Genome size and geographic range size in birds (#50951)

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Genome size and geographic range size in birds

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What causes that some species occur in small restricted areas while others are distributed in the entire world? Environmental heterogeneity increases with the area as the number of species does. Hence, a variety of biotic and abiotic conditions in species having large range sizes should enforce adaptations which are often linked with the genome size and the number of chromosomes. Therefore, there should be a positive association between genome size and geographic range size. Alternatively, high cognitive abilities should be favoured by natural selection to cope with the variety of conditions in organisms having large geographic ranges. We tested these hypotheses in birds, the most mobile terrestrial animals. Using phylogenetic partial least squares and phylogenetic path analyses we demonstrated that range size in birds is positively associated with genome size but not with the number of chromosomes. Moreover, brain mass had no effect on the range size and body mass possibly had a weak negative effect. However, our models explained a low proportion of variation in range size. Hence, selection indeed may impose larger genomes in birds occurring in larger areas but other explanations are likely.

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Abstract

What causes that some species occur in small restricted areas while others are distributed in the entire world? Environmental heterogeneity increases with the area as the number of species does. Hence, a variety of biotic and abiotic conditions in species having large range sizes should enforce adaptations which are often linked with the genome size and the number of chromosomes. Therefore, there should be a positive association between genome size and geographic range size. Alternatively, high cognitive abilities should be favoured by natural selection to cope with the variety of conditions in organisms having large geographic ranges. We tested these hypotheses in birds, the most mobile terrestrial animals. Using phylogenetic partial least squares and phylogenetic path analyses we demonstrated that range size in birds is positively associated with genome size but not with the number of chromosomes. Moreover, brain mass had no effect on the range size and body mass possibly had a weak negative effect. However, our models explained a low proportion of variation in range size. Hence, selection indeed may impose larger genomes in birds occurring in larger areas but other explanations are likely.

Key words: chromosomes, distribution, evolution, gene, macroecology

Introduction

There is enormous variation in the sizes of species' geographic ranges (Gaston 2003). Several explanations of the variation exist with leading hypotheses invoking traits such as body size (Cambefort 1994, Gaston & Blackburn 2000), dispersal ability (Lester et al. 2007, Laube et al. 2013) and niche breadth (Garcia-Barros & Romo Benito 2010). The increase in geographic range covaries with the environmental variability (e.g. climate) which is considered as a major selective force in the evolution (Lee-Yaw & Irwin 2012, Sayol et al. 2016, Liedtke et al. 2018). This suggests that species should possess numerous traits to live in the variable environment (Gaston & Blackburn 2000, Zamudio et al. 2016) and the traits should have strong heritable component thus be linked with the number of genes (Zhang et al. 2014). Hence, genome size may be an important predictor of the species range size but can also affect other features that are likely subject to natural selection.

The genome size in eukaryotes may be defined as the C-value which is the amount of DNA per haploid genome and number of chromosomes. There is a non-linear positive relationship between the genome size and the number of genes (Hou & Lin 2009). The eukaryotic genome is composed of a large amount of repetitive DNA, mobile elements, deletions, protein-coding exons and noncoding introns (John & Miklos 1988). However, the physical size of the genome has consequences for organismal fitness and may thus be subject to selection (Petrov 2001). Several concepts postulate an adaptive function for this extra DNA given that DNA abundance, rather than its information content, can have a direct and significant effect on phenotype (Petrov 2001). For instance, a larger genome size could be adaptive because it directly or indirectly increases nucleus and cell volumes (Cavalier-Smith 1978), body size (Gregory 2005), may buffer fluctuations in the concentration of enzymes or protects coding DNA from mutation (Hsu 1975, Janssen et al. 2018). Likewise, genome size correlates with cell life cycle complexity (Gregory 2002, Yu et al. 2019) and basal metabolism (Vinogradov 1997), tissue differentiation and developmental rates (Sessions & Larson 1987, Xia 1995, Wyngaard et al. 2005).

