1   **Missing the mammals for the trees: comparative biogeography of southern Appalachian**

2   **sky island biodiversity**

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10

11   **Abstract**

12   Sky islands are patches of relic ecosystems on mountaintops, often forest types, that were

13   previously connected in the geological past and are now patchily distributed. Whether a

14   particular sky island forest serves as an umbrella for conserving sky island fauna with a similar

15   patchy distribution is an open question. To address this, we systematically delineate sky islands

16   and identify spruce-fir-birch forest patches–southernmost boreal relics of the Pleistocene–in

17   relation to sky island mammal distributions in the southern Appalachians. Leveraging digitized

18   museum records and vegetation maps, we compare the distribution of sky island mammals to

19   one another as well as to the distribution of spruce-fir forest patches. We identify 10 southern

20   Appalachian mammals associated with high elevations andour results show that 5 of the 10

21   small mammal focal species do co-occur with large spruce-fir-birch (SFB) forest patches across

22   sky islands. These "spruce-fir associates" all occur on one or more sky islands lacking extensive

23   SFB forests. Furthermore, pairwise comparisons across all 10 focal species revealed significant

24   co-occurrence of SFB and non-SFB associates. Together, these results suggest that the

25   presence of SFB forest is not a sufficient "umbrella" for even spruce-fir associate mammals.

26   Conservation efforts focused exclusively on high-elevation forest types of the southern

27   Appalachian and elsewhere may, indeed, miss the mammals for the trees.

28   **Key words**: Appalachians, fragmented habitat, mountains, museum specimens, spruce-fir

29   **Teaser text**

30   On southern Appalachian mountaintops, pairwise comparisons between spruce-fir-birch forest

31   and 10 small mammals reveal discongruence between sky island habitat and its fauna.

32   Conservation efforts that focus solely on sky island habitat may, indeed, miss the mammals for

33   the trees.

34   **Introduction**

35   Mountains harbor unique biodiversity and serve as natural laboratories for studying climate-

36   driven shifts in species distributions (Love et al. 2023). In North America, high-elevation sky

37   islands are remnants of once-continuous boreal ecosystems that became fragmented as the

38   climate warmed following the Last Glacial Maximum (LGM; Burger et al. 2019). In the southern

39   Appalachians, which encompass western North Carolina, eastern Tennessee, and southern

40   Virginia, as temperatures rose, boreal forests tracked cooler, wetter conditions upslope

41   (Delcourt and Delcourt 1998; Jackson et al. 2000), and many cold-adapted mammals either

42   shifted their ranges northward or to higher elevations. These changes produced a patchwork of

43   isolated boreal forest patches and montane mammal populations on mountaintops now

44   surrounded by warmer lowland deciduous forests.

45   In northern New England, boreal forests—including red spruce (*Picea rubens*), and

46   yellow birch (*Betula alleghaniensis*)—extend to low elevations and even sea level. In the

47   southern Appalachians, by contrast, these boreal relic spruce-fir-birch (SFB) forests are highly

48   fragmented and restricted to the highest peaks (Cogbill and White 1991). Boreal mammals

49   show a parallel pattern: widespread at higher latitudes but confined to mountaintops in the

50   southern part of their range (e.g., *Glaucomys sabrinus*, *Myodes gapperi*, *Sorex* spp.). If these

51   mammals track suitable forest habitat, and SFB forest is most suitable for them, then the size

52   and connectivity of SFB patches should shape their distribution—consistent with the Constraint-

53   based Dynamic Island Biogeography (C-DIB) model (Burger et al. 2019). This fragmented

54   system of montane forests and elevation-restricted mammals offers a natural experiment to test

55   whether flora and fauna have shifted together since the LGM and whether their modern

56   distributions remain aligned.

57   Mapping SFB forest patches is essential for identifying habitat connectivity across this

58   sky island system. In the southern Appalachians, these forests now form an archipelago of high-

59   elevation patches, largely limited to cool, moist, north-facing slopes shaped by glacial–

60   interglacial cycles (Delcourt and Delcourt 1998; Cogbill and White 1991). Once widespread

61   during the LGM, they are now considered endangered ecosystems due to climate change, acid

62   rain, and other recent stressors (White 1984; Noss and Scott 1995). While the forest distribution

63   has been well characterized (e.g., White and Cogbill 1992; Koo et al. 2014; Kaylor et al. 2017),

64   the overlap with the distribution of high-elevation fauna remains poorly understood.

65   The extent to which sky island fauna overlap with forest types likely varies among

66   species and spatial scales. Many small mammals in the region—such as *Sorex* shrews, the

67   northern flying squirrel (*Glaucomys sabrinus*), and the southern red-backed vole (*Myodes*

68   *gapperi*)—exhibit traits characteristic of sky island endemism: high habitat specificity, limited

69   dispersal ability, and patchy distributions at high elevations (Sipe and Browne 2004; Arbogast et

70   al. 2005; Browne and Ferree 2007). County-level records and museum data showed that

71   several species are discontinuously distributed across the southern Appalachians (Campbell et

72   al. 2010), and population genetic studies revealed strong geographic structure, particularly

73   across barriers like the French Broad River (Arbogast et al. 2004; Sipe and Browne 2004;

74   Browne and Ferree 2007). In some species, such as *Sorex* shrews and *G. sabrinus*, populations

75   show genetic signatures of long-term isolation and small effective population sizes on the

76   northernmost islands.

77   For example, *Sorex fumeus* shows greater overall mountaintop isolation than *Sorex cinereus*

78   and both show similarly strong isolation on Whitetop Mountain, the northernmost sky island in

79   the region (Sipe and Browne 2004). At the regional scale, most studies define sky islands based

80   on SFB forest distribution, yet field surveys suggest that some species also occur in adjacent

81   northern hardwood or SFB ecotones at similar elevations (Knowles et al. 1989; Weigl et al.

82   1999; Menzel et al. 1999; Mallinoff et al. 2025). This raises a key question of our study: does a

83   narrow focus on present-day SFB distribution obscure broader patterns of habitat use among

84   sky island mammals?

85   To address this, we systematically delineated sky islands in the southern Appalachians

86   and assessed the distribution of high-elevation mammals across these fragmented landscapes

87   in relation to SFB forests. Using digitized museum records and vegetation maps, we compared

88   mammal occurrences to the spatial extent of SFB forest patches. We use descriptions for

89   subspecies when acknowledged, which is indicative of the unique evolutionary histories and

90   isolation of small mammal populations in the region.

91   This study focused on 10 small mammal species known to occur at high elevations.

92   These species differ in their degree of habitat specialization and elevational range (Figure 1).

93   The Carolina northern flying squirrel (*G. s. coloratus*), the most elevation-restricted of our study

94   species in the region, occurs between 1,000 and 1,830 meters in deciduous and coniferous

95   forests and is strongly associated with *Picea rubens* (red spruce), *Abes fraseri* (fraser fir), and

96 *Tsuga sp.* (hemlock) (Arbogast et al. 2005; Wells-Gosling and Heaney 1984). The rock or

97 yellow-nosed vole, *Microtus chrotorrhinus carolinensis*, inhabits talus slopes and mixed

98 mesophytic forests above 900 m (Komarek 1932; Kirkland and Jannet 1982; Orrock and Pagels

99 2003). The eastern woodland jumping mouse, *Napaeozapus insignis roanensis*, ranges from

100 900–2,000 m and is closely associated with spruce-fir and hemlock forests (Whitaker and

101 Wrigley 1972). *Parascalops breweri* is associated with a broad range of high elevation habitats

102 between 450–1,950 m, but due to its fossorial nature it may not require a particular vegetation

103 type (Hallett 1978, Laerm et al 2007). The rock shrew, *S. dispar*, occupies moss-covered talus

104 and cool, moist high-elevation habitats (Kirkland 1981), whereas the smoky shrew *S. fumeus*

105 prefers cool deciduous and coniferous forests at high elevations (Owen 1984; Ford et al. 2005).

