

1 New distributional opportunities with niche innovation in Eurasian snowfinches

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19 **Abstract**

20 This study explores the evolutionary history of ecological niche characters in the Eurasian snowfinch lineage.
21 Specifically, we use new analytical approaches to reconstruct ecological niche evolution, taking uncertainty in
22 knowledge of the ecological niche limits into account. We found an overall pattern of niche conservatism in
23 relation to both temperature and precipitation characteristics of niches, but for one dramatic niche evolution
24 event, in *Montifringilla nivalis*. Interestingly, this species is also that which has by far the broadest geographic
25 distribution among snowfinches. We conclude that an evolutionary change in niche characteristics perhaps
26 within *M. nivalis* (i.e., present in some and not all of its populations) made possible the broad, westward range
27 expansion of that species, thus changing the distributional potential of the snowfinch lineage dramatically.

28

29 **Keywords:**

30 Ancestral reconstruction, ecological niche, distribution, niche evolution, range expansion, snowfinch

31

32 **Introduction**

33 The field of distributional ecology is both new and old—old in the sense that biologists have been intensely
34 interested in geographic distributions of species since pre-Darwinian times, but new in the sense that a new suite
35 of tools and frameworks has brought new rigor and insight (Johnson et al., 2019; Randin et al., 2020; Zurell and
36 Engler, 2019). A question of particular interest has been the frequency with which ecological niches change over
37 phylogeny—the idea of phylogenetic niche conservatism has enabled the tools termed ecological niche
38 modelling (Peterson et al., 2011), and inspired speculation about implications for speciation rates (Wiens and
39 Graham, 2005). Although studies have attempted to address niche conservatism over phylogeny for the past two
40 decades (Graham et al., 2004; Kozak and Wiens, 2006; Peterson, 2009; Peterson et al., 1999), methodologies
41 have not always been appropriate and rigorous (Owens et al., 2020; Saupe et al., 2018; Warren et al., 2008),
42 which has led to a general overestimation of frequencies of ecological niche innovation (Peterson, 2011; Saupe
43 et al., 2018).

44 A set of novel tools has now clarified the sources of rampant bias in (over-)estimating evolutionary rates in
45 ecological niches over phylogenies (Owens et al., 2020), permitting rigorous identification of niche innovation
46 events. Specifically, these methods separate tolerance spectra of species into distinct bins, and score each bin
47 as to present, absent, or uncertain, the latter category referring to situations in which no environments are
48 available within areas accessible to species to permit conclusions of absence (Owens et al., 2020). The result is
49 a more conservative, but apparently much less biased, view of ecological niche innovation over phylogeny in
50 many groups (Ribeiro et al., 2016).

51 Perhaps most interesting is that these methods now allow identification of new distributional possibilities that
52 open with each niche evolution event, which we explore in this paper. The snowfinches are a lineage of Old
53 World sparrows that range across Eurasia, mostly in remote and high-montane regions, which has seen detailed
54 phylogenetic (e.g., Qu et al., 2006; Qu and Lei, 2009; Yang et al., 2006) and genomic (Qu et al., in review) study.
55 Here, we apply novel phylogenetic-reconstruction tools to the ecological niches of snowfinches, and explore the
56 distributional implications of the niche changes that have indeed occurred in the history of this group. This first
57 application and exploration of such questions in a relatively simple lineage presages a broader and more
58 comprehensive understanding of the changing distributional potential of lineages through time.

59

60 **Materials and Methods**

61 **Occurrence data**

62 Occurrence data for the snowfinch clade were obtained from eBird (<https://ebird.org/>; Sullivan et al., 2009), via
63 searches for *Montifringilla adamsi*, *M. nivalis*, *M. henrici*, *M. taczanowskii*, *M. blanfordi*, *M. ruficollis*, *M.*
64 *davidiana*, and *M. theresae*, although these taxa are often treated as belonging to three genera (*Montifringilla*,
65 *Onychostruthus*, and *Pyrgilauda*; Qu et al., 2006). We filtered the initial eBird query to remove long-distance,
66 broad-spatial-footprint reports for which geographic referencing would be imprecise by removing traveling counts
67 for which traveling distance was >10 km, and other protocols for which no traveling distance was given. The
68 initial count of occurrence data available across all of the species was 3266; however, after removing duplicate
69 records and keeping only one from each set of records separated by <10 km, we had only 1353 records
70 remaining. Sample sizes per species at this point ranged 41–805 (Fig. 1). For *Pyrgilauda theresae*, only two
71 records were available; because these two sites were closely similar in environmental characteristics, and in light
72 of the apparent close relationship of this species with *P. blanfordi* (with which it has been considered conspecific;
73 BirdLife International, 2020) but complete lack of high-quality tissue samples, we removed this species from the
74 analysis.

