

## **Supporting information**

**Daniel Sol, Joan Garcia-Porta, Cesar González-Lagos, Alex L. Pigot, Christopher Trisos & Joseph A. Tobias**

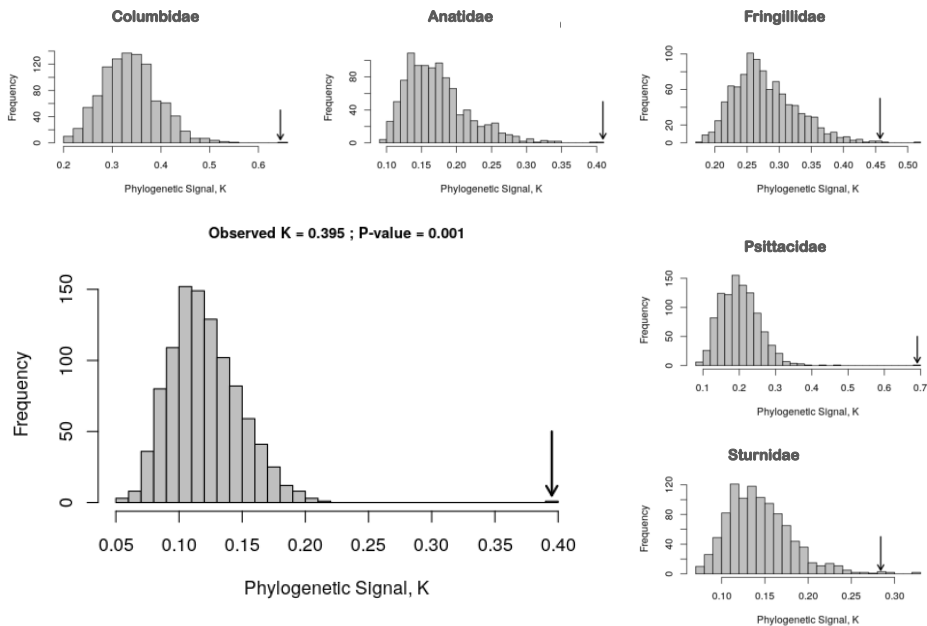
*A test of Darwin's conundrum in birds reveals enhanced invasion success in presence of close relatives*

### **This PDF file includes:**

Figure S1  
Tables S1 to S10

### **Other Supplementary Materials for this manuscript include the following:**

Data and codes, available in <https://doi.org/10.5281/zenodo.5076098>.



**Figure S1. Evidence for niche conservatism in all bird species sampled in the main analyses.** Main panel shows the complete sample ( $n = 1723$  species) and smaller panels show individual clades. The observed  $K$  is a multivariate estimation of phylogenetic effects for all major axes of ecological niche variation extracted from a Principal Coordinates Analysis (PCoA). Ecological niche data included morphological traits, diet and foraging strategy. All observed  $K$  values (illustrated by arrows) were higher than expected by randomly shuffling species in the phylogeny, whether estimated for all the species (invaders and natives) or for the five avian families better represented among the studied communities.

**Table S1.** Potential confounding variables used as co-variates in the models. For references, see the main text.

<i>Variable</i>	<i>Rationale</i>	<i>Measure</i>	<i>Source</i>
<i>Body size</i>	Body size may affect detectability	First principal component of a PCA of nine morphological traits	Pigot et al. (2020)
<i>Geographic range</i>	Species with broad geographical range may have increased probability of finding close relatives.	Number of cells where the species occurs from a 110x110 km equal area grid in a Behrman equal area projection	Jetz et al. (2014)
<i>ED</i>	Evolutionary distinctiveness of the exotic species may affect the probability of finding close relatives.	Weighted sum of the branch lengths from the root of the full avian tree to the tip, with weights determined as 1/number of tips sharing that branch	Jetz et al. (2012)
<i>Realm</i>	The realm of origin of the exotic species may affect the likelihood of finding close relatives.	Afrotropic, Australian, Indomalayan, Nearctic, Neotropic, Oceania and Palearctic	Pigot et al. (2020)
<i>Trophic level</i>	The trophic level can affect the density of the species.	Carnivore, Herbivore, Omnivore and Scavenger	Pigot et al. (2020)
<i>Native species richness</i>	A high number of native species in the sampled community can increase the likelihood of finding close relatives.	Total number of native species detected during the surveys	Published surveys
<i>Season</i>	The season where the survey was conducted can affect native species composition.	Breeding, Non-breeding and Year-round	Published surveys
<i>Survey method</i>	The method used to conduct the survey can affect species detectability.	Cell records, Line count, Line-point count and Point count	Published surveys

