

1 Letter

2 **Ecological traits influence the phylogenetic structure of bird species co-**  
3 **occurrences worldwide**

4

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25

26 **Statement of authorship:**

27 WDK & J-YB conceived the study, J-YB, WDK, J-CS formulated hypotheses, WDK and  
28 CHS compiled data, J-YB, WDK, BS, WLE and CT performed analyses, J-YB & WDK  
29 wrote the manuscript, all authors commented on draft manuscripts.

30

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32

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35

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43

44 **ABSTRACT**

45

46 The extent to which species' ecological and phylogenetic relatedness shape their co-  
47 occurrence patterns at large spatial scales remains poorly understood. By quantifying  
48 phylogenetic assemblage structure within geographic ranges of >8000 bird species, we  
49 show that global co-occurrence patterns are linked - after accounting for regional effects -  
50 to key ecological traits reflecting diet, mobility, body size, and climatic preference. We  
51 found that co-occurrences of carnivorous, migratory and cold-climate species are  
52 phylogenetically clustered whereas nectarivores, herbivores, frugivores and invertebrate-  
53 eaters tend to be more phylogenetically overdispersed. Preference for open or forested  
54 habitats appeared to be independent from the level of phylogenetic clustering. Our results  
55 advocate for an extension of the tropical niche conservatism hypothesis to incorporate  
56 ecological and life history traits beyond the climatic niche. They further offer a novel  
57 species-oriented perspective on how biogeographic and evolutionary legacies interact  
58 with ecological traits to shape global patterns of species coexistence in birds.

59

60 **INTRODUCTION**

61

62 How contemporary environmental gradients influence large-scale patterns of species  
63 diversity has been extensively studied (Gaston & Blackburn 2000; Hawkins *et al.* 2003),  
64 with increasing attention to the contribution of historical and evolutionary processes  
65 (Ricklefs 2004; Wiens & Donoghue 2004). The tropical niche conservatism hypothesis  
66 provides an integrative historical-environmental explanation to latitudinal changes in  
67 species richness and global-scale species co-occurrence patterns (Wiens & Donoghue  
68 2004). It suggests that climatic stability and large areas have favoured higher net  
69 diversification rates within the tropics, and that most tropical clades have been unable to  
70 expand into extra-tropical climates because of climatic specialization and niche  
71 conservatism. Macroecological studies that have found support for such historical  
72 processes underlying large-scale diversity gradients have been largely based on methods  
73 that focus on species assemblages which co-occur at particular locations (*e.g.* Cardillo  
74 2011; Kissling *et al.* 2012a). This approach takes a spatial focus, in contrast with  
75 macroevolutionary studies which often focus on how diversification can be explained by  
76 species traits, without an explicit spatial perspective (Bennett & Owens 2002; Bokma  
77 2004; Ackerly *et al.* 2006). A combined spatially-explicit and species-oriented  
78 perspective unifying these two frameworks is needed to provide an integrated perspective  
79 on the ecological and historical-evolutionary drivers of species co-occurrences  
80 (Villalobos *et al.* 2013, Tobias *et al.*, 2014).

81

82 Phylogenetic methods that have long been used to study the evolutionary structure of  
83 species co-occurrences in space rarely account for species' attributes (Webb *et al.* 2002;  
84 Cavender-Bares *et al.* 2009). The recent species-oriented concept of “phylogenetic fields”  
85 (Villalobos *et al.* 2013) overcomes this limitation by describing the phylogenetic  
86 structure of species co-occurrences within a given focal species' geographical range (Fig.  
87 1). A phylogenetic field quantifies the phylogenetic relatedness of all the species that co-  
88 occur with the focal species (Villalobos *et al.* 2013). Hence, the field is a property of a  
89 species, and provides a framework for linking macroscale species co-occurrence patterns  
90 to other species properties, such as ecological or life-history traits. Importantly,  
91 phylogenetic fields allow investigating how broad-scale historical processes such as  
92 speciation, extinction and dispersal combine to shape present-day co-occurrence patterns  
93 of evolutionarily-related species (Villalobos *et al.* 2013). For instance, allopatric  
94 speciation should promote low levels of range overlap among closely related species and  
95 thus overdispersed phylogenetic fields (Pigot & Tobias 2013), while high levels of  
96 overlap (clustered phylogenetic fields) could be the consequence of post-speciation range  
97 changes or localized radiations (Ericson 2012). Phylogenetic fields can also be shaped by  
98 species' dispersal abilities (Wiens & Donoghue 2004) and niche convergence or  
99 divergence among co-occurring species (Johnson & Stinchcombe 2007; Villalobos *et al.*  
100 2013). As a consequence, phylogenetic fields are likely to be related to specific traits that  
101 reflect variations in contemporary resource use (e.g. dietary adaptations, Silvertown *et al.*  
102 2006; Pigot & Tobias 2013), large-scale habitat or climatic preferences (Streelman &  
103 Danley 2003; Ackerly *et al.* 2006), dispersal behaviour (Belliure *et al.* 2000), and body  
104 size (Bokma 2004).

105

106 Birds are well suited for analyses of phylogenetic fields as their global distributions  
107 (BirdLife International & NatureServe 2011), ecological traits (Del Hoyo *et al.* 2013),  
108 and phylogenetic relationships (Jetz *et al.* 2012) are extensively described. Although  
109 allopatric speciation is thought to dominate bird diversification (Edwards 2005), fast  
110 transition rates to secondary sympatry (Pigot & Tobias 2013) and high levels of niche  
111 conservatism (Peterson *et al.* 1999) could make their phylogenetic fields prone to  
112 clustering (Fig. 1). Clustering of phylogenetic fields might be particularly pronounced for  
113 bird clades characterized by high diversification rates, isolated geographic occurrence,  
114 and low dispersal ability (Fig. 1), factors that increase the probability of localized  
115 speciation (Ricklefs 2006; Kisel & Barraclough 2010; Jetz *et al.* 2012). In contrast, low  
116 diversification rates, high dispersal ability, and strong competitive exclusion could trigger  
117 phylogenetic overdispersion (Fig. 1). Ecological traits related to bird habitat use, diet,  
118 body size, and mobility should therefore be associated with the structure of species'  
119 phylogenetic fields (Table 1). Reflecting deep-time evolutionary legacies (Ericson 2012),  
120 the relationships between phylogenetic fields and ecological traits in birds might also be a  
121 consequence of evolutionary conservatism.

122

123 Here, we tested whether phylogenetic fields are related to key ecological traits in more  
124 than 8000 terrestrial bird species (Fig. 1, Table 1). We first explored the imprint of  
125 biogeographical history on phylogenetic fields by investigating their regional variation.  
126 We then tested specific *a priori* hypotheses on the relationships between phylogenetic  
127 fields and species' ecological traits (see Table 1 for details and references). We expected

128 that (1) forest and open habitat species should differ in their degree of phylogenetic  
129 clustering; (2) species-rich dietary guilds in tropical areas (*e.g.* insectivores, frugivores  
130 and nectarivores) should show high levels of overdispersion; (3) high mobility (*i.e.*  
131 propensity to postnatal dispersal and irregular population-level dispersal events) should  
132 lead to phylogenetic overdispersion while regular migration should be related to  
133 clustering; (4) small-bodied species should show higher phylogenetic clustering than  
134 large-bodied species; and (5) as tropical niche conservatism has allowed only few  
135 families to expand outside the tropics, cold-climate species should have clustered  
136 phylogenetic fields. We show that the level of phylogenetic clustering and overdispersion  
137 in bird species co-occurrences worldwide is related to several of these key ecological  
138 traits, and that some of these relationships are affected by a strong historical-evolutionary  
139 component.

140

## 141 **MATERIAL AND METHODS**

142

### 143 **Bird distributions**

144

145 We compiled a comprehensive dataset of global bird distributions, representing  
146 conservative extent-of-occurrence extrapolations of the world-scale breeding ranges for  
147 9886 bird species (out of 9920 recognized extant species, BirdLife International &  
148 NatureServe 2011). Distribution maps were derived from a variety of sources, including  
149 >5.8 million specimen and Important Bird Area occurrences, other records (*e.g.*  
150 published literature, survey reports *etc.*), distribution atlases derived from systematic

151 surveys, distribution maps in field guides and other handbooks, and expert opinion  
152 (BirdLife International & NatureServe 2011). The dataset uses a globally consistent  
153 taxonomic standard and currently represents the best electronically available knowledge  
154 on global bird species occurrences. We overlaid these maps, originally in polygon format,  
155 onto a grid in cylindrical equal area projection with >39900 cells of  $110 \times 110$  km  
156 resolution (equivalent to c.  $1^\circ \times 1^\circ$  near the equator; Kissling *et al.* 2012b), from which  
157 we subsequently excluded cells with more than 50% of water and the Antarctic continent,  
158 retaining 10599 cells. This excludes many islands and thus 850 island endemic species,  
159 ensuring that our results were not affected by the high rates of recent man-driven  
160 extinctions that affected insular bird assemblages (Pimm *et al.* 2006). We further  
161 eliminated all families including at least one pelagic or marine species to exclude  
162 seabirds and terrestrial species with close marine relatives ( $n = 719$  species), and lumped  
163 34 species for taxonomic consistency with the phylogenetic data. We eventually deleted  
164 species for which all ecological traits ( $n = 28$ ) or phylogenetic information ( $n = 21$ ) were  
165 missing, and those whose restricted ranges prevented computation of phylogenetic fields  
166 ( $n = 70$ ). Our final set therefore included 8164 terrestrial and freshwater species. We  
167 assigned each species to the region (listed in Table S1: 19 among the 20 zoogeographic  
168 regions defined by Holt *et al.* 2013) encompassing most of its geographic range.