Interestingly, in animals, the genome size (C-value) and the number of chromosomes are weakly positively correlated with each other (Vinogradov 1988, Elliott & Gregory 2015). The number of chromosomes plays important functions in speciation, sex determination and developmental modes (King 1995, Warchałowska-Śliwa et al. 2011, Blackmon et al. 2017, Lucek 2018). Thus, it is possible that the number of chromosomes may also be positively associated with the variation in geographic range size (Guo et al. 2003, Martinez et al. 2017).

Among different organisms birds are the unique and useful model group to test many evolutionary hypotheses. They have constrained genome size compared to other vertebrates. However, avian genomic diversity covaries with adaptations to different lifestyles and convergent evolution of traits (Zhang et al. 2014). Most birds possess flight ability thus they are not as constrained by physical barriers as other organisms. Thus, range size in birds often correlates with dispersal abilities (Böhning-Gaese et al. 2006, Laube et al. 2013). A positive relationship was found between genome size and nucleus/cell size, as well as between genome size and wing loading index, which is interpreted as an indicator of adaptations for efficient flight (Andrews et al. 2009). Hence, one may expect that genome size may be positively linked with the geographic range size in birds.

The alternative (but not mutually exclusive) hypothesis is that large geographic ranges should favour enhanced cognitive skills enabling survival in varying conditions met across these ranges. Cognitive skills are connected with large brains (Reader & Laland 2002, Sol et al. 2005, Emery 2006) and considered to be linked with habitat generalism (Edmunds et al. 2016, Navarrete et al. 2016). Larger brains are indeed more likely to occur in bird species exposed to larger environmental variation throughout their geographic range (Sol et al. 2005, Sayol et al. 2016). Therefore, one may hypothesise that the geographic range size is positively correlated with the brain size. Also, the brain size is strongly correlated with body size (Minias & Podlaszczuk 2017). Thus, body size should always be considered as a covariate in studies on range size and genomes because there is well documented paradigm of overall positive association between body size and range size in animals (Gaston & Blackburn 2000, Newsome et al. 2019)

In this paper, we test the hypothesis that genome size, number of chromosomes and brain size as well as body size are positively associated with geographic range size in birds. Efficient testing of the causality of such relationships on a broad taxonomic scale has proven difficult in the past due to the inter-correlation of these biological traits and their phylogenetic non-independence. Thus, we used phylogenetic generalized least squares and path analyses to control for phylogeny and account for multicollinearity of variables.

Methods

Data collection

Data of bird species ranges were collected from BirdLife International (2019) (http://datazone.birdlife.org/species/requestdis). Data were manipulated in QGIS 3 Nosa. To calculate the area of species ranges we used Bonne equal-area transformation (ESRI: 54024). Only extant native ranges were used (Ravilious et al. 2015). The bird phylogenetic trees (Jetz et al. 2012, 2014) were created in nexus format online (http://birdtree.org). Unfortunately, birdtree.org did not provide any consensus tree of avian taxa. The sets of 1000 trees were downloaded for three data subsets (see below).

Data on species genome size were compiled from the Animal Genome Size Database (http://www.genomesize.com/search.php). This database contains data on both C-value and the number of chromosomes (much less data). We gathered data on the C-value of 637 bird species. To complete data on the number of chromosomes we also used data published by Kretschmer et al. (2018). Data on body mass were taken from Wilman et al (2014). Data on bird brain mass were compiled from three published sources (Fristoe et al. 2017, Minias & Podlaszczuk 2017, Tsuboi et al. 2018). In total, data on 311 species with both brain size and genome size were available. In total we had 65 species that have data on both genome size, chromosome number, brain size and body size All data used in analyses are available in the Supplementary material 1.

Data analysis

We computed three single consensus trees by using strict consensus methods implemented in PAUP* 4.0 (Swofford 2003) from the three sets of 1000 tree downloaded from the birdtree.org. Strict consensus methods show the tree group sequences only if that grouping appears in all of trees of the set. Three consensus trees were used in the subsequent statistical analyses. The branch-lengths for this tree were generated from the fitted branch lengths for the 1000 input trees, using the ‘consensus.edges’, function of the phytools R package (Revell 2012). Tree are visualized with Iroki software (Moore et al. 2020) and are in Figure 1 (2nd tree not shown).

