1   **Identifying the environmental drivers of corridors and predicting**

2   **connectivity between seasonal ranges in multiple populations of Alpine ibex**

3   **(*Capra ibex*) as tools for conserving migration**

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ABSTRACT

Seasonal migrations are central ecological processes connecting populations, species and ecosystems in time and space. Land migrations, such as those of ungulates, are particularly threatened by habitat transformations and fragmentation, climate change and other environmental changes caused by anthropogenic activities. Mountain ungulate migrations are neglected because they are relatively short, although traversing highly heterogeneous altitudinal gradients particularly exposed to anthropogenic threats. Detecting migration routes of these species and understanding their drivers is therefore of primary importance to predict connectivity and preserve ecosystem functions and services. The populations of Alpine ibex *Capra ibex*, an iconic species endemic to the Alps, have all been reintroduced from the last remnant source population. Because of their biology and conservation history, Alpine ibex populations are mostly disconnected. Hence, despite a general increase in abundance and overall distribution range, their conservation is strictly linked to the interplay between external threats and related behavioral responses, including space use and migration. By using 337 migratory tracks from 425 GPS-collared individuals from 15 Alpine ibex populations distributed across their entire range, we (i) identified the environmental drivers of movement corridors in both spring and autumn and (ii) compared the abilities of three modeling approaches to predict migratory movements between seasonal ranges of the 15 populations. Trade-offs between energy expenditure, food, and cover seemed to be the major driver of migration routes: steep south-facing snow-free slopes were selected while high elevation changes were avoided. This revealed the importance of favorable resources and an attempt to limit energy expenditures and perceived predation risk. Based on these findings, we provided efficient connectivity models to inform conservation of Alpine ibex and its habitats, and a framework for future research investigating connectivity in migratory species.

Keywords: Movement ecology; mountain ungulate; habitat selection; integrated step selection analysis; randomized shortest paths; cross validation; corridor mapping; migration conservation

INTRODUCTION

Global human-induced environmental changes are causing severe biodiversity loss, and habitat destruction and fragmentation are among the main causes of this decline (Newbold et al., 2016; Díaz et al., 2019). The development of linear infrastructures associated with human activities also contribute to impede species mobility (Torres et al., 2016). For instance, the extent of terrestrial mammalian movements was reduced by 50% in areas with a high human footprint compared with areas undisturbed by human activities (Tucker et al., 2018). By limiting animal movements between favorable habitats, human activities and infrastructures also reshape landscape connectivity (Taylor et al., 1993). Yet, connectivity is essential for individual and gene flows, for the local persistence of populations (Hanski, 1998), and for ecosystem functioning (Bauer & Hoye, 2014).

In the context of degraded connectivity, seasonal migrations, i.e., movements to track the spatiotemporal fluctuations in environmental conditions on seasonal ranges (Dingle & Drake, 2007), are of particular concern (Bolger et al., 2008). Most large herbivores, as primary consumers, migrate or may show migration propensity in heterogeneous and predictable habitats (Mueller at al., 2011, Teitelbaum et al., 2015). They are often restricted to well-defined corridors used by most migrants with low tendency to change migration routes when corridors are altered (see e.g., Xu et al., 2021). Migration can increase survival and reproduction through better access to high quality resources and reduced intra- and interspecific competition or predation risk (Avgar et al., 2014; Eggeman et al., 2016; van Moorter et al., 2021). However, migratory movements also imply energetic costs, and can be risky, or perceived as such, as animals may move through unfamiliar areas (Klaassen et al., 2014; Blagdon & Johnson, 2021). Hence, migration is a behavioral tactic whose fitness returns can vary through space and time, depending on individual traits, and spatial heterogeneity in occurrence and intensity of predation, harvesting, or competition in a population's range. Accordingly, migration can be partial, with some individuals that choose to migrate while others are resident, and with individual behavior that can change from year to year (Cagnacci et al., 2011). Given that migration can affect population dynamics and species persistence by shaping their spatio-temporal distribution, there is a crucial need to increase our understanding of the link between habitat use and drivers of movement during seasonal migration at a fine spatial scale, the resulting ecological connectivity of a landscape, and how human activities affect this connectivity level (Sawyer et al., 2011; Panzacchi et al., 2016).

117   Migration corridors and their environmental characteristics are well-documented in
118   spectacular collective and long-distance migrations in North American, Scandinavian or
119   African ungulates (Boone et al., 2006; Merkle et al., 2016; Panzacchi et al., 2016; Joly et al.,
120   2019) but are poorly known in most species (Kauffman et al., 2021). Recently, the focus has
121   been put on spring migration revealing how migratory species can surf the green wave by
122   tracking the green-up which moves like a wave across the landscape (Bischof et al., 2012;
123   Merkle et al., 2016). Although less spectacular, migrations also occur in mountain ungulate
124   populations occupying highly heterogeneous and fragmented landscapes (Herfindal et al.,
125   2019), which are under threats from rapid climate changes and increasing anthropogenic
126   pressure (Parmesan & Yohe, 2003; Schmeller et al., 2022). In mountain areas, green waves
127   occur along altitudinal gradients and therefore green wave surfing seems to not always fully
128   explain the choice of routes traveled between seasonal home ranges (Gaudry et al., 2015;
129   Herfindal et al., 2019; but see Semenzato et al., 2021 for seasonal tracking of the altitudinal
130   green and senescence wave). Several other factors can affect migration routes, particularly in
131   complex topographic landscapes. Indeed, in addition to the diversity of migratory portfolios,
132   migration is most often partial and takes place among multiple winter and summer ranges
133   (Crampe et al., 2007; Lowrey et al., 2020; Denryter et al., 2021) and, up to now, little is known
134   about migration patterns and migration routes for these mountain populations. Yet, this
135   information is essential to improve the conservation of migratory species (e.g., through the
136   establishment of protected areas, or to inform landscape planning; Mccollister & Manen, 2010)
137   and preserve the ecological functions and ecosystem services migratory species support
138   (Semmens et al., 2011). In this context, the importance of reliable connectivity maps for the
139   identification of realistic corridors has been stressed (Sawyer et al., 2011; Zeller et al., 2012).
140   A deeper understanding of the link between fine-grain habitat use and movements has been
141   particularly invoked and up-to-date algorithms have been developed and used to model
142   connectivity while accounting from iterative decisions of animals trading off exploration and
143   optimal use of their environment (Panzacchi et al., 2016; Goicolea et al., 2021). However,
144   population-specific movement analyses and connectivity predictions may be difficult to
145   generalize over species and contexts when relying on samples from a single population not
146   always representative of the species/habitat. Multi-populational analyses may be crucial to
147   extend population-specific knowledge to species conservation, but such comparative analyses
148   remain particularly scarce (Urbano, Cagnacci & Euromammals consortium, 2021).

