

1 *For: PeerJ Preprints*

2 Article type: Research article

3 Short title: Reverse diversity gradients in mammals

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7 **Historical contingency, niche conservatism and the tendency for**
8 **some taxa to be more diverse towards the poles**

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23 **Abstract**

24 Successful explanations for diversity gradients should account for both the generalized
25 tendency towards a higher tropical diversity and its exceptions. Moreover, identifying
26 exceptions to general trends, such as the latitudinal diversity gradient can give insight into
27 the mechanistic explanations responsible for structuring them. The Cenozoic biotic
28 exchange of mammals across the Bering land-bridge provides an illuminating case-study. It
29 allows comparing the diversity of clades that participated in the exchange (colonizers),
30 whose ancestors withstood the Beringian cold temperatures, with that of the clades that did
31 not participate (sedentaries). We find that assemblages of colonizers are more diverse
32 towards higher latitudes, opposing the traditional latitudinal diversity gradient which is
33 followed by sedentaries. Despite the long passage of time since this major dispersal event,
34 the geographic distribution of colonizers is more strongly correlated to the distributions of
35 other colonizers inhabiting a different continent than by the distribution of sedentary
36 species. These results highlight the importance of historical migrations and dispersal in
37 configuring present-day diversity gradients. Importantly, we also suggest that colonizers
38 may be particularly vulnerable to projected climate change because of the predicted
39 decrease in climate space in the extra-tropical realm where they are currently most diverse.

40

41

42 **Keywords:** Biotic exchange; niche conservatism; Bering land-bridge; diversification;
43 reversed diversity gradients; time-for-speciation effect; species richness.

44

45 Introduction

46 The latitudinal diversity gradient (LDG)—the tendency for species diversity to increase
47 toward the tropics—is perhaps one of the most ubiquitous pattern in ecology (Hawkins
48 2001). The literature on the LDG is vast due to the large number of hypotheses proposed to
49 account for it, but we still lack a single overarching explanation. Further complicating the
50 search for a single cause, there are numerous exceptions to the LDG, in which species
51 richness shows the reverse diversity gradient (Kindlmann et al. 2007; Morales-Castilla &
52 García-Valdés 2014). Examples of reverse gradients include: Lagomorpha (Rolland et al.
53 2014), Artiodactyla (Fergnani & Ruggiero 2015), migratory birds (Cook 1969; Morales-
54 Castilla et al. 2013; Storch et al. 2005), emydid turtles (Stephens & Wiens 2003), arboreal
55 ants (Ribas 2006), aphids (Dixon et al. 1987), ichneumonids (Gauld 1987; Gauld et al.
56 1992; Janzen 1981; Janzen & Pond 1975; Shaw 1994), mollusks (Valdovinos et al. 2003)
57 and, benthonic algae (Santelices 1980). If we consider the LDG not as a spatial pattern, but
58 as reflecting a climate-richness relationship – i.e. with richness peaking under warmer and
59 wetter climatic conditions – we find additional exceptions, for example, in the elevational
60 species richness patterns of treefrogs (Smith et al. 2007) and salamanders (Kozak & Wiens
61 2010), and in the tendency of some squamate reptile groups to show higher richness in arid
62 environments (Morales-Castilla et al. 2011; Wiens et al. 2013). Explanations proposed for
63 these less common gradients have generally been proposed *ad hoc*, for example, calling
64 upon differential habitat availability (Storch et al. 2005; Valdovinos et al. 2003), or biotic
65 interactions (Buckley et al. 2003), and do not widely generalize. We suggest that a general
66 explanation for the LDG must also be able to account for these, less common, reverse
67 gradients.

68 Climatic niche conservatism—the tendency of species to retain ancestral climatic
69 niches (Wiens & Donoghue 2004)—couple with the time-for-speciation effect—the
70 expectation of higher species richness for clades that have remained for longer in a given
71 environment) (Stephens & Wiens 2003) —have been proposed as a plausible explanation
72 for both the LDG and its exceptions. Niche conservatism predicts higher species richness
73 within ancestral environments, i.e. those occupied by species' ancestors, regardless whether
74 that environment is tropical or extra-tropical. This is because species are pre-adapted to
75 these ancestral conditions, and because clades would have had more time for diversification

76 in their ancestral environments (Wiens & Donoghue 2004). While niche conservatism as an
77 explanation for the LDG has frequently been referred to as the Tropical Conservatism
78 Hypothesis (TCH, (Wiens & Graham 2005)), it could also be applied to clades that
79 originated under extratropical conditions (Buckley et al. 2010b). The expectation for these
80 clades would be of higher species richness within temperate or cold regions (see figure 1).
81 Correlative support for the TCH is widespread (Buckley et al. 2010a; Hawkins & DeVries
82 2009; Hawkins et al. 2007); however, a more powerful test of the niche conservatism
83 hypothesis would be to evaluate predictions by contrasting diversity gradients between
84 taxon sets with differing biogeographic histories.