We used phylogenetic generalized least-squares (PGLS) models implemented in nlme package (von Hardenberg & Gonzalez-Voyer 2013, Pinheiro et al. 2019). We used Brownian motion correlation structure in model residuals to account for phylogenetic dependence among species (Münkemüller et al. 2012). Brownian motion is a popular model in comparative biology because it captures the way traits might evolve under a reasonably wide range of scenarios (Münkemüller et al. 2012, Harmon 2019). The dependent variable was bird species ranges size (in km^2). Primary explanatory variables were genome size (C-value) and the number of chromosomes. We also included covariates: body mass and brain mass (residuals form PGLS not explained by the body mass) because they are well linked with environmental variability and other species traits. Body and brain masses were logarithmically transformed. The number of available data varied among explanatory variables, therefore we built three models explaining range size variation in birds. The first model (637 species) had two explanatory variables: genome size and body mass. The second model (311 species) had three explanatory variables: genome size, body mass and relative brain mass. The third model (65 species) had four explanatory variables: genome size, the number of chromosomes, body mass, brain mass. Each model was tested against the null model (model with the intercept only), by likelihood ratio test and Nagelkerke pseudo-R square was a measure of model fit, calculated in companion R-package (Mangiafico 2020).

We used phylogenetic confirmatory path analyses (von Hardenberg & Gonzalez-Voyer 2013) based on prespecified candidate path models to test for the effects of traits on range variation in the R package ‘phylopath’(van der Bijl 2018). This approach allows comparing causal hypotheses of the relationship among traits disentangling direct from indirect effects while correcting for the non-independence of trait data due to common ancestry (Santini et al. 2019). Also, this approach deals with multicollinearity (Fig. 2) better than multivariate linear models because the variance in the response is partitioned among fewer predictors (Gonzalez-Voyer & von Hardenberg 2014). To build paths we used data from model 3rd which contained all explanatory variables. A total of 20 path model combinations were built with different configurations of these variables. We used a set of hypotheses depicted by directed acyclic graphs (Fig. 3) to minimise the number of models to test (Gonzalez-Voyer et al. 2016). The first set of models included the direct impact of each explanatory variable (Fig. 3). The second set of models included also indirect effects. We assumed that the effect of genome size may be mediated by the number of chromosomes, the effect of body mass may be mediated by genome size and the effect of brain mass may be indirect via brain mass (Martin 1981). The third set of models included more complex indirect associations (Fig. 3). Namely, we assumed that the effect of body mass may be mediated by both genome size and the number of chromosomes. Also, we expected that the effect of genome size may be mediated by the number of chromosomes. Finally, these sets of models were tested against the null model. Sets of models were compared using the C-statistic Information Criterion (*CICc*) corrected for small sample size

Results

The first PGLS model showed that genome size was positively associated with range size (Table 1, Fig. 4). Range size was negatively associated with body size (Table 1, Fig. 4). This model was statistically different from the null model (⍰^{2} = 11.543, P = 0.003) and explained 4 % of variation. The second PGLS model also revealed a positive association between range size and genome size (Table 1), a negative association between the range and body mass and no impact of residual brain mass (Table 1). This model also was statistically different from the null model (⍰^{2} = 11.249, P = 0.010) and explained 5 % of variation. The third PGLS model also showed that range size was associated with genome size and body mass but not with the number of chromosomes nor the residual brain mass (Table 1). This model was statistically different from the null model (⍰^{2} = 11.249, P = 0.010) and explained 17 % of variation in range sizes. Phylogenetic path analysis revealed that models with simple direct and indirect models had the highest support (Table 2). These models had higher support than models with direct effect only and more complex direct and indirect effects (Table 2). Estimated coefficients indicated that the statistically significant independent effect size (confidence intervals not overlapping with zero) had the genome size (Fig. 5).

Discussion

Large-scale patterns of spatial variation in species geographic range size are central to many fundamental questions in macroecology. However, the global nature of these patterns has remained contentious. Our study confirms our hypothesis that in birds the genome size is weakly positively related to geographic range size. Birds represent an example of a group in which genome size is correlated with active speciation. The amount of DNA gained by transposable element expansion is counteracted by DNA loss through large segmental deletions (Kapusta et al. 2017, Zhang et al. 2014). Thus, these contrasting forces may be the reason why statistical models explained a small proportion of variation in the range size. Also, there are other possible explanations of the variation in range size in birds mostly linked with environmental constraints, such as climate, geographic location and habitat (Orme et al. 2006, Laube et al. 2014, Zhang et al. 2014, Sayol et al. 2016).