149   Here, we investigated migration routes in several populations of Alpine ibex *Capra ibex*
150   across the Alps in order to model and predict connectivity between summer and winter ranges.
151   This mountain species of high patrimonial value went almost extinct during the XXth century
152   and recovered a large distribution thanks to intensive reintroduction programs (>55 000
153   individuals distributed across 178 populations; Brambilla et al., 2020). Even though most
154   populations stem from individuals that were naive to the areas they were introduced into,
155   seasonal migrations seem to occur in most populations. These migrations appear short in
156   distance between a low altitude wintering area and a higher summer range. Yet, populations are
157   still poorly connected, and drastic bottlenecks and founder effects have resulted in a very low
158   level of genetic diversity (Biebach & Keller, 2009). Thus, effective conservation of this species
159   and its habitats would highly benefit from better knowledge of the landscape characteristics
160   used by ibex during migration, and from an assessment of the connectivity offered by available
161   habitats. Owing to a unique GPS telemetry dataset from 425 ibex and 15 populations across the
162   entire distribution range of the species, we first aimed at determining the environmental drivers
163   of migratory tracks accounting for the many factors likely at play in an individual's choice of
164   routes. We specifically tested whether individuals (i) minimized energy expenditures and
165   difficulties to travel by avoiding elevation changes, rugged terrain and snowy areas as traveling
166   costs are paramount in all optimality models aiming at understanding the costs and benefits of
167   migration tactics (Holt & Fryxell, 2011), (ii) selected habitats offering food resources and
168   refuge from perceived predation risk, (iii) used visual landmarks (linear features such as ridges,
169   tree lines and valley bottoms) as "compasses" (Alerstam & Bäckman, 2018), and (iv) avoided
170   proximity to anthropogenic infrastructures (roads and ski areas; Table 1) during migration.
171   Then, we took advantage of the 15 populations monitored to compare connectivity assessments
172   when using either population-specific habitat selection criteria or criteria averaged over all
173   populations; and to perform external validation of the ability of our model to accurately predict
174   ibex migratory connectivity in the absence of any data on ibex locations, a crucial step to
175   provide reliable information for species migration conservation across its native range.

176

MATERIALS AND METHODS

178   <u>Study areas and GPS data</u>

179   We relied on a GPS dataset collected on 425 individual Alpine ibex (*Capra ibex*; 41% females
180   and 59% males; 77% being adults >4 years-old) from 15 reintroduced populations. Those

181   populations were distributed across the whole Alps (10 in France, 2 in Italy, 1 in Switzerland,

182   and 2 in Austria; Figure 1; latitudinal gradient: 44-47°N, longitudinal gradient: 6°-13°E and

183   altitudinal gradient: 1700-2700m). Alpine ibex can share habitats with northern chamois

184   (*Rupicapra rupicapra*), less frequently with red deer (*Cervus elaphus*) and roe deer (*Capreolus*

185   *capreolus*), and with livestock during summer (sheep, goats and cows). Grey wolf (*Canis lupus*)

186   is present in most of ibex distribution range, but predation occurs rarely on ibex.

187   Sample sizes varied between populations (minimum: 7 individuals in Hohe Tauern National

188   Park; maximum: 117 in the Bargy massif). Several types of collars were used (Vectronic: GPS

189   Plus, Vertex Plus, or Vertex Lite models; Lotek: 3300S or Litetrack models; Followit: Tellus

190   model). All models weighted <3% of individual body weight. They were programmed to record

191   ibex locations at variable frequencies and during variable periods (from 1 location per hour

192   during one year to 1 location per 6 hours during 2-3 years, Appendix S1), resulting in 1 068

193   seasonal tracks (an individual monitored during 1 year resulted in 2 potential migratory tracks).

194   Determining migratory status and migration tracks

195   The migratory status of each ibex (migrant or resident) and migration tracks (for migrants) were

196   visually determined using the application Migration Mapper^TM (version 2.3, Merkle et al., 2022;

197   see Appendix S2 for the parameters used). This application provides tools to visually identify

198   migrants, migration periods and tracks using the Net Squared Displacement (NSD; squared

199   Euclidean distance between the first locations of the GPS trajectory and the following one;

200   Börger & Fryxell, 2012; Appendix S3). Spring and fall migration periods and migratory tracks

201   started at the last location preceding the increase/decrease in the NSD and ended at the first

202   location when the NSD stabilized. Migratory movements were identified irrespective of

203   distance separating seasonal ranges as ibex exhibited several forms of migratory movements

204   within populations (short-altitudinal movements or long-distance movements). However, only

205   neat migrations (i.e., two movements between distinct seasonal ranges) were selected to reduce

206   uncertainty in the displayed behavior (see Appendix S4 for details on distance and altitudinal

207   interval between seasonal ranges of migrant and resident individuals).

208   Assessing environmental drivers of ibex migratory movements

209   *Environmental variables*

210   We investigated the influence of 11 environmental variables (see Appendix S5) that could affect

211   movement choices during migration (Table 1). We considered the total elevation change (sum

212 of changes in elevation values along a step), the ruggedness (Vector Ruggedness Measure;

213 Sappington et al., 2007) and a snow cover index (calculated as the total annual number of days

214 a pixel was covered by snow) as metrics reflecting the energetic costs and difficulties to travel

215 during migration. We used the northness (cosine of aspect derived from the same DEM) and

216 the snow cover index to reflect the accessibility and the quality of vegetation resources and the

217 presence of snow cover, as well as the availability of thermal shelters. Contrary to what is

218 commonly done in studies on migratory ungulates, we did not use vegetation variables or

219 derived metrics (NDVI, Instantaneous Rate of Green-Up; e.g. Bischof et al., 2012) as we judged

220 the information given by the northness and snow cover more relevant considering the short

221 duration and distance of ibex migrations (see results). As ibex mostly use open areas (Parrini et

222 al., 2009) and often steep slopes as refuge from perceived predation risk and human disturbance,

223 we expected forests to be avoided and proximity to slopes >40° to be selected during migration

224 (Grignolio et al., 2007; Iribarren & Kotler, 2012). We considered ridges, valleys and tree lines

225 as potential visual landmarks used for navigation (Alerstam & Bäckman, 2018). Finally, we

226 hypothesized that the proximity to roads and ski areas (i.e., human infrastructures that

227 occasionally occurred in the surrounding of ibex population ranges) would be avoided as both

228 can constitute barriers - physical barriers such as roads - or perceived as such because associated

229 with humans for both roads and ski areas.

230 *Habitat selection analyses during migration*

231 We used integrated Step Selection Analyses (iSSA; Avgar et al., 2016) to assess the

232 environmental drivers of ibex migratory movements. The habitat variables along (total

233 elevation change) or at the end (all other habitat variables) of each used movement step

234 (considered as the straight lines between recorded ibex locations) traveled by one individual

235 ibex during migration were compared with the habitat characteristics along/at the end of 15

236 available steps it could have traveled, using conditional logistic regressions (Fortin et al., 2005;

237 Thurfjell et al., 2014). We generated those available steps by sampling step lengths (corrected

238 to get three dimensional lengths using a DEM at a resolution of 25m, which are particularly

239 relevant in mountainous landscapes) and turning angles in parametric distributions (gamma

240 distribution for the step length and Von Mises distribution for the turning angles; Duchesne et

241 al., 2015) derived from the observed step length and turning angle distributions of the used

242 steps. We accounted for the variable step duration in our dataset by deriving specific

243 distributions for each step duration and checked if habitat selection was similar for the different

244 timesteps by using the method of Used Calibration Plots (see Appendix S6).

245   We scaled habitat variables across all populations (i.e., variables were centered and divided by

246   their standard deviation) to make their effect size comparable in iSSA outputs and we checked

247   for potential correlations between our variables using a Pearson correlation. Correlation

248   coefficients were > 0.3 for the variables forest and proximity to forest ($\rho = 0.5$) and for the

249   variables step length, log(step length) and total elevation change ($\rho = 0.6$ step length/log(step

250   length), $\rho = 0.6$ total elevation change/log(step length), $\rho = 0.9$ step length/total elevation

251   change).

