

Figure #	Figure title One sentence only	Filename This should be the name the file is saved as when it is uploaded to our system. Please include the file extension. i.e.: <i>Smith_ED_Fig1.jpg</i>	Figure Legend If you are citing a reference for the first time in these legends, please include all new references in the main text Methods References section, and carry on the numbering from the main References section of the paper. If your paper does not have a Methods section, include all new references at the end of the main Reference list.
Extended Data Fig. 1	<b>Global elevation changes since the mid-Piacenzian.</b>	lgea_ED_Fig1.eps	Pixels are at a 100 km × 100 km resolution and were calculated by subtracting past elevation in the mid-Piacenzian (~3 Ma) from the PRISM4 reconstruction from the ETOPO1 present-day elevation raster.
Extended Data Fig. 2	<b>Path analysis of hypothetical causal links among geologic and climatic factors and grid-based speciation rates in uplifted cells.</b>	lgea_ED_Fig2. eps	Uplifted cells were those with an increase in elevation since the Plio-Pleistocene (n = 3,780 cells) and we fitted a separate path analysis for a) mammals and b) birds. Parentheses show the lower and upper level 95% CI. Colours and lines as in Fig. 2.
Extended Data Fig. 3	<b>Path analysis of hypothetical causal links among geologic and climatic factors and grid-based speciation rates in eroded cells.</b>	lgea_ED_Fig3. eps	Uplifted cells were those with a decrease in elevation since the Plio-Pleistocene (n = 10,884 cells) and we fitted a separate path analysis for a) mammals and b) birds. Parentheses show the lower and upper level 95% CI. Colours and lines as in Fig. 2.
Extended Data Fig. 4	<b>Path analysis of hypothetical causal links among geologic and climatic factors and different worldwide grid-based speciation rates for mammals</b>	lgea_ED_Fig4. eps	Models were fitted to <b>a)</b> weighted mean $\lambda_{DR}$ ; <b>b)</b> weighted mean $\lambda_{BAMM}$ ; <b>c)</b> geometric weighted mean $\lambda_{DR-GM}$ ; and <b>d)</b> geometric weighted mean $\lambda_{DR-BAMM}$ in each of N = 14,664 cells. Parentheses show the lower and upper level

	and birds.		95% confidence intervals. Lines and colours as in Figure 2.
Extended Data Fig. 5	<b>Path analysis of hypothetical causal links among geologic and climatic factors and different grid-based speciation rates in uplifted cells.</b>	lgea_ED_Fig5. eps	Uplifted cells were those with an increase in elevation since the Plio-Pleistocene (n = 3,780 cells) and we fitted a separate path analysis for mammals and birds. Models were fitted to <b>a)</b> weighted mean $\lambda_{\text{BAMM}}$ ; <b>b)</b> geometric weighted mean $\lambda_{\text{BAMM - GM}}$ ; and <b>c)</b> geometric weighted mean $\lambda_{\text{DR - GM}}$ . Lines and colours as in Fig. 2.
Extended Data Fig. 6	<b>Path analysis of hypothetical causal links among geologic and climatic factors and different grid-based speciation rates in eroded cells.</b>	lgea_ED_Fig6. eps	Eroded cells were those with a decrease in elevation since the Plio-Pleistocene (n = 10,884 cells) and we fitted a separate path analysis for mammals and birds. Models were fitted to <b>a)</b> weighted mean $\lambda_{\text{BAMM}}$ ; <b>b)</b> geometric weighted mean $\lambda_{\text{BAMM - GM}}$ ; and <b>c)</b> geometric weighted mean $\lambda_{\text{DR - GM}}$ . Lines and colours as in Fig. 2.
Extended Data Fig. 7	<b>Path analyses of hypothetical causal links among geologic and climatic factors and grid-based speciation rates using 100 random trees in mammals and birds.</b>	lgea_ED_Fig7. eps	Models were fitted to <b>a)</b> all cells (n = 14,664); <b>b)</b> only uplifted cells (n = 3,780); and <b>c)</b> only eroded cells (n = 10,884 cells). Median values of effect sizes are shown with the lower and upper level 95% CI boundaries in parentheses. Lines and colours as in Fig. 2.
Extended Data Fig. 8	<b>Path analysis of hypothetical causal links among geologic and climatic factors and different grid-</b>	lgea_ED_Fig8. eps	There were 762 and 1923 species of mammals and birds with an age <3 Myr, respectively. Including only these species in our analyses resulted in excluding 363 and 242

	<p><b>based speciation rates over the last 3 million years.</b></p>		<p>cells where all mammals and bird species were older, respectively. We then calculated the weighted mean <math>\lambda_{BAMM}</math> in a) uplifted (n = 3719 cells) and b) eroded (n = 10,528 cells for mammals and birds, respectively). As in our main analyses, we found that historic changes in speciation had comparable effects on speciation to current elevation (compare panel a) to Fig S5a and panel b) to Fig S6a). This result was unsurprising given the strong correlation between speciation rates. Weighted mean <math>\lambda_{BAMM}</math> for species younger than 3Myr was strongly positively correlated with rates calculated for all species reported in the main text (<math>\rho = 0.87</math> and <math>0.93</math> for mammals and birds, respectively, <math>p &lt; 0.001</math> for both. Lines and colours as in Fig 2.</p>
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Item	Present?	Filename This should be the name the file is saved as when it is uploaded to our system, and should include the file extension. The extension must be .pdf	A brief, numerical description of file contents. <i>i.e.: Supplementary Figures 1-4, Supplementary Discussion, and Supplementary Tables 1-4.</i>
Supplementary Information	No		
Reporting Summary	Yes	lgea_reporting_summary.pdf	
Peer Review Information	Yes	<i>Tanentzap_PRfile.pdf</i>	

2

3 **Global topographic uplift has elevated speciation in mammals and**  
4 **birds over the last 3 million years**

5

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10

11 **Abstract**

12 Topographic change shapes the evolution of biodiversity by influencing both habitat  
13 connectivity and diversity as well as abiotic factors like climate. However, its role in  
14 creating global biodiversity gradients remains poorly characterised because geology,  
15 climate, and evolutionary data have rarely been integrated across concordant  
16 timescales. Here we show that topographic uplift over the last 3 million years  
17 explains more spatial variation in the speciation of all mammals and birds than the  
18 direct effects of paleoclimate change and both present-day elevation and  
19 temperature. By contrast, the effects of topographic changes are much smaller than  
20 those of present-day temperatures in eroded areas. Together, our results stress that  
21 historical geological processes rather than traditionally studied macroecological  
22 gradients may ultimately generate much of the world's biodiversity. More broadly, as  
23 the Earth's surface continues to rise and fall, topography will remain an important  
24 driver of evolutionary change and novelty.

25

26 **MAIN TEXT**

27 Understanding how abiotic processes influence the evolution of life on Earth has long  
28 fascinated scientists<sup>1</sup>. Integrating historical and present-day data on biodiversity and  
29 geology is necessary to determine the drivers of new species formation but has only  
30 been possible recently with the advent of more quantitative paleo-reconstructions<sup>2</sup>.  
31 Topographic changes directly promote the formation of new species by shaping the  
32 connectivity and environmental conditions of the Earth's surface<sup>3</sup>. First, uplift and  
33 erosion of land can create barriers to dispersal that increase the chances of  
34 reproductive isolation and ultimately allopatric speciation<sup>4</sup>. This process has been  
35 invoked to explain the high percentage of plant endemism in the world's mountains<sup>5</sup>.

36 Second, topographic change can create novel habitats and niches where new  
37 species evolve and diversify<sup>6</sup>. For example, ecological opportunity linked to the  
38 Andean uplift has been shown to drive the fast radiation of endemic lupines<sup>7</sup>.  
39 Together, these two mechanisms may explain why global species richness increases  
40 with topographic relief<sup>8</sup> and why high-elevation bird lineages speciate at faster rates  
41 than low-lying relatives<sup>9</sup>.

42

43 Topographic changes also indirectly promote speciation because they modify  
44 climate, which itself affects speciation in at least four ways. First, warmer  
45 temperatures at lower elevations may increase mutation rates, either directly through  
46 oxygen radical production<sup>10</sup> or faster metabolic rates that increase DNA synthesis<sup>11</sup>,  
47 and shorten generation times, thereby increasing the likelihood of speciation<sup>12,13</sup> but  
48 see<sup>14,15</sup>. Although endotherms may escape these effects by buffering their body  
49 temperatures<sup>16</sup>, warmer temperatures will reduce the costs of maintaining metabolic  
50 rates<sup>17</sup>. Lower thermoregulatory costs can release energy that enables large  
51 population sizes and promotes speciation by allowing more diverse ecological niches  
52 to be occupied<sup>18,19</sup>. Second, species interactions, such as competition, predation,  
53 and mutualism are a constant source of macroevolutionary change – so called Red  
54 Queen effects – and these are expected to be more intense at warmer  
55 temperatures<sup>20</sup>. Third, species tend to have wider thermal niches in colder climates  
56 because they experience greater temperature variation<sup>21</sup>. This broader niche can  
57 reduce opportunities for reproductive isolation and thus speciation if populations are  
58 consequently more widespread<sup>20,22</sup>. There may also be greater physiological costs of  
59 wider temperature adaptation that restricts the number of species that can employ  
60 this strategy<sup>18</sup>. Finally, greater climatic instability arising from topographic change  
61 may have promoted rapid and repeated ecological speciation by creating novel  
62 niches and increased ecological opportunity<sup>16,23</sup>. This relationship between climatic  
63 instability and speciation may, however, be non-linear, since higher speciation rates  
64 have also been linked with areas of high climatic stability like Pleistocene refugia<sup>24</sup>.  
65 Nevertheless, the complex interactions between climate and geology have not been  
66 explicitly modelled when attempting to explain patterns of biodiversity at large scales.