169

## 170 **Phylogeny**

171

172 We computed phylogenetic fields based on the recently published mega-phylogeny of the  
173 world's bird species (Jetz *et al.* 2012), which we pruned to the above-mentioned 8164



174 bird species. The original tree was inferred using a two-step protocol in which time-  
175 calibrated phylogenetic trees were estimated for well-supported bird clades and  
176 subsequently grafted onto a backbone tree representing deep phylogenetic relationships.  
177 In this procedure, about two thirds of bird species (6663) were represented by molecular  
178 information whereas the remaining species were assigned a phylogenetic position based  
179 on genus or higher taxa membership (*cf* Jetz *et al.* 2012 for methodological details). This  
180 tree currently represents the most comprehensive and up-to-date synthesis of  
181 phylogenetic information for birds, allowing species-level inference in spite of remaining  
182 uncertainty. To test the sensitivity of our results to phylogenetic uncertainty, we repeated  
183 all computations and statistical models using 100 trees randomly drawn from the set of  
184 10,000 trees provided by Jetz *et al.* (2012). These trees are realizations of the probability  
185 space of possible trees based on pseudo-posteriors of the original Monte Carlo Markov  
186 chains. The 10,000 trees were available for two separate backbones; we used those from  
187 the second-stage Ericson model for our analysis (available at <http://birdtree.org>, see  
188 details in Jetz *et al.* 2012).

189

## 190 **Traits**

191

192 We considered eight ecological traits corresponding to major differences in bird lifestyles  
193 and grouped them into five main trait categories: habitat, diet, mobility, body size and  
194 climatic preference (Table 1, family-level overview in Table S1). These traits are partly  
195 correlated due to biogeographic and evolutionary constraints. Since statistical removal of  
196 collinearity among multiple traits by multivariate statistical procedures would have

197 resulted in a loss of biological interpretability and a drastic reduction of sample size, we  
198 tested the effect of each trait separately, but explored correlations among traits using a  
199 Hill & Smith multivariate analysis (Hill & Smith 1976) on the 6266 species for which all  
200 traits were known (Appendix 1).

201

### 202 *Habitat preference*

203

204 We assigned each of the 8164 species to a binary habitat trait, separating forest from  
205 open-habitat species, derived from the habitats classification scheme (version 3.0) of the  
206 International Union for Conservation of Nature (IUCN, [www.iucnredlist.org](http://www.iucnredlist.org);  
207 downloaded April 2012). We defined forest species as those occurring in IUCN habitat  
208 classes 1.1–1.9 ( $n = 6396$ ). All other species occur in open habitats ( $n = 1768$ ).

209

### 210 *Dietary guilds*

211

212 For each species with dietary information ( $n = 8099$ ), we distinguished seven dietary  
213 categories (plants, seeds, fruits, nectar, invertebrates, carrions, vertebrates) from a  
214 comprehensive literature survey (Şekercioğlu *et al.* 2004; updated with Del Hoyo *et al.*  
215 2013). The relative importance of dietary categories for a given species' diet were  
216 ranked, with all scores adding up to 10 (see Kissling *et al.* 2012b for a similar  
217 methodology). Due to low sample sizes, we summed the scores of plants and seeds, and  
218 those of carrion and vertebrates, and then assigned each species to one of six dietary  
219 guilds according to the predominant diet (score > 5): frugivores ( $n = 1156$ ),

220 herbivores/seed eaters ( $n = 1037$ ), nectarivores ( $n = 454$ ), invertebrate eaters ( $n = 4745$ ),  
221 carnivores ( $n = 406$ ), and omnivores if none of the diet categories exceeded a score of 5  
222 ( $n = 301$ ).

223

#### 224 *Mobility*

225

226 We compiled four binary trait categories related to dispersal and migration (see Table 1,  
227 data also extracted from Del Hoyo *et al.* 2013) to describe species' mobility over large  
228 spatial extents ( $n = 8140$  species). The first two mobility traits corresponded to seasonal  
229 migrations across latitude ('long-distance migration',  $n = 1544$  migrants) or altitude  
230 ('altitudinal migration',  $n = 968$  migrants). The other two refer to a species' propensity to  
231 perform non-periodic long-distance dispersal events, either after leaving the nest  
232 ('postnatal dispersal',  $n = 422$  dispersers) or due to irruptive or irregular movements  
233 ('irregular dispersal',  $n = 956$  dispersers).

234

#### 235 *Body size*

236

237 Body size was represented by mean body mass across sexes (if available), retrieved from  
238 Dunning (2008) for a total of 6314 species. Data were log-transformed prior to statistical  
239 analyses to reduce the effects of extreme values.

240

#### 241 *Climatic preference*

242

243 We approximated species' climatic preferences ( $n = 8164$ ) as the average temperature it  
244 encounters over its geographic range (*i.e.* the mean temperature across the grid cells in  
245 which it occurs). Temperature data ( $^{\circ}\text{C} \times 10$ ) were averaged from annual means retrieved  
246 from Worldclim version 1.4 ([www.worldclim.org](http://www.worldclim.org); Hijmans *et al.* 2005). As a  
247 supplement, we further calculated species' range-level average net primary productivity  
248 and mean range latitude (data described in Appendix 2): these two variables were highly  
249 correlated with temperature and associated results are therefore only presented as  
250 supplementary information in Appendix 2.

251

## 252 **Calculation of phylogenetic fields**

253

254 Phylogenetic fields quantify the phylogenetic structure of species co-occurrence within a  
255 focal species' geographical range (Villalobos *et al.* 2013) by comparing the observed  
256 phylogenetic dispersion in the pool of species co-occurring with the focal species to a  
257 null expectation (Villalobos *et al.* 2013). We calculated phylogenetic fields with a  
258 modified version of the Net Relatedness Index (NRI, Webb *et al.* 2002) for all focal  
259 species occurring in more than one grid cell. Our index ("focal" NRI:  $\text{NRI}_{\text{F}}$ ) was defined  
260 as a standardized effect size varying from overdispersed phylogenetic fields (negative  
261 values) to clustered phylogenetic fields (positive values):

$$262 \quad \text{NRI}_{\text{F},i,t} = -1 \times \frac{\text{MPD}_{\text{F},i,t,\text{obs}} - \text{mean}(\text{MPD}_{\text{F},i,t,\text{rand}})}{\text{standard deviation}(\text{MPD}_{\text{F},i,t,\text{rand}})}$$

263  $\text{MPD}_{\text{F},i,t,\text{obs}}$  is the observed mean pairwise phylogenetic distance (in million years)

264 between a given focal species  $i$  and the  $n$  species it co-occurs with, for a given

265 phylogenetic tree  $t$ , calculated with a computationally efficient algorithm (Tsirogiannis *et*

266 *al.* 2012). It differs from the mean pairwise distance measure which usually underlies the  
267 NRI (Webb *et al.* 2002) in that it includes only the distances between the focal species  
268 and the  $n$  co-occurring species, rather than all pairwise distances in the assemblage. Thus,  
269 the  $NRI_F$  is more a property of the focal species than of the whole assemblage.  
270  $MPD_{F,i,t,rand}$  is the null distribution of  $MPD_F$  values for focal species  $i$ , and tree  $t$  across  
271 100 null model replicates. The species pools used in the null model were constrained by  
272 two conditions. First, a species could only be drawn for the null expectation if it occurred  
273 in at least one of the regions (sensu Holt *et al.* 2013) in which the focal species is present.  
274 Hence,  $MPD_{F,i,t,obs}$  is compared to a null expectation drawn from a regional (rather than  
275 global) species pool, ensuring that worldwide differences in phylogenetic fields are not  
276 simply driven by differences in species richness among zoogeographic regions. Second,  
277 the probability of drawing a given species was proportional to its range size, which  
278 implies that large-ranging species are more likely to be drawn than range-restricted  
279 species. Hence, the  $NRI_F$  accounts for differences in species' range sizes as well as in the  
280 richness of regional species pools. We preferred this null expectation over one based on a  
281 global species pool or one where species are drawn independently of geographic range  
282 size because it relates range-wide co-occurrences to the specific region in which a focal  
283 species is present, and it minimizes any spurious effects related to differences in species  
284 range sizes.