252   The logistic regressions included the 11 environmental variables, step length, log of step

253   length and cosine of turning angles (Avgar et al., 2016). We chose to include the step length

254   and turning angles in iSSA without interactions with habitat variables to simplify our models,

255   except for the interaction between step length and elevation change. We fitted one model for

256   each season (i.e., spring or autumn migration) and each of the 15 populations. For 6 populations

257   in spring and 5 in autumn, the variables "forest" and "proximity to ski areas" were excluded

258   from models as forest or ski areas were rare or absent in the distributional range of those

259   populations. We chose to fit models at population scale because we were more interested in

260   modeling migratory movements at the population scale. Accounting for sex-specific differences

261   can be important for a species like Alpine ibex knowing to exhibit different patterns of

262   movements between sexes (Herfindal et al., 2019). However, numbers of migrant females (or

263   even migrant animals) were too small in several populations to test sex-specific differences (see

264   Appendix S7). We investigated if habitat selection results differed between sexes in Appendix

265   S8. We fitted models using the *clogit* function from the package *survival* in R V. 4.2.2

266   (Therneau, 2022, R Core Team, 2022). We conducted a model selection based on AICc with

267   the *dredge* function in package *MuMIn* (Bartoń, 2022). The coefficients from the best models,

268   i.e., models with an ΔAICc <2, were averaged using the *model.avg* function in the package

269   *MuMIn*. We did not include "individual" as a random effect as the models did not converge

270   correctly when doing so. We finally produced Used Habitat Calibration plots (UHC plots;

271   Fieberg et al., 2018) using mixed-effect Poisson models (Appendix S9) to check for the

272   agreement between model predictions and values of our covariates observed at or along used

273   steps (Appendix S6).

274   <u>Building and validating models of migratory connectivity in ibex</u>

275   We proceeded in four steps (see below and step III of Figure 2) to build and validate

276   connectivity models based on the 15 populations to perform three different validation

277 procedures (i.e., using three different pairs of training/validation datasets; Figure 2) designed
278 to understand how our models could inform different management measures. The first
279 procedure ("leave 10% of whole data out") seeks to understand if based on all information we
280 have on ibex habitat selection we can predict migratory movements of non-marked individuals
281 in monitored populations. We used the second procedure ("leave 10% of population data out)
282 to assess if based on data from a limited number of animals in a population we can predict
283 where other animals should migrate. Finally, the third procedure ("leave one population out")
284 evaluates if based on all information we have we can predict migratory movements in
285 populations without monitoring.

286 For each seasonal migration (i.e., spring or fall), we first selected habitat variables
287 previously identified as having a significant effect in at least 8/15 populations. To assess if
288 variables had a significant effect, we computed the 95% confidence intervals (CI) for selection
289 coefficients resulting from the model averaging. A coefficient was significant if its CI non-
290 overlapped with 0. We included these variables to fit average seasonal iSSA models on three
291 different training datasets. Second, we used those averaged seasonal iSSA models to build three
292 different resistance maps for each population. Third, we modeled connectivity between winter
293 and summer ranges using the Randomized Shortest Path algorithm on each resistance map
294 (Panzacchi et al., 2016). Finally, we used 2 different methods to evaluate the performance of
295 our three connectivity models by comparing their predictions to the different validation datasets
296 previously set aside.

1. Sampling training and validation datasets

298 We built three different combinations of training/validation datasets, which were then used to
299 build resistance maps and model three corresponding connectivity maps. Specifically, we first
300 fitted two seasonal iSSA using 90% of the whole dataset (Figure 2; 'leave 10% of whole data
301 out' approach), and second, we fitted population-specific seasonal iSSA models with 90% of
302 the population-specific dataset as a training dataset ('leave 10% of population data out'
303 approach). For those two approaches, the remaining 10% of migratory tracks served as
304 validation datasets and the 90%/10% sampling procedure was repeated 250 times to assess
305 uncertainty around connectivity predictions. Third, we fitted iSSA with data from all
306 populations but one, and used data from the discarded population for validation, and repeated
307 this for the 15 populations ('leave one population out' approach).

308   *2. Building resistance maps*

309   We then used the different iSSA models to compute seasonal resistance maps that display the

310   relative avoidance of each pixel by an ibex migrating through the landscape. To do so, we

311   multiplied each raster of environmental variables by the corresponding coefficient provided by

312   the iSSA model fitted with a given data source. Then, we summed those rasters and applied the

313   inverse logit function to get habitat selection maps representing the relative probability that an

314   ibex selected a pixel during migration. The RSP algorithm uses a resistance map to model the

315   connectivity, to obtain resistance maps, we applied the inverse function to those habitat

316   selection maps considering that the cost of movement is higher in avoided habitats (Keeley et

317   al., 2016; Zeller et al., 2018).

318   *3. Modeling connectivity between summer and winter ranges*

319   We defined seasonal ranges as 95% kernel areas derived from the corresponding seasonal

320   locations (Worton, 1989), using *kernelUD* function from *adehabitatHR* package (h parameter

321   was set to 400; Calenge, 2022). We restricted our analyses to seasonal ranges connected by

322   migratory tracks to limit our connectivity predictions to the areas actually used by GPS-collared

323   migrant ibex. We used the Randomized Shortest Paths approach to model connectivity (RSP;

324   Saerens et al., 2009; Panzacchi et al., 2016; implemented in the *passage* function from R

325   package *gdistance*; van Etten, 2022) between 10 points randomly sampled within each pair of

326   summer and winter ranges. This algorithm estimates the number of times an ibex would cross

327   each pixel of the resistance map during migration. As in other algorithms relying on the graph

328   theory (e.g., least-cost path and circuit theory), the resistance map is represented as a graph with

329   individuals moving from nodes to nodes (i.e., the center of the pixels) along links/edges with

330   variable costs depending on the values of the resistance map. The RSP computes the least-cost

331   path, the path which minimizes the distance and costs accumulated along a trajectory joining a

332   source and a destination. The RSP algorithm also integrates a stochasticity parameter θ which

333   allows measuring the degree of departure from two extreme strategies, i.e., random-walk (full

334   exploration of neighboring nodes), when θ = 0, or least-cost path (i.e., optimal exploitation of

335   the landscape by minimizing total costs) for the highest value of θ (see Appendix S10). This

336   allows accounting for intermediate strategies between the two most commonly used methods

337   to model movements in connectivity analyses. We obtained two connectivity maps (one per

338   season) for each training dataset using an optimized stochasticity parameter θ (Appendix S10).

339   We finally obtained three unique connectivity maps (one per training dataset) by averaging the

340   two seasonal connectivity maps for each training dataset.

4. Validating connectivity maps

342   We used two different methods to evaluate the accuracy of our connectivity predictions. First,

343   we ranked each used step traveled by ibex during migration versus the 15 associated available

344   steps they could have travelled (already sampled for iSSA analyses; see section *Habitat*

345   *selection analyses during migration*) based on connectivity values at the end of each step and

346   assigned them a value between 1 (lowest connectivity) and 16 (highest connectivity; ranking

347   method; McClure et al., 2016; Goicolea et al., 2021). If accurately predicted, the average rank

348   of used steps should be higher than those of available steps. Second, we converted connectivity

349   values to percentile connectivity values (e.g., the 95th percentile corresponds to the 5% highest

350   values of the connectivity map) and delineated five connectivity corridors as the 80th, 85th, 90th,

351   95th, and 99th connectivity percentiles. We then calculated the percentage of ibex locations

352   collected during migration included in each connectivity corridor as a metric of predictive

353   performance of our connectivity models (representation in corridors; Poor et al., 2012; Zeller

354   et al., 2018; Goicolea et al., 2021). As the percentage of ibex locations during migration that

355   fall within a given corridor is strongly dependent on the area of this corridor, we also computed

356   the proportion of locations in the corridor divided by the corridor surface to get an index of

357   accuracy of connectivity predictions (Appendix S11). We applied both validation methods

358   (ranking and representation in corridors) on the three validation datasets we set aside previously

359   to validate our three approaches to compute connectivity maps.