67

68 Finally, geological history can promote speciation because it influences present-day  
69 abiotic factors like elevation and climate. Speciation may be favoured in areas with

70 high present-day elevation, such as if topographic relief increases the range of  
71 available niches for species to fill<sup>6</sup>, in addition to any effects from the large historical  
72 changes in topography. Thus, the effect of elevational change on both historic and  
73 present-day conditions must be considered to quantify accurately which mechanisms  
74 are more important drivers of speciation. However, to date, large-scale studies have  
75 only correlated present-day elevation with species richness<sup>8</sup> and speciation rates<sup>9</sup>,  
76 without testing direct causal links between topographical change and speciation.  
77 These causal links have only been established for particular mountain ranges<sup>25</sup> or  
78 small groups of species<sup>26,27</sup>, with no large-scale synthesis.

79

80 Here we quantified how much of the present-day spatial variation in speciation rates  
81 of mammals and birds was explained by climate and geology and their changes  
82 since the Plio-Pleistocene approximately 3 million years ago (Ma). By integrating  
83 paleoreconstructions in a path analysis framework, we *i*) estimated the direct and  
84 indirect effects of historical changes in elevation on speciation rates; and *ii*)  
85 compared these historical effects on speciation rates to those of present-day  
86 elevation (Fig. 1). Analysing paleoclimatic data allowed us to quantify how much of  
87 the effect of geology on speciation rates was mediated by climate, namely  
88 temperature. As elevation changes can arise from both the gain and loss of  
89 topography, which we respectively termed uplift and erosion, we determined if these  
90 two opposing processes had contrasting effects on speciation. The relatively fine  
91 spatial resolution (100 x 100 km) of the paleo-relief model<sup>28</sup>, allowed us to model  
92 changes worldwide rather than only in mountains as considered previously<sup>8,9</sup>  
93 (Extended Data Fig. 1).

94

## 95 **Results**

96 We found that speciation rates increased most in areas with the greatest increases in  
97 elevation from the Plio-Pleistocene (Fig. 2). We separately analysed 3,780 and  
98 10,884 100-km grid cells that underwent uplift and erosion, respectively, since the  
99 mid-Piacenzian. The positive effect of elevation gain on speciation rates was stronger  
100 than that of present-day elevation and outweighed the effects of both temperature in  
101 the present-day and its historical change (Fig. 3a). Consequently, speciation rates  
102 increased by a mean of 11% (95% confidence interval, CI: 9 to 13%) and 10% (95%  
103 CI: 8 to 12%) in mammals and birds, respectively, for a 1 standard deviation (SD)

104 gain in elevation of 195 m above the mean change in uplift cells of 144 m. Both the  
105 direct and indirect effects of elevation change contributed to these results. Greater  
106 historical uplift strongly influenced present-day elevation and subsequently  
107 temperature and speciation (Fig. 2). Overall, in uplift areas, the total effects of  
108 elevation on speciation rates were larger than the effects of temperature when  
109 aggregating both these direct and indirect effects (Fig. 3c). Historical changes in  
110 temperature and elevation were also much stronger drivers of speciation in uplifted  
111 areas than the present-day values of these variables (Fig. 3e).

112

113 Erosion had contrasting effects to those of uplift. Although elevation change causing  
114 erosion promoted speciation (Extended Data Fig. 3), it was directly correlated with  
115 5.5- and 11.9-times lower speciation rates than uplift for mammals and birds,  
116 respectively (Figs 3a, b). For example, a 1 SD reduction in elevation beneath the  
117 mean temporal change of -115 m in eroded cells increased speciation only by a  
118 mean of 2% (95% CI: 1 to 3%) and 1% (95% CI: <1% to 2%) in mammals and birds,  
119 respectively. Instead, temperature, primarily present-day values, had the strongest  
120 effect on speciation rates in eroded grid cells (Fig. 3b,d). Historical changes of both  
121 elevation and temperature had weaker effects than present-day values (Fig. 3f).

122

123 The strong effect of topographic change on speciation rates diminished when we  
124 analysed all areas together irrespective of whether they underwent uplift or erosion,  
125 highlighting the importance of separating these processes (Fig. 4a). In mammals,  
126 higher present-day elevation and greater elevation change were similarly directly  
127 associated with faster speciation rates (Extended Data Fig. 4). Only elevation change  
128 and not present-day values were directly positively associated with speciation in birds  
129 (Extended Data Fig. 4). Elevation overall (i.e., when aggregating effects of both  
130 present-day and historical changes) explained less variation in speciation rates in  
131 birds than temperature. In mammals, these overall effects were similar (Fig. 4b). This  
132 result in mammals may have been partly explained by opposing effects on speciation  
133 rates cancelling each other out, as we found positive and negative effects of  
134 historical changes and present-day temperature, respectively (Fig. 4b). The effect of  
135 the historical changes and the present-day values of the abiotic variables were also  
136 comparable in mammals, with the latter stronger predictors in birds (Fig. 4c).

137

138 Our results were robust to alternative metrics of speciation rates and to topological  
139 uncertainty in the mammal and bird phylogenies. First, we repeated the path  
140 analyses using alternative estimates of spatially explicit speciation rates (see  
141 Methods). Mirroring our main results (Figs 2-4), these alternative analyses showed  
142 that uplift and erosion had contrasting effects on speciation rates (Extended Data  
143 Figs. S5 and S6). Second, we confirmed that the estimated effect sizes on speciation  
144 rates obtained with the Maximum Clade Credibility (MCC) trees for mammals and  
145 birds (Figs 2-4) were within the confidence intervals of the effect sizes obtained when  
146 running the analyses with 100 random trees from the posterior distributions of the  
147 phylogenetic reconstructions (Extended Data Fig. 7). Finally, our results were  
148 unchanged when we repeated our analyses using spatially explicit speciation rates  
149 estimated only over the period of our paleo-elevation data, i.e. last 3 Ma (Extended  
150 Data Fig. 8).

151

## 152 **Discussion**

153 Here we found that historical elevation uplift explained more spatial variation in  
154 speciation of two large vertebrate classes than the direct effects of present-day  
155 environmental conditions. Higher-elevation lineages have been previously shown to  
156 speciate at faster rates in global mountains<sup>9</sup>. By incorporating reconstructions of past  
157 topography and climate, our findings expand on this association by showing that gain  
158 in elevation more strongly promotes recent speciation rates than simply the presence  
159 of high present-day elevation. More broadly, these results point to the importance of  
160 both direct and indirect historical processes for explaining spatial patterns of  
161 biodiversity. While these historical processes have often been appreciated<sup>8</sup>, their  
162 importance has not yet been rigorously quantified alongside more traditional  
163 macroecological gradients like in present-day temperature and elevation.

164

165 Geological uplift generally decreases surface temperatures and increases the rate of  
166 temperature change<sup>30,31</sup>, but this relationship has rarely been explicitly modelled  
167 when quantifying the role of abiotic factors on speciation. Higher rates of past  
168 temperature change have been shown to be associated with increased speciation  
169 rates and species turnover in mountains<sup>9</sup>. For example, colonisations and radiations  
170 during the Pleistocene interglacial and glacial periods are one of the main drivers of  
171 recent speciation in temperate regions<sup>32,33</sup>. By using path analyses, we expanded on

172 these results and estimated that the direct contributions of changes in elevation and  
173 temperature on speciation were comparable at a global scale.

174

175 Our analyses also revealed that opposing geologic forces like surface uplift and  
176 erosion have contrasting effects on biodiversity. In areas where elevation increased  
177 from the Pleistocene, this gain in elevation had the largest positive effect on  
178 speciation rates (Fig. 3a). This result may arise because areas with active uplift have  
179 increased habitat complexity, new niches, and biogeographic barriers, all of which  
180 can increase reproductive isolation and ultimately cause speciation<sup>34,35</sup>. By contrast,  
181 in areas where elevation decreased from the Pleistocene, the effect of geological  
182 change on speciation was much smaller (Fig. 3b). These regions where erosion was  
183 large may have lost habitat diversity and experienced greater extinction rates, e.g.,  
184 analogous to the maturity phase on oceanic islands<sup>36</sup>. Temperature may therefore  
185 remain a stronger predictor of speciation rates than habitat diversity in these eroded  
186 areas.