85 Testing the niche conservatism hypothesis requires information on historical niches.
86 However, data on species ancestral distributions are rarely available (Springer et al. 2011).
87 One approach is to assign ancestral niches based on species present-day distributions
88 (Buckley et al. 2010a); but current methods for reconstructing ancestral climate niches,
89 which are a product of a species' geographic distribution, can be highly unreliable (Kozak
90 & Wiens 2010). An alternative, but less explored approach, is to use information on
91 historical biogeography to characterise species climatic origins. For example, major
92 historical dispersal events, such as biotic exchanges, have helped in understanding
93 comparisons between contemporary versus ancestral mammalian body size patterns
94 (Morales-Castilla et al. 2012). The biotic exchanges that occurred during the Cenozoic are
95 reasonably well documented, with detailed information in the fossil record allowing
96 identification of the mammalian genera that participated (or not) in the biotic exchange
97 across the Bering land bridge (Tedford et al. 2004; Woodburne & Swisher 1995). In this
98 example, even if the precise geographical origins of the mammal species remain unclear,
99 we can assume with reasonable confidence that their ancestors crossing the Bering bridge
100 must have been generally well adapted to withstand the lower temperatures that
101 characterised Beringia towards the end of the Cenozoic (Lavrushin & Alekseev 2005). We
102 can thus assume that colonizers (species with ancestors that crossed the Bering land bridge)
103 likely descend from cold-adapted ancestors, whereas sedentaries (species with ancestors
104 that were not part of the biotic exchange across the Bering land bridge) might have more
105 tropical ancestry, reflecting the earlier diversification of mammal lineages in the tropical
106 biome (Buckley et al. 2010a).

107 Here we evaluate the niche conservatism hypothesis by contrasting diversity
108 gradients between Holarctic mammal faunas grouped according to their participation in the
109 Bering biotic exchange. We compared diversity gradients between colonizer and sedentary
110 taxa, and tested the following three linked predictions related to the niche conservatism
111 hypothesis. First, if crossing Bering were a useful proxy for ancestral niches, we predict
112 sedentaries would conform to the classical LDG in both the Palaeartic and the Nearctic, as
113 observed for all mammals globally (Davies et al. 2008), whereas colonizers would show a
114 reverse gradient with more species at high latitudes and within colder areas. Second, we
115 would expect environment-richness models for colonizers to perform better at predicting
116 species richness of colonising lineages in their area of origin than species richness of
117 sedentaries. Third, we predict negative temperature-richness relationships for colonizers
118 and positive ones for sedentaries.

119

120 **Material and Methods**

121 *Empirical Data*

122 We obtained range maps for all Palaeartic and Nearctic non-volant terrestrial mammal
123 species from (Schipper et al. 2008) and rasterized them on a *ca.* 100 x 100 Km equal-area
124 grid comprising 2,244 cells in the Nearctic and 4,162 cells in the Palaeartic. Nearctic and
125 Palaeartic biogeographic regions were delimited according to the mammalian
126 zoogeographic domains in (Rueda et al. 2013). We used biogeographic regions rather than
127 smaller domains (i.e. sub-continents) because their delineation implicitly represents
128 geographic extents with homogeneous biogeographic histories.

129 Mammal species within each domain were classified according to whether or not they
130 fell within genera that participated in the Bering biotic exchange (i.e. colonizers versus
131 sedentaries). To identify the genera that crossed the Bering land bridge we followed the
132 palaeontological literature documenting the fossil record of the Nearctic and the Palaeartic
133 through the Pliocene-Pleistocene (Bell et al. 2004; Tedford et al. 2004; Webb & Barnosky
134 1989; Woodburne & Swisher 1995). For some species, we used familial (rather than
135 generic) associations due to the lack of resolution in the fossil record (e.g. families
136 Erinacidae, Soricidae and Talpidae, see Woodburne & Swisher 1995; and see electronic
137 supplementary material, Appendix S1). Mammal taxonomy was standardised to Wilson &

138 Reeder (2005), and the resulting dataset encompassed a total of 865 species classified
139 within the following three major groups: (i) *P-N colonizers*, (ii) *N-P colonizers*, and (iii) *P*
140 *and N sedentaries*. We considered as colonizers the species belonging to genera that
141 dispersed from the Palaearctic to the Nearctic (“P-N colonizers”), or from the Nearctic to
142 the Palaearctic (“N-P colonizers”). In addition, we considered two sub-groups within the P
143 and N sedentaries: (iv) *confamilial sedentaries*, representing species belonging to non-
144 colonizing genera but falling within families that contained colonizer genera, and (v) *old*
145 *colonizers*, including species that were not identified as colonizers but which fall within
146 cosmopolite genera present in both the Palaearctic and the Nearctic. Confamilial
147 sedentaries could be more similar to colonizers due to phylogenetic relatedness, while old
148 colonizers might have crossed Bering prior to the Plio-Pleistocene or might be actual
149 colonizers for which we lack a detailed fossil record (see Table 1 for number of taxa and
150 details of each group).

151

152 *Environmental models*

153 To make cross-predictions of species richness among assemblages of colonizers, we
154 followed the macroecological modelling approach (MEM hereafter), which models species
155 richness against a set of environmental variables. MEMs have proven useful as a
156 conservative alternative to stacking species distribution models in order to make
157 assemblage level predictions of species richness (Dubuis et al. 2011b; Guisan & Rahbek
158 2011). We used MEMs rather than stacked species distribution models because the latter
159 have shown a tendency to over-predict species richness (Dubuis et al. 2011a). The goal was
160 to quantify the ability of MEMs for colonizers calibrated on their biogeographic region of
161 origin to predict species richness of their biogeographic region of current occupancy (see
162 Table 1).

163 First, we used five environmental variables (see below) commonly used to model
164 mammalian species richness (Hawkins et al. 2012) to build MEMs of species richness for
165 both colonizer and sedentary groups within each biogeographic region. Second, for
166 colonizers, we used the MEMs constructed on their biogeographic region of origin to make
167 predictions of species richness on their colonized region. Third, we used MEMs for

168 colonizers constructed on their biogeographic region of current occupancy to predict
169 species richness of sedentary species in that same biogeographic region.