RESULTS

Identification of migrant ibex

362   Among the 1068 seasonal tracks available in our GPS dataset, we identified 337 migratory

363   tracks (169 in spring, 168 in autumn), distributed between multiple winter and summer ranges

364   within each population. On average, the proportion of seasonal tracks identified as migration

365   was 45% (SD 22.5) over the 15 populations, confirming partial migration. However, it varied

366   greatly between populations, from 13% to 75% in the Bargy and Champsaur populations,

367   respectively (considering populations with enough animals to estimate this proportion). On

368   average, migrant ibex traveled 12 km (SD 8) of topographic distance, with population means

369   that varied from 6 to 22 km and an individual maximum of 62 km. In spring, those migratory

370 tracks lasted 3.5 days (SD 3.6) on average and occurred around May 27 (SD 27 days), while in

371 autumn they lasted 6.3 days (SD 6.3) on average and occurred around October 30 (SD 29 days).

372 Habitat selection during migration

373 In both spring and autumn, ibex traveled in areas with less total elevation change (192.4 m on

374 average for 6 hours) than if they had moved randomly (207.1 m, 7% less; significant in 11/15

375 populations in spring and 13/15 in autumn; Figure 3). They also selected for proximity to

376 refuges from perceived predation risk (slopes > 40°; 11/15 populations in spring and 10/15 in

377 autumn) and avoided north-oriented areas (10/15 populations in both seasons). During autumn

378 migration only, they also avoided areas expected to be the first covered by snow and where

379 snow may accumulate (snow cover index; 7/15). By contrast, neither anthropogenic

380 infrastructures (proximity to ski resorts and roads) nor linear structures considered as potential

381 landmarks (proximity to ridges, valley bottoms and tree lines) influenced ibex migratory tracks

382 during either season.

383 Connectivity modeling

384 The three modeling methods performed relatively well and produced similar predictions of ibex

385 migratory corridors. About half of the migratory tracks were in areas with high connectivity,

386 falling in the 95th connectivity percentile corridor (50.4% (SD 14.7) for "leave one population

387 out"; 51.9% (SD 11.8) for "leave 10% of population data out" and 53.1% (SD 13.7) for "leave

388 10% of whole data out"; Figure 4). The percentage of tracks included in the predicted corridor

389 increased rapidly for lower values of the predicted connectivity corridor, as more than 90% of

390 the tracks were included in the 80th connectivity percentile. The best stochasticity value θ in

391 the Randomized Shortest Path algorithm was equal to 0.1 (Appendix S10). This intermediate

392 value largely outperformed the lower ($\theta=0$; totally random movements) and upper limits ($\theta=3$;

393 deterministic movements) resulting in intermediate connectivity patterns between the diffuse

394 connectivity corridors obtained with the circuit theory approach and the narrow and simple

395 least-cost path that prevented from alternative routes (Figure 5).

396 According to the ranking validation method, the three connectivity modeling approaches tested

397 (i.e., 'leave 10% of whole data out', 'leave 10% of population data out' and 'leave one

398 population out') provided connectivity maps that predicted ibex migratory movements better

399 than random surfaces (see Figure 5 for examples, and Appendix S12). The mean and median

400 ranks of used steps in the three validation datasets were all>8, with values from 9 to 11

401 depending on the population, although variability was important (1st quartile and 3rd quartile

402   ranging from 5 to 14 depending on populations; Appendix S13). However, within populations

403   results were similar whatever the training dataset used.

404   Comparable proportions of locations of migratory tracks were included in connectivity

405   corridors for the three modeling approaches: between 93.7 – 94.0% of locations in the 80th

406   connectivity percentile corridors and between 14.9 – 15.7% in the 99th connectivity percentile

407   corridors (Figure 4, Appendix S14). There was heterogeneity between populations in the

408   accuracy of the predictive models of connectivity, but within the same population, the three

409   connectivity models gave similar results (Appendix S14). The ratio of the proportion of

410   locations included in the corridor over the corridor surface was superior for the 95th and 99th

411   percentile corridors. Therefore, these connectivity corridors captured on average the highest

412   proportion of ibex locations within the smallest surface but the variability in this ratio over the

413   15 populations was high (Appendix S11).

DISCUSSION

415   Relying on a dataset assembling 337 migratory tracks collected in 15 Alpine ibex populations

416   distributed across the Alps, we identified the environmental predictors of corridors in this

417   endemic and emblematic short-distance and altitudinal migrant species. While consistently

418   limiting energetically-costly elevation change, ibex migrated mostly in south-facing snow-free

419   slopes and close to steep areas providing refuges from perceived predation risk. By contrast,

420   neither the landmarks (ridges, tree lines, valley bottoms) hypothesized as visual cues for ibex

421   navigation, nor human infrastructures (ski areas and roads, when present) affected ibex

422   migratory movements. The randomized shortest path algorithm revealed an intermediate

423   movement strategy in Alpine ibex, trading off optimization and exploration during migratory

424   movements. The abilities of the three modeling methods we compared to predict migratory

425   connectivity from the results of those movement analyses, relying either on population-specific

426   or multipopulational approaches, were comparable. They provided efficient connectivity

427   models to inform conservation of Alpine ibex and its habitats, and a framework for future

428   research investigating connectivity in migratory species from multi-populational datasets.

429   In addition to spring green wave tracking, evidenced in commonly-studied long-distance

430   migrations from North American, Scandinavian and African ungulates, we revealed other

431   predictors, more scarcely investigated, may also drive Alpine ibex during both spring and

432   autumn migration. By focusing on south-facing snow-free slopes, they may partly benefit from

433   emerging vegetation during spring migration (although we did not fully investigate the green

434   wave hypothesis, see Methods; but see Semenzato et al., 2021), while limiting energetically-

435   costly movements in snow-covered areas. Limiting energy expenditures seemed particularly

436   important in Alpine ibex that also strongly avoided high elevation changes during migration,

437   yet relatively short in distance and duration. This behavior may be adaptive in the steep and

438   rugged terrain in which ibex migration occurs (see Passoni et al., 2021 for another example in

439   roe deer *Capreolus capreolus*). Indeed, when traveling through unfamiliar areas for migration,

440   Alpine ibex selected for proximity to steep slopes, i.e. habitats generally used by mountain

441   ungulates to limit perceived predation risk (Grignolio et al., 2007, see also Marchand et al.,

442   2015 for Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp.; Baruzzi et al., 2017 in

443   chamois *Rupicapra rupicapra*). Altogether, these results suggest the persistence of the energy-

444   food-cover trade-off, i.e. the most important predictor of ungulate habitat selection all year

445   round (Lima & Dill, 1990; Houston et al., 1993; Mysterud & Østbye, 1999), as a major driver

446   of Alpine ibex migration routes. This trade-off may also explain the intermediate movement

447   strategy of migrant ibex trading off optimization and exploration during migratory movements,

448   as revealed by the randomized shortest paths algorithm. By contrast, none of the landmarks

449   tested seemed to be used by migrant ibex as compass for navigation during migration. Yet,

450   recent studies revealed how natural landscape features can be used by mountain ungulates,

451   including Alpine ibex, to delimit their seasonal home ranges and constitute cognitive maps to

452   gather and memorize spatially explicit information for navigation (Seigle-Ferrand et al., 2022).