187

188 Mammals and birds responded somewhat differently to the abiotic gradients we  
189 studied, potentially reflecting contrasting ecological strategies. The effects of present-  
190 day elevation were stronger in mammals than in birds, which were themselves more  
191 strongly affected by current temperature (Fig. 2). Elevation creates physical barriers  
192 to dispersal, contributing to smaller ranges in mammals<sup>37</sup>. The resulting reductions in  
193 gene flow may mean that geographic isolation is more easily associated with  
194 speciation in mammals than in birds<sup>38</sup>. By contrast, speciation may be more strongly  
195 associated with temperature in birds because variation in temperature creates larger  
196 differences in the timing and extent of mating than in mammals<sup>39</sup>, and thus more  
197 chances for reproductive isolation. Future work should test how the effects of  
198 geological processes on biogeography vary with the life history and dispersal  
199 strategies of organisms. Exploring whether speciation rates vary across communities  
200 with contrasting morphospaces would also elucidate the role of ecological strategies  
201 in speciation driven by environmental change.

202

203 Integrating climatic, geologic and biologic datasets is essential to untangle the  
204 mechanisms that generate life on Earth<sup>2</sup>. Our study used such an integrative  
205 approach to uncover and quantify the role of geological changes as drivers of

206 biodiversity at unprecedented taxonomic and geographic scales. One limitation is  
207 that we were unable to estimate the uncertainty related to the paleo-reconstructions  
208 as quantitative estimates do not yet exist. As novel paleo-altimetric methods are  
209 further refined and more precise reconstructions of past elevation are generated<sup>40,41</sup>,  
210 the association between speciation and geological changes can be improved and  
211 assessed in older epochs than the Plio-Pleistocene. Only through these joint  
212 analyses of biological processes and their surrounding abiotic factors, as Von  
213 Humboldt proposed<sup>2</sup>, can we begin to comprehend the mechanisms that generate  
214 new species.

215

## 216 **Methods**

### 217 *Phylogenies and species distribution data*

218 We analysed widely used and near-complete phylogenies accounting for  
219 phylogenetic uncertainty. For terrestrial mammals, we first obtained 100 random  
220 trees from the pseudoposterior provided by<sup>42</sup>. Following<sup>43</sup>, we recalibrated these  
221 100 trees with the dates from<sup>44</sup> using PATHd8<sup>45</sup>. We then used the recalibrated 100  
222 trees to obtain a Maximum Clade Credibility (MCC) tree using TreeAnnotator  
223 v.1.8.2<sup>46</sup>. For birds, we estimated the MCC Tree with *phangorn*<sup>47</sup> using 100 random  
224 trees from the updated version of the posterior distribution in<sup>29</sup>. As all downstream  
225 results were virtually identical between the MCC trees and the 100 random trees  
226 (Extended Data Fig. 7), we present only the former in the Main Text.

227

228 Distribution data were obtained from the International Union for the Conservation of  
229 Nature (IUCN) Red List for mammals (version 5.2) and from Birdlife International  
230 (version 6.0) for birds. We collated the phylogenetic and distribution data by  
231 standardising the species names using the IUCN and Birdlife taxonomies to obtain a  
232 final dataset of 4633 and 9622 species of mammals and birds, respectively.

233

### 234 *Speciation rate estimates*

235 We estimated two species-specific speciation rates ( $\lambda$ ) in two different ways using the  
236 mammal and bird phylogenies. First, we calculated the DR statistic (herein  $\lambda_{DR}$ ,<sup>29</sup>.  
237 This metric is calculated for each species as the inverse of the equal splits measure,  
238 i.e., the sum of the branch lengths separating a tip from the root where each  
239 successive branch from the tip is multiplied by a factor of 0.5 to give greater weight to

240 branches closer to the present<sup>48</sup>. Second, we used Bayesian Analysis of  
241 Macroevolutionary Mixtures (BAMM<sup>49</sup> to obtain tip estimates of speciation rates -  
242 herein  $\lambda_{\text{BAMM}}$ ) while accounting for rate heterogeneity both across lineages and  
243 through time and accommodating for non-random taxon sampling. Sampling fractions  
244 for BAMM were implemented at the family level by dividing the number of species  
245 present in the tree in a family by the number of species described in that family  
246 according to the IUCN and Birdlife taxonomies (see above). Each BAMM analysis  
247 was run for 50 million generations with priors generated by the function  
248 *setBAMMpriors* in the R package *BAMMtools*<sup>49</sup> and the *expectedNumberOfShifts*  
249 parameter was set to 50. We discarded the initial 5 million generations as *burn-in* and  
250 we confirmed that the Effective Sample Size for the log-likelihood and the number of  
251 rate shifts were above 200. Although the reliability of BAMM estimates has been  
252 questioned<sup>50,51</sup>, simulations show that robust estimates of  $\lambda$  can be estimated with  
253 large datasets like ours<sup>52,53</sup>.

254

255 Both of our speciation rates were conditioned on evolutionary history in the recent  
256 past. Specifically, rates estimated along the terminal branches of phylogenetic trees  
257 represent the waiting time in the present-day before a lineage will undergo another  
258 speciation event<sup>54</sup>. These estimates of present-day speciation rates can be robustly  
259 estimated despite considerable uncertainty about diversification histories deeper  
260 within phylogenetic trees<sup>55</sup> and without paleontological data to inform rate  
261 estimation<sup>52,53</sup>. Speciation rates, unlike diversification rates, are also generally robust  
262 to the effect of unmeasured extinction events<sup>54</sup>. For all these reasons, present-day  
263 speciation rates are widely used to explain spatial patterns of biodiversity<sup>14,15,54</sup> and  
264 we used them in our analyses.

265

#### 266 *Spatial variation in speciation rates*

267 We mapped speciation rates by overlaying species ranges with a grid of 100 km by  
268 100 km cells. This approach allowed us to account for variation in local species pools  
269 among grid cells. Following past studies<sup>14,29</sup>, we then computed the speciation rate  
270 for individual grid cells with at least one mammal and one bird species. We estimated  
271 the arithmetic mean of  $\lambda_{\text{BAMM}}$  and  $\lambda_{\text{DR}}$  for the species present in each cell but  
272 weighted each species by the inverse of their range (i.e. the number of grid cells  
273 where they occurred), herein weighted mean  $\lambda$ . Weighting decreases the contribution

274 of widespread species to the overall mean in each cell. Second, we calculated the  
275 geometric mean of  $\lambda_{\text{BAMM}}$  and  $\lambda_{\text{DR}}$  by weighting species by the inverse of their range  
276 (herein “weighted geometric mean  $\lambda_{\text{BAMM/DR}}$ ”).

277

### 278 *Abiotic gradients*

279 We estimated present-day elevation across the grid cells using a 1-arc minute (ca.  
280 1.9 km resolution) global relief model from the United States National Oceanic and  
281 Atmospheric Administration (ETOPO1<sup>56</sup>). We masked the sea values, re-projected  
282 the raster to an equal-areas projection, and overlaid it onto the 100x100 km grid of  
283 cells used for speciation estimates. Then, we computed mean values of elevation for  
284 each cell in the grid. Past elevation was derived from a 1-degree (ca. 111 km  
285 resolution) global reconstruction of topography in the mid-Piacenzian (~3 Ma,  
286 PRISM4<sup>28</sup>). As above, sea values were masked and the paleo-relief model was re-  
287 projected before computing mean elevation per cell in the grid. We estimated the  
288 historical change in elevation as the difference in mean elevation per cell between  
289 the present and past (Extended Data Fig. 1). Cells where the mean past elevation  
290 was negative, corresponding with 10.7% of the total and almost exclusively within the  
291 oceans, were discarded to ensure land masses were present for the entirety of our  
292 comparisons.

293

294 A 2.5 arc-minute (ca. 4.6 km resolution) global temperature raster was obtained for  
295 present-day and past conditions (M2 Late Pliocene, ~3.3Ma) from Worldclim<sup>57</sup> and  
296 Paleoclim<sup>58</sup>, respectively. As above, rasters were re-projected and overlaid with the  
297 grid of speciation estimates to compute the mean present and change in temperature  
298 (present minus past) for each cell.

299

### 300 *Statistical analyses*

301 We tested how speciation rates varied with historical changes and present-day  
302 elevation and temperature using path analysis. This framework allowed us to  
303 incorporate our proposed cause-effect relationships among the predictor variables.  
304 Using the R package *piecewiseseem*<sup>59</sup>, we modelled the direct and indirect effects on  
305 grid-based speciation rates (e.g., weighted mean  $\lambda_{\text{DR}}$ ) from both present-day  
306 elevation and temperature and their historical changes. The indirect effects were  
307 mediated by historical changes in elevation and temperature determining the

308 present-day values of each variable, and thus speciation rates. We also assumed  
309 that historical changes in elevation could influence historical changes in temperature  
310 and that present-day elevation influenced present-day temperatures (Fig. 1). All  
311 predictor variables were centred and scaled and both present-day elevation and  
312 speciation rates were log-transformed. No collinearity was detected among the  
313 predictors (i.e., Spearman's  $\rho$  was  $< 0.6$  for all pairwise comparisons). Preliminary  
314 analyses revealed significant spatial autocorrelation in the residuals of the linear  
315 regressions (Moran's  $I \lambda_{DRmammals} = 0.479$ ,  $p$ -value  $< 0.001$ ; Moran's  $I \lambda_{DRbirds} = 0.568$ ,  
316  $p$ -value  $< 0.001$ ), so we implemented spatial simultaneous autoregressive (SAR)  
317 error models with the R package `spdep`<sup>60</sup>. A test of missing paths in our model also  
318 identified a need to include a link from historical changes in elevation to present-day  
319 temperature (Fig. 1). We did not include any further missing paths that linked  
320 present-day conditions to historical changes, which would have been nonsensical  
321 and created bidirectional relationships in our model. Total effects on speciation rates  
322 for each predictor were calculated by adding the direct and indirect effects.