170 The five environmental variables used to build the MEMs were: (1) mean annual
171 temperature and temperature seasonality (Bio 1 and 4, respectively, from WorldClim;
172 Hijmans et al. 2005); (2) annual average Net Primary Productivity, extracted from Imhoff
173 et al. (2004; data available at <http://sedac.ciesin.columbia.edu/es/hanpp.html>); (3) mean
174 annual precipitation (Bio 12, from WorldClim; Hijmans et al. 2005); (4) range in elevation
175 (data available at http://www.ngdc.noaa.gov/seg/cdroms/ged_iiia/datasets/a13/fnoc.htm);
176 and (5) a measure of mesoclimatic variation derived from the interaction between
177 temperature and topography (mean annual temperature [$+21^{\circ}\text{C}$] x range in elevation).

178 MEM fits were stimulated by averaging the predictions of four common modelling
179 techniques (Dubuis et al. 2011b): generalized linear models (GLMs; McCullagh & Nelder
180 1989), generalized additive models (GAMs), which are a non-parametric version of GLMs
181 (Hastie & Tibshirani 1990); and two machine learning methods based on decision trees,
182 generalized boosted models (GBMs; Friedman et al. 2000; Ridgeway 1999) and random
183 forests (RF; Breiman 2001). Since the relationship between species richness and annual
184 temperature was non-linear, GLMs also included a quadratic term for this variable. Both
185 GLMs and GAMs were fit assuming a Poisson distribution and a logarithmic link function
186 (i.e. logistic regression). GBMs and RFs were computed using a maximum of 500 trees.

187 We tested if the five environmental variables included in the models accounted for
188 the spatial autocorrelation in species richness by analysing autocorrelation in model
189 residuals. For this, we computed Moran's I values for the raw richness data of each species
190 group as well as for the averaged residuals generated by each MEM. MEMs were
191 constructed in R (R Development Core Team, 2011) with the libraries 'glm2' (Marschner
192 2011), 'gam' (Hastie 2008), 'gbm' (Ridgeway 2007) and 'randomForest' (Liaw & Wiener
193 2002) and autocorrelation analyses were run in SAM v.4.0 (Rangel et al. 2010). We
194 inspected the variable importance metrics to detect potential differences in the main drivers
195 of richness variation between species groups and/or regions (see electronic supplementary
196 material, Appendix S2).

197

198 *Evaluation and comparison of environmental models*

199 To evaluate the model performance, we used a tenfold cross-validation procedure
200 with 1,000 iterations. The original dataset was split into two, with models fitted to 70% of
201 the data and verified on a 30% hold-out set. Split-sample iterations were computed for
202 MEMs for each subset of species in each region. Model accuracy was assessed with
203 Spearman correlations between fitted species richness (estimated from the 70% modelled
204 set) and predicted species richness (from the 30% hold-out set).

205 In some cases, species within the P-N and N-P colonizer sets belong to the same
206 genera, a stronger correlation between their MEMs might then be attributed to the
207 phylogenetic closeness among congeneric species. We explored potential for bias by testing
208 the ability of MEMs for colonizers to predict species richness of sedentary confamilials.

209

210 *Phylogenetic models*

211 To test for differences in the environment-richness relationships between colonisers and
212 sedentaries we used phylogenetic generalized least squares models (PGLS; Freckleton et al.
213 2002) on the slopes of the richness-temperature relationship within mammal families. The
214 slopes of the richness-temperature relationship were obtained for each mammalian family
215 by fitting GLS logistic regression models (see above). Mammal families were classified as
216 colonizer if they contained one or more colonizing genera. To account for additional factors
217 that might mediate the environment-richness relationships, we included average log-body
218 mass and log-range size, both computed at the family level. We accounted for uncertainty
219 in the phylogenetic hypothesis by running analyses on a random sample of 100 trees from
220 the posterior distribution of the complete mammal phylogeny in (Faurby & Svenning
221 2015). Each of the sampled trees was pruned to a single tip for each included family.
222 Phylogenetic analyses were performed in the R library 'caper' (Marschner 2011).

223

224 **Results**

225 Colonizers showed inverse latitudinal species richness patterns regardless of the
226 biogeographic domain and irrespective of whether P-N colonizers (figure 2a), N-P
227 colonizers (figure 2b) or Old colonizers (figure 2c) were considered. Overall, assemblages
228 of colonizers are more species-rich across temperate and high latitudes than within the
229 lowest latitudes of the Nearctic and the Palaearctic. P-N colonizers showed highest species

230 richness concentrated in Alaska and the northern half of the Nearctic and, coinciding with
231 Mongolia, Siberia and mountainous regions of the Palaearctic (figure 2a). Assemblages of
232 N-P colonizers show a similar species richness pattern with higher species richness along
233 the Rockies and the Appalachians in the Nearctic (figure 2b). Species richness of Old
234 colonizers is also higher along the Rockies in the Nearctic and in Mongolia in the
235 Palaearctic (figure 2c) and does not conform to the LDG. In contrast, species richness
236 patterns for sedentary species follow the pattern expected by the LDG, regardless of
237 whether P and N sedentaries (figure 2d) or confamilial sedentaries (figure 2e) are
238 considered. Assemblages of sedentary species clearly present increasing species richness
239 with decreasing latitude in both the Nearctic and the Palaearctic.

240 Results from averaged MEMs utilizing five environmental predictors explain most of
241 variation in species richness for assemblages of both colonizers and sedentaries ($R^2 > 0.7$).
242 Hence, richness predicted by MEMs highly correlates with observed species richness in all
243 cases (Spearman's $\rho > 0.834$) (Table 1). Outcomes from the four modelling techniques are
244 consistent in their predictive ability (Spearman's $\rho > 0.736$) and in identifying temperature
245 and net primary productivity as the predictors more strongly associated with species
246 richness of P-N colonizers and N-P colonizers, respectively (see electronic supplementary
247 material for details, Appendix S2). Model verification confirms that MEMs are accurate
248 overall, and that models for P-N colonizers consistently yield better predictions than
249 models for N-P colonizers (see electronic supplementary material, Appendix S3).