453   Further research is hence needed to investigate the importance of other navigation

454   cues/mechanisms, and more generally other drivers of migration corridors identified in other

455   contexts/species (e.g., memory; Bracis & Mueller, 2017, Merkle et al., 2019; social learning

456   and cultural transmission; Jesmer et al., 2018) that were not investigated here in absence of data

457   to do so.

458   Combined with the randomized shortest paths algorithm, the results of three modeling

459   methods relying either on population-specific or multi-population approaches provided reliable

460   and comparable connectivity maps. Both the "ranking" and "representation in corridors"

461   validation approaches indicated relatively high levels of agreement between connectivity

462   corridors and actual migratory tracks, although the dispersion associated with reliability

463   measurements was high. Indeed, in several populations, some predicted high-use areas were

464   not used by ibex, or inversely, ibex used areas that were not predicted as providing high

465 connectivity. Thus, factors such local idiosyncrasies in landscape features may be involved at
466 the population level.

467 Despite obvious topographic, climate and anthropogenic differences in the areas used
468 by the 15 studied populations across the whole Alps, contributing to the differences in
469 movement strategies across populations (Figure 3), we chose to fit iSSA with environmental
470 variables that had significant influence in most populations, and to average the resulting
471 resistance maps over both seasons (spring and autumn; see Figure 2). This probably contributed
472 to increasing uncertainty in connectivity predictions as inter-population differences were
473 ignored. However, when assessed with the same validation approach (here "representation in
474 corridors", easily translatable into management/conservation measures; McClure et al., 2016),
475 the performance of our connectivity models was comparable or better than those reported in
476 other studies (here, 73-78% locations in the 90th percentile corridor, 68-72% in Poor et al.,
477 2012 - pronghorn *Antilocapra americana*; 65% in Zeller et al., 2018 - puma *Puma concolor*;
478 42% in Goicolea et al., 2021 - Iberian lynx *Lynx pardinus*). Besides, those average connectivity
479 models may be more reliably transferable or generalizable to other populations/contexts over
480 the species' distributional range and even in the absence of any data. Therefore, it may
481 constitute an invaluable tool for the conservation of this endemic and emblematic species and
482 its habitats.

483 Even though we did not find any major effects of human infrastructures that could
484 impede ibex migration (i.e. ski areas and roads, probably due to their scarcity in the vicinity of
485 areas where ibex have been reintroduced), climate warming and the development of human
486 activities and infrastructures, particularly present in the Alps (Parmesan & Yohe, 2003;
487 Schmeller et al., 2022), could reshape movement corridors of alpine animals in the near future
488 (see an example with pronghorn, Zeller et al., 2021). In addition, despite the numerical success
489 of the species reintroduction programs over the Alps, Alpine ibex still face important
490 conservation issues (e.g., dramatically low genetic diversity, lack of functional meta-
491 populations; Biebach & Keller, 2009; Brambilla et al., 2021) and migration corridors remain
492 poorly protected outside. In this context, preserving and (re-)establishing connectivity within
493 and between ibex populations will probably be a major conservation issue in the next decades,
494 and tools such as our connectivity models could be particularly helpful.

495 More generally, our study also provided an original methodological framework for
496 future research and conservation efforts dedicated to connectivity analysis and predictions of

497 movements other than migration. Here, the three different approaches (i.e., 'leave 10% of whole

498 data out', 'leave 10% of population dataset out' and 'leave one population out') revealed no

499 major differences in accuracy of corresponding connectivity predictions. Thus, our models

500 could be used to predict migratory movements in monitored populations with either enough

501 data, using population-specific model, or using data from all populations. Moreover, we could

502 predict movements in populations where no GPS data are available but seasonal range locations

503 are known or predicted with habitat selection models. With the advent of animal tracking over

504 the last decades, and the generalization of initiatives aiming at gathering those GPS data in

505 common databases (e.g. Movebank, Euromammals, Biologging initiative, Global Initiative for

506 Ungulate Migrations; Kauffman et al., 2021; Urbano, Cagnacci & Euromammals consortium,

507 2021), multi-population analyses will develop and testing the reliability of population-specific

508 versus multi-population connectivity predictions is crucial, particularly in a context of demand

509 and need around conserving and restoring connectivity within species distribution ranges.

510

511 **ACKNOWLEDGMENTS**

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534 **CONFLICT OF INTEREST STATEMENT**

535 The authors declare no competing interests.

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833 **TABLES**

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835 Table 1: Hypotheses tested in the integrated Step Selection Analyses and their corresponding

836 predictions.

Hypotheses	Covariables	Predictions	References
Ibex minimize energy expenditures and traveling difficulties	Total elevation change	Ibex should perform steps with relatively low total elevation change	Passoni et al., 2021
	Ruggedness	Ibex should avoid rugged terrain which tends to increase movement costs and reduce visibility	Wall et al., 2006; Halsey & White, 2017
	Snow cover index	Ibex should avoid snowy areas which impede ibex movements	Richard et al., 2014; Sheppard et al., 2021
Ibex select areas that can provide forage, security and thermal shelters	Northness	Ibex should prefer south exposed terrain as they present snow-free areas with access to early growing vegetation in spring or thermal shelters in autumn	
	Proximity to refuges (steep slopes)	Ibex should stay close to steep slopes to reduce perceived predation risk	Grignolio et al., 2007; Iribarren & Kotler, 2012
	Forest	Ibex should avoid forests as they prefer open habitats, being primarily grass roughage eaters	Parrini et al., 2009

Ibex use landmarks for orientation	Proximity to ridges	Ibex should select for proximity to ridges and follow ridges during their migration	
	Proximity to valley bottoms	Ibex should avoid to go down to valley bottoms in spring when migrating up the mountain but opposite in autumn	
	Proximity to tree lines	Ibex should use tree lines as a landmark to follow in some populations but not in others	
Ibex avoid human-linear infrastructures	Proximity to roads	Ibex should avoid roads constituting physical barriers or because associated with humans	Seigle-Ferrand et al., 2022
	Proximity to ski areas	Ibex should avoid ski areas because associated with humans	Dickie et al., 2020