75

76 **Climate data**

77 Data summarizing variation in climatic dimensions across Eurasia were obtained from the Chelsa climate
78 database (<http://chelsa-climate.org/>), which summarize global climates over the period 1979–2013 (Karger et al.,
79 2017). Data layers had a spatial resolution of 30", or approximately 1 km at the Equator. We excluded from
80 analysis four variables that combine temperature and precipitation information (bio 8, bio 9, bio 18, bio 19), to
81 avoid problems deriving from odd spatial artefacts (Escobar et al., 2014). Variables used can be obtained using
82 the code provided in Supplementary Data, file name: Commented_script.pdf

83

84 **Phylogenetic hypotheses**

85 We explored initially three distinct phylogenetic hypotheses: (1) a coalescent tree constructed by ASTRAL II
86 (Mirarab and Warnow, 2015) based on 2000 trees randomly extracted from birdtree (<http://birdtree.org/>) that
87 contains seven species, including all snowfinch species except *M. henrici*, (2) a Bayesian consensus tree
88 generated using BEAST2 (Bouckaert et al., 2014) based on 13 mtDNA of all snowfinch species except *P.*
89 *theresae*, and (3) a coalescent tree based on maximum likelihood analyses of 13 mtDNA constructed with
90 RAxML (Stamatakis, 2014) using ASTRALII (Supplementary Data, Fig. S1 has the summary). One species (*P.*
91 *theresae*) was excluded from analysis owing to the small number of occurrence records ($n = 2$), which reduced
92 the accuracy with which niche limits could be detected; what is more, the best phylogenetic hypothesis available
93 to us did not include this taxon. The consensus phylogenetic tree for tree 2 (see above) was obtained from a
94 total of 135,003 trees in the *a posteriori* distribution, among which only a single tree had a different topology; all
95 remaining trees presented the same topology and varied only in branch length (Supplementary Data, Fig. S2).
96 Occurrence data and phylogenetic trees are available in Supplementary Data, file name: Initial_data.zip.

97

98 **Data Analysis**

99 We focused our data analysis on the challenge of reconstructing the evolutionary history of fundamental niches
100 in the snowfinch radiation. Ecological niches of species were characterized in single environmental dimensions
101 at a time—the methodology was designed and coded this way for simplicity, and because numbers of
102 occurrence data are insufficient for multivariate analyses for many or most species. All of our analyses follow
103 methods presented by Owens et al. (2020), following insights into the importance of considering uncertainty in
104 such reconstructions (Saupe et al., 2018)—Owens et al. (2020) offered detailed justifications of methodological
105 decisions (summarized below), and presented a set of tools that supports all of the analyses conducted in this
106 study.

107

108 **Accessible area hypotheses**

109 In light of the relatively good abilities of snowfinch species as regards movement, and exploring and detecting
110 areas presenting suitable conditions (Brambilla et al., 2019), we used a relatively broad area for defining
111 species-specific accessible areas (termed **M**, see Soberón and Peterson, 2005), which in turn are the areas
112 across which niche models should be calibrated (Barve et al., 2011). We defined accessible areas for each
113 species as the area within 5° around the occurrence records of each species. Accessible areas of species in the
114 Himalaya region were further limited to only areas above 2500 m elevation (Fig. 1; Supplementary Data, Table
115 S1). All of these processes were executed in QGIS 3.10.0 (QGIS Development Team, 2019). Supplementary
116 Data (file name: Initial_data.zip) contains shapefiles of the **M** hypotheses used.