106 In contrast, *M gapperi*, occupies SFB, northern hardwood, and ecotone habitats across a range

107 of elevations (Merritt 1981; Tisell et al. 2023). In the study region, the southern bog lemming

108 (*Synaptomys cooperi stonei*) inhabits more open high-elevation habitat, including wet meadows

109 and bogs (Rose and Linzey 2021). *Sorex cinereus* occurs broadly in high-elevation mesophytic

110 habitats (Whitaker 2004), and the Appalachian cottontail (*Sylvilagus obscurus*) has the widest

111 elevational range of our study species, occurring in dense woody understory regardless of forest

112 type (Apodaca et al. 2020).

113 Based on these natural histories, we predicted that the most elevation-restricted

114 species—*G. sabrinus*, *M. chrotorrhinus*, *S. fumeus, N. insignis,* and *S. dispar*—would show the

115 strongest associations with SFB forest patches. Meanwhile, we predicted that the habitat

116 generalist species—*P. breweri*, *M. gapperi*, *S. cooperi*, *S. cinereus*, and *S. obscurus*—would

117 have weak or no association with SFB forest patches because they occur across a broader

118 range of habitats, including spruce–hardwood ecotones and northern hardwood forests. For

119 both groups of species, either elevation-restricted or generalists we do not expect there to be

120 "perfect" associations because each study species can be found within other forest types across

121   their ranges. Finally, we evaluated species co-occurrence patterns across sky islands to assess

122   how habitat connectivity and elevation structure the distribution of the region's montane

123   mammal community. If the species with the strongest SFB associations also tend to co-occur

124   with each other but not the species with weak or no SFB associations, this would suggest that

125   environmental and/or trait filtering plays a key role in structuring the SFB small mammal

126   community. Alternatively, if the species with the strongest SFB associations tend to also co-

127   occur with the non-SFB associates, this would suggest that environmental and/or trait filtering

128   are less important and instead, species interactions and/or resource availability play more

129   prominent roles in structuring the SFB small mammal community.

130   **Methods**

131   To define the study area, we used the northernmost island (Whitetop, VA) as the northern

132   cutoff, interstate 81 as a western cutoff due to its position along the transition between high to

133   low elevation, and the area above 400 m in elevation in the southern Appalachians (Figure 2, 3).

134   While some study species are known to occur. adjacent to the study region(e.g., Black

135   Mountain, Kentucky; (Barbour 1951) we focused our study to encompass SFB forest islands.

136   The elevation and geographic cutoffs enabled us to capture a wide breadth of elevation, while

137   excluding the lowland areas which were outside the scope of this study. To this end, we

138   downloaded the USGS Digital Elevation Model (DEM) at 30 m resolution (USGS 2022). The

139   area above 400 m was converted to a polygon using the Raster to Polygon tool in ArcGIS Pro

140   (3.4.2). We used this polygon to extract elevation, vegetation cover, and to spatially filter

141   mammal records downloaded for the region from the Global Biodiversity Information Facility

142   (GBIF, see Identifying Sky Island Mammals section). All data were projected to Universal

143   Transverse Mercator Zone 17 (NAD 1983) and processed in ArcGIS Pro 3.4.2.

144   **Delineation of sky islands**

145   To define the physical sky island archipelago, we used the minimum elevation where the

146   sky island habitat (i.e. SFB forest) is found. This method captures all the high elevation areas

147   that have the potential to be classified as this forest type. To find this value, we filtered the

148   LANDFIRE National Vegetation Cover (NVC) dataset (30 meter resolution; LANDFIRE 2016) to

149   include only pixels classified as Central and Southern Appalachian Spruce-Fir-Hardwood Forest

150   (consisting mainly of red spruce, *Picea rubens,* Fraser fir, *Abies fraseri,* and yellow birch, *Betula*

151   *alleghaniensis* (SFB)). We calculated the Cohen's Kappa statistic (K) for this landcover type

152   based on the quality assessment data made available from LANDFIRE, in which ground-based

153   and model-based landcover classifications can be compared. Cohen's Kappa calculates the

154   agreement between two observers, in this case the LANDFIRE model and the ground-based

155   data, while accounting for agreement or disagreement based on chance. The K statistic for

156   Central and Southern Appalachian Spruce-Fir-Hardwood forest was 0.75, which is considered

157   as substantial agreement (Landis & Koch 1977). Based on the USGS elevation and LANDFIRE

158   NVC data, the minimum elevation for this forest type in the study region was 1,093 m. We then

159   used the Extract By Attributes and Raster to Polygon tool to obtain only the areas above 1,093

160   m from the USGS DEM.

161   A common challenge in studying island and island-like systems is how to systematically

162   and objectively delineate island areas, especially in cases where small satellite "island" peaks

163   cluster around a larger core island. To address this, we used the Dissolve Boundaries and

164   Group by Proximity tools to merge islands larger than 10 km² that are within 1 km of each other,

165   based on geodesic distance. Several islands were clustered in their own group, and islands that

166   belong to a group consisting of more than 1 island are labeled using letter notation (e.g. islands

167   1a and 1b belong to the same cluster; Figure 3).

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169

Identifying sky island mammals

Natural history is paramount to ecological studies, and much previous work has identified southern Appalachian sky island mammals based on this knowledge. We take an additional approach to identify sky island mammals based on all regional museum records for Mammalia. This method enables us to capture the elevation distribution of all mammals in the study region and determine species in high elevation areas. We downloaded all regional (see study region definition above) occurrence records (N=28,099) for Mammalia that included coordinates from the Global Biodiversity Information Facility (GBIF) on October 24, 2024 (GBIF DOI:10.15468/dl.sf7c4b). Additional occurrence records for southern Appalachian small mammals were reviewed from the following collections: University of Georgia (GMNH, N=8,321), University of North Carolina Wilmington (UNCW, N=130), Appalachian State University (ASU, N=227), and the North Carolina State Museum of Natural Sciences (NCSM, N=1,228).

Occurrence records were filtered using the following criteria: voucher specimens from the present day (excludes occurrences from iNaturalist and the Paleobiology Database), less than 1 km of coordinate uncertainty (to control for data quality in assigning occurrences to islands), and non-volant (excludes bats). To determine each species' elevation distribution, we obtained the USGS elevation in meters for each occurrence with the Extract Values to Points tool. Point-derived elevation could introduce some error in our estimations, particularly in a topographically complex landscape. To evaluate our estimation of elevation, we estimated the mean elevation within three different buffer thresholds around the occurrence points: 1 km, 500 m, and 250 m. For each threshold, we conducted Type II OLS regression between the point-derived elevation and the mean elevation within the buffer radius (Supplementary Data SD1). Based on this analysis, we found that the 250 m radius had the highest slope (0.97), meaning the point-derived elevation captured the most variation in elevation within the surrounding

195   landscape. We further estimated elevation distributions using the extracted valuesmean,

196   median, interquartile range, and quartiles of elevation from records with < 250 m of coordinate

197   uncertainty and with >5 occurrences within the study region. (Supplemental Data SD2, SD3). In

198   a first pass, we defined sky island species as having a mean elevation greater than 1,093 m

199   (lowest elevation cutoff for regional SFB, see above). Further natural history information in the

200   published literature was used in determining high elevation species, resulting in the addition of

201   *Microtus chrotorrhinus*, and exclusion of the cloudland deermouse (*Peromyscus maniculatus*)*,*

202   and red squirrel (*Tamiasciurus hudsonicus*)*,* (see references in Supplemental Data SD1).