**Table S2.** Occurrence of invasive bird species in the context of their evolutionary relatedness to native species in recipient communities. Results shown are from Bayesian binomial mixed models accounting for variation in the occurrence of invading species as a function of their mean ( $MD_{Phy}$ ) phylogenetic distance to native species. Comparisons are made between communities in the same region. Variables are defined in Table S1; CI is the credible interval.

<i>Predictors</i>	<i>Log-Odds</i>	<i>CI (95%)</i>
<i>Intercept</i>	-5.59	-9.21 – -1.65
<i>MD<sub>Phy</sub></i>	1.41	0.48 – 2.47
<i>Habitat alteration: High</i>	2.46	1.26 – 3.70
<i>Body size</i>	-0.22	-0.52 – 0.13
<i>Season: Non-breeding</i>	-0.15	-0.87 – 0.65
<i>Season: Year-round</i>	-0.87	-1.70 – -0.03
<i>Survey: Line count</i>	0.98	-0.85 – 3.04
<i>Survey: Line-point count</i>	3.84	0.51 – 8.21
<i>Survey: Point count</i>	1.31	-0.61 – 3.29
<i>Geographic range size (log-transformed)</i>	0.99	0.23 – 1.93
<i>ED (log-transformed)</i>	0.57	-1.00 – 2.05
<i>Native species richness</i>	0.01	-0.01 – 0.01
<i>Trophic level: Herbivore</i>	-0.67	-2.35 – 0.82
<i>Trophic level: Omnivore</i>	-0.39	-2.08 – 1.12
<i>Realm: Australian</i>	0.52	-1.06 – 2.08
<i>Realm: Indomalayan</i>	0.56	-0.96 – 2.09
<i>Realm: Nearctic</i>	-0.05	-1.63 – 1.84
<i>Realm: Neotropic</i>	0.19	-1.54 – 1.58
<i>Realm: Palearctic</i>	1.22	0.08 – 2.43
<i>MD<sub>Phy</sub>*Habitat alteration (High)</i>	-3.23	-5.01 – -1.44
<b>Random Effects</b>		
$\sigma^2$	3.29	-
$\tau_{00phylo}$	0.91	-
$\tau_{00region}$	0.69	-
$\tau_{00species}$	0.75	-
<i>ICC</i>	0.42	-
<i>N<sub>phylo</sub></i>	62	-
<i>N<sub>species</sub></i>	62	-
<i>N<sub>region</sub></i>	46	-
<i>Observations</i>	3326	-
<i>Marginal R<sup>2</sup> / Conditional R<sup>2</sup></i>	0.179 / 0.317	-

**Table S3.** Occurrence of invasive bird species in the context of their evolutionary relatedness to native species in recipient communities. Results shown are from Bayesian binomial mixed models accounting for variation in the occurrence of invading species as a function of their nearest ( $ND_{Phy}$ ) phylogenetic distance to native species. Comparisons are made between communities in the same region. Variables defined in Table S1.