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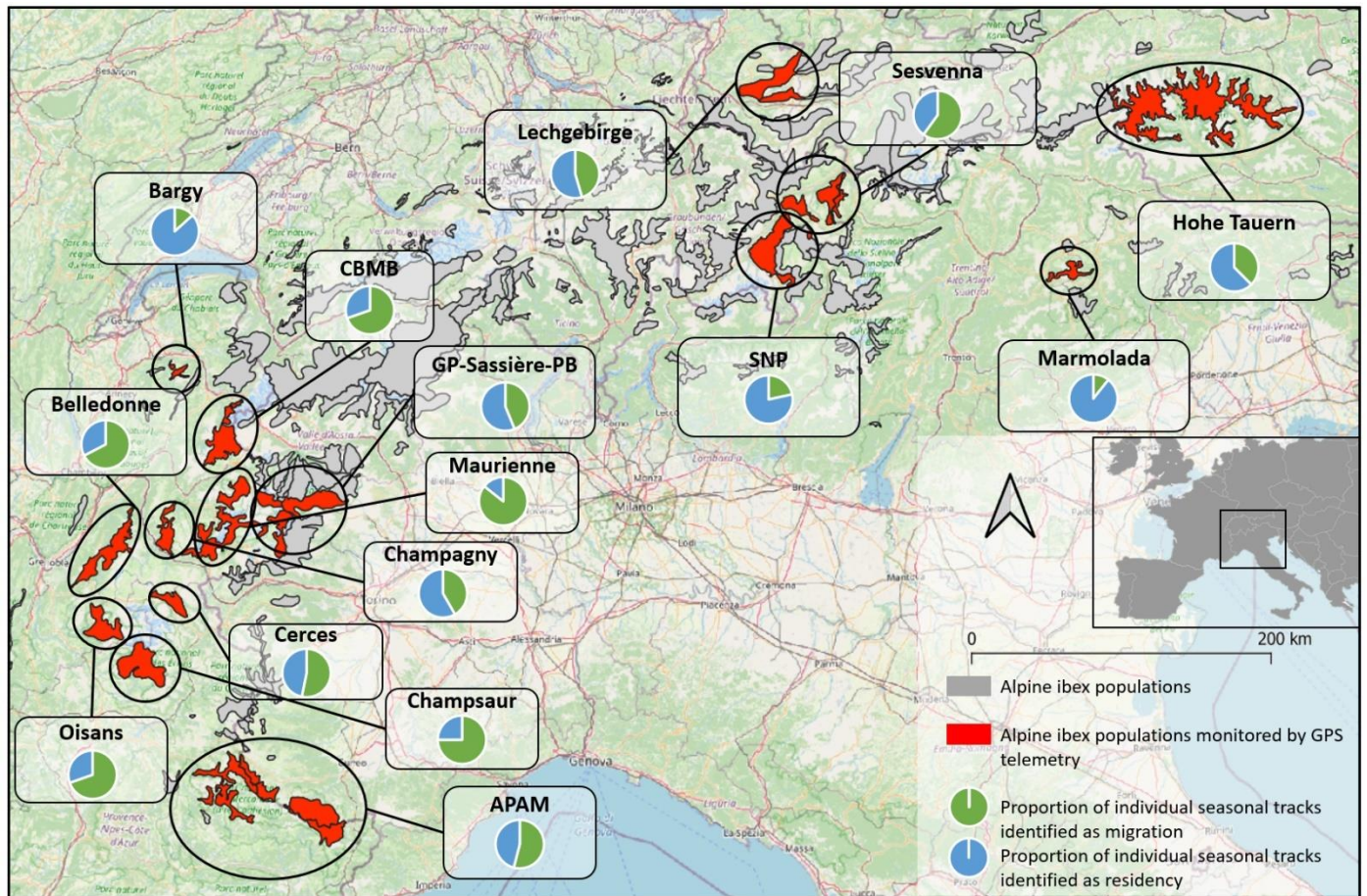
855   <u>Figure 1:</u> Location of the 15 Alpine ibex *Capra ibex* populations monitored by GPS telemetry

856   (red) over the distributional range of the species (gray; source: Brambilla et al., 2020); see

857   Appendix S1 for more details. The pie charts display the proportion of individual seasonal

858   tracks identified as migration (green) or residency (blue) within each population (see below and

859   Appendix S3 for details on individual status identification).

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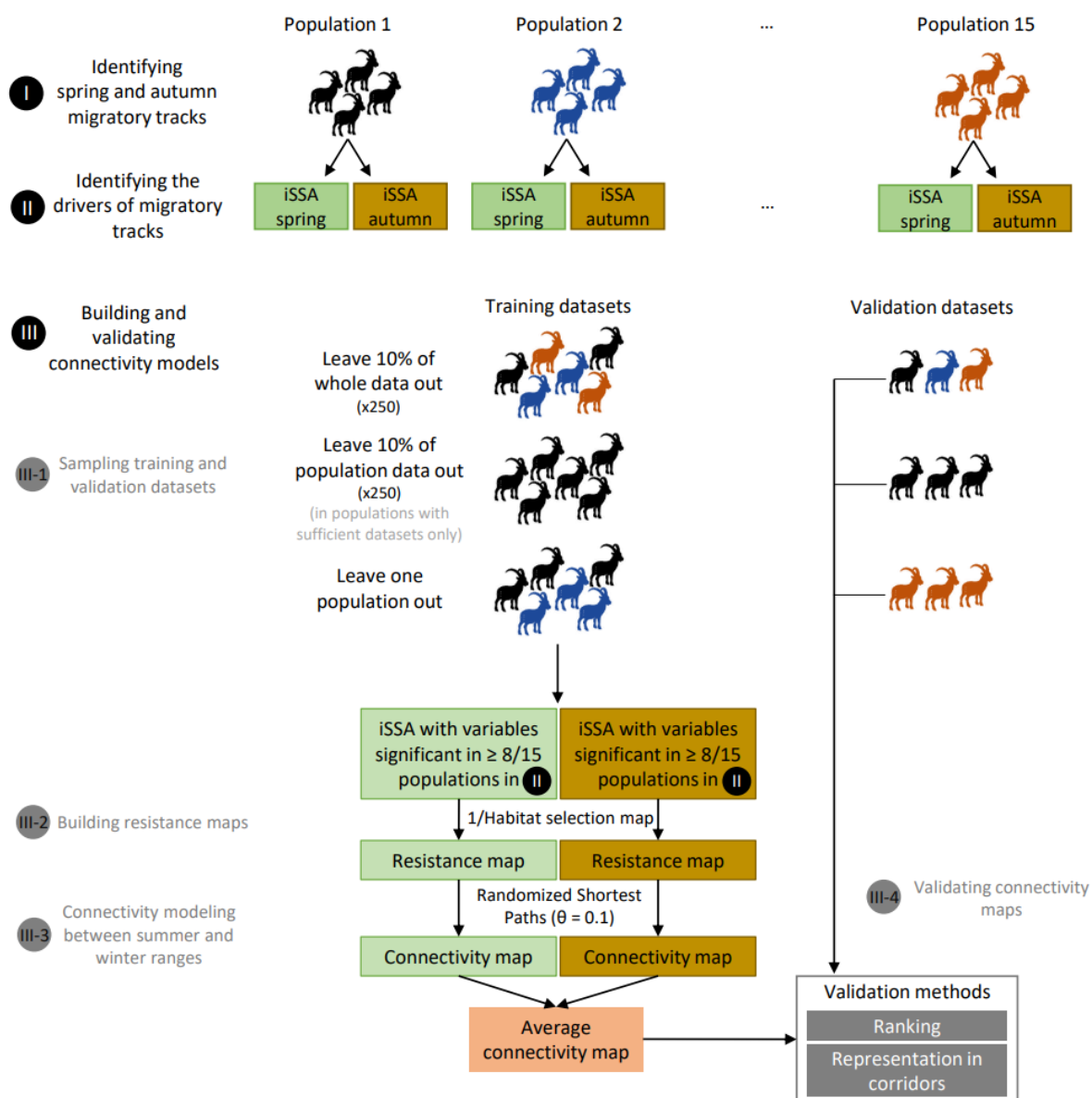
Figure 2: Methodological workflow scheme. First, we identified seasonal migratory tracks. Second, we fitted integrated Step Selection Analyses (iSSA) for each population to identify environmental drivers of spring and autumn migrations. Third, we sampled three different training and validation datasets: leave 10% of whole data out, leave 10% of population data out and leave one population out. The three training datasets were used in iSSA with the environmental variables identified as significant in at least 8/15 populations. We built three (one per training dataset) different resistance maps (250 times for "leave 10% of whole data out" and "leave 10% of population data out") for each population and season and modeled connectivity based on these resistance maps using the Randomized Shortest Path algorithm (θ = 0.1; Appendix S10). Finally, for each training dataset, we averaged the two seasonal

873 connectivity maps and combined this average connectivity map with the corresponding

874 validation datasets to perform the 'ranking' 'and 'representation in corridors' validation

875 methods.