117 We inspected the occurrence data carefully for errors and inconsistencies. In particular, we checked the
118 occurrences for consistencies with known ranges of each species (BirdLife International, 2020), and examined

119 environmental characteristics of each occurrence point to detect potential outliers (Supplementary Data, file
120 names: Histograms_joined.pdf and Ranges_joined.xlsx). We then inspected visualizations of the distributions of
121 points with respect to each of the environmental dimensions, in which we focused on the extreme 5% of variable
122 values inside **M** (2.5% on each side). The environmental range within **M**, which is crucial to establishing
123 conditions under which a species is absent, was constrained to exclude rare values across **M** that either the
124 species has not been able to explore or are so scarce that the species may not have been detected there.

125

126 **Ecological niche characters**

127 We developed tables of character values for all species for each environmental dimension, summarizing ranges
128 of variable values occupied by each species and manifested across each species' **M** (Supplementary Data, file
129 name: Character_tables_joined.xlsx). This summary of variable values in **M** and for occurrences allowed us to
130 recognize values of the variable for which the species is present (value = 1), absent (value = 0), or its presence
131 is uncertain (value = ?). Uncertainty was assigned in cases in which the occupied range abutted the
132 environmental limit of the **M** area, such that at what value the species' niche limit is manifested cannot be
133 established (see Owens et al. 2020 for details). To permit detailed analysis and explicit consideration of
134 uncertainty in our reconstructions, environmental ranges were divided into equal-width bins, each of which was
135 subjected to phylogenetic reconstruction independently (see below). These methodological steps were taken
136 using the package nichevol 0.1.19 (Cobos et al., 2020) in R 3.6.1 (R Core Team, 2019).

137

138 **Ancestral reconstruction of niches**

139 Ancestral niche reconstructions were performed using the three phylogenetic hypotheses available for these
140 taxa and the tables of characters described above. We used maximum parsimony (MP) and maximum likelihood
141 (ML) methods to perform reconstructions for all 15 variables, resulting in 30 processes per phylogenetic tree. We
142 used the nichevol package, which internally uses the function "asr_max_parsimony" from castor (Louca, 2020)
143 and the function "ace" from ape (Paradis and Schliep, 2018), to perform MP and ML reconstructions,
144 respectively. MP reconstructions were done with "all equal" transition costs, whereas ML reconstructions were
145 done using the "equal rates" model.

146 We sampled 1 out of every 100 trees from the *a posteriori* distribution of trees (for tree 2 only), and developed
147 MP and ML reconstructions on each of those 1350 trees to explore variability in our results. Reconstructed niche
148 characters were categorized as 0 = absence, 0.5 = unknown, and 1 = present. To summarize variability, we
149 averaged the 1350 outcomes for each current and ancestral species in each environmental dimension. Under
150 this scheme, highly variable results will end in values in between the three recategorized states; whatever the
151 case, values closer to 0.5 reflect uncertain or unknown states, whereas values close to 0 or 1 are much more
152 certain. These analyses were performed using nichevol and base functions of R.

153

154 **Characterization of niche evolution**

155 To detect environmental values that represent niche evolution between ancestors and descendant species, we
156 compared reconstructed niches of ancestor species with those of corresponding descendant species to identify
157 episodes of niche expansion, retraction, or stasis. This comparison was achieved as follows: (1) expansion is
158 manifested as absence in ancestor and presence in descendant for a given “bin” of environmental values; (2)
159 retraction is manifested as presence in ancestor and absence in descendant; and (3) stasis is the conclusion
160 when states are equivalent in ancestor and descendant, and in any comparison in which no evidence indicates
161 difference because the character of either ancestor or descendant is unknown (see details in Owens et al.,
162 2020).

163 To identify geographic areas inside species' **M** areas that are related to niche changes detected, we queried the
164 **M** areas for environmental variable values that correspond to either niche expansion or retraction—given the
165 results obtained. We developed such geographic assessments for the four taxa (*M. nivalis*, *M. henrice*, *P.*
166 *davidiana*, and *P. blanfordi*) for which niche evolution was detected, using results obtained for tree 2 and MP
167 reconstructions. We performed these tasks using the R packages raster 3.0.7 (Hijmans, 2019), rgdal 1.4.8
168 (Bivand et al., 2019), and nichevol. Maps were developed in QGIS. Code for performing all analysis presented is
169 included in Supplementary Data, file name: Commented_script.pdf.