Interestingly, we found that body mass in the multivariate models and path analyses was negatively correlated with the range size. It contradicts most of former findings that were considered as a paradigm of macroecology (Cambefort 1994, Gaston & Blackburn 2000). This finding should be investigated in more detail in other taxa because it may change our understanding of the role of body size in shaping range sizes. Body size depends on genome size (rather than the opposite) thus it may indicate that genetic factors are primary causative variables and body mass may be in fact linked with species distribution indirectly.

We also did not find the effect of the relative brain mass on the range size despite former study reported the positive association between the environmental variation and the brain size (Sayol et al. 2016). Larger brains allow for increased intelligence (i.e. information processing capacities) that is under strong selection (Reader & Laland 2002, Sol et al. 2005) The possible explanation is that in the scale of geographic range the environmental variation may be too high for cognitive skills to adjust bird behaviour. In that case, the adaptations for varying conditions should evolve, which may be linked with the genome size.

Study limitations

Several issues should be taken into account when interpreting results. First, the explained variation is low, thus statistical significance does not necessary mean biological meaning. Moreover, our sample sizes in analyses were limited by the availability of data on chromosome numbers. Used methods assume that relationships are linear, which is not necessary a good assumption. On the other hand, non-linear methods do not include phylogenetic relations among species. Also, species ranges are not constant and used data on range have well known limitations but not better options exist at that scale of study.

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Literature

Andrews CB, Mackenzie SA, Gregory TR. 2009. Genome size and wing parameters in passerine birds. *Proceedings of the Royal Society B.* **276:** 55–61 DOI:10.1098/rspb.2008.1012.

BirdLife International. 2019. Important Bird Areas factsheet: Isla Diego de Almagro. Downloaded from http://www.birdlife.org (accessed 20 November 2019)

Blackmon H, Ross L, Bachtrog D. 2017. Sex Determination, Sex Chromosomes, and Karyotype Evolution in Insects. *Journal Heredity* **108:** 78–93 DOI:10.1093/jhered/esw047.

Böhning-Gaese K, Caprano T, van Ewijk K, Veith M. 2006. Range Size: Disentangling Current Traits and Phylogenetic and Biogeographic Factors. *American Naturalist* **167:** 555–567 DOI:10.1086/501078.

Cambefort Y. 1994. Body-size, abundance, and geographical distribution of Afrotropical dung beetles (Coleoptera, Scarabaeidae). *Acta Oecologica* **15:** 165–179

Cavalier-Smith T. 1978. Nuclear volume control by nucleoskeletal DNA, selection for cell volume and cell growth rate, and the solution of the DNA C-value paradox. *Journal of Cell Science* **34**: 247–278

Edmunds NB, Laberge F, McCann KS. 2016. A role for brain size and cognition in food webs. *Ecology Letters* **19:** 948–955 DOI:10.1111/ele.12633.

Elliott TA, Gregory TR. 2015. What's in a genome? The C-value enigma and the evolution of eukaryotic genome content. *Philosophical Transactions of the Royal Society B.* **370:** 20140331 DOI:10.1098/rstb.2014.0331.

Emery NJ. 2006. Cognitive ornithology: the evolution of avian intelligence. *Philosophical Transactions of the Royal Society B*. **361:** 23–43 DOI:10.1098/rstb.2005.1736.

Fristoe TS, Iwaniuk AN, Botero CA. 2017. Big brains stabilize populations and facilitate colonization of variable habitats in birds. *Nature Ecology and Evolution* **1:** 1706–1715 DOI:10.1038/s41559-017-0316-2.

Garcia-Barros E, Romo Benito H. 2010. The relationship between geographic range size and life history trait: is biogeographic history uncovered? A test using the Iberian butterflies *Ecography* **33:** 392–401 DOI:10.1111/j.1600-0587.2010.06269.x.