203   **Identify co-occurrence of spruce-fir-birch forest and sky island mammals**

204   Using the Near tool (ArcGIS Pro 3.4.2) we assigned occurrences to an island based on

205   the geodesic distance to the closest island. These data were used to populate a

206   presence/absence matrix (Supplementary Data SD4).

207   While there are many ways to measure co-occurrences among species (e.g. the C-

208   score, which measures the degree of competitive exclusion within a community), we chose the

209   Jaccard/Tanimoto Similarity (JTS) index because our primary interest was the pairwise co-

210   occurrence between small mammal species and the SFB forest patches. We calculated this

211   index for all pairs of small mammal species as an exploratory step with the aim to catalyze

212   further investigation into species interactions (e.g. checkerboards) within this system, which

213   would require more focused analyses beyond the scope of this study. To determine co-

214   occurrences, we used the R package *jaccard* (Chung et al. 2018) to calculate pairwise JTS

215   indices among each species and against the SFB island distributions. These indices were

216   based on the presence/absence matrix constructed in the previous step. To calculate the JTS

217   index for a pair of species, this method compares the vector of SFB island presences for

218   species A against species B. The resulting index is the ratio of the intersection (# SFB islands

219   where species A and B both occur) to the union (sum of # SFB islands where species A and B

220 both occur, where just species A occurs, and where just species B occurs). To determine

221 statistical significance, we used the bootstrapping method of Chung et al. (2019). In short, this

222 bootstrapping method creates a null expectation of the JTS that preserves the proportion of

223 each species' SFB island presences. Statistical significance is based on deviation from this

224 expected value.

225 **Results**

226 **Delineation of sky islands**

227 We identified 33 independent sky islands, 6 of which had SFB forest patches >10km^2 including

228 Great Smoky Mountains, Attakulla (Mt. Mitchell), Grandfather Mountain, Roan Mountain, Black

229 Balsams, and Mt. Rogers (Figure 3, 4). Grandfather and Roan mountains were clustered

230 together, and the Black Balsams were clustered with 3 other islands that did not contain large

231 patches of SFB based on the clustering method described above.

232

233 **Identifying sky island mammals**

234 Across all mammal species in the study area, we curated 11,105 records from GBIF and

235 digitized additional museum specimens. Species include: *S. fumeus* (N=4,993), *S. cinereus*

236 (N=4,526), *M. gapperi* (N=1,286), *N. insignis* (N=150), *S. dispar* (N=58), *S. cooperi* (N=56), *P.*

237 *breweri* (N=39) *M. chrotorrhinus* (N=26), *S. obscurus* (N=6)*,* and *G. sabrinus* (N=4)*.* Literature

238 search resulted in additional island presences for *G. sabrinus* and *S. obscurus* (Supplementary

239 Table 1; presence matrix)). Maps of occurrences are included in Figure 4.

240

241 **Mammal comparisons with SFB forest**

242   Five species had significant distributions with SFB forest, meaning the intersection of

243   occurrences (species A and B) to the union (islands where at least one of A or B occurs) was

244   greater than expected by chance. SFB forest associates had the the following Jaccard/Tanimoto

245   similarity indices, which range from 0 (never co-occur) to 1 (always co-occur): *N. insignis* (0.67)*,*

246   *G. sabrinus* (0.5)*, , Parascalops breweri* (0.45), *Synaptomys cooperi* (0.45), and *S. dispar* (0.63)

247   (Figure 5). We did not expect *S. cooperi* to overlap with SFB forest (JTS=0.45, *P*<0.05).

248
249   **Regions of overlap among mammals**

250   Among mammals, 11 of 18 significant (*P*<0.05) connections had JTS indices above

251   0.5.*G. sabrinus* co-occurs with 5 other species, including 2 that do not co-occur with SFB forest

252   (*M. chrotorrhinus* and *M. gapperi*) and 3 that do (*N. insignis, S. dispar*, and *S. cooperi*. (Figure

253   5). *Sorex fumeus* had the fewest connections to other species (2, *S. cinereus* and *M. gapperi*).

254   In general, the southern portion of our study area (south of the French Broad river)

255   harbored a large proportion of occupied islands. The Great Smoky Mountains (island 16) and

256   the Black Balsams (island 18a) contained all but one species (Figure 4, Supplemental Table 2).

257   Mt. Rogers (island 1b), while it had a large spruce-fir patch, contained only 5 out of 10 species

258   (*S. fumeus, S. cinereus, M. gapperi, N. insignis, P. breweri*). *Sorex fumeus* occupied the most

259   islands (N=23), while *M. chrotorrhinus* emerged with the most restricted distribution on only 2

260   islands (Great Smoky Mountains and Black Balsams).

261   **Discussion**

262   We find discongruence between SFB forest (the high elevation habitat) and the distributions of

263   high elevation small mammals in the southern Appalachians. Out of the ten small mammals we

264   studied, 5 of them (*S. dispar, G. sabrinus, P breweri, S. cooperi,* and *N. insignis*) are statistically

265   associated with spruce-fir-hardwood forest. Across all small mammal species, 21 pairs co-

266   occur, and 12 of those pairs included at least 1 species that was not a spruce-fir associate

267   (Figure 5). Finally, some islands without large patches of spruce fir (Max Patch (15b), Sandy

268   Mush (15a), and the Unicoi mountains (20)) contained almost every mammal species

269   (Supplementary Data SD4). Together, these results suggest that the presence of large spruce-

270   fir patches does not serve as an umbrella for all high elevation species. In fact, all high elevation

271   mammal species were found on at least one island *lacking* large patches of SFB. Eighteen sky

272   islands containing high elevation mammal species would be missed entirely if mountains with

273   spruce-fir patches were the only basis of conservation in the region.

274   We propose several possible explanations for this pattern of discongruence among high

275   elevation species and spruce-fir forest. First, within and among species, there may be local

276   adaptations that explain the discongruence and patchiness of occupancy. Four of the 10 study

277   species are either regionally unique species (*Sylvilagus obscurus*) or subspecies (*Synaptomys*

278   *cooperi stonei* Howell 1927*, Microtus chrotorrhinus carolinensis* Komarek 1932*,* and *Glaucomys*

279   *sabrinus coloratus* Handley 1953). This suggests localized adaptation or at least unique

280   evolutionary lineages, which could be further isolated by major rivers (e.g. French Broad,

281   Pigeon) that surround several mountain ranges. It is clear, then, that there is a need to evaluate

282   how connectivity and relative isolation among islands has contributed to evolutionary histories at

283   the species and population scales. Habitat suitability models could be used to test whether

284   unoccupied islands in the present day were ever connected to other islands in the past (e.g.

285   Rocha-Méndez et al. 2024). If a habitat suitability model reveals that an island was suitable and

286   connected in the past (e.g. last glacial maximum) and is unoccupied but suitable in the present,

287   this would suggest recent population extinctions of sky island species (Burger et al. 2019). Mt.

288   Rogers (island 1b) one of the northernmost islands in our study system, could be one such

289   island, since it does contain a large patch of spruce fir but only 1 of the spruce-fir associates.

290   The historical biogeography of the region is further complicated by the possibility that

291   small boreal mammals may be more closely associated with other tree species or patchily

292 distributed resources that are present both within and outside of SFB forest. For example, small

293 mammals in their northern distribution vary in specialization on particular nuts, fungi, and fruits;

294 additionally, they augment their life history in response to masting events (Stephens et al. 2024,

295 Willems et al. 2025). More complex analysis could model the co-occurence of sky island

296 mammals with the patchiness of other resources, such as sugar maples, beech, etc., not

297 represented by spruce and fir, and other sky island mammal species. Further study of sky island

298 mammals in the southern Appalachians should integrate measures of isolation (e.g. population

299 genetics) and habitat suitability modeling to further evaluate how historical island connectivity

300 generates current discongruences among species.