170

171 **Results**

172 The snowfinch lineage is broadly distributed across Eurasia, with highest species richness on and around the
173 Qinghai-Tibet Plateau. Of the seven species analyzed, five species show a quite-similar distributional pattern:
174 that is, *Montifringilla adamsi*, *M. henrici*, *Onychostruthus taczanowskii*, *Pyrgilauda blanfordi*, and *P. ruficollis*, all
175 have geographic distributions along the Himalayas, and extending northward onto the Qinghai-Tibet Plateau
176 (Fig. 1). One exception is *P. davidiana*, which is distributed more to the north, across the Gobi Desert region of
177 Mongolia, with a southernmost outlier population in central China. The most dramatic exception, however, is that
178 of *M. nivalis*, which has a wide distribution mirroring that of *P. davidiana* in the east, but that then extends into the
179 mountains of Central Asia, through the Levant, and across southern Europe.

180 We developed ancestral state reconstructions for 15 bioclimatic variables (i.e., all save for four that show odd
181 spatial artefacts), but patterns in each variable were largely parallel, at least among temperature variables and
182 precipitation variables separately. Patterns of niche evolution across distinct phylogenetic trees were also similar
183 (especially for temperature), as a consequence, we present only our reconstructions for annual mean
184 temperature and annual precipitation, and all of the remaining reconstructions are available in Supplementary
185 Data, file name: Reconstruction_figures.zip. MP reconstructions for temperature (Fig. 2) were mostly highly
186 conserved, such that only in *M. nivalis* were changes of more than a single bin of environmental values noted. In

187 precipitation, our ancestral reconstructions (Fig. 3) showed a broad ancestral niche, which then manifested
188 retractions in *M. henrici*, *O. taczanowskii*, *P. ruficollis*, and *P. davidiana*. ML reconstructions for the 15 bioclimatic
189 variables were consistent and parallel with the MP reconstructions, but ancestral states less well defined, such
190 that clear conclusions were difficult. The ML reconstructions are shown in Supplementary Data, file name:
191 Reconstruction_figures.zip.

192 Checking how much our ancestral state reconstructions varied among the 1350 trees sampled from the *a*
193 *posteriori* distribution, we observed low variability. Indeed, for MP reconstructions, we observed no variability
194 whatsoever in reconstructions based on different trees (which again, differed only in minor ways in terms of
195 branch lengths). For ML reconstructions, results varied little, but no change was >0.08 along the spectrum from 0
196 to 1 in unsuitability to suitability (values of 0.5 representing uncertainty; Supplementary Data, file name:
197 Variability_in_reconstructions_joined.xlsx).

198 Areas within the **M** for each species were queried to detect areas presenting conditions that are involved in
199 recent niche evolution events (i.e., expansions or retractions). The most dramatic such events concerned *M.*
200 *nivalis* (Fig. 4). In which the niche expansion event occurred since the split of *M. nivalis* from *M. henrici*, dated
201 perhaps at 2.6 mya (Gebauer et al., 2006; although based on a weak molecular clock approach), such that many
202 sectors of the western portion of the range of the species are under conditions that represent newly derived parts
203 of the species' ecological niche. Temperature changes in the niches of *M. henrici* and *P. davidiana* had much
204 more subtle geographic implications (Supplementary Data, Fig. S3).

205 The changes that we observed in niche with respect to precipitation were chiefly in the form of niche retractions
206 (Fig. 3). These changes affected only the peripheral parts of the **M** areas for each species, as can be observed
207 in Supplementary Data, Fig. S3. That is, in each case, areas presenting conditions from which the niche has
208 recently retracted were along the more remote parts of the **M** area of the species.

209

210 Discussion

211 The concept of the Hutchinsonian Duality (Colwell and Rangel, 2009) becomes quite significant in pondering the
212 results that we obtained in this study. That is, species exist in two linked spaces—geographic and environmental,
213 and they must conserve a nonzero range potential in each of those spaces to avoid extinction (Peterson, 2009).
214 This point is partly self-evident—that is, if a species' geographic range area approaches nil, or if conditions
215 across that range all become unsuitable, the species will go extinct. However, the explorations presented in this
216 study, in which we detect niche evolution *via* rigorous phylogenetic analyses that explicitly take into account
217 uncertainty, and then examine the geographic implications, point to some subtleties. For example, the niche
218 expansion observed in temperature tolerance of *M. nivalis* (Fig. 2) made possible massive geographic
219 expansions in the geographic potential of the lineage (Fig. 4), yet the even larger changes in the form of niche
220 retractions in precipitation values detected for other species, covered much smaller areas (Fig. S3).

