local adaptation of Brown-capped Rosy Finch in Colorado, USA (DeSaix et al. 2022).

4.2 | Current Niche Versus Historical Niche

Current distribution models indicated that the threshold for unsuitable distance to rugged terrain has increased over time at the species range order. The population-order effect of distance to rugged terrain, which was negative in the historical model, remained negative in the current model but became uncertain, with the range of its estimated effects including zero (Figure 4). At the population order, suitable habitats in the current model also tended to have a lower frequency of peaks (Figure 5), suggesting reduced dependence on this topographic feature compared to the historical model. At the individual order, suitable current habitats were located farther from spur and hollow landforms than in the historical model (Figure 5). These shifts across all hierarchical orders from historical to current modelled niches are consistent with an interpretation that the species has become more flexible since the historical period in its use of areas farther from cliffs and other rugged features, suggesting a possible niche expansion.

On the other hand, the amount of snow, as Snow Water Equivalent, was influential in the current population–order niche but not in the historical model. At the individual order, the current niche model indicated that suitable SNRF habitats today have more summer frost-free days than they did in the historical model. These findings imply that increasing summer frost-free days could decrease snowpack persistence, forcing SNRF to become more flexible regarding the distance from their nests to snowfields.

Our predicted current distribution showed that the suitable habitat area has declined since the historical period and that upward range shifts of approximately 47.8 and 283 m have occurred at species range and population orders, respectively. These changes could be due to decreased summer snowpack persistence. Since the 1950s, the Sierra Nevada has experienced 15%–30% declines in April 1 snowpack (SWE), driven largely by warming temperatures leading to a mean shortened snow season length of 14 days and shifts from snow to rain at lower elevations (Belmecheri et al. 2016; Mote et al. 2018). Notably, these modelled shifts are of a similar order to the 178 m future upward shift projected for Brown-capped Rosy-Finches under climate change in Colorado (DeSaix et al. 2022). They