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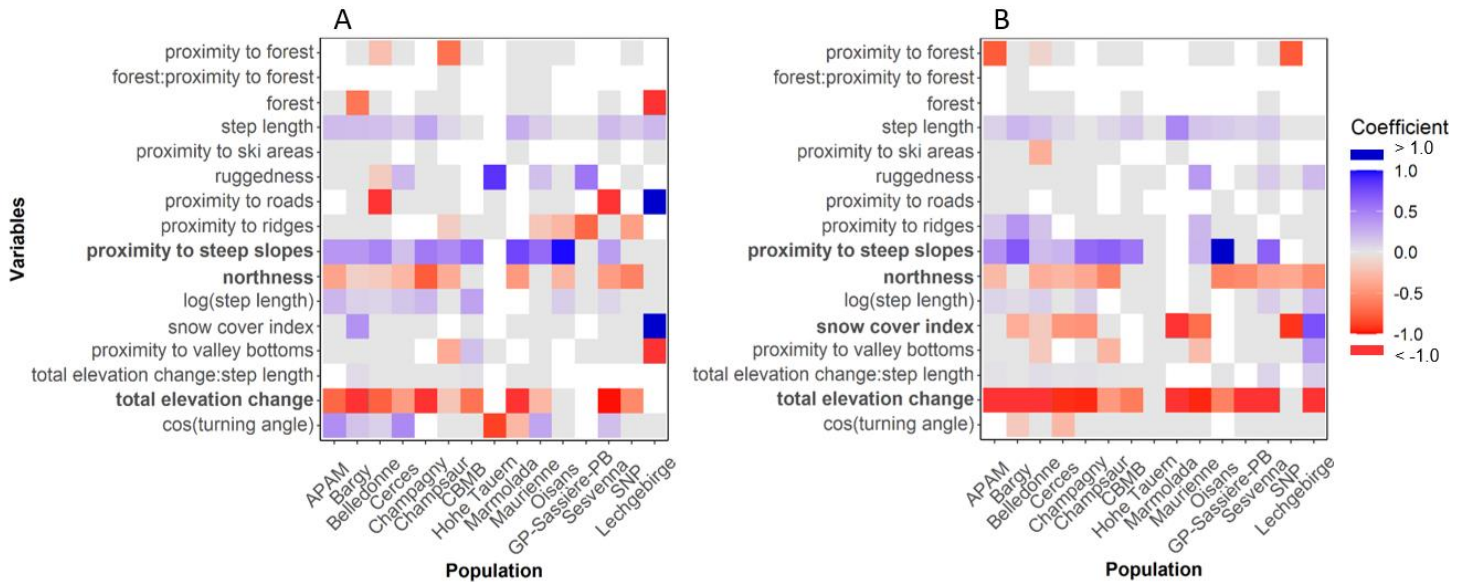
877 Figure 3: Coefficients provided by population-specific model-averaged (models with ΔAICc <

878 2) integrated Step Selection Analyses investigating the influence of environmental variables on

879 movement steps performed by Alpine ibex from 15 populations during spring (A) or autumn

880 (B) migration. Blue and red cells represent variables that were selected or avoided for migratory

881 movements, respectively. Grey cells represent non-significant coefficients. We calculated the

882 95% confidence interval (CI) of coefficients resulting from the model averaging. A coefficient

883 was significant if its CI non-overlaps with zero. White cells represent cases for which the

884 influence of a focal habitat variable could not be tested (not retained during model selection).

885 A variable name is in bold type if its selection coefficient was significant in at least 8/15

886 populations.