285

## 286 **Statistical analyses**

287

288 We first used an ordinary-least-squares (OLS) linear regression model with a normally  
289 distributed error term (referred to as ‘non-phylogenetic regression’) to relate species’  
290  $NRI_F$  to a suite of species’ ecological traits. For categorical traits (habitat preference,  
291 dietary guild and mobility), parameters were made identifiable by setting a reference  
292 category to 0. For body mass and temperature preference (continuous variables), we  
293 reported the linear slope coefficient. Because not all traits were measured for all species  
294 (see above, “Traits”) and because our aim was to investigate the magnitude of the fields-  
295 trait relationships rather than to compare the effects among trait categories, we performed  
296 five separate models: (i) forest vs. open habitat use; (ii) dietary guild; (iii) mobility  
297 (postnatal dispersal + irregular dispersal + long-distance migration + altitudinal  
298 migration); (iv) body size, and (v) climatic preference. In all models, we additionally  
299 included the core zoogeographic region of the focal species’ occurrence as a covariate to  
300 account for biogeographic differences in phylogenetic fields. In this region effect, each  
301 species is attributed to the region hosting the largest fraction of its range (see “Bird  
302 distributions”, above). We used Akaike’s Information Criterion (AIC, Burnham &  
303 Anderson 2002) to measure the gain of likelihoods of models with sets of traits, as  
304 compared to models with zoogeographic region only (discriminating models separated by  
305 more than two AIC units).

306

307 We also investigated the phylogenetic component of the trait effects with generalized  
308 least square regressions (hereafter “phylogenetic regression”, implemented under the  
309 `phylolm` R library, Ho & Ané 2013) to test whether the effect of traits on phylogenetic  
310 fields contains a deep evolutionary signal. We used the same fixed effect structures as in

311 non-phylogenetic regressions, but additionally imposed a correlated error structure based  
312 on a phylogenetic distance matrix that assumes Pagel's evolutionary model (Pagel 1999).  
313 The associated parameter (Pagel's  $\lambda$ ) increases towards 1 as the phylogeny has an  
314 increasing impact on model structure (Pagel 1999).

315

### 316 **Sensitivity analyses**

317

318 We assessed the sensitivity of the relationships between phylogenetic fields and traits to  
319 phylogenetic uncertainty by performing the non-phylogenetic and phylogenetic  
320 regressions for 100 separate phylogenetic trees and their associated phylogenetic field  
321 distributions. We reported the regression coefficients  $\pm$  95% confidence intervals  
322 separately for each of these 100 models in the results. We further evaluated the influence  
323 of marginally overlapping species by re-computing phylogenetic fields and re-estimating  
324 their relationships with traits, restricting species assemblages to those species overlapping  
325 by more than 5% or 10% with the focal species' geographic range (Appendix 3).

326

## 327 **RESULTS**

328

### 329 **Structure of bird phylogenetic fields**

330

331 Birds phylogenetic fields varied widely across the 8164 species (Fig. 2). Overall, 49% of  
332 the species ( $n = 4017$ ) had overdispersed phylogenetic fields, while 40% ( $n = 3282$ ) had  
333 clustered phylogenetic fields. Only 865 phylogenetic fields (11%) did not exhibit any

334 clear phylogenetic structure (95% confidence intervals overlapping 0, Fig. 2). Across  
335 species-rich bird families (with >100 species), rails and allies (Rallidae), birds of prey  
336 (Accipitridae), and the toucans and barbets (Ramphastidae) had the most clustered  
337 phylogenetic fields whereas ovenbirds (Furnariidae), sunbirds (Nectariniidae), and  
338 cisticolas (Cisticolidae) were particularly overdispersed (for a list with  $NRI_F$  averaged at  
339 the family level see Table S2). As expected, phylogenetic fields showed regional  
340 variation according to the focal species' core zoogeographic region of occurrence (Fig.  
341 3): Eurasian, Central Asian and Nearctic species had the most clustered fields, while  
342 species with the most overdispersed fields occurred in tropical areas, especially in Africa  
343 and South America.

344

#### 345 **Relationships between phylogenetic fields and traits**

346

347 Sample sizes were relatively large across all trait categories, ensuring that trait effects  
348 were reasonably well estimated even for the less common categories. Models with sets of  
349 traits in addition to a region effect exhibited lower AIC than models with a region effect  
350 only, indicating that all life history traits except habitat preference contributed to explain  
351 phylogenetic fields (Table 2). Open-habitat and forest species did not differ in their field  
352 structures (Table 2, Fig. 4A). Dietary guild had a strong effect in non-phylogenetic  
353 regressions (Table 2), mainly driven by the high level of clustering in carnivore species  
354 (Fig. 4B). Omnivores exhibited the highest variance in their phylogenetic fields among  
355 all guilds, and nectarivores and herbivores were the most overdispersed, although the  
356 confidence intervals of their regression parameters partly overlapped with invertebrate-



357 eaters and frugivores. Among mobility traits, the most clustered phylogenetic fields were  
358 related to altitudinal and latitudinal migratory behaviours, while postnatal and irregular  
359 dispersal showed a weaker clustering effect (Fig. 4C). In non-phylogenetic regression,  
360 body mass was positively correlated with the level of clustering, indicating that large  
361 species had the most clustered fields (Fig. 4D). Finally, warm-climate species had more  
362 overdispersed fields than cold-dwelling ones (Fig. 4E).

363

### 364 **Imprint of phylogeny**

365

366 Pagel's  $\lambda$  was close to 0.4 in all phylogenetic regressions (Table 2), suggesting that  
367 phylogenetic fields contain a signal related to the clade's evolutionary history.  
368 Accordingly,  $\Delta$ AIC indicated that the effect of dietary guilds on phylogenetic fields  
369 disappeared when including a phylogenetic covariance matrix, while body mass and  
370 mobility still improved the models relative to a region only model, but to a smaller extent  
371 than in non-phylogenetic regressions (Table 2). The effects of altitudinal and latitudinal  
372 migrations persisted in phylogenetic regressions, contrary to those of postnatal and  
373 irregular dispersal (Fig. 4C). Furthermore, the effect of body mass was reversed, with  
374 large-bodied species being more overdispersed than smaller ones after accounting for  
375 phylogeny. Finally, and contrary to all other traits, species' climatic preference improved  
376 the AIC more in phylogenetic than in non-phylogenetic regressions (Table 2), but its  
377 regression coefficients remained largely similar, with warmer-climate species having  
378 more overdispersed phylogenetic fields than cold-dwelling species (Fig. 4E).

379

380 **Sensitivity to phylogenetic uncertainty, marginal species, and multi-trait**  
381 **correlations**

382

383 The Hill & Smith analysis on the set of species for which all traits were available ( $n =$   
384 6266) revealed associations among traits (Appendix 1). For instance, carnivory was  
385 associated with large body mass, high rates of postnatal and irregular dispersal and  
386 preference for open habitats. Moreover, frugivore species were mainly associated with  
387 warm climates, and to a lesser extent with forested habitats and sedentariness. Finally,  
388 altitudinal or latitudinal migrants were negatively associated with warm climates,  
389 highlighting their ability to breed in strongly seasonal (*e.g.* northern latitude) habitats.

390

391 Phylogenetic fields showed little variation across the 100 randomly sampled phylogenetic  
392 trees (Fig. 2), and our conclusions on trait effects were thus not substantially affected by  
393 uncertainty in the underlying phylogenetic trees (Fig. 4). Removing marginal species did  
394 not qualitatively change the results (compare Fig. 4 with figures in Appendix 3).

395

396 **DISCUSSION**

397

398 Quantifying phylogenetic fields across broad biogeographical scales offers a novel  
399 species-oriented perspective to test hypotheses on geographical patterns of co-occurrence  
400 (Villalobos *et al.* 2013). Applying this approach, we present the first comprehensive  
401 analysis of relationships between ecological traits and the phylogenetic structure of bird

402 assemblages worldwide. Accounting for regional species pools and range size, we found  
403 that some bird species tend to co-occur with close relatives, while others tend to co-occur  
404 with distant relatives (overdispersion), with a trend towards clustering in extra-tropical  
405 species. We found that species' ecological characteristics explained a substantial  
406 proportion of species co-occurrence patterns at large spatial scales, but the intensity of  
407 their influence as well as their phylogenetic signal varied substantially from trait to trait.  
408 Effects of diet and body size on phylogenetic fields showed deep evolutionary signals,  
409 whereas effects of mobility and climatic preference appeared to be less evolutionarily  
410 constrained. Species that only marginally co-occurred with a focal species had little  
411 impact on the magnitude of trait signals in phylogenetic fields.

412

### 413 **Patterns of phylogenetic clustering and overdispersion**

414

415 About half of the bird species showed phylogenetic overdispersion in the co-occurrence  
416 structure of conspecifics. This overdispersion could be explained by the predominance of  
417 allopatric speciation associated with low secondary rates of sympatry (e.g. in Furnariidae,  
418 Table S2, Pigot & Tobias 2013, Tobias *et al.* 2014), which has been suggested to  
419 dominate among terrestrial birds (Edwards 2005). However, 40% of bird species had  
420 clustered phylogenetic fields, indicating that sym- and parapatric speciation and/or  
421 allopatric speciation with high secondary rates of sympatry could also be common among  
422 birds. In addition to speciation mode, biogeographic history of a region could also be a  
423 mediating factor (Figure 1). Interestingly, phylogenetic fields were strongly affected by  
424 region, with species of northern temperate and arctic regions showing high levels of

425 clustering whereas tropical species tended to have overdispersed fields. This pattern  
426 contrasts with previous results for Neotropical bats, for which overdispersion in  
427 phylogenetic fields has been found at northern (rather than tropical) latitudes (Villalobos  
428 *et al.* 2013). Across the bird clade, we suggest that only few families have been able to  
429 colonize and diversify in colder realms (consistent with tropical niche conservatism,  
430 Wiens & Donoghue 2004; Hawkins *et al.* 2006), leading to a predominance of clustering  
431 in extra-tropical regions. Distributional constraints imposed by current and past climatic  
432 changes on Arctic-Siberian species could further explain the high levels of clustering  
433 compared with more southern species (Hortal *et al.* 2011). This is consistent with higher  
434 clustering in regions that have been climatically unstable in the past, relative to regions  
435 with low paleoclimatic temperature oscillations (Kissling *et al.* 2012a). However, it could  
436 also indicate that allopatric speciation associated with high secondary rates of sympatry is  
437 most common in harsh and unstable environments, which requires further testing.