250 MEMs for colonizers (see summary statistics in Table 2) at their biogeographic
251 region of origin predicted substantial variation in species richness at their biogeographic
252 region of destination (P-N colonizers $R^2 = 0.502$; N-P colonizers $R^2 = 0.310$, Table 3). The
253 cross-predictive ability among MEMs of Old colonizers was weaker than that among
254 MEMs of colonizers in both the Nearctic ($R^2 = 0.340$) and the Palaearctic ($R^2 = 0.114$) (see
255 Table 3). Furthermore, MEMs predictions among colonizers significantly outperformed
256 predictions between sedentaries and colonizers, regardless of whether all sedentary species,
257 or sedentary confamilials were accounted for (figure 3; Table 3). Spatial autocorrelation did
258 not affect our results since Moran's I correlograms showed little or no autocorrelation in
259 MEMs residuals, indicating that most spatial variation in species richness was accounted
260 for by the environmental predictors (see electronic supplementary material, Appendix S4).

261 PGLS models confirmed a significant effect of being colonizer on the temperature-
262 richness relationships at the family level (see electronic supplementary material, Appendix
263 S5). As expected, colonizer clades tend to show negative temperature-richness relationships
264 while sedentary clades increase in species richness with increasing temperature, and
265 differences are significant as shown by a phylogenetic ANOVA (p -value = 0.040 ± 0.019 ;
266 figure S5 in Appendix S5). Further, being colonizer is significant after controlling for
267 phylogenetic relatedness (p -value = 0.048 ± 0.008), after including body mass as a
268 covariate (p -value = 0.020 ± 0.016), and is marginally significant after including both
269 body-mass and range size as covariates (p -value = 0.072 ± 0.032 ; see Table S5 in Appendix
270 S5). These results support all three predictions.

271

272 Discussion

273 Our results evidence that the contemporary geographic distribution of species can be
274 partially explained by historical events of dispersal and subsequent conservatism of
275 ancestral climatic preferences. This is particularly true if historical dispersal took place
276 across a corridor such as the Bering Strait that would have acted as a strong environmental
277 filter only allowing cold-adapted species to pass. Despite the long time-period spanned
278 since the analysed Plio-Pleistocene biotic exchanges through Bering, species with cold-
279 adapted ancestors are still preferably distributed within the colder climates at higher
280 latitudes (see figure 2). In contrast, species richness of sedentary clades that did not cross
281 the Bering Strait conform to the pattern of increasing diversity with decreasing latitude
282 predicted by the LDG. The marked divergence between colonizers and sedentaries is
283 confirmed by both geographically and phylogenetically explicit analyses and, offer a
284 compelling mechanism able to simultaneously explain why most taxonomic groups are
285 more diverse in the tropics while other taxa would show inverse latitudinal diversity
286 gradients.

287 Far from novel, the fact that most clades increase their diversity towards the equator
288 and certain clades are more diverse towards the poles has been long acknowledged and
289 intensely studied (Fergnani & Ruggiero 2015; Rolland et al. 2014). However,
290 encompassing explanations for such a pattern have remained elusive. For instance, in
291 Buckley et al. (Buckley et al. 2010a), the authors analysed the variation in climate-richness

292 relationships as a function of clade age for all world's mammals. They found that negative
293 temperature–richness relationships are strongly phylogenetically constrained and that,
294 overall, clades with negative temperature–richness relationships tend to be younger. The
295 existence of many young clades with positive temperature–richness relationships (Buckley
296 et al. 2010a) suggests that mechanisms complementary to age should be assessed. While
297 our results cannot be extrapolated to all mammals, they combine a specific historical event
298 of dispersal and phylogenetic niche conservatism, to robustly explain differences in
299 climate–richness relationships across clades. For the 28 families of mammals in our study,
300 those with genera that participated in the biotic exchange through Bering are significantly
301 more likely to show negative climate–richness relationships, even after controlling for
302 phylogenetic relatedness, for body size and for range size (see Appendix S5).

303 The ability of MEMs to cross-predict species richness among assemblages of
304 colonizers from one biogeographic region to the other may be related to phylogenetic
305 relatedness among the subsets of colonizers (i.e. their species belong to the same genera).
306 This is, ancestral environmental preferences would have been conserved through evolution
307 and thus, closely related species distribute in similar environments within different
308 biogeographic domains. Accordingly, phylogenetic niche conservatism expects closely
309 related species to be more similar in their traits than expected by chance (Losos 2008). A
310 twofold approach allowed us inspecting to what extent the stronger predictive ability of
311 MEMs amongst colonizers was due to phylogenetic relatedness.

312 First, we compared the ability of phylogenetic relationships to account for proxies of
313 the environmental tolerances (extracted from the environmental distributions of species,
314 regarding temperature and net primary productivity) of each subset of colonizer and
315 sedentary species (see electronic supplementary material, Appendix S6). Consistently with
316 cross-predictions among MEMs, we found that phylogenetic filters selected for temperature
317 and productivity yielded stronger predictions among colonizers than between sedentary and
318 colonizer species. Nonetheless, we found predictions based on phylogenetic relationships to
319 be generally weak (see electronic supplementary material, Appendix S6). Second, if
320 phylogenetic relatedness was the sole mechanism behind the similarities in the distributions
321 of colonizers across continents, then MEMs for Old colonizers should also predict species
322 richness from one biogeographic region to the other. MEMs among Old colonizers partially

323 predicted species richness across biogeographic regions, but these predictions were weaker
324 than among P and N colonizers (Table 2).