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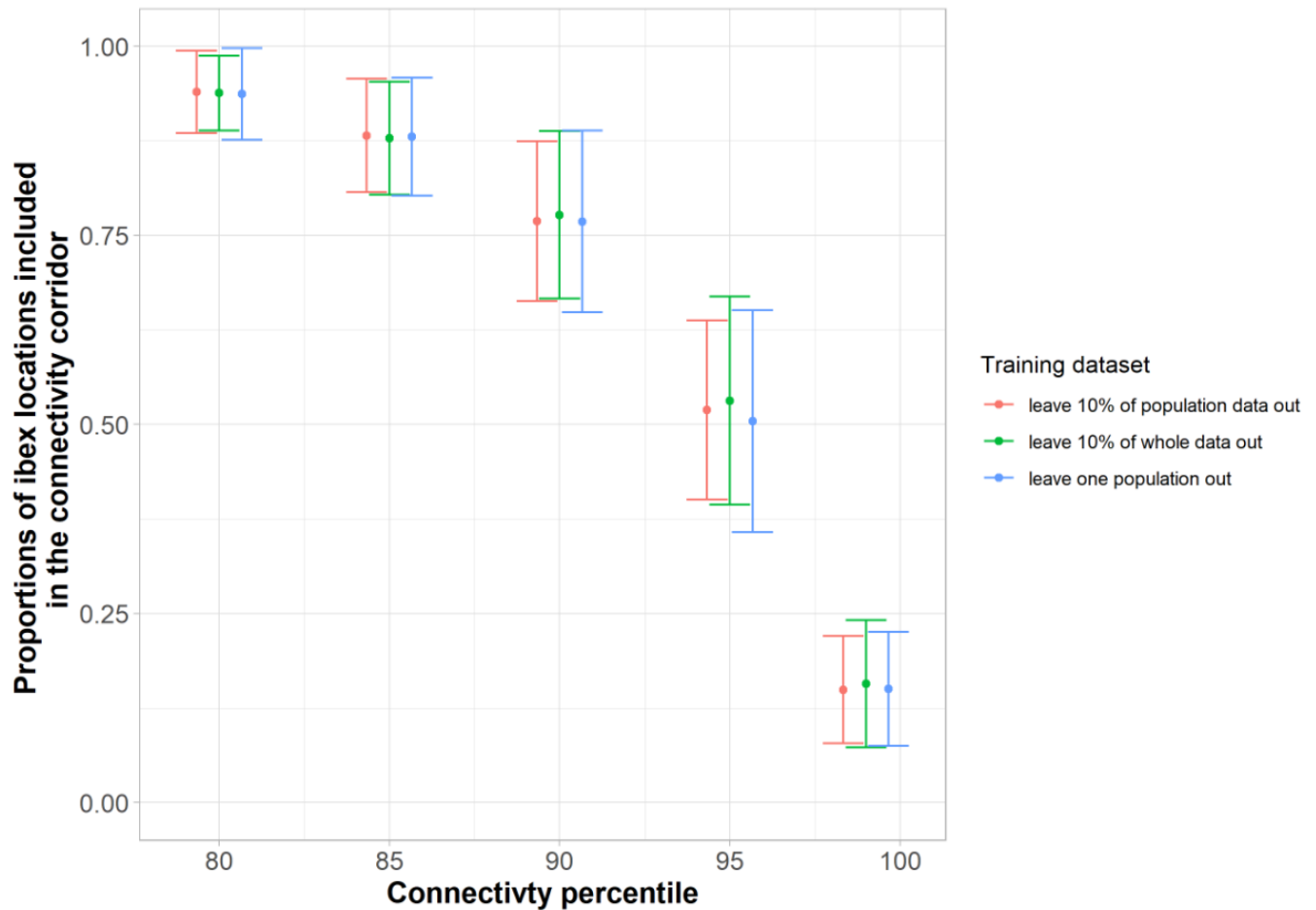
Figure 4: Results of the second validation method, representation in corridors (Goicolea et al., 2021). Proportions of ibex locations from migratory tracks included in the different connectivity corridors defined as the 80th, 85th, 90th, 95th and 99th connectivity percentiles. For the three modeling processes, the mean proportion calculated over the 15 populations is displayed with its standard deviation.
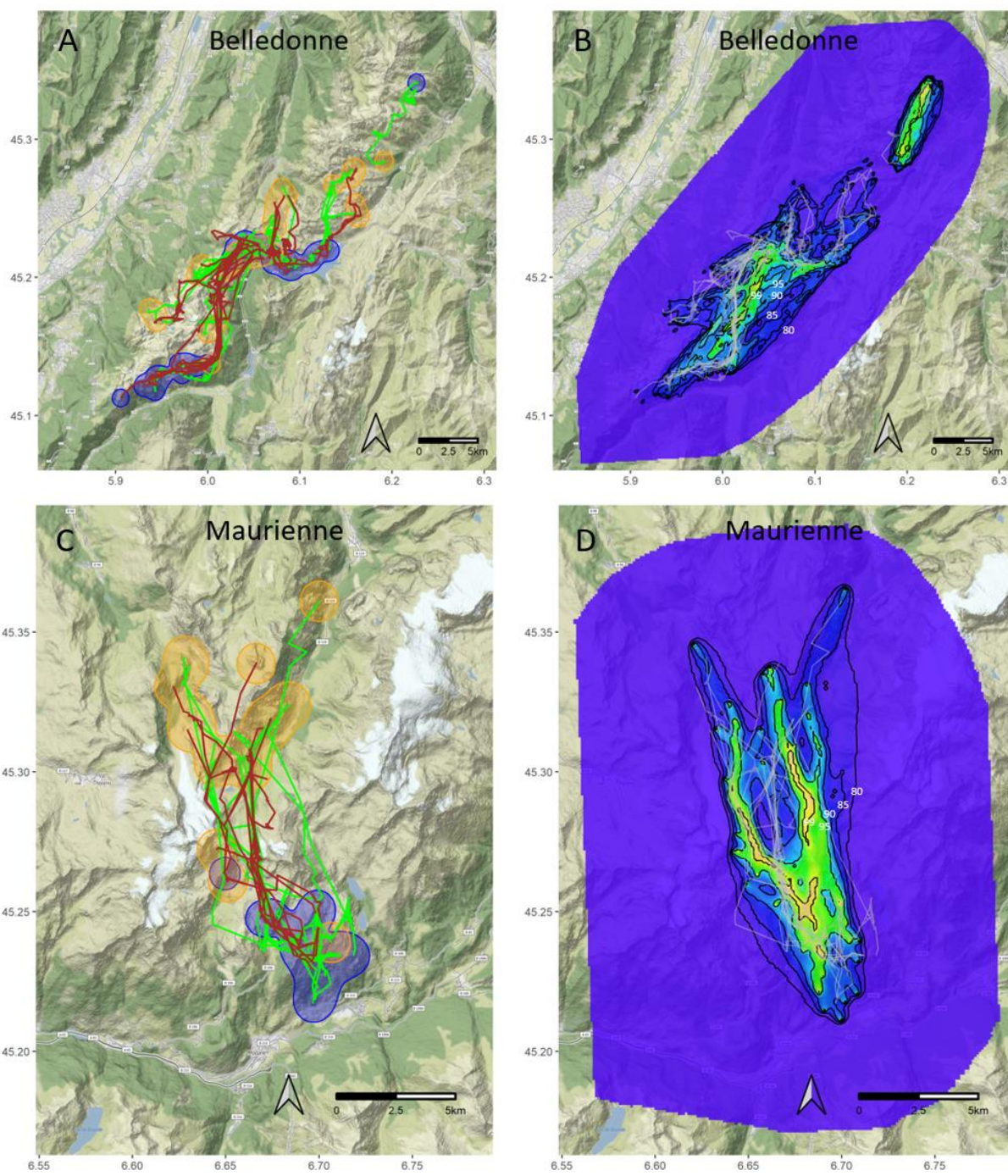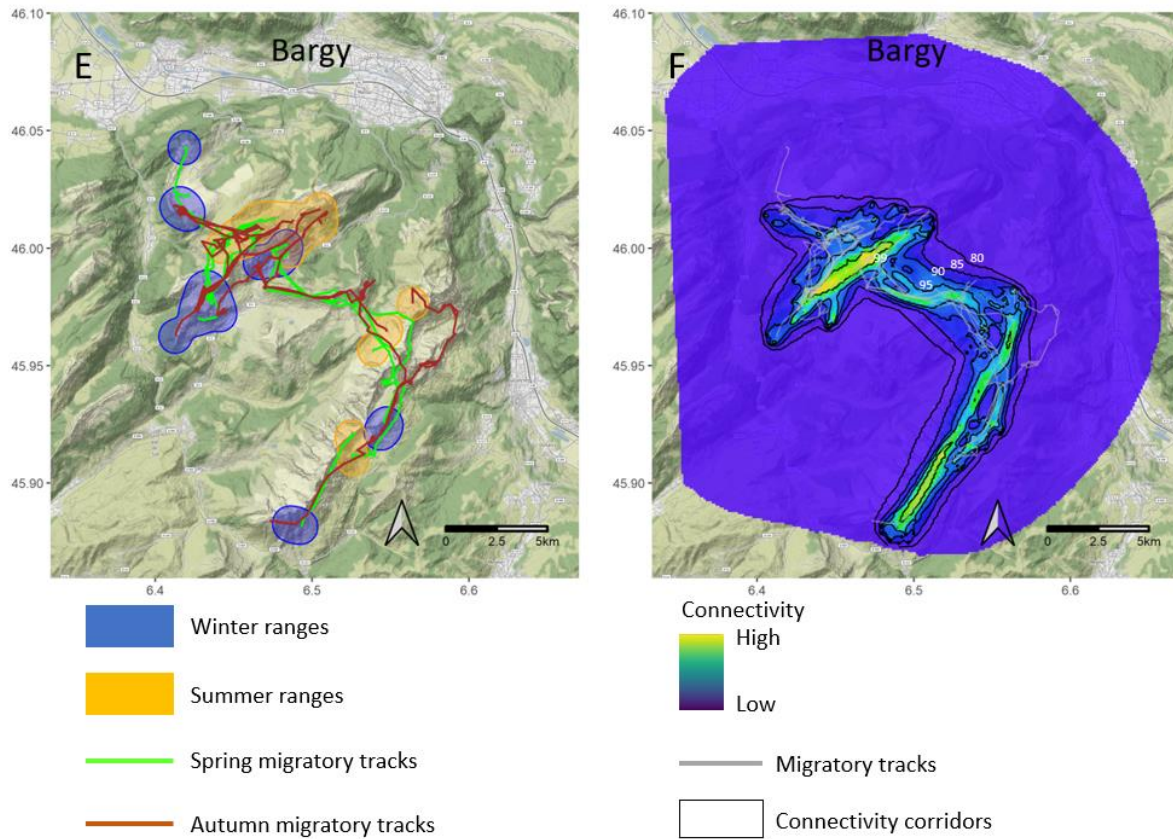
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Figure 5: Examples of connectivity modeling. Observed migration routes (spring in green and autumn in brown) and summer and winter ranges (orange and blue) of Alpine ibex from Belledonne, Maurienne and Bargy populations (A, C and E). Connectivity maps obtained from the "leave 10% of whole data out" dataset (B, D and F). The black lines delineate the connectivity corridors as defined in the 'representation in corridors' validation method.

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