221 Although analyses of ecological niche evolution in phylogenetic contexts have been developed now for more
222 than 20 years (Graham et al., 2004; McCormack et al., 2010; Rice et al., 2003), they were rather universally
223 compromised by lack of ability to take into account accessible areas for each species and associated uncertainty
224 regarding suitability limits (Saupe et al., 2018). With the development of methods that are designed to take
225 uncertainty into account explicitly (Owens et al., 2020), however, the potential arises for lineage-specific
226 reconstruction of change events, which in turn permits assessment of which parts of a species' range are "old"
227 *versus* "new" distributional potential.

228 In this study, we took advantage of these methods, and applied them to a lineage that is admittedly quite simple,
229 particularly as regards temperature niches. That is, the snowfinch species all exist under a single, rather simple,
230 temperature niche (-8–7°C), with the sole exception of *M. nivalis*. This latter species, however, appears to have
231 been able to spread massively westward, to cover much of southern Europe, thanks to one niche expansion
232 event, to a niche of (-9–20°C). Indeed, careful inspection of Fig. 4 suggests that the niche expansion may
233 actually have happened in a subset of the species' populations: the eastern populations occur dominantly under
234 the ancestral part of the niche, whereas the western populations occur dominantly under the derived part of the
235 niche. In light of this rather recent niche innovation event, one could advance a hypothesis of refugial origin of *M.*
236 *nivalis*, likely around the Qinghai-Tibet Plateau (Qu et al., 2006; Qu and Lei, 2009; Yang et al., 2006), with
237 subsequent expansion across much of Eurasia, although a detailed phylogeographic study remains to be
238 conducted.

239 Considerable speculation has revolved around the question of whether niche evolution would elevate or reduce
240 speciation rates (Culumber and Tobler, 2016; Wiens, 2004; Wogan and Richmond, 2015). That is, one could
241 imagine niche evolution allowing a species to overcome distributional barriers, and thereby avoid the population
242 isolation that would lead to speciation. On the other hand, niche evolution might allow the species to "explore"
243 novel distributional situations, which might afford possibilities for colonization of new areas and possible
244 opportunities for speciation. Previous analyses of this question (e.g., (Kozak and Wiens, 2006)) have been
245 compromised by the rampant over-estimation of evolutionary dynamics that inevitably results when availability of
246 areas and associated uncertainty are not considered in ancestral niche reconstructions (Saupe et al., 2018).
247 Using virtual-world simulation approaches, Saupe et al. (2019) found variable effects of niche breadth on
248 speciation rates, with strong effects when climate change is rapid (e.g., abrupt climate change events in glacial-
249 interglacial cycles), but comprehensive analyses have yet to be developed.

250 In a broader sense, identifying geographic regions and key populations involved in evolutionary changes in
251 ecological niches could prove crucial in identifying target populations for further research aimed at understanding
252 genomic mechanisms underlying niche innovation. That is, functional genomic studies necessarily seek
253 population pairs that are minimally differentiated or separated by independent periods of evolution in isolation
254 (Lamichhaney et al., 2017), so as to avoid a background of evolutionary change in the broader genome. Studies
255 such as this one have considerable potential to make these comparisons more specific—see, e.g., the eastern

256 *versus* western populations of *M. nivalis*, which are closely related, but which may differ in niche characteristics.
257 Another area for future exploration and analysis in other taxa (snowfinch species tend to be broadly sympatric, at
258 least in broad brush-strokes) could be the degree to which areas detected as niche retraction correspond to
259 barriers to gene flow among speciating lineages.

260

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264

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269

270 **Data accessibility**

271 R script and data used in this study, including occurrence data, shapefiles summarizing our hypotheses of
272 accessible areas, and the three phylogenetic trees, are available online at
273 <https://doi.org/10.6084/m9.figshare.12915971>. The climatic data used in this study can be obtained using the
274 script provided.

275

276 **Author Contributions**

277 All authors designed research and compiled data; M.E.C. performed analyses; A.T.P. and M.E.C. wrote the
278 paper; all authors reviewed and approved the manuscript.