<i>Predictors</i>	<i>Log-Odds</i>	<i>CI (95%)</i>
<i>Intercept</i>	-3.95	-7.57 – 0.27
<i>ND<sub>Phy</sub></i>	0.41	-0.16 – 0.96
<i>Habitat alteration: High</i>	1.43	0.88 – 2.01
<i>Body size</i>	-0.19	-0.45 – 0.05
<i>Season: Non-breeding</i>	-0.09	-0.85 – 0.83
<i>Season: Year-round</i>	-0.83	-1.75 – 0.02
<i>Survey: Line count</i>	0.79	-1.28 – 3.25
<i>Survey: Line-point count</i>	3.61	-0.13 – 7.68
<i>Survey: Point count</i>	1.15	-1.08 – 3.74
<i>Geographic range (log-transformed)</i>	0.69	-0.15 – 1.56
<i>ED (log-transformed)</i>	0.81	-0.74 – 2.32
<i>Native species richness</i>	0.01	-0.01 – 0.01
<i>Trophic level: Herbivore</i>	-0.72	-2.08 – 0.91
<i>Trophic level: Omnivore</i>	-0.48	-2.01 – 1.24
<i>Realm: Australian</i>	0.47	-0.91 – 1.96
<i>Realm: Indomalayan</i>	0.64	-0.86 – 2.01
<i>Realm: Nearctic</i>	0.07	-1.77 – 1.80
<i>Realm: Neotropic</i>	0.21	-1.08 – 1.45
<i>Realm: Palearctic</i>	1.51	0.34 – 2.54
<i>ND<sub>Phy</sub>*Habitat alteration (High)</i>	-2.53	-3.61 – -1.49
<b>Random Effects</b>		
$\sigma^2$	3.29	-
$\tau_{00phylo}$	0.36	-
$\tau_{00region}$	0.91	-
$\tau_{00species}$	0.89	-
<i>ICC</i>	0.39	-
<i>N<sub>phylo</sub></i>	62	-
<i>N<sub>species</sub></i>	62	-
<i>N<sub>region</sub></i>	46	-
<i>Observations</i>	3326	-
<i>Marginal R<sup>2</sup> / Conditional R<sup>2</sup></i>	0.190 / 0.318	-

**Table S4.** Invasion success of bird species in the context of their evolutionary relatedness to native species in recipient communities. Results shown are from Bayesian Gaussian mixed models accounting for variation in the abundance of invading species in communities where it was present as a function of their mean ( $MD_{Phy}$ ) phylogenetic distance to native species. Variables defined in Table S1.

<i>Predictors</i>	<i>Estimates</i>	<i>CI (95%)</i>
<i>Intercept</i>	-6.16	-8.91 – -3.39
<i>MDPhy</i>	-0.84	-1.54 – -0.15
<i>Habitat alteration: High</i>	1.58	0.68 – 2.47
<i>Body size</i>	0.01	-0.15 – 0.16
<i>Season: Non-breeding</i>	0.26	-0.39 – 0.92
<i>Season: Year-round</i>	0.18	-0.56 – 0.92
<i>Survey: Line count</i>	-0.01	-1.85 – 1.82
<i>Survey: Line-point count</i>	0.08	-2.53 – 2.81
<i>Survey: Point count</i>	0.38	-1.48 – 2.17
<i>Geographic range (log-transformed)</i>	0.87	0.25 – 1.46
<i>ED (log-transformed)</i>	0.12	-0.83 – 1.02
<i>Native species richness</i>	-0.03	-0.04 – -0.02
<i>Trophic level: Herbivore</i>	-0.47	-1.37 – 0.46
<i>Trophic level: Omnivore</i>	-0.64	-1.62 – 0.33
<i>Realm: Australian</i>	0.31	-0.71 – 1.31
<i>Realm: Indomalayan</i>	0.65	-0.23 – 1.56
<i>Realm: Nearctic</i>	0.88	-0.27 – 2.04
<i>Realm: Neotropic</i>	0.46	-0.60 – 1.44
<i>Realm: Palearctic</i>	1.01	0.26 – 1.78
<i><math>MD_{Phy}</math>*Habitat alteration (High)</i>	-2.17	-3.60 – -0.73
<b>Random Effects</b>		
$\sigma^2$	1.67	-
$\tau_{00phylo}$	0.09	-
$\tau_{00region}$	0.61	-
$\tau_{00species}$	0.19	-
<i>ICC</i>	0.35	-
$N_{phylo}$	64	-
$N_{species}$	64	-
$N_{region}$	51	-
<i>Observations</i>	1673	-
<i>Marginal <math>R^2</math> / Conditional <math>R^2</math></i>	0.250 / 0.386	-

**Table S5.** Invasion success of bird species in the context of their evolutionary relatedness to native species in recipient communities. Results shown are from Bayesian Gaussian mixed models accounting for variation in the abundance of invading species as a function of their nearest ( $ND_{Phy}$ ) phylogenetic distance to native species in the recipient community. Variables defined in Table S1.