323

#### 324 **Data availability**

325 The raw data that support the findings of this study are available from: the National  
326 Oceanic and Atmospheric Administration for present-day elevation in ETOPO1 with  
327 the identifier doi:10.7289/V5C8276M, United States Geological Survey for paleo-  
328 elevation in PRISM4 (hyperlink:  
329 [https://geology.er.usgs.gov/egpsc/prism/4\\_data.html](https://geology.er.usgs.gov/egpsc/prism/4_data.html)), Worldclim for present-day  
330 temperatures (hyperlink: <http://www.worldclim.org>), figshare for paleo-temperatures  
331 with the identifier doi:10.6084/m9.figshare.c.4126292.v1, International Union for  
332 Conservation of Nature Red List for mammal distributions (hyperlink:  
333 <http://www.iucnredlist.org>), Birdlife for bird species distributions (hyperlink:  
334 <http://datazone.birdlife.org>), supplementary materials of Methods in Ecology and  
335 Evolution for the mammal phylogeny with the identifier doi: 10.1111/j.2041-  
336 210X.2011.00103.x, and supplementary data of Nature for the bird phylogeny with  
337 the identifier doi: 10.1038/nature11631.

338

#### 339 **Code availability**

340 All code required to reproduce the analyses from the raw data is available at  
341 <https://figshare.com/s/977f006d2ed37bd4b4ef>

342

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348

### 349 **Author Contributions Statement**

350 J.I. conceived the study. J.I. and A.J.T. designed the study. J.I. performed all  
351 analyses. Both J.I. and A.J.T. co-wrote the manuscript.

352

### 353 **Competing Interests Statement**

354 The authors declare no competing interests.

355

### 356 **Figure Legends**

357 **Figure 1. Hypothesised framework of cause and effect between speciation**  
358 **rates and both climatic and geologic variables.** We considered change in  
359 elevation and temperature to be the difference between present-day and mid-  
360 Piacenzian (~3 Ma) values.  $T$  = annual mean temperature.

361

362 **Figure 2. Path analysis of hypothetical causal links among geologic and**  
363 **climatic factors and worldwide grid-based speciation rates in uplifted cells (i.e.**  
364 **with an increase in elevation since the Plio-Pleistocene) for a) mammals and b)**  
365 **birds.** Positive, negative and non-statistically significant ( $p$ -value  $> 0.05$ )  
366 relationships are indicated by blue, red and grey arrows, respectively. The width of  
367 the arrows is proportional to the standardised effect size shown by adjacent  
368 numbers. Numbers are only reported for those effect sizes that cause at least a 5%  
369 change in a response for each standard deviation change in the corresponding  
370 predictor. Confidence intervals given in Extended Data Fig. 2.  $T$  = temperature.  
371 Speciation rate ( $\lambda$ ) was estimated as the weighted mean in each of  $N = 3,780$  grid  
372 cells after<sup>29</sup>.

373

374 **Figure 3. Total (direct + indirect) effects from path analysis of elevation and**  
375 **temperature variables on speciation rates for uplifted ( $N = 3,780$ ) and eroded ( $N$**

376 = 10,884) cells in mammals and birds. Effects were estimated for a & b) separate  
377 predictors of both change and present-day values in each of elevation and  
378 temperature; c & d) all predictors related to elevation and temperature; and e & f) all  
379 predictors related to historical changes and present-day values of a variable. Values  
380 are standardised effect sizes and are only shown where they cause at least a 5%  
381 change in a response for each standard deviation change in the corresponding  
382 predictor. *T* = temperature. Speciation rate was estimated as in Fig. 2.

383

384 **Figure 4. Total (direct + indirect) effects from path analysis of elevation and**  
385 **temperature variables on grid-based speciation rates in mammals and birds.**

386 Effects were calculated for: a) the four predictors in Fig. 2; b) all predictors related to  
387 elevation and to temperature; and c) all predictors related to historical changes and  
388 present-day values of a variable. *T* = temperature. Speciation rate estimated as in  
389 Fig. 2 and effect sizes shown only where they change responses by  $\geq 5\%$  as in Fig. 3.