325 Together, these results suggest that the effects of phylogenetic relatedness manifest
326 preferably at the generic level or below since predictions made among models of
327 confamilial species are significantly weaker than predictions among congenics (Table 2).
328 Recent works (Khaliq et al. 2015; Olalla-Tárraga et al. 2011) have provided evidence for
329 conservatism of climatic tolerances. In particular, conservatism of tolerance to cold
330 temperatures has been shown to manifest more clearly at the generic level for mammals
331 (Olalla-Tárraga et al. 2011). Overall, phylogenetic relatedness seems not enough to explain
332 the conservatism of cooler climatic niches shown by colonizers. Considering that they share
333 a common biogeographic history would be needed to understand the current distribution of
334 species whose ancestors crossed Beringia.

335 Alternatively to explanations based on niche conservatism (Wiens & Donoghue
336 2004) and on the time that clades had to diversify (Stephens & Wiens 2003), other
337 evolutionary mechanisms may underlay our findings. Differences in diversification rates
338 (i.e. speciation minus extinction) between tropical and temperate regions have often been
339 invoked to explain why the tropics harbour the highest diversity (Chown & Gaston 2000;
340 Mittelbach et al. 2007). However, studies referring to diversification rates to explain
341 diversity gradients often provide contradictory results (Soria-Carrasco & Castresana 2012;
342 Weir & Schluter 2007). Surprisingly, and despite the expectation for higher net
343 diversification rates within the tropics, there are examples of higher temperate
344 diversification for mammals (Rolland et al. 2014; Weir & Schluter 2007). All the same,
345 even the literature in diversification rates recurs to both the age and the geographic origin
346 of the clades, to explain differences in speciation rates (Rolland et al. 2014; Soria-Carrasco
347 & Castresana 2012). For example, (Rolland et al. 2014) found higher diversification within
348 temperate regions for the order Lagomorpha and the family Talpidae, which was
349 interpreted based in their origin within temperate Asia and the time that clades would have
350 had to diversify *in situ*. To assess the extent to which diversification rates would affect our
351 results, we compared net diversification rates and Lineage Through Time (LTT) plots
352 between colonizer and sedentary mammals. We found little difference in diversification
353 rates among colonizers and sedentaries and a more recent diversification of colonizers (see

354 electronic supplementary material, Appendix S7), which would coincide with some
355 colonizers' diversification posterior to pre-Plio-Pleistocene Beringian biotic exchanges.
356 Nevertheless, these analyses suggest that we can rule out rates of evolution as a cause for
357 the observed differences in species richness among exchanged and non-exchanged
358 mammals, consistent with previous findings (McPeck & Brown 2007; Soria-Carrasco &
359 Castresana 2012); but see (Rolland et al. 2014).

360 Admittedly, our results might be limited by not considering extinct taxa. A number of
361 extinct mammal genera are identified as participants in the biotic exchange through the
362 Bering land bridge (Tedford et al. 2004; Woodburne & Swisher 1995). For example, most
363 taxa present in the Plio-Pleistocene record identified by (Bell et al. 2004) (see figure 7.2
364 therein) have become extinct. What would be the diversity pattern of exchanged species if
365 extinct species were still alive? A likely answer is that the observed pattern of higher
366 temperate species richness for colonizers would be reinforced. This conjecture stems from
367 the fact that many extinct genera were distributed across the northernmost latitudes of the
368 Holarctic (e.g. genera *Mammuthus* or *Coelodonta*) (Lorenzen et al. 2011), and that the
369 regions witnessing more extinctions were those where climate change was more severe
370 (Nogués-Bravo et al. 2010). Furthermore, most of the orders encompassed by our analyses
371 have shown higher extinction rates within the temperate regions (Rolland et al. 2014).
372 These facts indicate that it is unlikely that the distributions of most extant species belonging
373 to exchanged genera across temperate, polar or mountainous regions (figure 2a-b) be due to
374 higher extinctions of colonizers within lower latitudes.

375 Global mammalian diversity gradients emerge through addition of markedly different
376 clade-specific patterns (Buckley et al. 2010b; Isaac 2005). Global diversity patterns can be
377 'deconstructed' in a number of ways to understand the underlying processes. Common
378 approaches include studying distributional patterns for individual taxonomic groupings (i.e.
379 orders, families) (Cooper & Purvis 2010); to deconstruct the patterns attending to traits
380 such as body size (Terribile et al. 2009); or, grouping taxa according to phylogenetic
381 characteristics – i.e. the length of the terminal branches (Davies & Buckley 2012). Here, we
382 propose to deconstruct diversity patterns by selecting subsets of species according to their
383 biogeographic history. Our results support this choice since neither taxonomic grouping (at
384 the family level) nor phylogenetic relatedness, account for the observed patterns as strongly

385 as historically defined groupings do (Table 2). Although this approach may not be
386 recommendable for any study of niche conservatism, it proves suited for taxa with inverse
387 LDG patterns, or taxa whose distributions are suspected to be strongly influenced by
388 biogeographic history.

389

390 **Conclusions**

391 All our predictions are supported by data and show a strong influence of deep historical
392 biogeographic events over contemporary diversity patterns. Mammal species whose
393 ancestors colonized a new continent by crossing the Bering land-bridge preferably
394 distribute across cooler latitudes. Further, their environmental preferences resemble more
395 those of other colonizers in a different continent than the environmental affinities of
396 sedentary species. Logically, the environmental preferences of ancestors are not perfectly
397 conserved, which is expected given that the evolutionary process consists of accumulation
398 of change through time. The mammal genera that participated in the Beringian biotic
399 exchange expanded their ranges longitudinally across the Holarctic even crossing
400 continents, but seemingly, did not expand as much their latitudinal ranges (figure 2). Niche
401 conservatism would have prevented species whose ancestors were adapted to high latitude
402 climates from colonizing and expanding towards tropical latitudes. In sum, the combination
403 of past dispersal events and the longer time to diversify within cold environments while
404 constrained by the retention of ancestral niches, can explain the inverse LDG patterns
405 observed for colonizers. Our findings not only add to our understanding of how diversity
406 patterns are configured through time, but they also might have implications for the effects
407 that ongoing global change could have over extant species adapted to temperate and cold
408 environments. Cold-adapted species have also shown to maintain the environmental
409 preferences of their ancestors through time, and might be at risk if the geographic extent of
410 cooler niches shrinks in a future.