438

#### 439 **Trait and niche conservatism**

440

441 For some traits (especially dietary preferences and body size) parameter estimates  
442 differed between non-phylogenetic and phylogenetic regressions. This indicates an  
443 imprint of trait conservatism on phylogenetic fields and suggests that such ecological  
444 characteristics have evolved little after the early separation of ancestors. However, more  
445 recent trait evolution within clades (Peterson *et al.* 1999; Ericson 2012) might also have  
446 occurred at a much finer scale than our coarse trait categorizations, as proposed for  
447 instance in the dietary preferences or specialization of New World warblers (Mac Arthur

448 1958). The relatively higher proportion of carnivores at northern latitudes, as compared  
449 with that of frugivores, seed eaters or invertebrate eaters, could explain the relative  
450 overdispersion of other dietary guilds in our results (see the bimodal latitudinal species  
451 richness gradient for carnivores in Kissling *et al.* (2012b)). Interestingly, the diet trait  
452 effect on phylogenetic fields disappeared in phylogenetic regressions, indicating that  
453 carnivory is a highly conserved dietary strategy within the avian tree of life. An even  
454 more pronounced change in parameter estimates between non-phylogenetic and  
455 phylogenetic regression occurred for body size (from overdispersion to clustering),  
456 suggesting that body size shows larger trait conservatism than coarse dietary strategies. In  
457 contrast to body size and diet, however, the effect of climatic preference on phylogenetic  
458 fields did not show an evolutionary signal. Hence, we hypothesize that much of the  
459 widely recognized tropical niche conservatism (Wiens & Donoghue 2004) may actually  
460 arise via constraints imposed by species ecological traits such as body size and dietary  
461 preference rather than directly via their range-wide climatic niches.

462

### 463 **Migration vs. dispersal**

464

465 Migratory behaviour had a detectable imprint on phylogenetic fields whereas dispersal  
466 behaviour had no or at most a weak effect. In line with our hypothesis (Table 1),  
467 altitudinal and latitudinal migrants showed clustered phylogenetic fields relative to non-  
468 migratory birds, maybe because the evolution of migratory behaviour adds up with low  
469 flexibility in habitat preferences, nesting phenology or physiological constraints  
470 (Böhning-Gaese *et al.* 1998). However, the same clustering effect might also arise from

471 habitat or geophysical constraints, as these can confine migratory birds to certain regions.  
472 For instance, many altitudinal migrants are found in association with mountain ranges  
473 (*e.g.* Andes, Himalaya), whereas latitudinal migrants usually use the seasonal excess of  
474 resources at northern latitudes (Hurlbert & Haskell 2003). In contrast to migrants and  
475 non-migrants, species with high (irregular or postnatal) dispersal ability did not differ in  
476 phylogenetic fields relative to less mobile species. We acknowledge that our coarse  
477 dispersal categories might disregard an influence of dispersal behaviour on phylogenetic  
478 fields, and that additional analyses with actual dispersal distances would be desirable in  
479 future analyses. However, such direct dispersal estimates are extremely difficult to  
480 quantify and hence are lacking for the majority of bird species (Dawideit *et al.* 2009).

481

#### 482 **Correlations among multiple traits**

483

484 Some of the effects of individual traits on phylogenetic fields could be mediated by  
485 correlations among multiple traits (Appendix 1). For instance, the effect of body size  
486 could at least in part mediate the overdispersion of dietary guilds relative to carnivory.  
487 Frugivory, preference for warm temperature and sedentariness are also strongly related  
488 (Appendix 1). This indicates that climatic niche conservatism will be difficult to  
489 disentangle from the effects of ecological and morphological traits for some bird species  
490 (*e.g.* frugivores and non-migratory birds), as covariation between climate and ecological  
491 adaptations might be due to indirect climatic effects on large-scale distributions of higher  
492 trophic levels (Kissling *et al.* 2007). Finally, latitudinal migration was negatively related  
493 to warm climate preference and frugivory, which indicates that some ecological strategies

494 are exclusive (*i.e.* obligate frugivores occur in tropical climates and are not latitudinal  
495 migrants). In spite of these correlations, none of the investigated traits were fully  
496 represented by the other traits and thus each of them deserves a separate examination.  
497 Although it is clear that phylogenetic fields of individual bird species are ultimately  
498 shaped by the joint influence of suites of inter-related traits, it is challenging to identify  
499 which characteristics drive the response of a species to selection pressures, and hence  
500 mediates evolution. From our multi-trait analysis (Appendix 1), we suggest that frugivory  
501 and warm-climate preference, body mass and carnivory, and long-distance latitudinal  
502 migration are key ecological traits shaping broad-scale species co-occurrence patterns in  
503 birds.

504

## 505 **CONCLUSION**

506

507 Using a novel species-oriented phylogenetic perspective, we provide evidence that key  
508 ecological traits —on top of regional effects— shape geographical patterns of species co-  
509 occurrence in birds worldwide. Some trait effects on phylogenetic fields (*e.g.* via body  
510 size and diet) are deeply conserved in the bird tree of life whereas others are not (*e.g.*  
511 climatic preference). This suggests that a more differentiated theory of ‘tropical niche  
512 conservatism’ needs to be developed that does not only focus on climatic niches (Wiens  
513 & Donoghue 2004), but also takes various ecological and life history traits into account.  
514 Beyond the traits used in our study, other factors such as the fine-scale division of  
515 resources and space (often approximated by morphological measurements, Grant 1968)  
516 or host-pathogen dynamics (Ricklefs 2010) could also contribute to shape the

517 phylogenetic and geographic structure of species co-occurrences. Furthermore,  
518 intraspecific variation in a species' phylogenetic field could be quantified for each grid  
519 cell of a species geographic range. This would allow investigating how phylogenetic  
520 structure in co-occurrence varies from a species' range core to its margins, where abiotic  
521 conditions often become harsher (Sexton *et al.* 2009). We therefore suggest that, in line  
522 with our results, shifting from a purely site-based to a species-oriented, range-wide  
523 approach may be especially fruitful to understand how species' evolutionary histories and  
524 current ecological conditions combine to shape large-scale gradients of biodiversity and  
525 species coexistence.

526

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528

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743

744 **SUPPLEMENTARY MATERIALS**

745

746 **Table S1:** Summary of ecological traits and sample sizes.

747 **Table S2:** List of bird families included in the analyses, with number of species per  
748 family and average phylogenetic fields  $\pm$  SD over 100 replicates of the phylogenetic tree.

749 **Appendix 1:** Multivariate exploration of the relationships among bird species' ecological  
750 traits

751 **Appendix 2:** Relationships between phylogenetic fields and species' mid-range latitude  
752 and range-averaged net primary production.

753 **Appendix 3:** Effects of marginal co-occurrences on phylogenetic fields – trait  
754 relationships.

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767 **TABLES**

768

769 **Table 1:** Key ecological traits of birds and related hypotheses on how they might  
 770 influence the phylogenetic structure (overdispersion, clustering) of species co-  
 771 occurrences (‘phylogenetic fields’) at biogeographic scales.