390

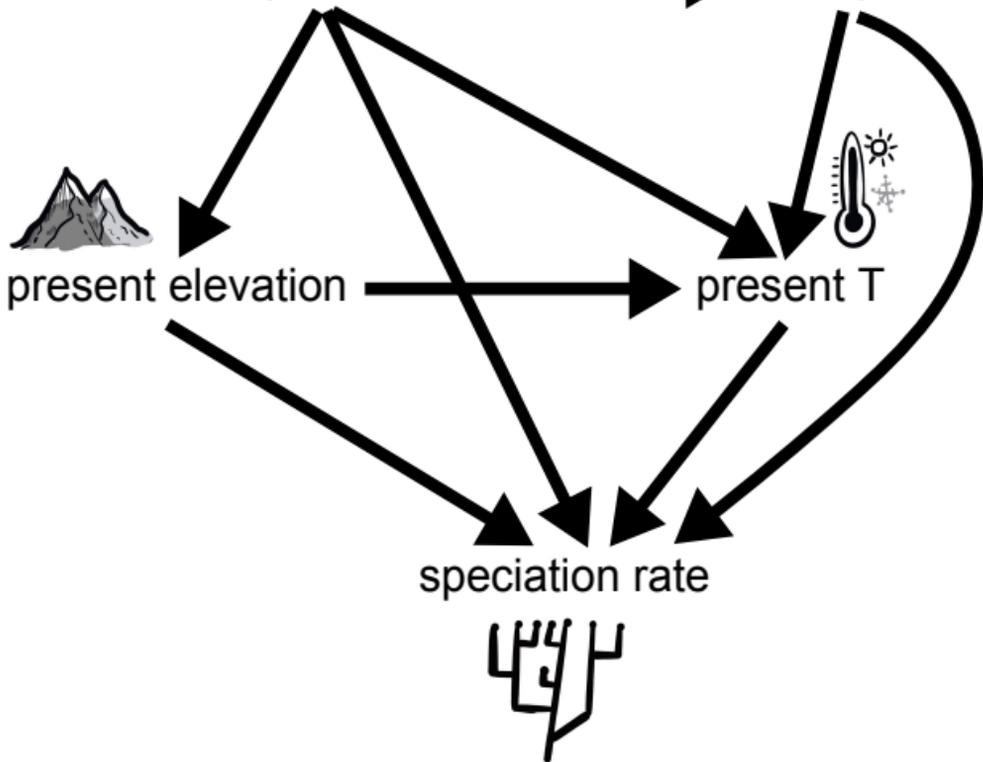
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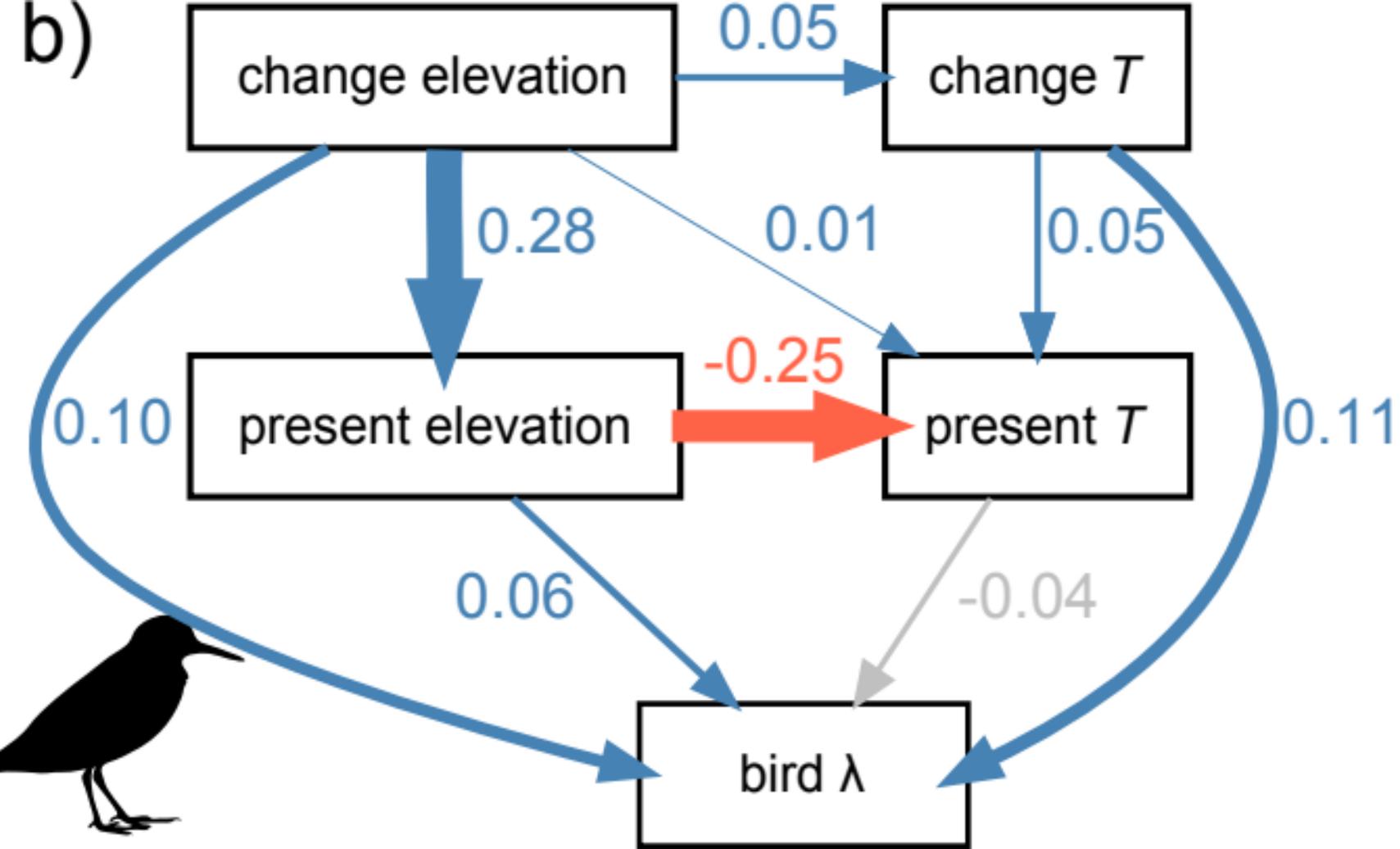
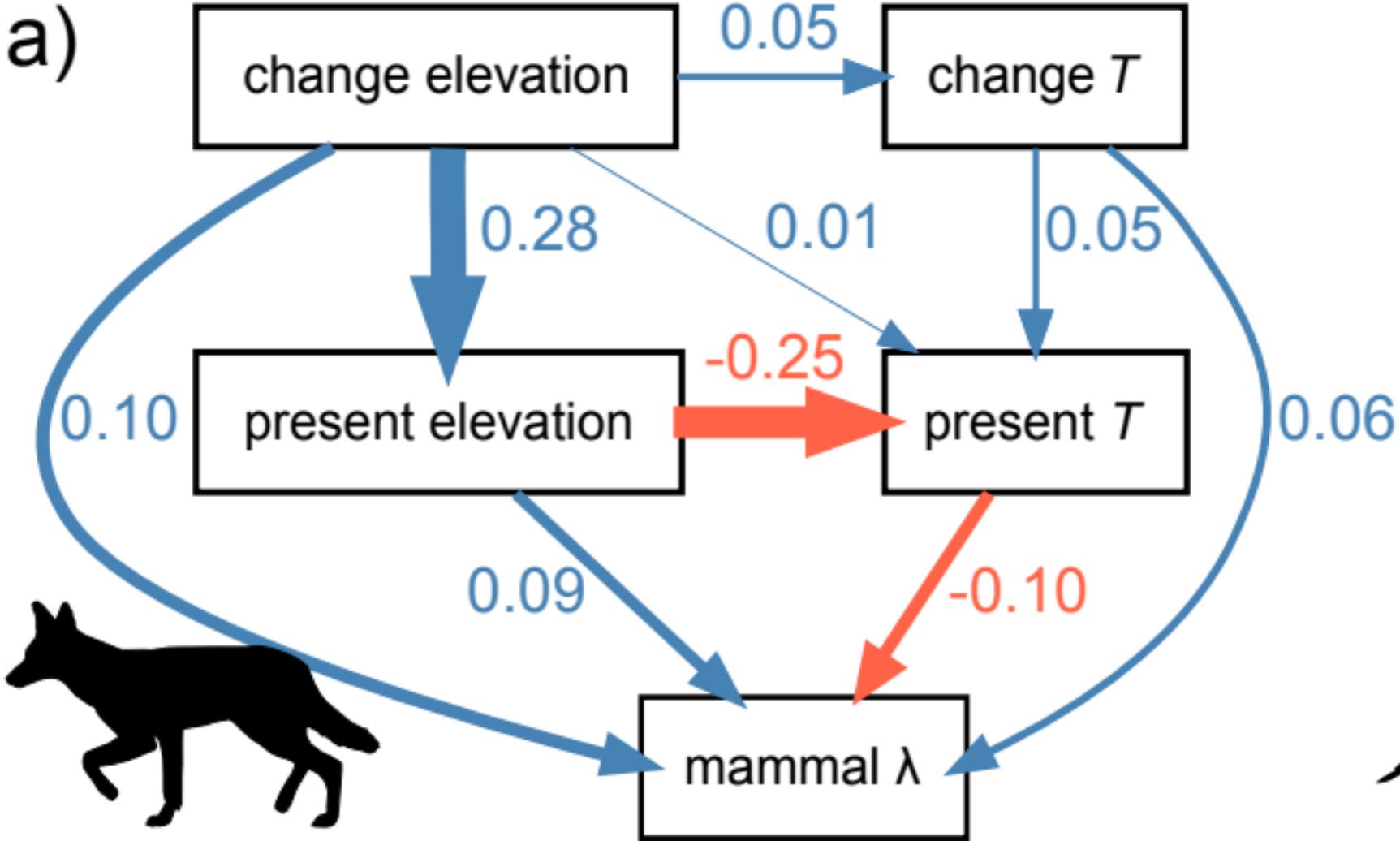
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- 532





# Uplifted areas



a)

elevation gain	0.14	0.12
present elevation	0.12	0.06
change in T	0.06	0.11
present T	-0.10	

c)

elevation (gain + present)	0.26	0.18
temperature (change + present)		0.11

e)

change (elevation gain + T)	0.20	0.23
present (elevation + T)		0.06

# Eroded areas



b)

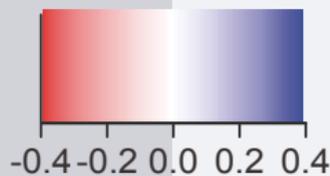
		elevation loss
0.07		present elevation
		change in T
-0.23	-0.43	present T

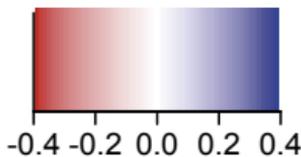
d)

0.09		elevation (loss + present)
-0.20	-0.42	temperature (change + present)

f)

0.06		change (elevation loss + T)
-0.17	-0.40	present (elevation + T)





a)

change elevation

0.06

present elevation

0.09

0.05

change  $T$

present  $T$

-0.23

-0.33

b) elevation (change + present)

0.15

0.09

temperature (change + present)

-0.19

-0.29

c) change (elevation +  $T$ )