301 Second, species-specific ecologies and species interactions may explain the patchiness

302 and discongruence among sky island species. The co-occurrence of small mammals and

303 spruce-fir forest at the island scale may not necessarily mean that the species co-occur at

304 smaller scales in sympatry or syntopy. For example, among the insectivorous shrews, *S.*

305 *fumeus* and *S. cinereus* co-occur, but *S. dispar* does not, likely because of its unique

306 association with talus slopes.. Although the *S. fumeus* and *S. cinereus* pairing has a high

307 Jaccard score (0.83), *S. fumeus* might rely more heavily on millipedes than other arthropods,

308 allowing the 2 species to co-occur (Linzey and Linzey 1973). Competition could also be

309 prevalent among other high elevation species with similar diets. *Synaptomys cooperi, M.*

310 *gapperi,* and *M. chrotorrhinus,* whose diets tend to be more herbaceous, tend to co-occur more

311 with species that have non-herbaceous diets; however *M. gapperi* is more of an opportunist and

312 consumes plant materials, insects, and fungi (Merritt 1981, Stephens et al. 2020). *Synaptomys*

313 *cooperi*, while generally low-density, thrives in the absence of competition (Rose and Linzey

314 2021), which may facilitate its survival in isolated areas if competitor species are locally

315 extirpated. Among the spruce-fir associates, which do not tend to co-occur, fungi makes up a

316 large portion of their diets, specifically *Endogene* (*G. sabrinus*: Weigl et al. 1999, *N. insignis*:

317 Linzey and Linzey 1973, *M. chrotorrhinus*, second to an herbaceous diet: Linzey and Linzey

318 1973, Kirkland and Jannett 1982), with the exception of the insectivore *S. dispar* (Richmond and

319 Grimm 1950, Conaway and Pfizer 1952). Those species with broad diets, such as *S. cooperi*

320 and *S. obscurus,* emerged among the most widespread among the islands, although *S.*

321 *obscurus* alternates seasonally between herbaceous and woody material, and sometimes

322 spruce needles (Edelman 2019). *Synaptomys cooperi* consumes vegetation, some fungi

323 (*Endogene*), roots where it occupies forests, and some insect larvae (Rose and Linzey

324 2021).Finally, the topographically complex landscape of the southern Appalachians could

325 contribute to biodiversity more so than habitat associations. A linear regression revealed that

326 species richness had a slightly positive, but significant, relationship to maximum elevation

327 (Supplementary Data SD5; slope=0.012; R^2=0.63; P<0.05). Further studies may build on those

328 such as that of Mallinoff et al. (2025) should evaluate contribution of both vegetation and

329 climatic gradients in the biogeography of the region.

330   Our study deployed a new technique to delineate sky islands that could be applied to

331 other taxa in the region that are known to have patchily distributed populations (e.g. spruce-fir

332 moss spider (*Microhexura montivaga*) and the northern and southern pygmy salamanders

333 (*Desmognathus organi & wrighti*)). While previous studies of sky islands have used elevation

334 cutoffs to determine island area, we additionally used a clustering approach to resolve instances

335 of several small satellite islands surrounding a larger island. Furthermore, our classification

336 approach revealed connections between islands that were previously unrecognized. For

337 example, one cluster that consisted of islands 9a and 9b (Roan Mountain and Grandfather

338 Mountain, respectively), has typically been considered as separate islands in the past (Sipe and

339 Brown 2004, Brown and Ferree 2007). Their connectivity may have conservation importance.

340 Localized extreme weather events, such as hurricane Helene (2024), had detrimental effects on

341 the spruce-fir forest at Roan Mountain and presumably the small mammal community, while

342   Grandfather Mountain was minimally affected. In this case, Grandfather Mountain could serve

343   as a source area to "rescue" Roan populations, as seen in other island systems (Brown and

344   Kodric-Brown 1977). The clustering approach employed in this study may have had broader use

345   to other island systems such as cities, oceanic archipelagos, and landbridge islands to

346   objectively and systematically delineate island cluster areas.

347   Our systematic approach to delineating sky islands and compiling known localities of

348   small mammals in the study area will be useful for future studies. However, we caution that

349   these localities may not represent all extant populations of these species in the study area. An

350   exhaustive survey of all high-elevation sites in the region was not feasible in this study. Yet, the

351   results of this study do not hinge on complete sampling of all sky islands. We found 5 of our 10

352   mammal species to be statistically associated with spruce-fir among islands. But all of these

353   species were found on islands lacking SFB entirely. The timeline of collection across species

354   (Supplementary Figure 2) is unlikely to affect these distributions because many of the

355   mountaintops have been protected for the last century, including national parks (e.g. Great

356   Smoky Mountains, Blue Ridge Parkway) and forests (e.g. Nantahala, Pisgah). There may be

357   additional specimens that remain in "dark" collections that have not been digitized, however,

358   species' distributions in this study were based on voucher specimens that were either available

359   on GBIF or located in 1 of the 4 regional collections listed above. It is possible that those islands

360   did contain spruce-fir prior to human arrival and European colonization that were subsequently

361   transformed or logged driving local extirpation of SFB. Field surveys of the pollen record and

362   small mammals throughout the region and in poorly-surveyed sky islands will better inform the

363   dynamic distributions biodiversity in the region over long (e.g., terminal Pleistocene) and short

364   (e.g., pre-colonial) time scales

365   **Conclusion**

366   Montane biodiversity is increasingly threatened by climate change and human activity, making it

367   critical to develop robust, scalable tools for understanding and conserving sky island systems.

368   Here, we present a systematic and quantitative approach to delineating sky islands and

369   assessing mammal distributions in the southern Appalachians—an approach that can be

370   extended to other mountain regions globally. Our findings demonstrate that sky islands are not

371   uniform units: species vary in their association with forest types, reflecting distinct ecological

372   requirements and evolutionary histories. While some high-elevation mammals are frequently

373   associated with spruce-fir forest, their presence on islands lacking extensive spruce-fir suggests

374   that forest type alone is not a sufficient proxy for mammal habitat. Significant co-occurrence

375   between spruce-fir and non–spruce-fir associates brings into question whether spruce-fir forests

376   serve as sufficient umbrella habitats for montane mammal conservation. The take home

377   message from our results is that conservation strategies that focus solely on forest types may,

378   quite literally, miss the mammals for the trees. By integrating species-specific distributions with

379   dynamic landscape features, our framework offers an integrative tool and systemic approach for

380   identifying sky island species and conservation priorities worldwide.

381

389   **Conflict of interest**

390   None declared.

Supplementary Data

    Supplementary Data SD1.—Coordinate uncertainty sensitivity analyses.
    Supplementary Data SD2.—Distributions of southern Appalachian species' museum records across elevation and time.
    Supplementary Data SD3.—Elevation distributions of study species.
    Supplementary Data SD4.—Presence matrix across islands.
    Supplementary Data SD5.—Regression of maximum elevation and species richness.

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576 **Fig. 1**.—Elevation distributions of the ten study species in relation to spruce-fir birch (SFB)

577 forest in the southern Appalachians. Asterisks indicate species we predicted to be associated

578 with SFB forest.

579 **Fig. 2**.—Data pipeline depicting the workflow from downloaded data to generate presence

580 matrices.

581 **Fig. 3**.—Distribution of 33 study islands >1,093 m elevation (medium gray) with the study region

582 (light gray). Islands are numbered north to south, where letter notation indicates islands

583 belonging to the same cluster. Major rivers are depicted in B. The righthand table lists island IDs

584 with island names. Black cells indicate islands with spruce-fir birch (SFB) forest patches

585 >10km^2.