772

Trait	Description	Hypotheses	Potential processes	References
<b>Habitat preference</b>				
Forest vs. open habitats	Whether a species prefers open or forested habitats	Forest and open-habitat birds show different levels of phylogenetic structure, but the direction of the effect is unclear	The spatial grain of resource distribution differs among forests and open habitats	<i>Cueto and De Casenave 1999</i>
<b>Diet</b>				
Dietary guild	Species are divided into six dietary guilds according to their dominant diet (frugivores, herbivores/seed eaters, nectarivores, insectivores, carnivores, omnivores)	Overdispersion in tropical guilds (e.g. insectivores, frugivores, nectarivores)	Ecological competition limits geographical co-occurrence of closely-related species	<i>Kissling et al. 2012b; Pigot &amp; Tobias 2013</i>
<b>Mobility</b>				

Postnatal dispersal	Whether post-fledging long-distance dispersal occurs or not	High rates of dispersal favour overdispersion	Dispersal creates opportunities for extra-range colonization and allopatric speciation over evolutionary time scales	<i>Belliure et al. 2000</i>
Irregular dispersal	Irruptive or irregular movements			
Long-distance migration	Whether periodic (seasonal) migration along latitudinal gradients occurs or not	Restricted opportunities for allopatric speciation promote clustering	In spite of their high mobility, migratory species exhibit low physiological, behavioral and ecological flexibility	<i>Böhning-Gaese et al. 1998</i>
Altitudinal migration	Whether periodic (seasonal) migration along elevational gradients occurs or not			
<b>Body size</b>				
Body mass	Body mass in grams (species-level average, continuous trait)	Body mass is negatively correlated with clustering	Smaller species might diversify faster than large-bodied species, and the latter might be more affected by competitive exclusion	<i>Bokma 2004; Olson et al. 2009</i>
<b>Climatic preference</b>				

Temperature optimum	Average temperature over a species' geographic range	Overdispersion in tropical species, clustering in cold-climate species	Tropical niche conservatism, with few families having dispersed outside the tropics	<i>Wiens &amp; Donoghue 2004; Hortal et al. 2011</i>
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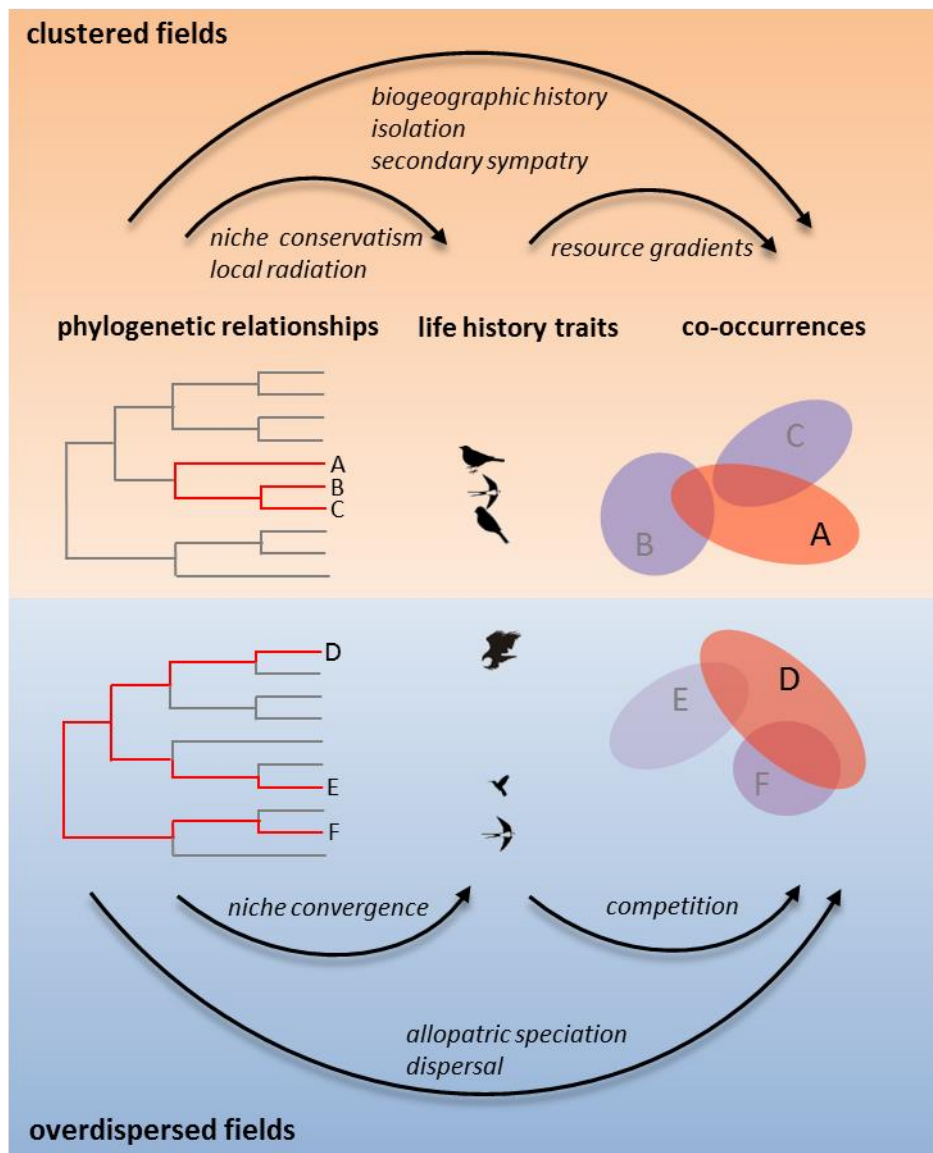
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792 **Table 2.** Performances of regression models relating bird species' phylogenetic fields to  
793 their ecological traits.  $\Delta$ AIC values express the difference between a model with species'  
794 traits + main zoogeographic region of occurrence, and a model with regions only.  
795 Positive  $\Delta$ AIC values  $>2$  (highlighted in bold) indicate that ecological traits improve the  
796 likelihood of the model relative to a model with regions only. Pagel's  $\lambda$  measures the  
797 strength of the phylogenetic correlation structure in phylogenetic regressions.  $\Delta$ AIC and  
798 Pagel's  $\lambda$  are shown as mean  $\pm$  SD over 100 models in which phylogenetic fields and  
799 phylogenetic covariance matrices (in phylogenetic regressions) are derived from 100  
800 phylogenetic trees drawn from Jetz et al. (2012)'s original Monte Carlo Markov chains.

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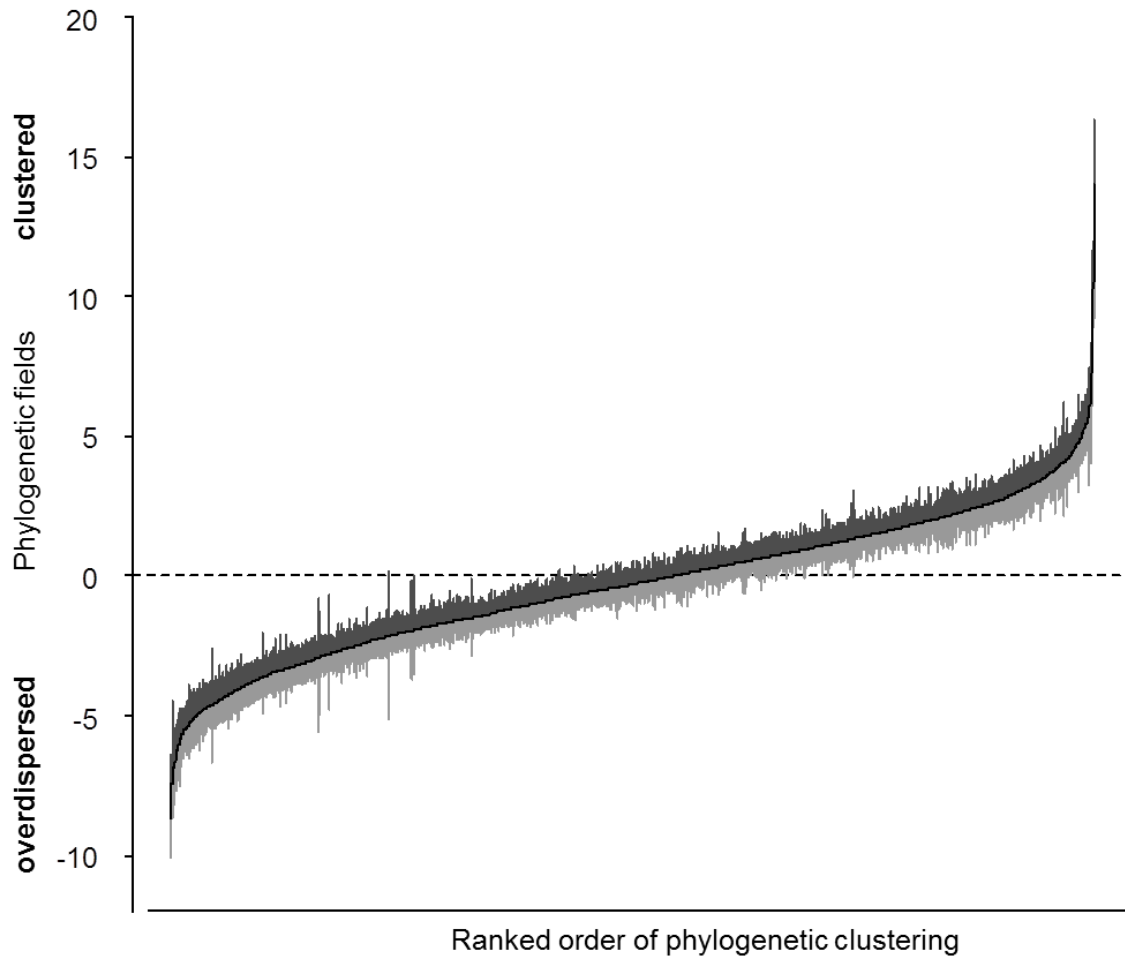
Trait category	Non-phylogenetic regression	Phylogenetic regression	
	$\Delta$ AIC	$\Delta$ AIC	Pagel's $\lambda$
<b>Habitat use</b>	$-1.23 \pm 0.57$	$-0.64 \pm 0.49$	$0.44 \pm 0.03$
<b>Dietary guild</b>	<b><math>169.66 \pm 7.94</math></b>	$-16.24 \pm 0.70$	$0.44 \pm 0.03$
<b>Mobility</b>	<b><math>121.59 \pm 6.45</math></b>	<b><math>67.07 \pm 5.56</math></b>	$0.44 \pm 0.03$
<b>Body size</b>	<b><math>131.12 \pm 10.47</math></b>	<b><math>3.83 \pm 0.89</math></b>	$0.44 \pm 0.03$
<b>Temperature</b>	<b><math>63.63 \pm 7.28</math></b>	<b><math>91.00 \pm 9.54</math></b>	$0.43 \pm 0.03$