411

412 **Acknowledgements**

413 I.M.-C. received support by the Fonds de Recherches du Québec - Nature et Technologies
414 (FQRNT) programme, Projet de Recherche en Équipe and is currently supported by a
415 Postdoctoral Fellowship by the Programa Propio de la Universidad de Alcalá. The Ministry

416 of Economy and Competitiveness of Spain awarded a grant to M.A.R. (CGL2013-48768-
417 P).

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586

587 **Figure captions**

588

589 **Figure 1.** Scheme modified from (Wiens & Donoghue, 2004) depicting how niche
590 conservatism and the time-for-speciation effect (Stephens & Wiens, 2003) would also apply
591 to a clade originated within an extra-tropical region (i.e. temperate region). That clade
592 would accumulate more species through the diversification process within the region of
593 origin. The lower panel shows how for equal diversification rates, a clade of temperate
594 origin would accumulate more species than a tropical clade at a given moment t_1 (modified
595 from Mittelbach *et al.*, 2007).

596

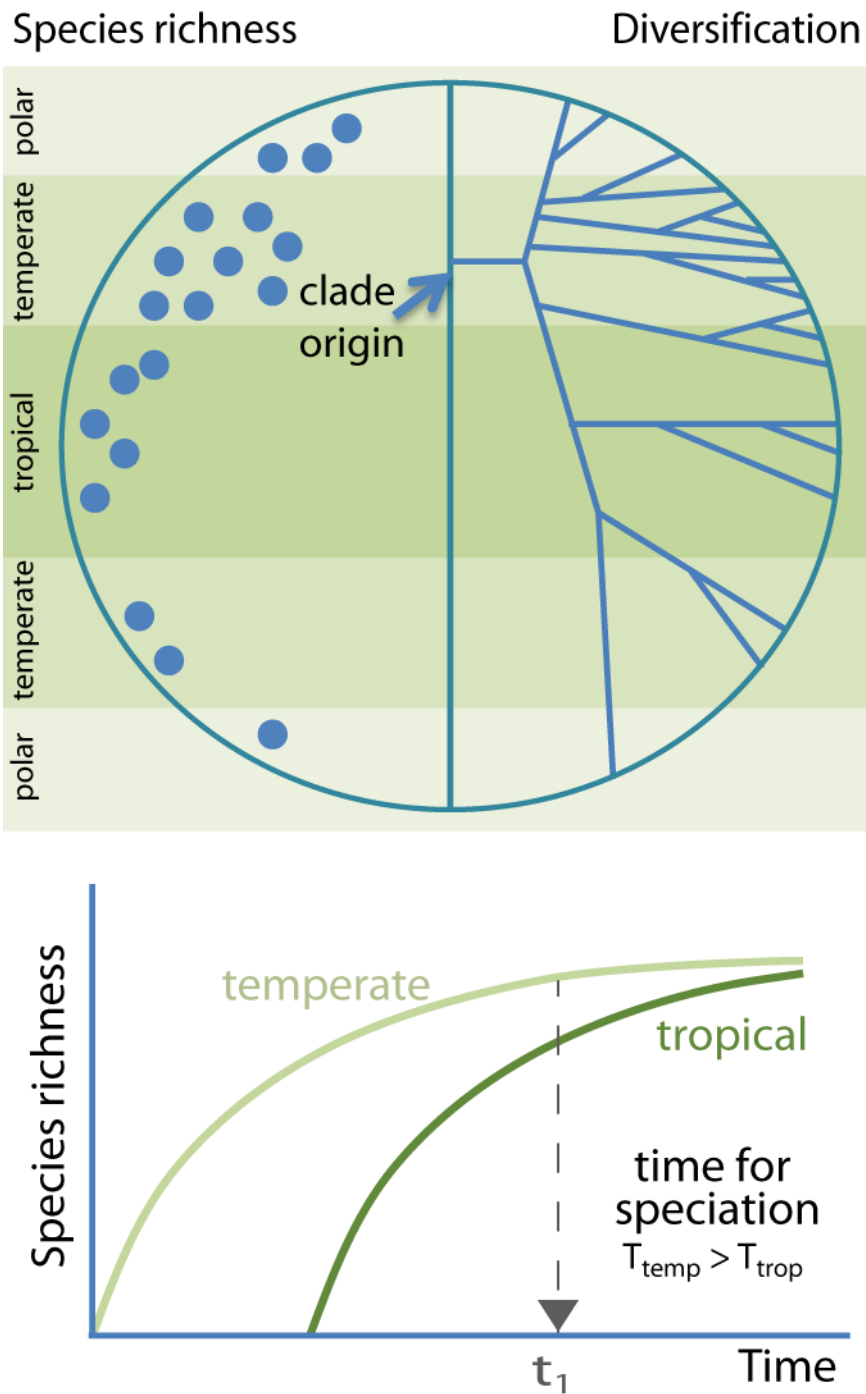
597 **Figure 2.** Species richness gradients for species of Nearctic and Palaeartic non-volant
598 mammals grouped as follows: (A) richness of P-N colonizers ($n = 127$), (B) richness of
599 exchanged species to the Nearctic ($n = 126$), (C) richness of exchanged species to the
600 Palaeartic ($n = 172$), (D) richness of all non-exchanged species ($n = 572$), and, (E) species
601 richness of con-familial non-exchanged species ($n = 219$). Grey arrows indicate the
602 direction of the biotic exchange for the groups of exchanged species.