586 **Fig. 4**.—Distributions of high elevation mammals across the southern Appalachian sky islands

587 (>1,093 m). Black areas indicate presences, while gray areas indicate absences. Museum

588 occurrence records are indicated with open circles, while literature records are indicated with

589 open squares. GLSA: *Glaucomys sabrinus*; MICH: *Microtus chrotorrhinus*; MYGA: *Myodes*

590 *gapperi*; NAIN: *Napaeozapus insignis*; PABR: *Parascalops breweri*; SOCI: *Sorex cinereus*;

591 SODI: *Sorex dispar*; SOFU: *Sorex fumeus*; SYCO: *Synaptomys cooperi*; SYOB: *Sylvilagus*

592 *obscurus*.

593   **Fig. 5**.—Pairwise Jaccard/Tanimoto Similarity indices between small mammals and SFB forest

594   (top row) and between small mammal species (remaining rows). Black cells indicate significant

595   (*P*<0.05) co-occurrences. Silhouettes are from phylopic.org, except for NAIN, which was made

596   by the authors. *Glaucomys sabrinus* illustrated by Chloe Schmidt. Others are in the public

597   domain. GLSA: *Glaucomys sabrinus*; MICH: *Microtus chrotorrhinus*; MYGA: *Myodes gapperi*;

598   NAIN: *Napaeozapus insignis*; PABR: *Parascalops breweri*; SOCI: *Sorex cinereus*; SODI: *Sorex*

599   *dispar*; SOFU: *Sorex fumeus*; SYCO: *Synaptomys cooperi*; SYOB: *Sylvilagus obscurus*.

Fig. 1.—Elevation distributions of the ten study species in relation to spruce-fir birch (SFB) forest in the southern Appalachians. Asterisks indicate species we predicted to be associated with SFB forest.
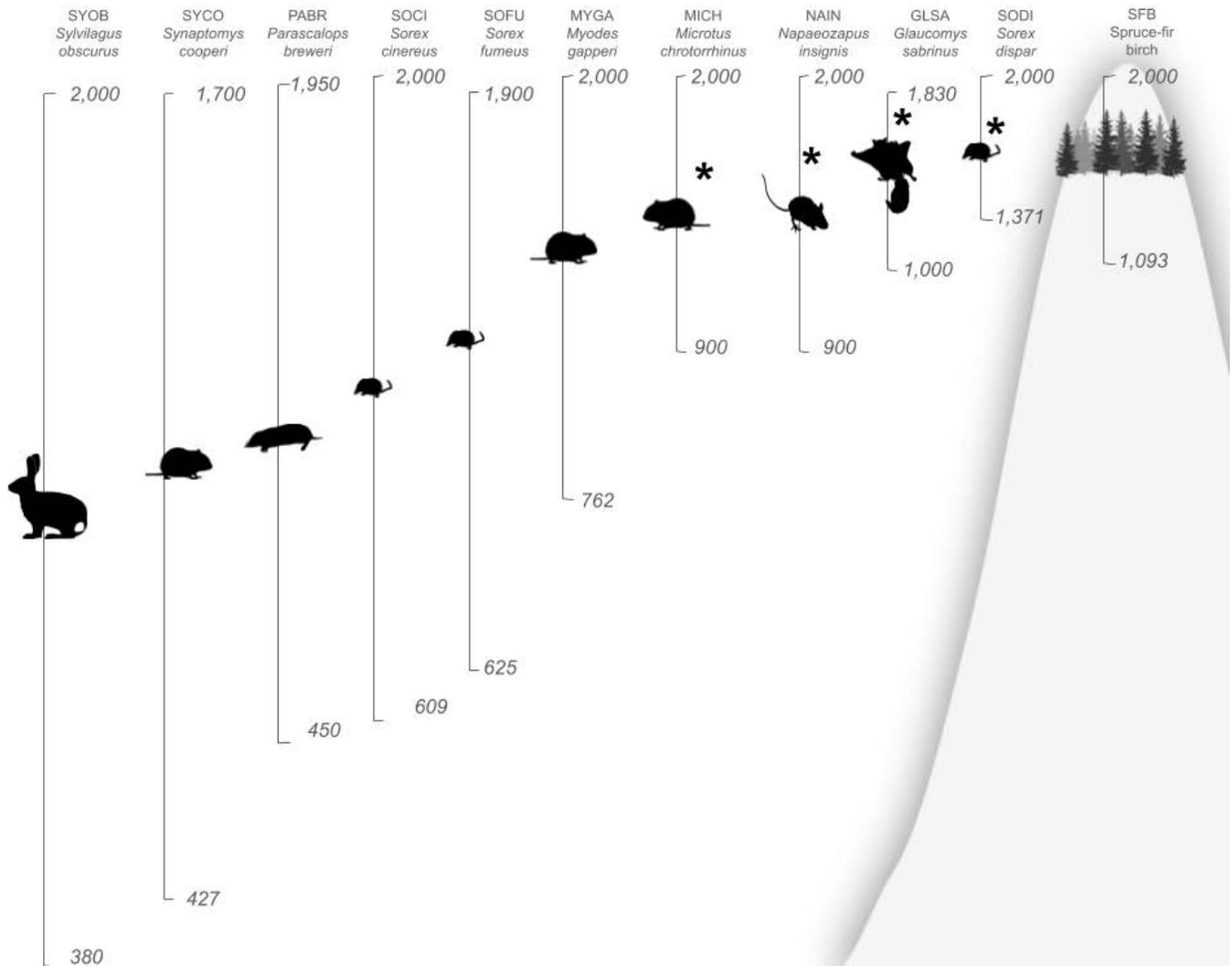
Fig. 2.—Data pipeline depicting the workflow from downloaded data to generate presence matrices.

LANDFIRE National Vegetation Cover

USGS Digital Elevation Model

33 islands

Elevation cutoff of spruce-fir-hardwood forest: 1,093 meters

11,144 voucher specimens across 10 species

Assign occurrences to closest island

Voucher specimens from GBIF and digitization efforts:
<1km coordinate uncertainty
Non-volant
Present day
Mean elevation >1,093 meters
High elevation quartiles