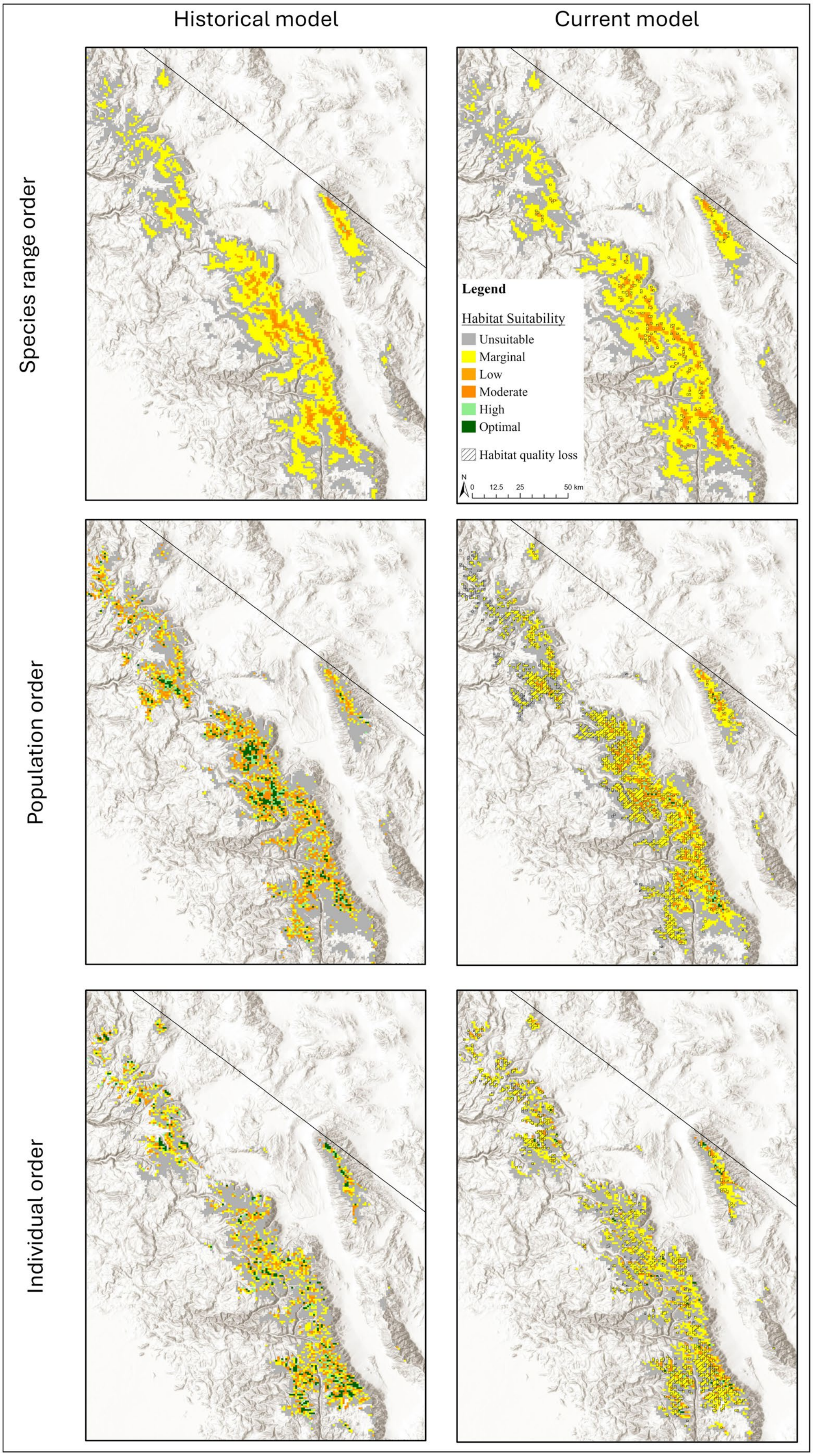

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FIGURE 6 | Habitat suitability prediction maps for historical and updated current models, depicting species range, population, and individual habitat selection orders. The base map is the World Hillshade Map (Esri 2023). Habitat suitability categories were determined through sensitivity analysis to evaluate the response of various classifications to changes in percentile thresholds. Hatched areas in the updated current prediction maps highlight regions where suitable habitats have degraded to marginal or unsuitable categories. Maps are rendered on a common geography (≥ 3000 m elevation within the maximum available habitat). Categories represent bins of model-predicted expected counts (relative index) and were used for relative comparisons. See Data S1 for projected maps.