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281 **Figures**

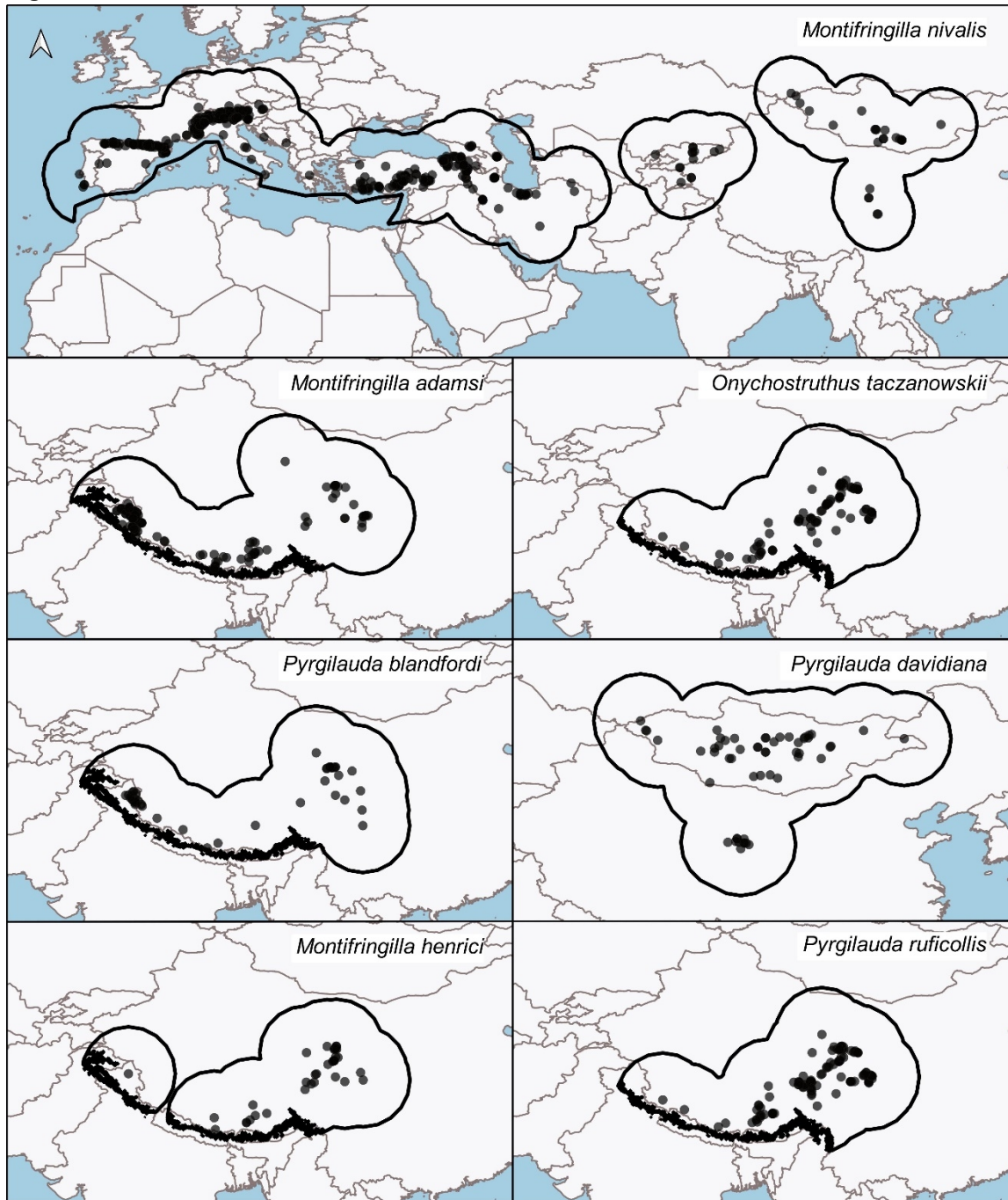