Voucher Specimens

Presence matrix

spp.	A	B
1	1	0
2	1	1
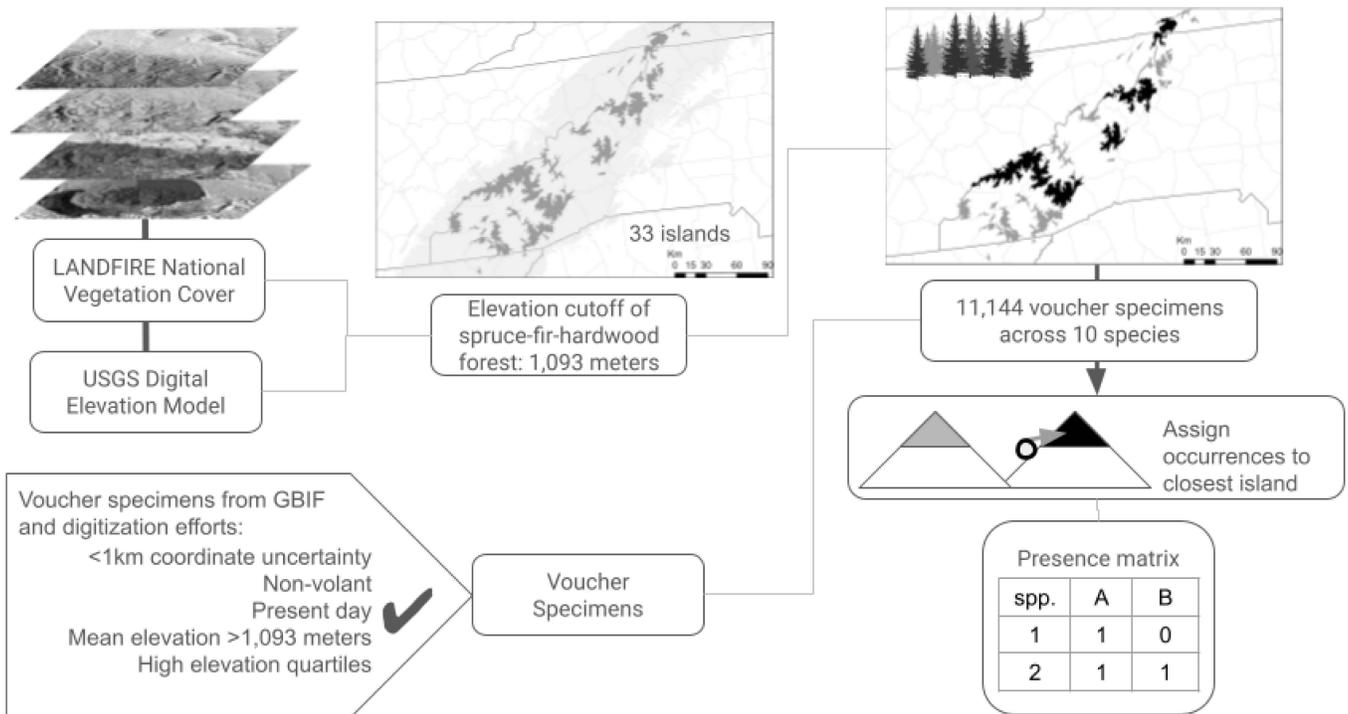
Fig. 3.—Distribution of 33 study islands >1,093 m elevation (medium gray) with the study region (light gray). Islands are numbered north to south, where letter notation indicates islands belonging to the same cluster. Major rivers are depicted in B. The righthand table lists island IDs with island names. Black cells indicate islands with spruce-fir birch (SFB) forest patches >10km^2.

ID	Island Name
1a	Blue Spring Gap
1b	Mt. Rogers
2	Buck Mountain
3	Iron Mountain, north peak
4	Iron Mountain, south peak
5	Holston Mountain
6a	Three Top Mountain
6b	Elk Knob
7	Vaught Gap
8a	Thunder Hill
8b	Flat Top
9a	Roan Mountain
9b	Grandfather Mountain
10	Howard's Rock
11	Big Bald
12	Attakulla (Mt. Mitchell)
13	Crabtree Falls
14	Spring Mountain
15a	Sandy Mush
15b	Max Patch
16	Great Smoky Mountains
17	Cowee Mountain
18a	Black Balsams
18b	Highlands Plateau
18c	Windy Gap
18d	Rabun Bald
19	Cheoah Bald
20	Unicoi
21	Joanna Bald
22	Junalaska
23a	Nantahala Falls Creek
23b	Nantahala
24	Brasstown Bald

Fig. 4.—Distributions of high elevation mammals across the southern Appalachian sky islands (>1,093 m). Black areas indicate presences, while gray areas indicate absences. Museum occurrence records are indicated with open circles, while literature records are indicated with open squares. GLSA: *Glaucomys sabrinus*; MICH: *Microtus chrotorrhinus*; MYGA: *Myodes gapperi*; NAIN: *Napaeozapus insignis*; PABR: *Parascalops breweri*; SOCI: *Sorex cinereus*; SODI: *Sorex dispar*; SOFU: *Sorex fumeus*; SYCO: *Synaptomys cooperi*; SYOB: *Sylvilagus obscurus*.
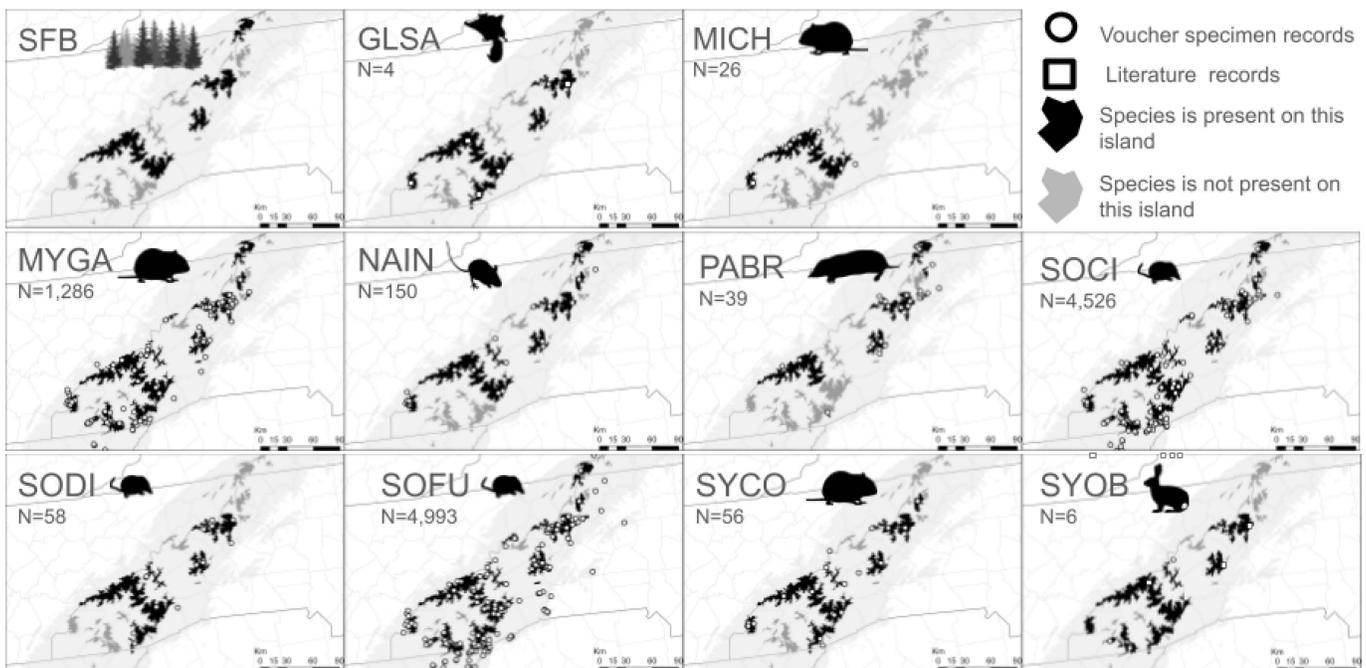
Fig. 5.—Pairwise Jaccard/Tanimoto Similarity indices between small mammals and SFB forest (top row) and between small mammal species (remaining rows). Black cells indicate significant (*P*<0.05) co-occurrences. Silhouettes are from phylopic.org, except for NAIN, which was made by the authors. *Glaucomys sabrinus* illustrated by Chloe Schmidt. Others are in the public domain. GLSA: *Glaucomys sabrinus*; MICH: *Microtus chrotorrhinus*; MYGA: *Myodes gapperi*; NAIN: *Napaeozapus insignis*; PABR: *Parascalops breweri*; SOCI: *Sorex cinereus*; SODI: *Sorex dispar*; SOFU: *Sorex fumeus*; SYCO: *Synaptomys cooperi*; SYOB: *Sylvilagus obscurus*.