603

604 **Figure 3.** Comparison among MEMs' cross-predictions between exchanged species from
605 the biogeographic region of origin to the biogeographic region of destination (green) and
606 MEMs of non-exchanged species predicting species richness of exchanged species (yellow)
607 within the Nearctic (A) and the Palaeartic (B). Frequency distributions of errors of both
608 cross-predictions (i.e. among MEMs of exchanged species and among MEMs of non-
609 exchanged and exchanged species) are also shown for the Nearctic (C) and the Palaeartic
610 (D).

611

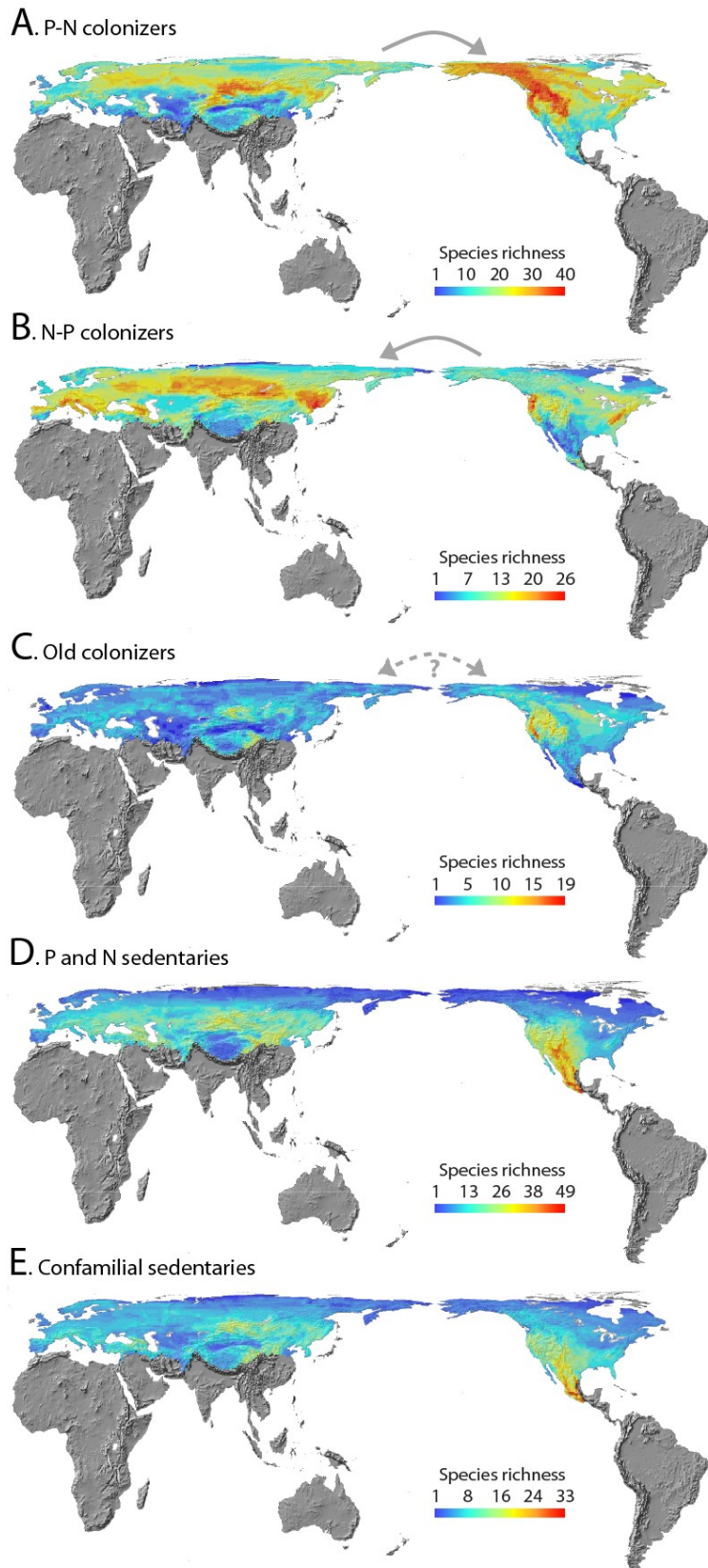
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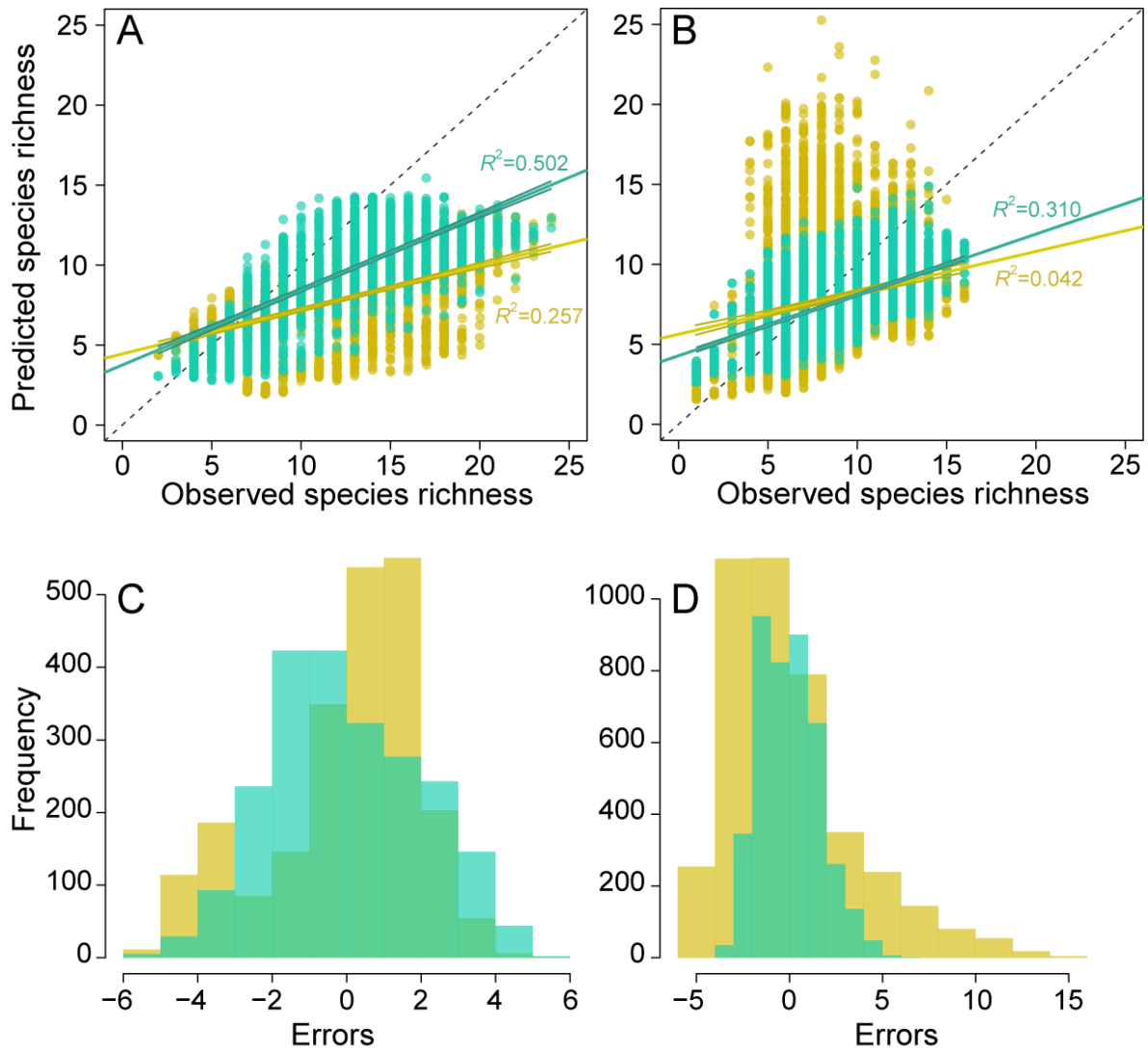
614 Figure 1.