<i>Predictors</i>	<i>Estimates</i>	<i>CI (95%)</i>
<i>Intercept</i>	-6.39	-9.24 – -3.54
<i>ND<sub>Phy</sub></i>	-0.31	-0.77 – 0.17
<i>Habitat alteration: High</i>	0.79	0.35 – 1.21
<i>Body size</i>	-0.02	-0.19 – 0.17
<i>Season: Breeding</i>	0.25	-0.38 – 0.91
<i>Season: Year-round</i>	0.18	-0.53 – 0.87
<i>Survey: Line count</i>	-0.19	-1.85 – 1.62
<i>Survey: Line-point count</i>	-0.07	-2.51 – 2.53
<i>Survey: Point count</i>	0.23	-1.47 – 2.07
<i>Geographic range (log-transformed)</i>	0.83	0.20 – 1.44
<i>ED (log-transformed)</i>	0.05	-0.91 – 1.02
<i>Native species richness</i>	-0.03	-0.04 – -0.02
<i>Trophic level: Herbivore</i>	-0.52	-1.44 – 0.45
<i>Trophic level: Omnivore</i>	-0.66	-1.67 – 0.41
<i>Realm: Australian</i>	0.41	-0.62 – 1.46
<i>Realm: Indomalayan</i>	0.71	-0.23 – 1.61
<i>Realm: Nearctic</i>	0.99	-0.16 – 2.18
<i>Realm: Neotropic</i>	0.62	-0.46 – 1.65
<i>Realm: Palearctic</i>	1.06	0.24 – 1.81
<i>ND<sub>Phy</sub>*Habitat alteration (High)</i>	-1.28	-2.23 – -0.30
<b>Random Effects</b>		
$\sigma^2$	1.67	-
$\tau_{00phylo}$	0.15	-
$\tau_{00region}$	0.58	-
$\tau_{00species}$	0.19	-
<i>ICC</i>	0.36	-
<i>N<sub>phylo</sub></i>	64	-
<i>N<sub>species</sub></i>	64	-
<i>N<sub>region</sub></i>	51	-
<i>Observations</i>	1673	-
<i>Marginal R<sup>2</sup> / Conditional R<sup>2</sup></i>	0.238 / 0.386	-

**Table S6.** Occurrence of invasive bird species in the context of their functional relatedness to native species in recipient communities. Results show Bayesian binomial mixed models accounting for variation in the occurrence of invading species as a function of their mean functional distance ( $MD_{Func}$ ) to native species in the recipient communities. Functional distance is calculated from a set of ecologically informative functional traits, including morphology, diet and habitat use. Comparisons are made between communities in the same region, accounting for the degree of habitat alteration.

<i>Predictors</i>	<i>Log-Odds</i>	<i>CI (95%)</i>
Intercept	-1.20	-2.78 – 0.23
$MD_{Func}$	2.11	-0.11 – 4.35
Habitat alteration: High	7.07	4.62 – 9.55
$MD_{Func}$ *Habitat alteration (High)	-15.57	-21.30 – -9.96
<b>Random Effects</b>		
$\sigma^2$	0.01	
$\tau_{00}$	0.24	
ICC	0.03	
$N_{phylo}$	71	
$N_{species}$	71	
$N_{region}$	53	
Observations	3431	
Marginal $R^2$ / Conditional $R^2$	0.020 / 0.312	



**Table S7.** Occurrence of invasive bird species in the context of their functional relatedness to native species in recipient communities. Results are from Bayesian binomial mixed models accounting for variation in the occurrence of the invader across communities from a same region as a function of their nearest functional distance ( $ND_{\text{Funct}}$ ) to native species in the recipient communities. Comparisons are made between communities in the same region, accounting for the degree of habitat alteration.

<i>Predictors</i>	<i>Log-Odds</i>	<i>CI (95%)</i>
Intercept	2.41	0.90 – 3.92
$ND_{\text{Funct}}$	-8.18	-11.70 – -4.84
Habitat alteration: High	-3.18	-4.24 – -2.16
$ND_{\text{Funct}} * \text{Habitat alteration (High)}$	9.69	6.31 – 13.35
<b>Random Effects</b>		
$\sigma^2$	0.01	
$\tau_{00}$	0.24	
ICC	0.03	
$N_{\text{phylo}}$	71	
$N_{\text{species}}$	71	
$N_{\text{region}}$	53	
Observations	3431	
Marginal $R^2$ / Conditional $R^2$	0.019 / 0.312	

**Table S8.** Invasion success of bird species in the context of their functional relatedness to native species in recipient communities. Results are from Bayesian Gaussian mixed models accounting for variation in the abundance of the invader in communities where it was present as a function of their mean functional distance ( $MD_{Funct}$ ) to native species in the recipient communities. Comparisons are made between communities in the same region, accounting for the degree of habitat alteration.