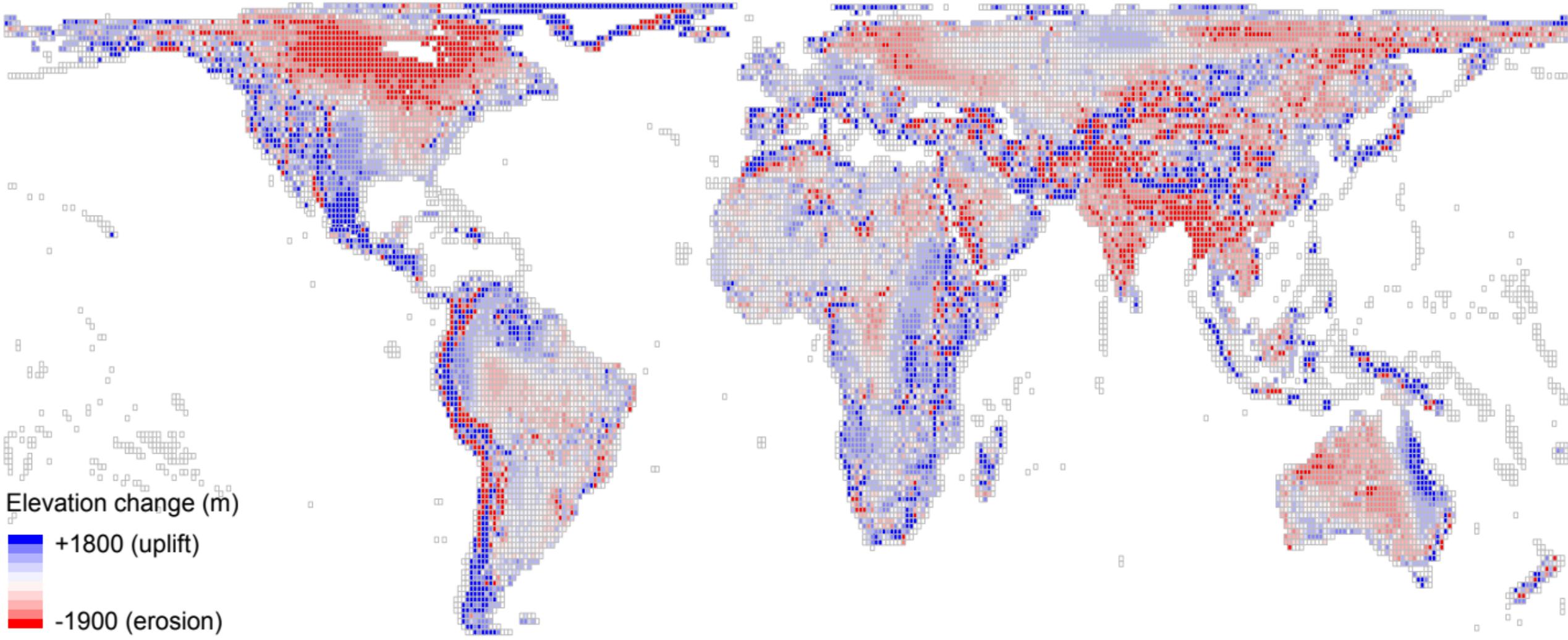
0.10

0.08

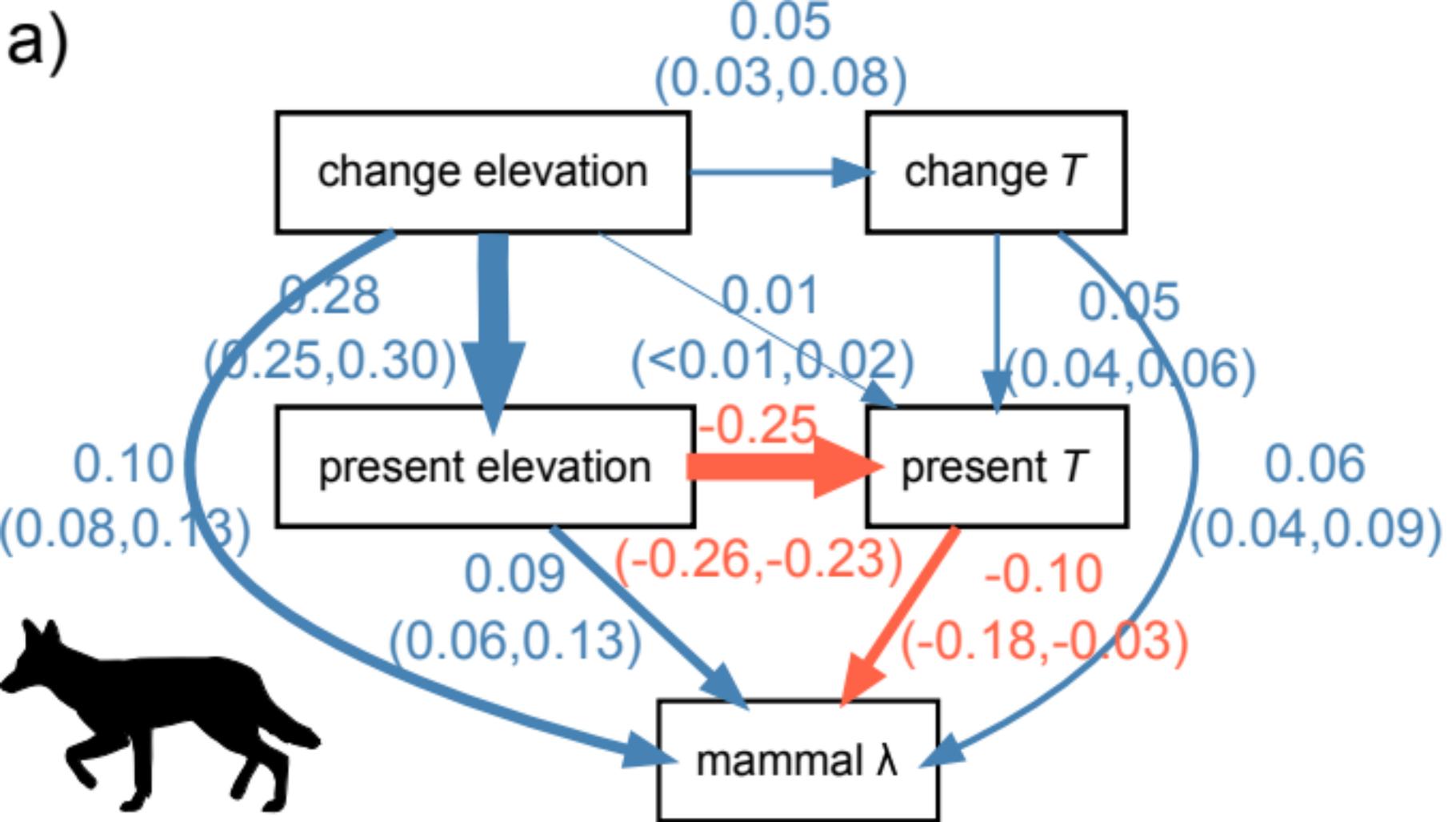
present (elevation +  $T$ )

-0.14

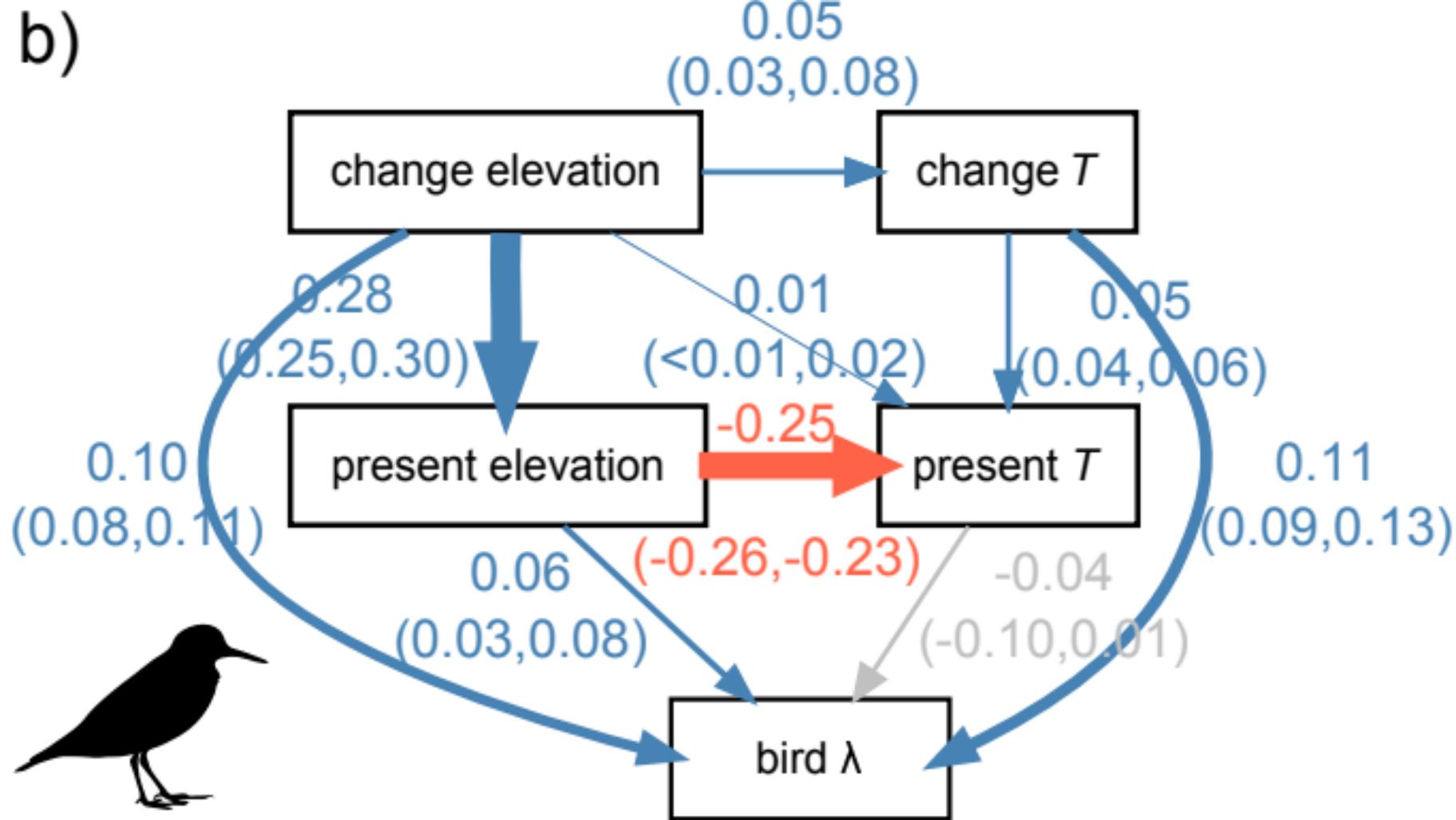
-0.28



a)