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617 Figure 2.



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619 Figure 3.

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621

622 **Table 1.** Mammal groups used for the study of species richness gradients in the Palaeartic
 623 and the Nearctic. Each group comprises species belonging to genera that either remained in
 624 their native region (“sedentary” species), or colonized the other region by crossing the
 625 Bering Strait during the Plio-Pleistocene (“colonizer” species). Species belonging to genera
 626 present in both regions that might have crossed Bering prior the Plio-Pleistocene have been
 627 identified as a separate group (i.e. “Old colonizers”). Species confamilial to colonizer
 628 species but belonging to genera that did not cross Bering are identified as “confamilial
 629 sedentaries”.

Native region	Colonized region	Colonizer/ Sedentary	Group name	Current number of taxa					
				Holarctic		Palaeartic		Nearctic	
				Genera	Species	Genera	Species	Genera	Species
Palaeartic	Nearctic	Colonizer	P-N colonizers	22	127	14	79	21	58
Nearctic	Palaeartic	Colonizer	N-P colonizers	35	170	24	90	14	83
Palaeartic & Nearctic	-	Old colonizer	Old colonizers	10	136	10	67	10	73
Palaeartic & Nearctic	-	Sedentary	Confamilial sedentaries	78	217	45	99	36	120
Palaeartic & Nearctic	-	Sedentary	P and N sedentaries	170	568	103	292	77	280

631

632 **Table 2.** Summary of Goodness of fit of averaged Macro-Ecological Models (MEMs) of
 633 species richness for P-N and N-P colonizers. Both Spearman's ρ and R^2 are indicative of
 634 relationships between predicted and observed species richness values. All Spearman
 635 correlations were significant ($P < 0.001$).

Taxa	Biogeographic Region	n	Spearman's ρ	R^2
P-N colonizer	Nearctic (destination)	2244	0.922	0.859
	Palaeartic (origin)	4162	0.834	0.701
N-P colonizer	Nearctic (origin)	2244	0.872	0.772
	Palaeartic (destination)	4162	0.843	0.723

636
 637

638 **Table 3.** Cross-predictions among MEMs of colonizers and sedentaries at the
 639 biogeographic region of origin predicting species richness at the biogeographic region of
 640 destination.

MEM	Predicted species richness	Spearman's ρ	p -value <	R^2
P-N colonizers in Palaeartic	P-N colonizers in Nearctic	0.679	0.001	0.502
	N sedentaries	0.204	0.001	0.053
	N confamilial sedentaries	0.508	0.001	0.255
N-P colonizers in Nearctic	N-P colonizers in Palaeartic	0.521	0.000	0.310
	P sedentaries	0.244	0.001	0.049
	P confamilial sedentaries	0.244	0.001	0.042
Old colonizers in Palearctic	Old colonizers in Nearctic	0.610	0.001	0.340
Old colonizers in Nearctic	Old colonizers in Palearctic	0.344	0.001	0.114

641
 642