	GLSA	MICH	MYGA	NAIN	PABR	SOCI	SODI	SOFU	SYCO	SYOB
SFB	0.50	0.29	0.33	0.67	0.45	0.32	0.63	0.26	0.45	0.31
GLSA		0.33	0.50	0.50	0.36	0.47	0.60	0.39	0.58	0.60
MICH			0.17	0.33	0.08	0.16	0.25	0.13	0.30	0.20
MYGA				0.42	0.40	0.85	0.39	0.78	0.47	0.57
NAIN					0.58	0.47	0.45	0.39	0.58	0.33
PABR						0.53	0.31	0.43	0.33	0.25
SOCI							0.37	0.83	0.45	0.55
SODI								0.30	0.70	0.47
SOFU									0.43	0.52
SYCO										0.56

Jaccard/Tanimoto Similarity (JTS) index

dissimilar 0   similar 1

More likely to co-occur than expected by chance
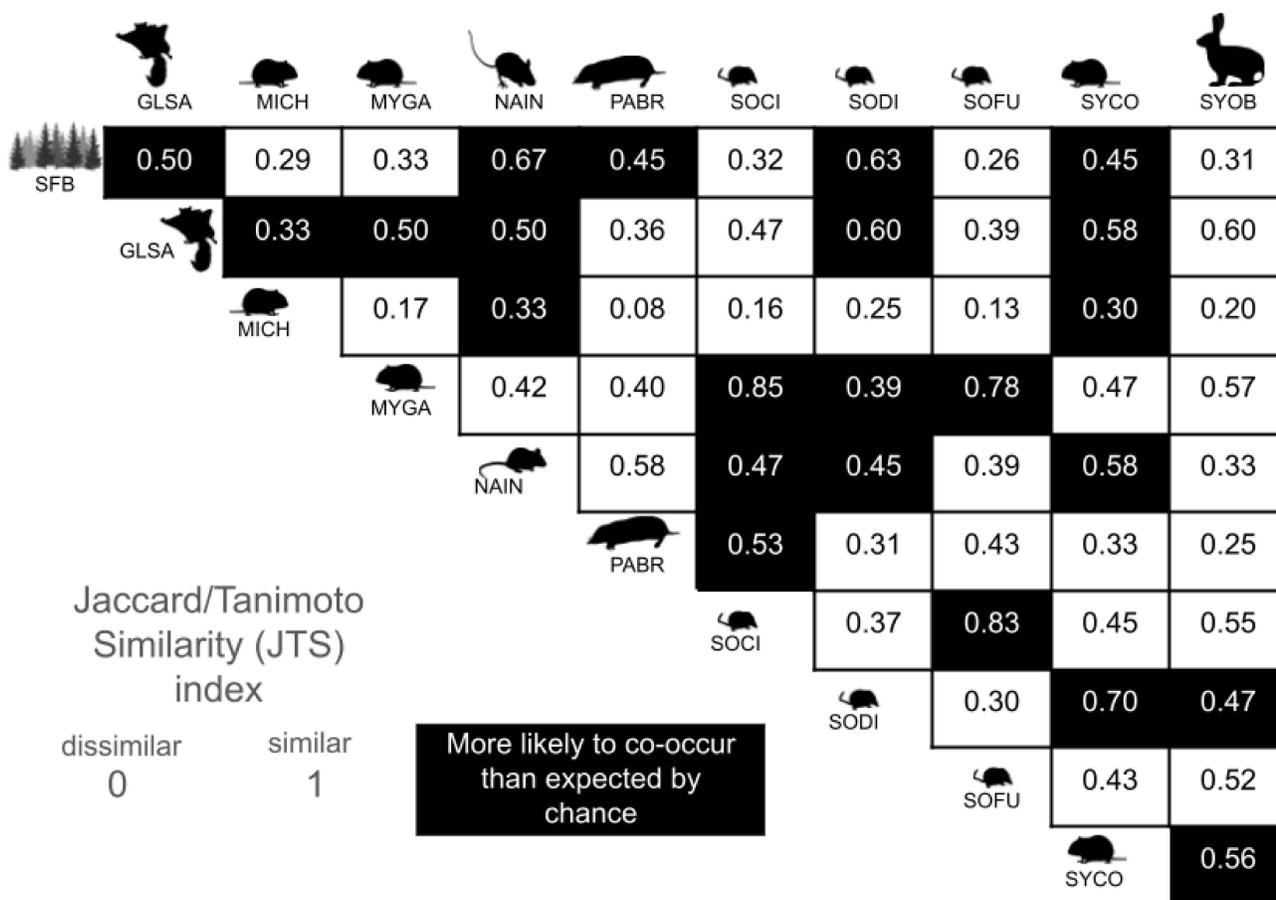
**Supplemental Figure 2:** Type II OLS Regression to evaluate the sensitivity of point-derived elevation (m) to coordinate uncertainty at three thresholds (1 km, top right; 500 m, bottom right; 250 m, bottom left).