<i>Predictors</i>	<i>Estimates</i>	<i>CI (95%)</i>
Intercept	-4.01	-5.01 – -3.05
$MD_{Func}$	-1.92	-3.66 – -0.18
Habitat alteration: High	4.24	2.61 – 5.92
$MD_{Func}$ *Habitat alteration (High)	-8.81	-12.74 – -4.99
<b>Random Effects</b>		
$\sigma^2$	0.88	
$\tau_{00}$	1.79	
ICC	0.33	
$N_{phylo}$	64	
$N_{species}$	64	
$N_{region}$	51	
Observations	1673	
Marginal $R^2$ / Conditional $R^2$	0.041 / 0.373	

**Table S9.** Invasion success of bird species in the context of their functional relatedness to native species in recipient communities. Results are from Bayesian Gaussian mixed models

accounting for variation in the abundance of the invader in communities where it was present as a function of their nearest phylogenetic distance ( $ND_{\text{Funct}}$ ) to native species in the recipient communities. Comparisons are made between communities in the same region, accounting for the degree of habitat alteration.

---



---

<i>Predictors</i>	<i>Estimates</i>	<i>CI (95%)</i>
Intercept	-3.60	-4.60 – -2.66
$ND_{\text{Funct}}$	-2.45	-4.95 – -0.00
Habitat alteration: High	-1.65	-2.40 – -0.90
$ND_{\text{Funct}} * \text{Habitat alteration (High)}$	3.79	1.37 – 6.20
<b>Random Effects</b>		
$\sigma^2$	0.94	
$\tau_{00}$	1.74	
ICC	0.35	
$N_{\text{phylo}}$	64	
$N_{\text{species}}$	64	
$N_{\text{region}}$	51	
Observations	1673	
Marginal $R^2$ / Conditional $R^2$	0.021 / 0.371	

**Table S10.** Predictive power of models for the effect of mean ( $MD_{\text{Phy}}$ ) and nearest ( $ND_{\text{Phy}}$ ) phylogenetic distance on invasiveness (abundance) when these predictors are used alone or in combination with functional diversity ( $MD_{\text{Funct}}$  and  $ND_{\text{Funct}}$ ) and/or habitat alteration (ALT, categorized as high and low alteration levels). ELPD (with associated standard error, se) is the

expected log pointwise predictive probabilities for models based on the Widely Applicable Information Criterion (WAIC) and expressed as differences in relation to the best model.

<b>Models for mean distances</b>	<b>elpd diff</b>	<b>se diff</b>
<i>Abundance ~ MD<sub>phy</sub> + MD<sub>Funct</sub>*ALT + (1   phylo) + (1   species) + (1   region)</i>	0.0	0.0
<i>Abundance ~ MD<sub>phy</sub>*ALT + MD<sub>Funct</sub>*ALT + (1   phylo) + (1   species) + (1   region)</i>	-1.8	1.1
<i>Abundance ~ MD<sub>phy</sub>*ALT + MD<sub>Funct</sub> + (1   phylo) + (1   species) + (1   region)</i>	-5.6	4
<i>Abundance ~ MD<sub>phy</sub> + (1   phylo) + (1   species) + (1   region)</i>	-17.4	6.7
<i>Abundance ~ MD<sub>Funct</sub> + (1   phylo) + (1   species) + (1   region)</i>	-17.5	6.8

<b>Models for nearest distances</b>	<b>elpd diff</b>	<b>se diff</b>
<i>Abundance ~ ND<sub>phy</sub>*ALT + ND<sub>Funct</sub>*ALT + (1   phylo) + (1   species) + (1   region)</i>	0.0	0.0
<i>Abundance ~ ND<sub>phy</sub> + ND<sub>Funct</sub>*ALT + (1   phylo) + (1   species) + (1   region)</i>	-1.1	2.3
<i>Abundance ~ ND<sub>phy</sub>*ALT + ND<sub>Funct</sub> + (1   phylo) + (1   species) + (1   region)</i>	-1.5	2.7
<i>Abundance ~ ND<sub>Funct</sub> + (1   phylo) + (1   species) + (1   region)</i>	-14.3	7.4
<i>Abundance ~ ND<sub>phy</sub> + (1   phylo) + (1   species) + (1   region)</i>	-16.0	7.8