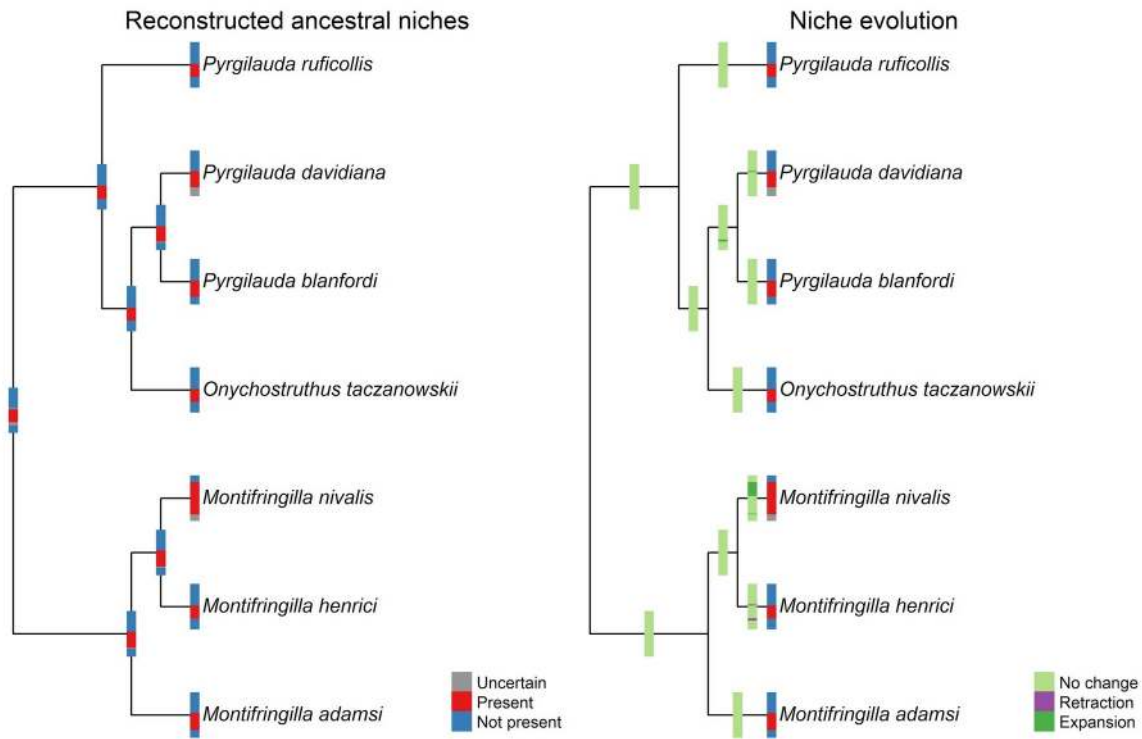
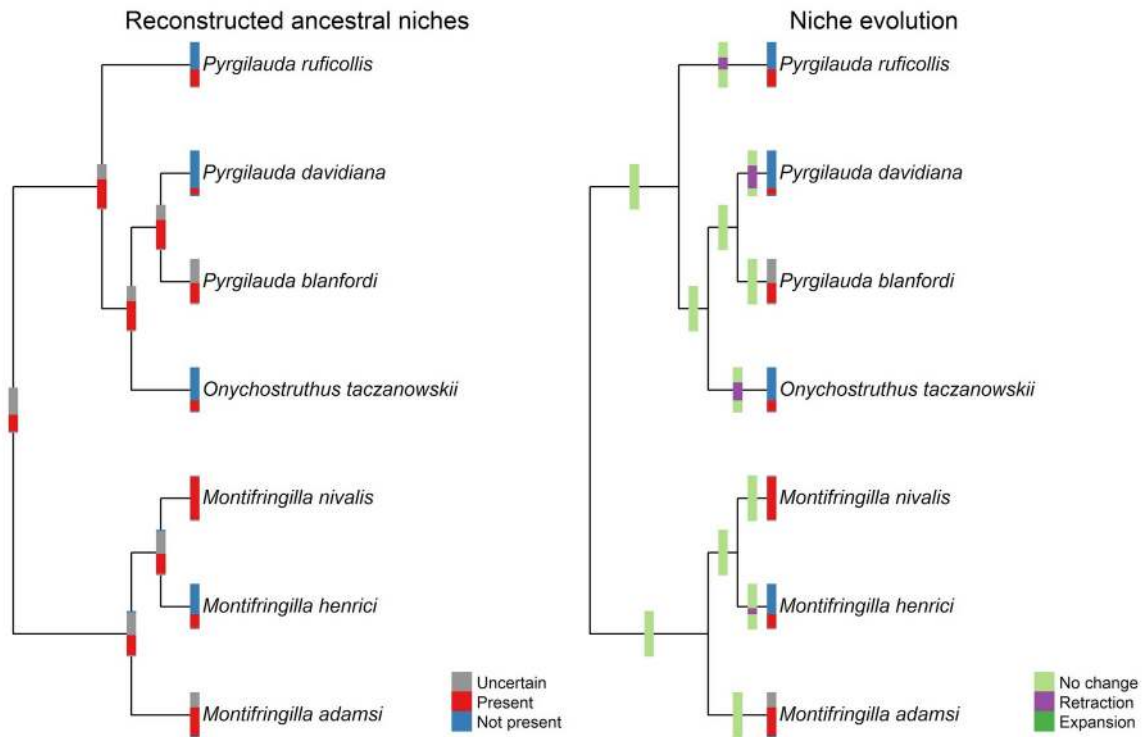