Gaston KJ, Blackburn TM. 2000. *Pattern and Process in Macroecology*. Oxford: Blackwell Publishing.

Gaston KJ. 2003. *The Structure and Dynamics of Geographic Ranges*. Oxford: Oxford University Press.

Gonzalez-Voyer A, Gonzalez-Suarez M, Vila C, Revilla E. 2016 Larger brain size indirectly increases vulnerability to extinction in mammals. *Evolution* **70:** 1364–1375 DOI:10.1111/evo.12943.

Gonzalez-Voyer A, von Hardenberg A. 2014. An introduction to phylogenetic path analysis. In: Garamszegi LZ, ed. *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology*. Berlin, Heidelberg: Springer-Verlag, 201–229.

Gregory TR. 2002 Genome size and developmental complexity. *Genetica* **115:** 131–146 DOI:10.1023/A:1016032400147.

Gregory TR. (ed) 2005. *The Evolution of the Genome*. San Diego: Elsevier.

Guo QF, Kato M, Ricklefs RE. 2003. Life history, diversity and distribution: a study of Japanese pteridophytes. *Ecography* **26:** 129–138 DOI:10.1034/j.1600-0587.2003.03379.x.

Harmon LJ. 2019. *Phylogenetic Comparative Methods*. CC-BY 2019. Available from: https://lukejharmon.github.io/pcm/pdf/phylogeneticComparativeMethods.pdf

Hou Y, Lin S. 2009. Distinct Gene Number-Genome Size Relationships for Eukaryotes and Non-Eukaryotes: Gene Content Estimation for Dinoflagellate Genomes. *PLoS ONE* **4(9):** e6978 DOI:10.1371/journal.pone.0006978.

Hsu TC. 1975. A possible function of constitutive heterochromatin: the bodyguard hypothesis. *Genetics* **79 (Suppl.):** 137–150.

Janssen A, Colmenares SU, Karpen GH. 2018. Heterochromatin: Guardian of the genome. *Annual Review of Cell and Developmental Biology* **34:** 265–288 DOI: 10.1146/annurev-cellbio-100617-062653.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. *Nature* **491:** 444–448 DOI:10.1038/nature11631.

Jetz W, Thomas GH, Joy JB, Hartmann K, Redding D, Mooers AO. 2014. Global Distribution and Conservation of Evolutionary Distinctness in Birds. *Current Biology* **24**: 1–12 DOI:10.1016/j.cub.2014.03.011.

John B, Miklos GLG. 1988. *The Eukaryotic Genome in Development and Evolution*, Allen & Unwin.

Kapusta A, Suh A, Feschotte C. 2017. Dynamics of genome size evolution in amniotes. *Proceedings of the National Academy of Sciences USA*. **114 (8):** E1460–E1469 DOI:10.1073/pnas.1616702114.

King M. 1995 *Species Evolution*. Cambridge: Cambridge University Press.

Kretschmer R, Ferguson-Smith M, de Oliveira E. 2018. Karyotype Evolution in Birds: From Conventional Staining to Chromosome Painting. *Genes* **9:** 181 DOI:10.3390/genes9040181.

Laube I, Korntheuer H, Schwager M, Trautmann S, Rahbek C, Böhning-Gaese K. 2013. Towards a more mechanistic understanding of traits and range sizes. *Global Ecology and Biogeography* **22:** 233–241 DOI:10.1111/j.1466-8238.2012.00798.x.

Lee-Yaw JA, Irwin DE. 2012. Large geographic range size reflects a patchwork of divergent lineages in the long-toed salamander (*Ambystoma macrodactylum*). *Journal of Evolutionary Biology* **25:** 2276–2287 DOI:10.1111/j.1420-9101.2012.02604.x.

Lester SE, Ruttenberg BI, Gaines SD, Kinlan BP. 2007. The relationship between dispersal ability and geographic range size. *Ecology Letters* **10:** 745–758 DOI:10.1111/j.1461-0248.2007.01070.x.