Radius threshold	Intercept	Slope (± 95% CI)
1km	171.524	0.846 (0.843-0.850)
500m	79.922	0.930 (0.928-0.931)
250m	30.273	0.973 (0.972-0.973)
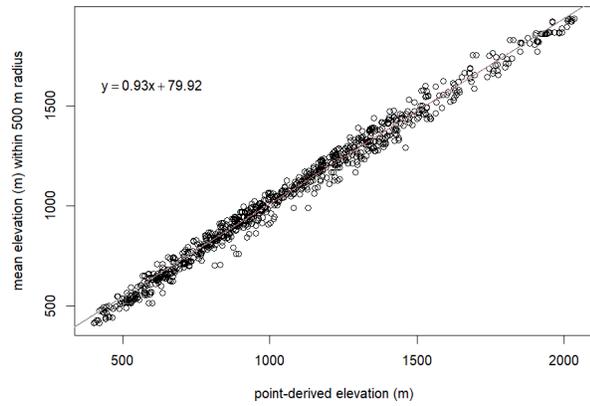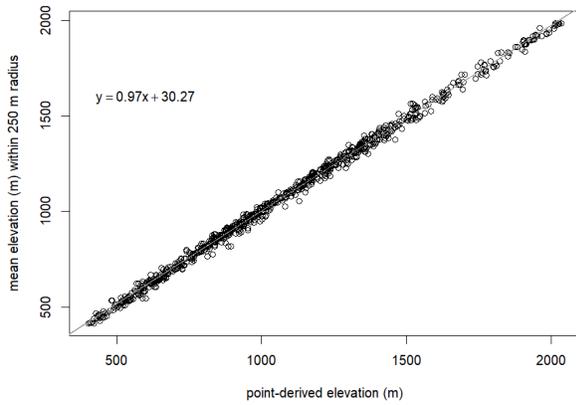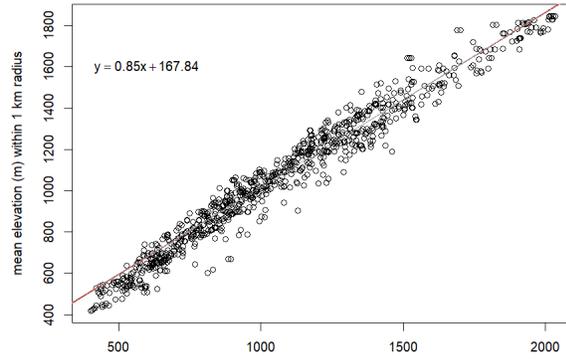
Supplemental Figure 1: A) elevation distributions of non-volant mammals in the southern Appalachians based on museum records with more than 5 occurrences. Gray band shows the elevation distribution of spruce-fir-hardwood forest according to the USGS National Vegetation Cover dataset. B) Temporal distributions of selected study species represented by museum occurrences.
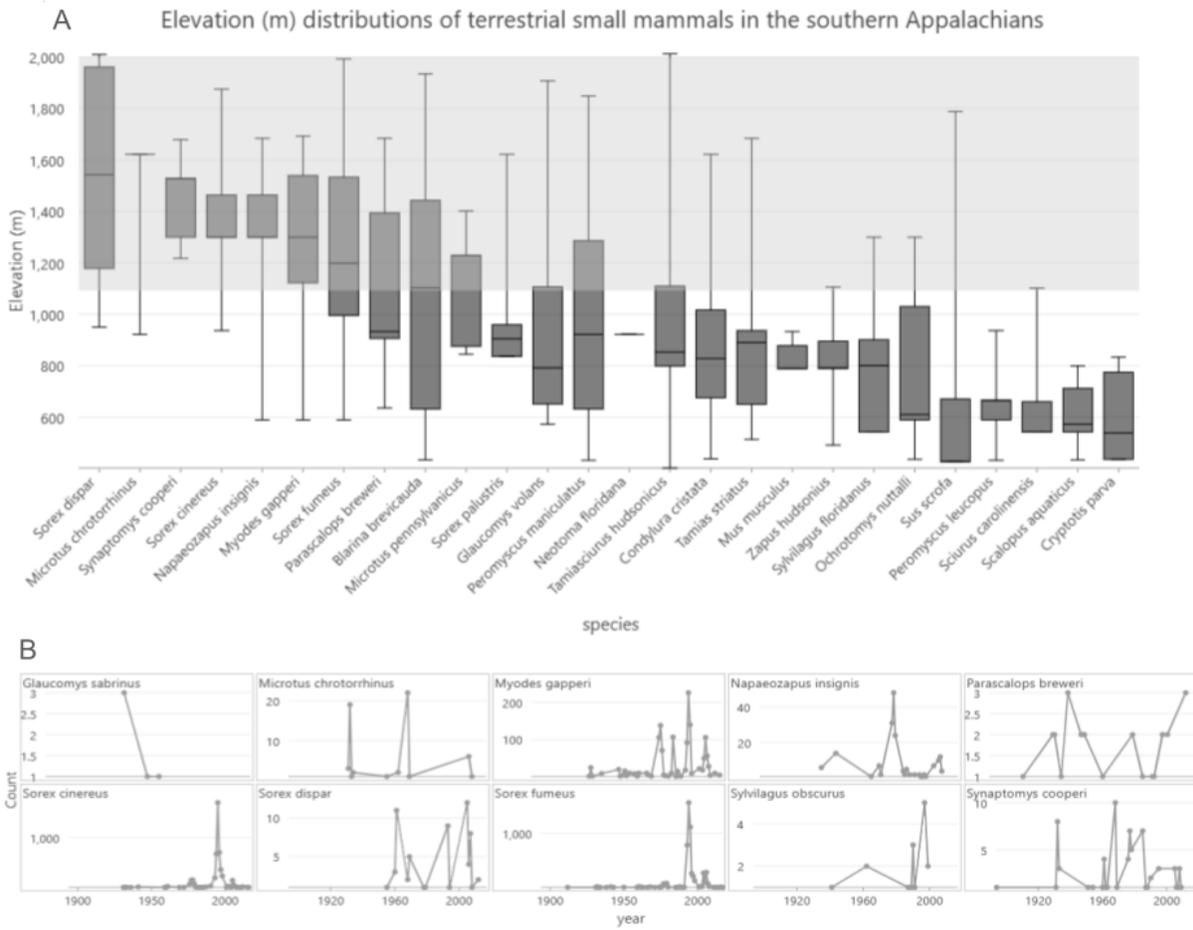
For *Napaeozapus insignis*, this filtering process excluded the only known two specimens from Sandy Mush (island 15a) and so these occurrences were reviewed and confirmed through the literature (Anderson 2008). While *Sorex fumeus* had a mean elevation less than 1,093 meters (mean = 1,040), this species was included because it has been considered a sky island species and was found to have population structure that reflects high elevation areas in past literature

(e.g. Sipe & Browne 2004). *Peromyscus maniculatus* was excluded from the analysis due to its widespread distribution across several habitat types. *Parascalops breweri* was excluded because of its fossorial nature and so may not be associated with any particular vegetation type (Hallett 1978, Laerm et al 2007), however due to its high mean elevation this species merits further work to understand its ecology. *Tamiasciurus hudsonicus* was excluded due to its broad elevation range.

Supplemental Table 1: Mean, median, quartiles, interquartile range (IQR), minimum, and maximum of selected sky island species.

Species	Min	First quartile	Median	Third quartile	Max	Interquartile range	Mean
Glaucomys sabrinus	1,464	1,464	1,464	1,575.25	1,909	111.25	1,575.25
Synaptomys cooperi	421	1,329.25	1,507	1,626.50	2,033	297.25	1,454.25
Sorex dispar	722	1,045.25	1,405	1,919	2,010	873.75	1,441.71
Sylvilagus obscurus	541	1,120	1,656	1,679	1,876	559	1,392.83
Napaeozapus insignis	590	1,300	1,311	1,507	2,034	207	1,343.31
Myodes gapperi	546	1,166	1,311	1,504	2,027	338	1,305
Sorex cinereus	444	1,086	1,273	1,420	2,010	334	1,256.32
Microtus chrotorrhinus	733	837	1,173	1,622	1,622	785	1,240.77
Parascalops breweri	516	964	1,153	1,453	2,033	489	1,215.31
Sorex fumeus	442	850	994	1,220	2,034	370	1,040.49

Supplemental Table 2: Presence matrix of all nine small mammal species across islands >1,093 meters in elevation. Asterisks (*) indicate presences known only from the literature (SOFU: *Sorex fumeus*, SOCI: *Sorex cinereus*, NAIN: *Napaeozapus insignis*, MYGA: *Myodes gapperi*, GLSA: *Glaucomys sabrinus* (reference: Weigl et al. 1999), SYOB: *Sylvilagus obscurus* (reference: Diggins 2020), MICH: *Microtus chrotorrhinus*, SODI: *Sorex dispar*, SYCO: *Synaptomys cooperi*.

Island ID	Island name	GLSA	MICH	MYGA	NAIN	PABR	SOCI	SODI	SOFU	SYCO	SYOB
1a	Blue Spring Gap								1		
1b	Mt. Rogers			1	1	1	1		1		
2	Buck Mountain								1		
3	Iron Mountain, north										
4	Iron Mountain, south										
5	Holston Mountain										
6a	Three Top Mountain				1	1	1		1		
6b	Elk Knob			1	1	1	1		1	1	
7	Vaught Gap										
8a	Thunder Hill			1			1	1	1		
8b	Flat Top						1	1	1		
9a	Roan Mountain	1		1	1	1	1	1	1	1	1
9b	Grandfather Mountain	1*		1	1	1	1	1	1	1	1*
10	Howard's Rock			1				1	1		
11	Big Bald										1
12	Attakulla (Mt. Mitchell)	1		1	1	1	1	1	1	1	1*
13	Crabtree Falls										
14	Spring Mountain			1					1		
15a	Sandy Mush			1			1	1	1	1	1
15b	Max Patch								1	1	1
16	Great Smoky Mountains	1*	1	1	1	1	1	1*	1	1	1*
17	Cowee Mountain										
18a	Black Balsams	1*	1	1	1		1	1	1	1	1*
18b	Highlands Plateau	1*		1			1	1	1	1	1*
18c	Windy Gap	1*		1	1		1		1		1*
18d	Rabun Bald	1*		1			1		1		1*
19	Cheoah Bald										
20	Unicoi	1*		1	1		1		1	1	1
21	Joanna Bald										1
22	Junalaska										
23a	Nantahala Falls Creek			1				1	1		1
23b	Nantahala			1				1	1		1
24	Brasstown Bald			1				1	1		

Supplemental Figure 3: Linear regression of relationship between maximum elevation (m) and species richness across islands. R^2 = 0.63, P<0.05.