Fig. 1. Occurrence records and hypotheses of areas that have been accessible to each species over relevant time periods (M) for the seven species of snowfinches of interest.



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288 **Fig. 2.** Results of maximum parsimony reconstructions of ecological niche evolution for seven species of
289 snowfinches using annual mean temperature. Temperature is shown in a spectrum from low temperature at the
290 bottom of the bar to high temperature for the upper part of the bar. To obtain better visualizations, the length of
291 branches was not considered in plots (but see Supplementary Data, Fig. S1).



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Fig. 3. Results of maximum parsimony reconstructions of ecological niche evolution for the seven species of snowfinches using annual precipitation. Precipitation is shown in a spectrum from low precipitation at the bottom of the bar to high precipitation for the upper part of the bar. To obtain better visualizations, the length of branches was not considered in plots (but see Supplementary Data, Fig. S1).

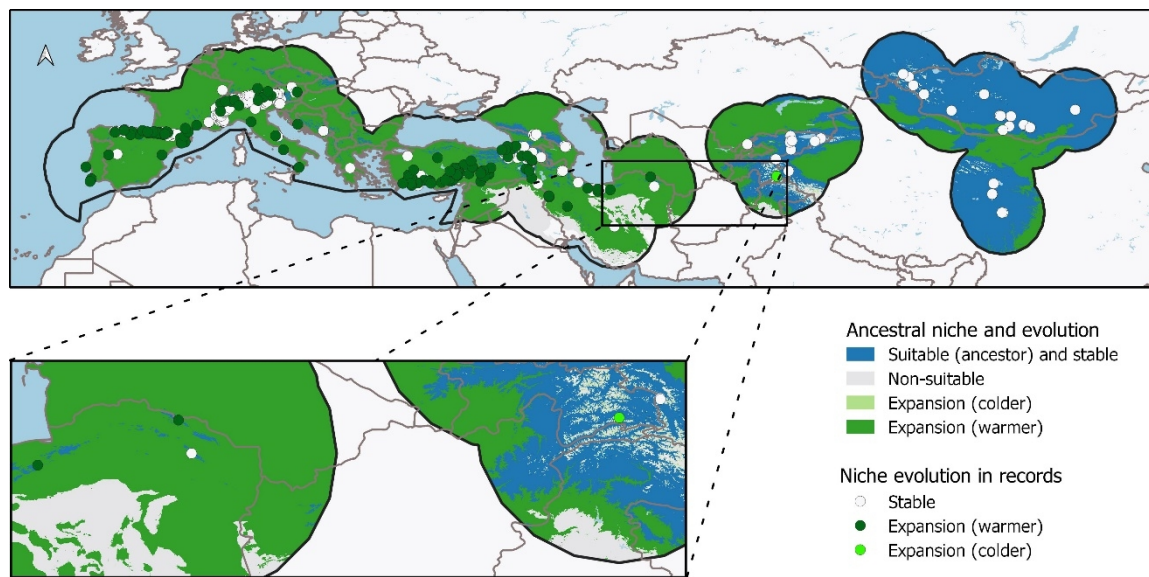


Fig. 4. Regions inside the accessible area (**M**) of *Montifringilla nivalis* and records of this species that present conditions detected as an expansion of niche compared to its ancestor. Variable represented is the mean annual temperature. Expansion in temperature was towards higher and lower values of this variable (see Fig. 2).