## FIGURE LEGENDS

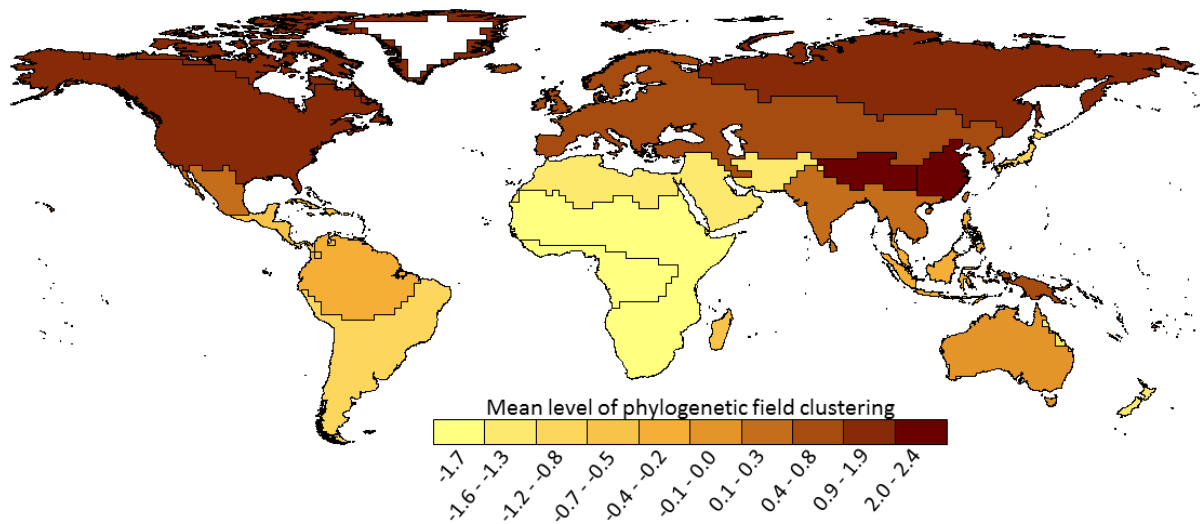


**Figure 1.** Conceptual representation of phylogenetic fields based on phylogenetic relationships, traits and species co-occurrences. Phylogenetic fields reflect the phylogenetic structure of the species assemblage that occurs within the geographic range of a focal species. For species A, the co-occurrences of species B and C lead to a clustered field (shown in red in the phylogeny), while species D has a phylogenetically overdispersed field with species E and F. Several evolutionary, biogeographic, and ecological processes may affect species co-occurrences and can be mediated via species traits.

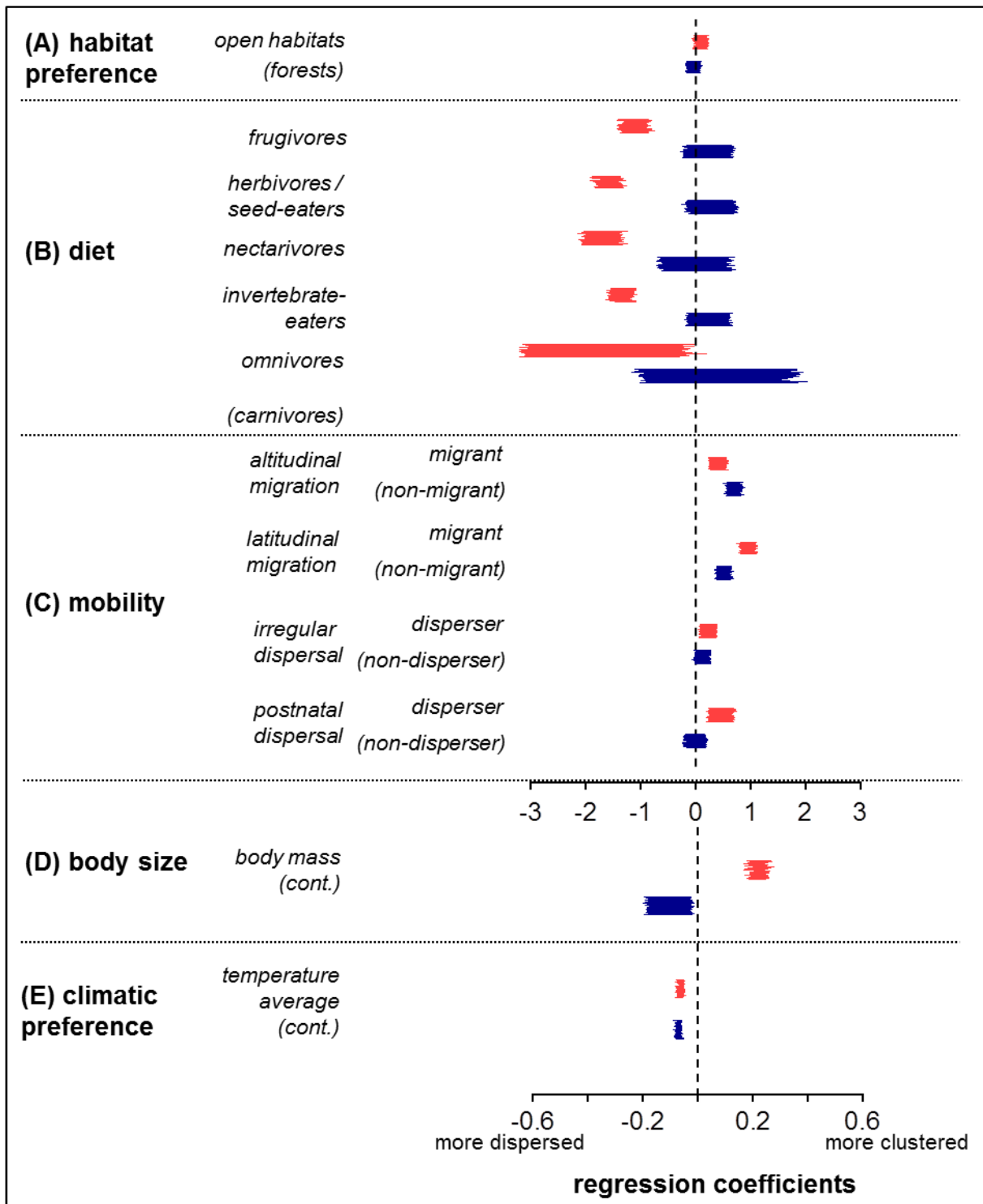




**Figure 2.** Distribution of phylogenetic fields of 8164 bird species, ranked by increasing order of phylogenetic clustering. Phylogenetic fields vary from species that co-occur with less closely related species across their geographic range (overdispersion, negative values) to those that co-occur with more closely related species (clustering, positive values) compared to a null expectation of phylogenetically random assemblages. For each species, phylogenetic fields are represented by their mean (solid line) and 5–95% quantiles (grey shades) across 100 replicated phylogenetic trees.



**Figure 3.** Variation of bird phylogenetic fields across zoogeographic regions. The map shows phylogenetic fields averaged across all species present in each of the 19 regions, from regions dominated by overdispersed fields (lighter colors) to clustered fields (darker colors). Quantile classification is shown.



**Figure 4.** Effects of ecological traits on phylogenetic fields of birds, estimated as regression coefficients in non-phylogenetic regressions (red) and phylogenetic regressions (blue). The 95% confidence intervals are reported for 100 models, each based on a different phylogenetic tree drawn from Jetz et al. (2012)’s original Monte Carlo Markov chains. For categorical traits