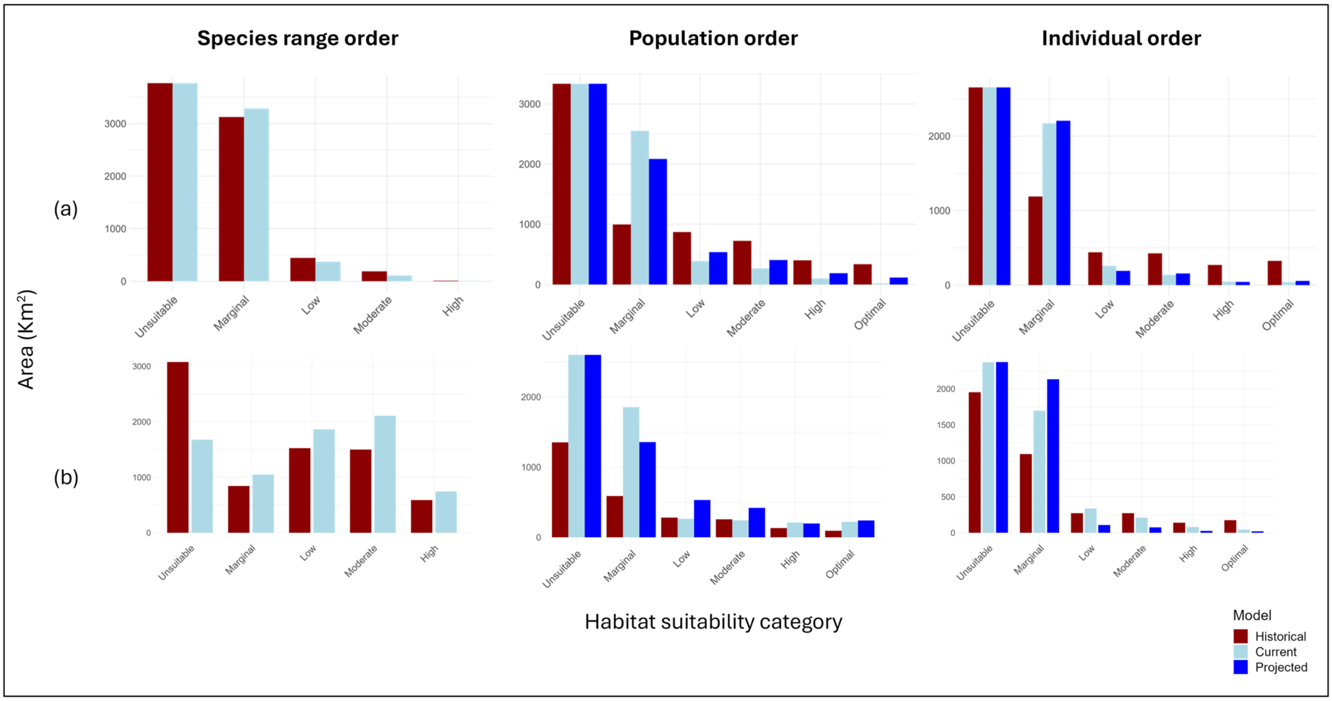

FIGURE 7 | Comparison of habitat suitability areas across historical, current (updated historical model with the current dataset), and projected (projection of historical model into the current time period) models for species range, population and individual habitat selection orders: (a) within the full environmental extent and (b) within the comparable-environment subset. Bars represent the total area (log scale, km^2) for each habitat suitability category. The species range model does not have a projected map since the historical model does not include bioclimatic variables. Categories represent bins of model-predicted expected counts (relative index) and were used for relative comparisons.

also align with broader patterns of climate-driven distribution changes in Sierra Nevada avian communities Tingley and Beissinger (2009) in which 50 of 53 bird species have already tracked their climate niche toward wetter/cooler or warmer conditions since the early 20th century. Although Tingley and Beissinger (2009) did not include SN Rosy-Finch, our results indicate that this alpine specialist is likewise shifting to higher elevations.

Overall, our results are consistent with SNRF having experienced both ecological niche breadth expansion (utilising a broader range of habitats or resources in response to changing environmental conditions; Yoder et al. 2010) and geographical niche contraction (Wiens 2011) to cope with climate change over the last century. A broader niche in harsh environments, such as alpine habitats, enables species to exploit a wider range of resources (McKinney and Lockwood 2001). This aligns with the Range Shift-Niche Breadth Hypothesis, which posits that as species shift their range, they may simultaneously broaden their niche to adapt to new or altered conditions, enhancing their chances of survival (Lancaster 2022). Broadening the niche can increase resilience to environmental changes by allowing species to utilise more diverse resources (Mermillon et al. 2021). At the same time, tracking climate niches along elevational gradients by moving upslope in response to warming temperatures and tree cover encroachment into alpine ecosystems can mitigate the effects of environmental changes (Bani et al. 2018). There are many examples of species niche expansion in response to environmental changes (Clavel et al. 2011; Mermillon et al. 2021). However, high alpine species have limited options because their ranges are restricted by elevational upper limits (Freeman et al. 2019).

Within the comparable environment subsets, we observed consistent niche shifts within shared environmental space: at the species range order, the share of suitable classes increases while unsuitable declines; at the population order, class shares reallocate, with gains at the upper suitability tail alongside increases in marginal and unsuitable categories, indicating redistribution rather than net increase; and at the individual order, higher quality classes contract while marginal expands, consistent with the use of lower quality microhabitats under warmer, less snow-persistent summers. Because these contrasts are evaluated inside predefined ranges of key predictors, they are unlikely to reflect out-of-range extrapolation artefacts (novelty Type I; Mesgaran et al. 2014). These results support a niche shift and remain compatible with niche expansion within the shared environmental envelope, although relative abundance and niche responses at the finest order of habitat selection appear constrained by recent warming.