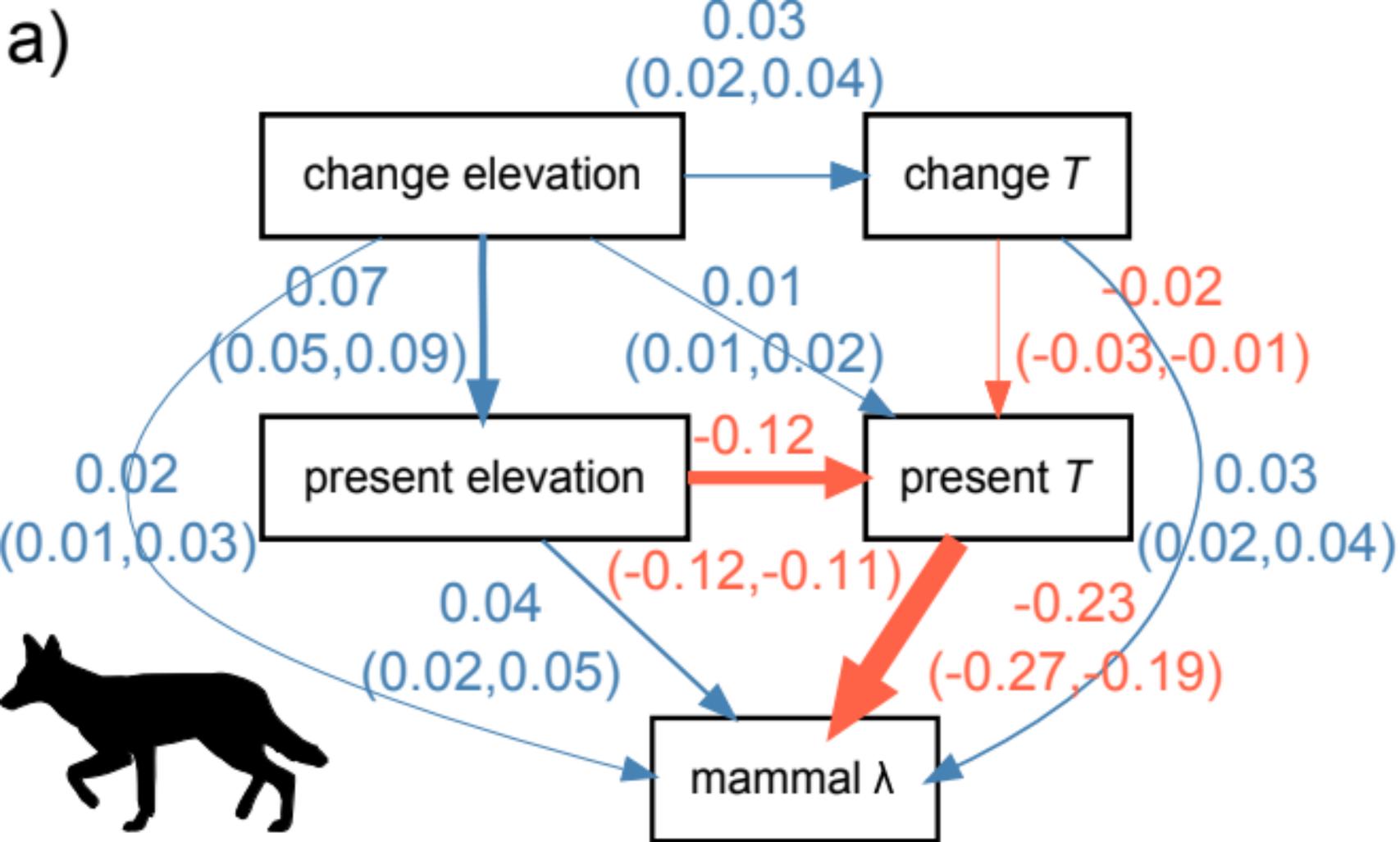


b)

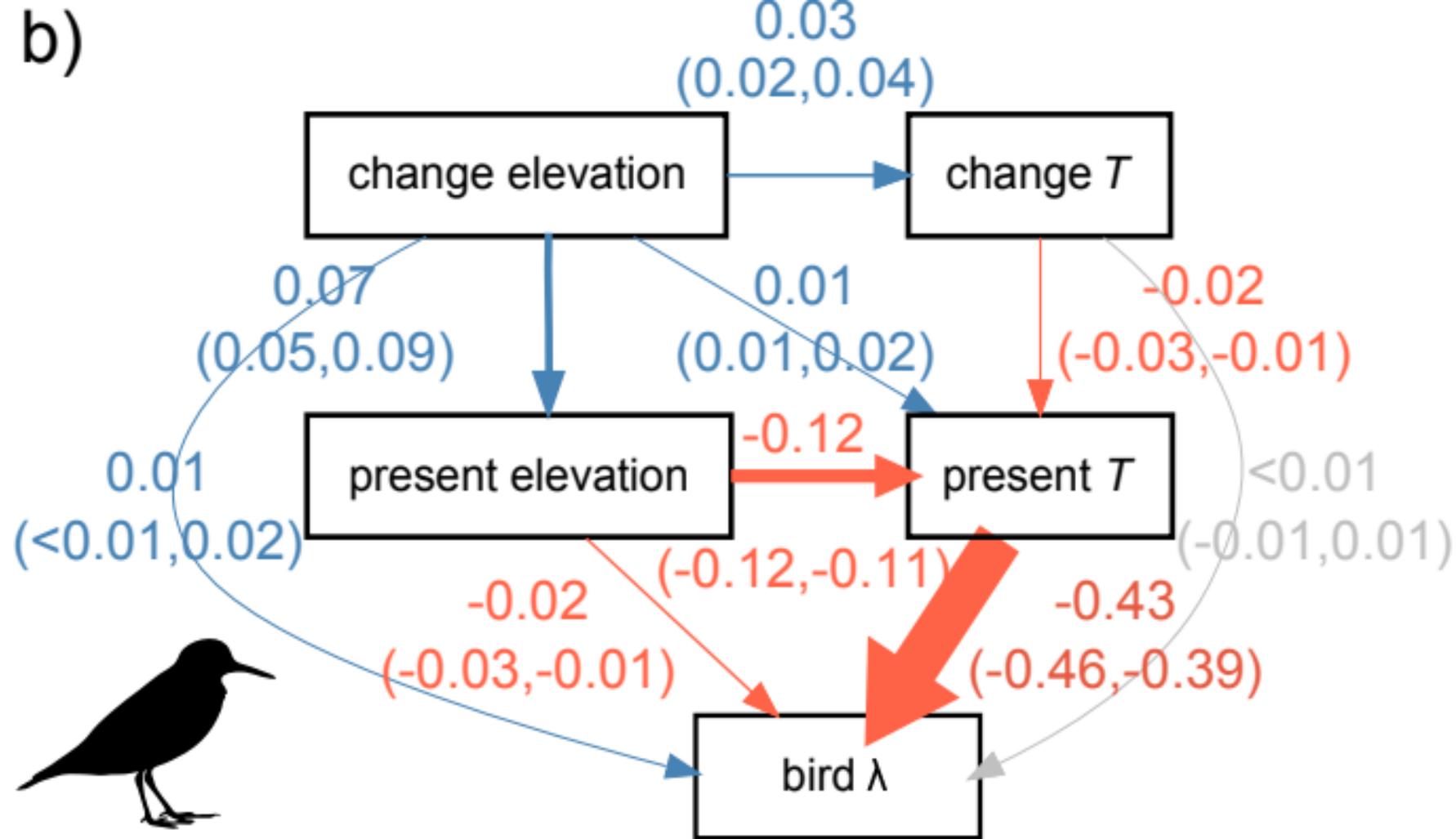




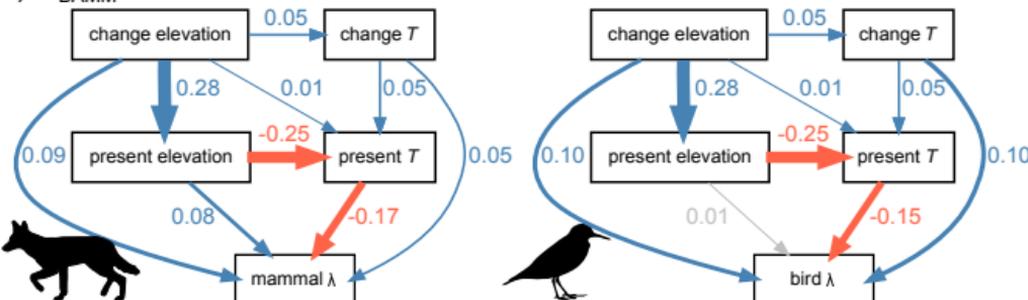
a)