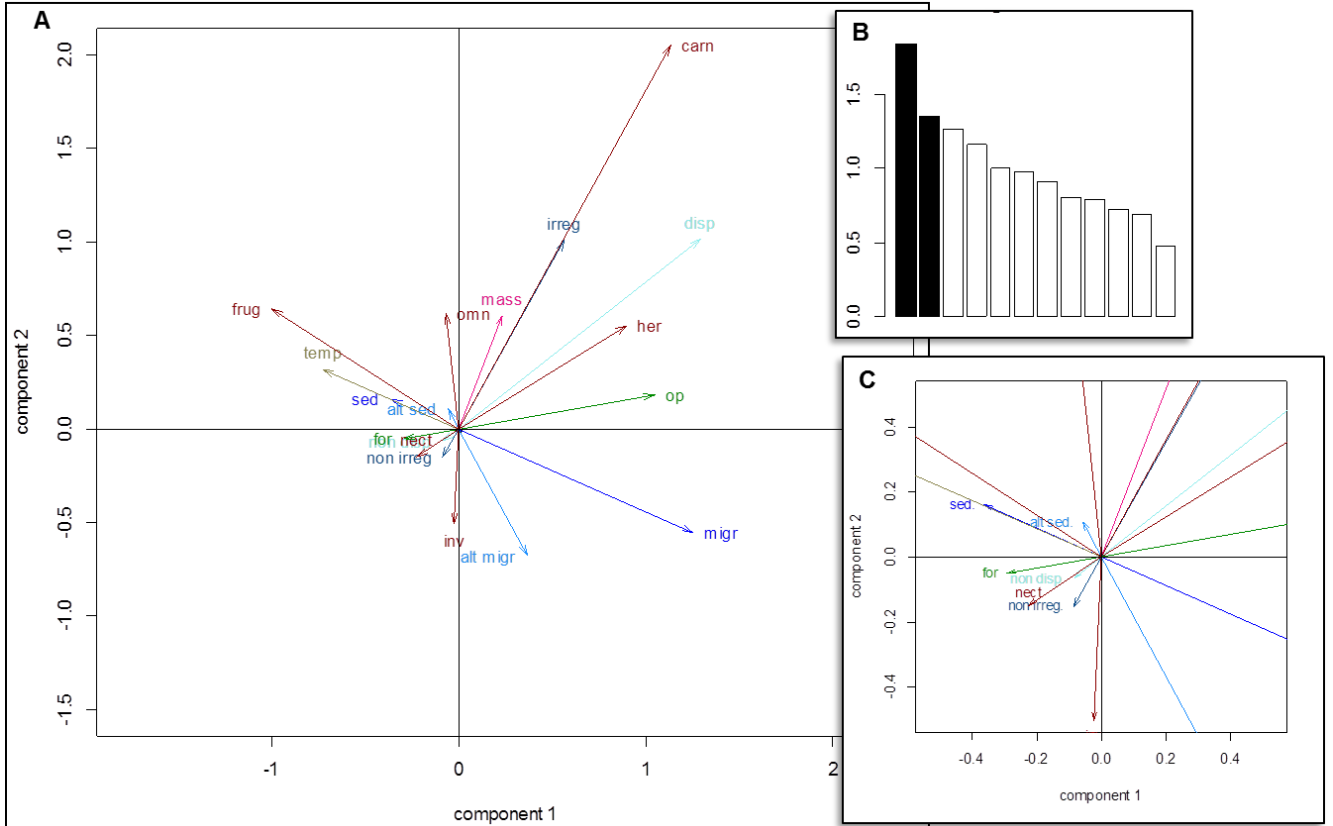
(A: habitat preference; B: dietary guilds; C: mobility), effects are expressed as the difference of phylogenetic fields relative to a reference level fixed to 0 (in brackets). Slope coefficients are reported for continuous traits (D: body size and E: climatic preference). All regressions include species' main zoogeographic region of occurrence as a covariate.

## APPENDIX 1

### Correlations among ecological traits in 6266 bird species, as revealed by a Hill & Smith analysis.

**Figure S4.** (A) Scores of each trait on the two first components of the Hill & Smith multivariate space. Directions of arrows reflect the correlation between traits and the two components. Lengths of arrows are proportional to the influence of traits on each component. Each trait category is represented in a different color (green: habitat preference; red: dietary guild; blue: mobility; pink: body mass; brown: temperature preference). (B) Barplot of the eigenvalues; the two first components retained for the analysis are shown in black. (C) Zoom on the center of the multivariate space. Habitat preference: open-habitat (**op**) vs forest (**for**) – Dietary guilds: carnivores (**carn**), herbivores and seed eaters (**her**), frugivores (**frug**), invertebrate eaters (**inv**), nectarivores (**nect**), omnivores (**omn**) – Mobility: latitudinal migrants (**migr**) vs sedentary species (**sed**), altitudinal migrants (**alt migr**) vs sedentary species (**alt sed**), postnatal dispersers (**disp**) vs non dispersing species (**non disp**), irregular dispersers (**irreg**) vs non dispersing species (**non irreg**) – Body mass (continuous variable: **mass**) – Temperature preference (continuous variable: **temp**)





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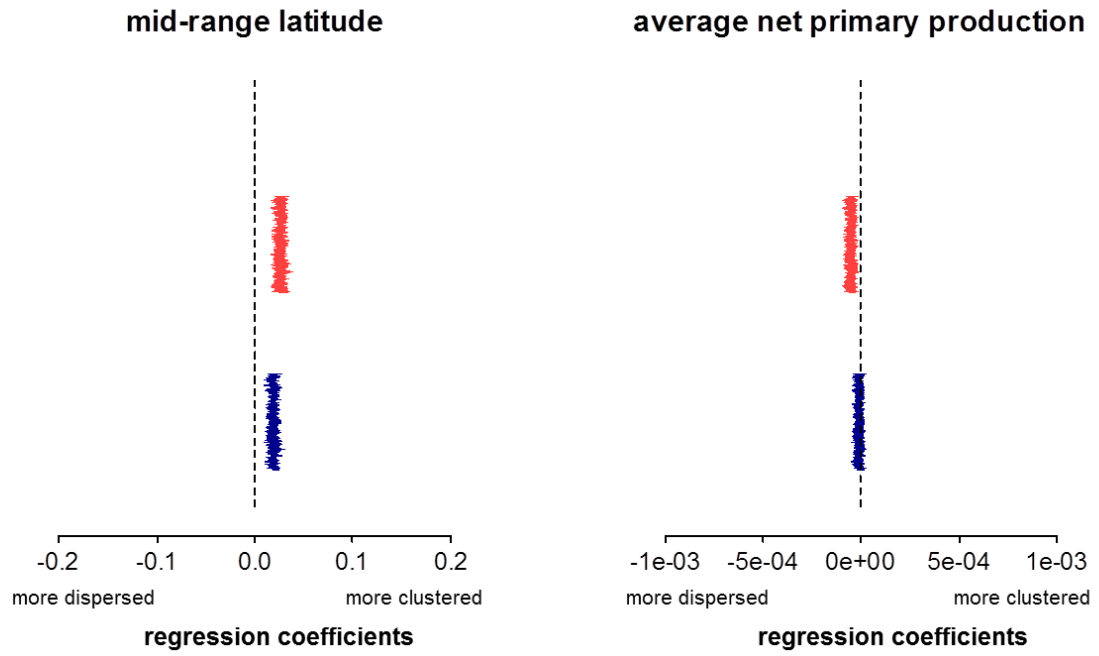
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5 **APPENDIX 2**

6 **Relationships between phylogenetic fields and species' mid-range latitude and**  
7 **range-averaged net primary production.**

8

9 **Figure S1.** Effects of ecological traits on phylogenetic fields of birds, estimated as  
10 regression coefficients in non-phylogenetic regressions (red) and phylogenetic  
11 regressions (blue). (A) Mid-range latitude was computed for the 8164 bird species as the  
12 average latitude of the centroids of grid cells embedded in each species' distribution. (B)  
13 Net Primary Production is expressed in gC/m<sup>2</sup>/y from the MODerate resolution Imaging  
14 Spectroradiometer (MODIS, Zhao et al. 2005). Data are available at a resolution of  
15 approximately 1 km and mean values were extracted for each grid cell, then averaged  
16 over each of the 8164 bird species' range. 95% confidence intervals are reported for 100  
17 models, each based on a different phylogenetic tree drawn from Jetz et al. (2012)'s  
18 original Monte Carlo Markov chains. Slope coefficients are reported for both traits. The  
19 two regressions include species' main zoogeographic region of occurrence as a covariate.  
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**REFERENCES**

Zhao, M. S., F. A. Heinsch, R. R. Nemani, and S. W. Running. 2005. Improvements of the MODIS terrestrial gross and net primary production global data set. *Remote Sensing of Environment* 95:164-176.



29 **APPENDIX 3**

30 **Effects of marginal co-occurrences on phylogenetic fields – trait relationships.**

31

32 To investigate how marginally co-occurring species influence the relationship between  
33 phylogenetic fields and traits, we recomputed the  $NRI_{FS}$  by excluding species present on  
34 less than 5% or 10% of the focal species' range. We subsequently re-evaluated the non-  
35 phylogenetic and phylogenetic regressions in the same way as described for the main  
36 analysis.  $\Delta AIC$  and Pagel's  $\lambda$  are given in Tables S3 (5% threshold) and S4 (10%  
37 threshold), framed similarly as Table 2 in the main text. Figures S2 (5% threshold) and  
38 S3 (10% threshold) are interpreted similarly as Figure 4 (main text).