The concept of scale is crucial to consider when studying ecological and evolutionary processes associated with niche breadth and range shifts. These shifts can involve both expansion into newly suitable habitats and contraction from formerly occupied areas, processes driven by local colonisation and adaptation at the population and individual levels (Lancaster 2022). While our study was correlative rather than mechanistic, applying hierarchical habitat selection theory provided some evidence regarding relationships between SNRF niche breadth and range shifts. This framework also helps generate testable hypotheses about species' ecological and evolutionary responses to environmental change. By combining historical and current habitat models, we gain a more robust understanding of constraints shaping suitable habitats and can better inform and interpret future modelling efforts aimed at projecting climate change impacts. Future studies should therefore test these potential mechanisms of adaptation with targeted field data, moving beyond correlative inferences to elucidate how climate-driven changes influence species distribution and persistence.

Heterogeneous topography of alpine landscapes can partially mitigate the impacts of climate change on alpine species by providing local thermal refugia (Seastedt and Vaccaro 2001). We included a variety of topographic variables in our models to capture these microhabitats, and our findings suggest that such refugia do offer some buffering capacity. However, the overall declines we observed in modelled suitable habitat underscore that refugia alone may not offset broad-scale warming trends particularly for a species with complex, spatially distributed breeding requirements (Dobrowski 2011).

This research is a first step in understanding the status and trends in SNRF breeding habitat selection and suitability and the impact of climate change. Forecasting the future impact of climate change, along with considering possible adaptation mechanisms and deepening our knowledge about nest site selection, wintering habitats, population parameters and population structure in the SNRF could all inform effective management of this species. Field-based estimates of SNRF densities in breeding habitats could also be combined with our findings to estimate change in overall abundance of this range-restricted species over the last several decades and update its conservation status.

Our approach based on hierarchical habitat selection theory effectively isolated key variables at each order of habitat selection, even under limited sample sizes, allowing us to refine suitable habitat from broader to finer orders. Indicator variable selection and spike-and-slab priors provided a robust means of identifying the most influential scales of effect and covariates, underscoring the importance of scale in species-habitat relationships. Updating historical models with current data further illuminated how the niche and distribution of this alpine specialist have shifted over time (Jackson and Fahrig 2015; Wiens 2011).

4.3 | Conservation Implications

This hierarchical modelling framework and variable selection approach is readily transferable to other range-restricted or data-limited species. By targeting the most relevant variables and scales of a given species, researchers can generate more reliable historical reconstructions and refine present-day habitat suitability assessments. Such insights can then inform future forecasting efforts, enabling conservation practitioners to plan strategies under environmental-change scenarios. In this way, adopting hierarchical habitat selection theory and scales of effects offers a powerful toolkit for understanding and predicting the distributions of species facing rapid climatic and landscape transformations.

Author Contributions

Conceptualization: R.G.A., K.R., M.B.H., E.S.Z. Methodology: R.G.A. Formal analysis: R.G.A. Data curation: T.M.B., R.G.A., K.L., G.H. Validation: R.G.A., M.B.H., E.S.Z. Visualization: R.G.A. Writing – original draft: R.G.A. Writing – review and editing: R.G.A., K.R., M.B.H., E.S.Z., T.M.B., K.L., G.H.

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Ethics Statement

All fieldwork was conducted in compliance with the following permits: National Park Service Research Permits (annually renewed), including YOSE-2023-SCI-0039 (Yosemite) and SEKI-2024-SCI-0016 (Sequoia–Kings Canyon); California Department of Fish and Wildlife Scientific Collecting Permit (S-190610001-22081-001, annually renewed), and U.S. Forest Service Special Use Permits for field activities on Inyo, Sierra, and Stanislaus National Forests, issued annually by the respective ranger districts.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and code supporting the findings of this study are openly available in the Dryad Digital Repository at 10.5061/dryad.1c59zw47b.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70128.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Supporting information.