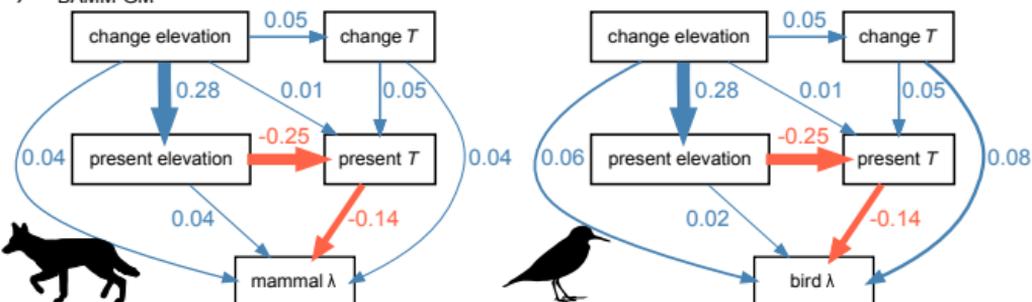
b)



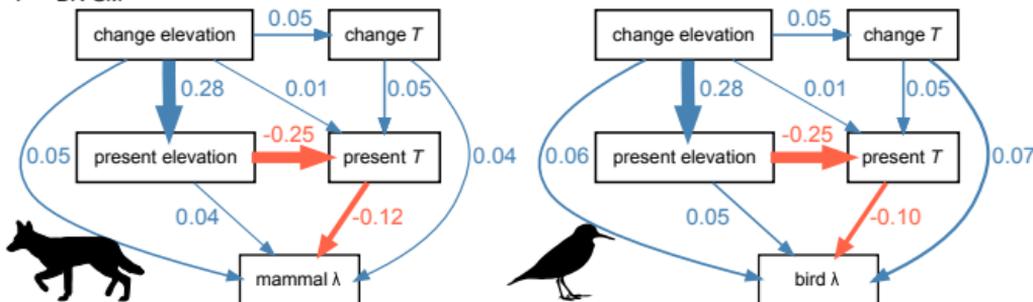
a)  $\lambda$  BAMM



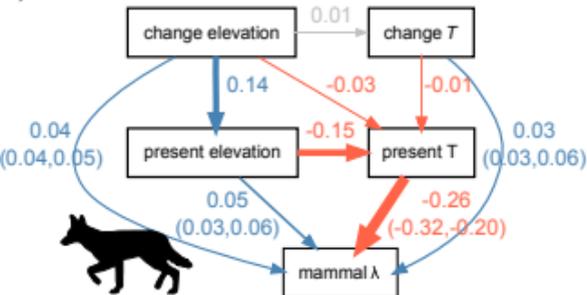
b)  $\lambda$  BAMM-GM



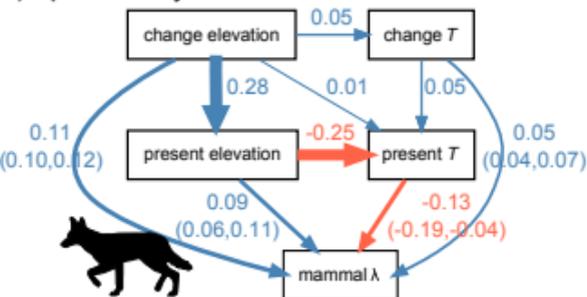
c)  $\lambda$  DR-GM



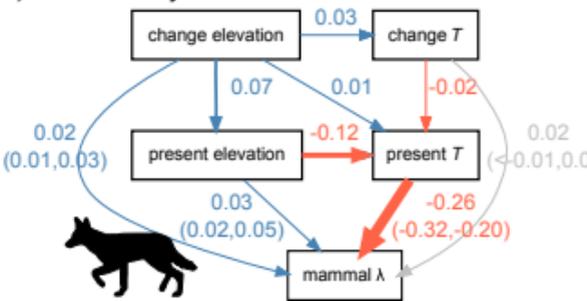
a) all cells



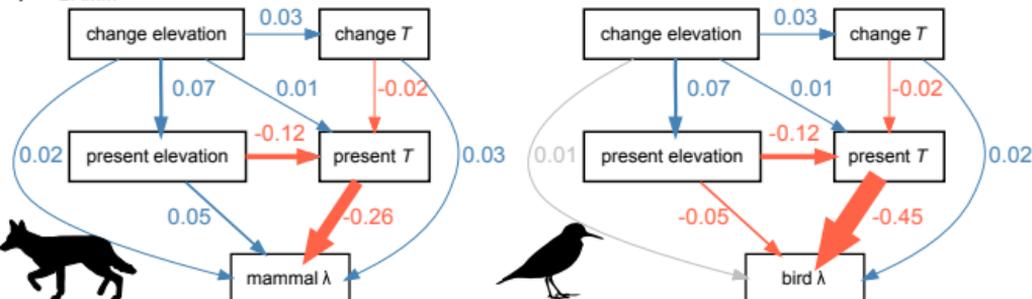
b) uplifted only



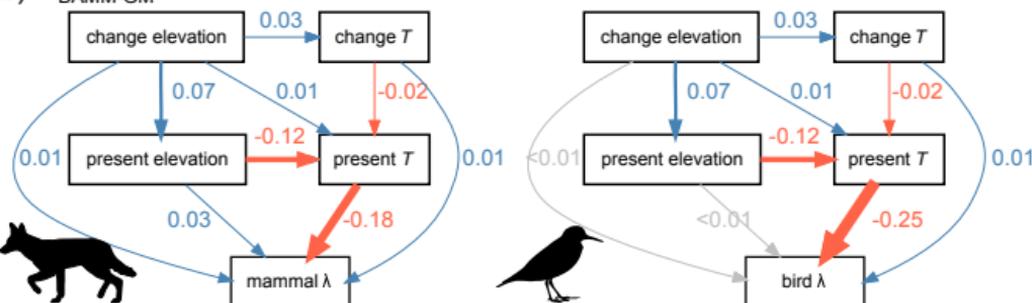
c) eroded only



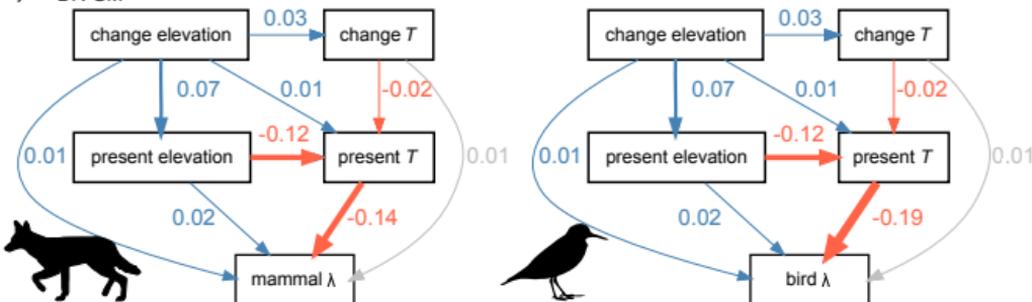
a)  $\lambda$  <sup>BAMM</sup>



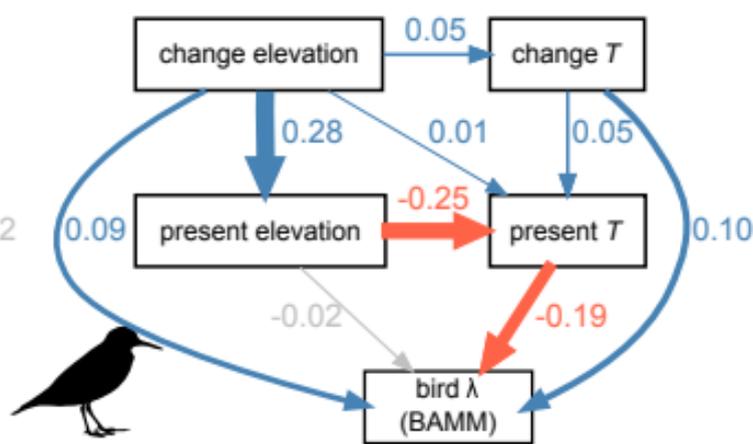
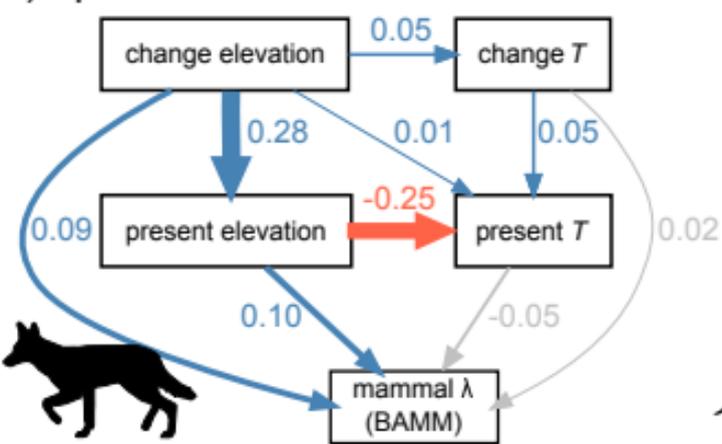
b)  $\lambda$  <sup>BAMM-GM</sup>



c)  $\lambda$  <sup>DR-GM</sup>



a) uplifted



b) eroded