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52 **Table S3.**

Trait category	Non-phylogenetic regression	Phylogenetic regression	
	$\Delta$ AIC	$\Delta$ AIC	Pagel's $\lambda$
Habitat use	0.50 $\pm$ 1.49	-1.55 $\pm$ 0.40	0.46 $\pm$ 0.03
Dietary guild	<b>497.49<math>\pm</math>28.58</b>	-5.21 $\pm$ 0.67	0.46 $\pm$ 0.03
Mobility	<b>111.26 <math>\pm</math> 7.93</b>	<b>40.58 <math>\pm</math> 4.36</b>	0.46 $\pm$ 0.03
Body mass	<b>490.60 <math>\pm</math> 34.69</b>	-0.85 $\pm$ 0.44	0.48 $\pm$ 0.03
Temperature	<b>73.74 <math>\pm</math> 8.02</b>	<b>134.61 <math>\pm</math> 13.08</b>	0.45 $\pm$ 0.03

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54 **Table S4.**

Trait category	Non-phylogenetic regression	Phylogenetic regression	
	$\Delta$ AIC	$\Delta$ AIC	Pagel's $\lambda$
Habitat use	0.42 $\pm$ 1.57	-1.35 $\pm$ 0.43	0.47 $\pm$ 0.03
Dietary guild	<b>632.20<math>\pm</math>38.18</b>	-5.87 $\pm$ 0.75	0.46 $\pm$ 0.03
Mobility	<b>123.34 <math>\pm</math> 8.64</b>	<b>28.31 <math>\pm</math> 2.62</b>	0.47 $\pm$ 0.03
Body mass	<b>659.54 <math>\pm</math> 45.02</b>	-1.12 $\pm$ 0.36	0.50 $\pm$ 0.03
Temperature	<b>76.10 <math>\pm</math> 8.83</b>	<b>147.20 <math>\pm</math> 15.44</b>	0.46 $\pm$ 0.03

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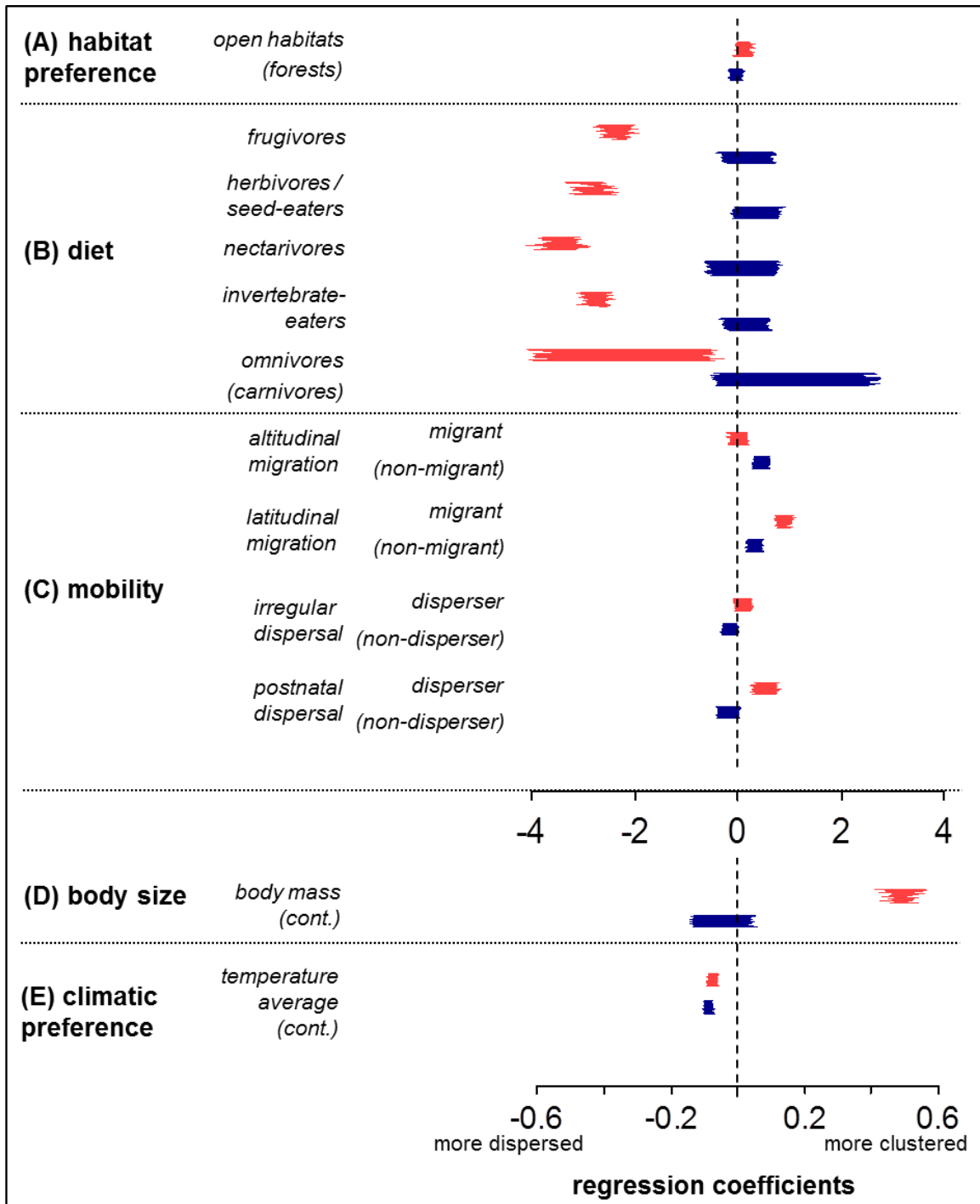
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67 **Figure S2.** Trait effects on phylogenetic fields (for details see Fig. 4 in main text). Here,  
 68 phylogenetic fields were calculated by excluding species which co-occur with the focal  
 69 species over less than 5% of its range.

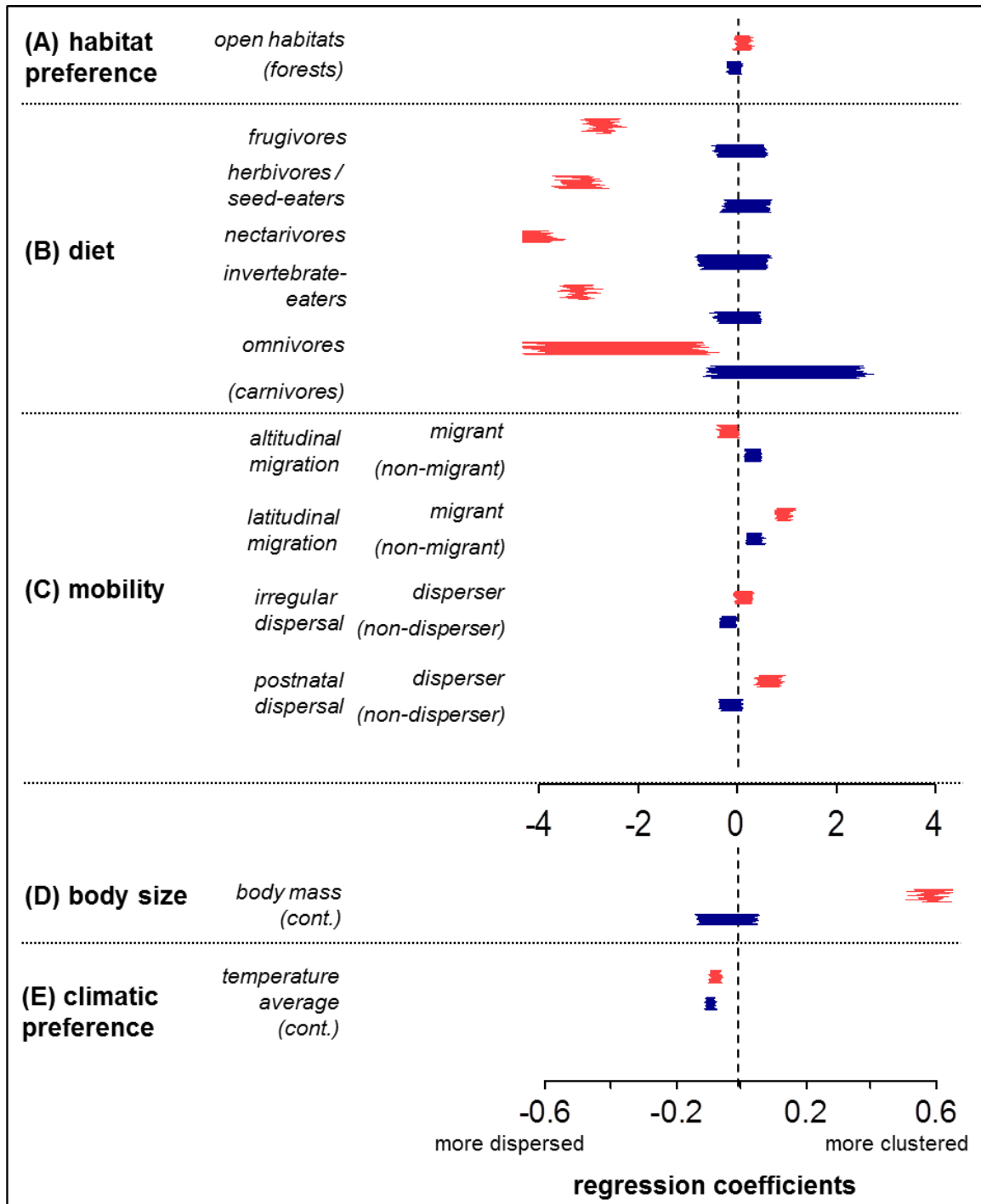
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72 **Figure S3.** Trait effects on phylogenetic fields (for details see Fig. 4 in main text). Here,  
 73 phylogenetic fields were calculated by excluding species which co-occur with the focal  
 74 species over less than 10% of its range.

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