Liedtke HC, Gower DJ, Wilkinson M, Gomez-Mestre I. 2018. Macroevolutionary shift in the size of amphibian genomes and the role of life history and climate. *Nature Ecology and Evolution* **2**: 1792 DOI: 10.1038/s41559-018-0674-4.

Lucek K. 2018. Evolutionary Mechanisms of Varying Chromosome Numbers in the Radiation of Erebia Butterflies. *Genes* **9(3):** 166 DOI:10.3390/genes9030166.

Mangiafico S. 2020. rcompanion: Functions to Support - Extension Education Program Evaluation. R package version 2.3.25. https://CRAN.R-project.org/package=rcompanion

Martin RD. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* **293:** 57–60 DOI: 10.1038/293057a0.

Martinez PA, Jacobina UP, Fernandes RV, Brito C, Penone C, Amado TF, Fonseca CR, Bidau CJ. 2017. A comparative study on karyotypic diversification rate in mammals. *Heredity* **118(4):** 366–373 DOI:10.1038/hdy.2016.110.

Minias P, Podlaszczuk P. 2017. Longevity is associated with relative brain size in birds. *Ecology and Evolution* **7:** 3558–3566 DOI:10.1002/ece3.2961.

Moore RM, Harrison AO, McAllister SM, Polson SW, Wommack KE. 2020. Iroki: automatic customization and visualization of phylogenetic trees. *PeerJ* **8:** e8584 DOI:10.7717/peerj.8584.

Münkemüller T, Lavergne S, Bzeznik B, Dray S, Jombart T, Schiffers K, Thuiller W. 2012. How to measure and test phylogenetic signal. *Methods in Ecology and Evolution* **3:** 743–756 DOI:10.1111/j.2041-210X.2012.00196.x.

Navarrete AF, Reader SM, Street SE, Whalen A, Laland KN. 2016. The coevolution of innovation and technical intelligence in primates. *Philosophical Transactions of the Royal Society B.* **371:** 20150186 DOI:10.1098/rstb.2015.0186.

Newsome TM, Wolf C, Nimmo DG, Keller Kopf R, Ritchie EG, Smith FA, Ripple WJ. 2019. Constraints on vertebrate range size predict extinction risk. *Global Ecology and Biogeography* **29:** 76–86 DOI:10.1111/geb.13009.

Orme CDL, Davies RG, Olson VA, Thomas GH, Ding TS, et al. 2006. Global patterns of geographic range size in birds. *PLoS Biology* **4(7):** e208 DOI:10.1371/journal.pbio. 0040208.

Petrov DA. 2001. Evolution of genome size: new approaches to an old problem. *Trends in Genetics* **17:** 23–28 DOI:10.1016/s0168-9525(00)02157-0.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2019. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-142, https://CRAN.R-project.org/package=nlme

Ravilious C, Goodman L, Bodin B, Runsten L, Osti M. 2015. Using spatial information to support decisions on safeguards and multiple benefits for REDD+. Step-by-step tutorial v1.0: Extracting and processing IUCN Red List species data using a vector method in a combination of QGIS 1.8 and 2.8. Prepared on behalf of the UN-REDD Programme. UNEP World Conservation Monitoring Centre, Cambridge, UK.

Reader SM, Laland KN. 2002 Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences USA* **99(7):** 4436–4441 DOI:10.1073/pnas.062041299.

Revell LJ. 2012. phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3:** 217–223 DOI:10.1111/j.2041-210X.2011.00169.x.

Santini L, González-Suárez M, Russo D, Gonzalez-Voyer A, von Hardenberg A, Ancillotto L. 2019. One strategy does not fit all: Determinants of urban adaptation in mammals. *Ecology Letters* **22:** 365–376.

Sayol F, Maspons J, Lapiedra O, et al. 2016. Environmental variation and the evolution of large brains in birds. *Nature Communications* **7:** 13971 DOI:10.1038/ncomms13971.

Sessions SK, Larson A. 1987. Developmental correlates of genome size in Plethodontid salamanders and their implications for genome evolution. *Evolution* **41:** 1239–1251 DOI: 10.1111/j.1558-5646.1987.tb02463.x.

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L. 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences USA* **102:** 5460–5465 DOI:10.1073/pnas.0408145102.

Swofford DL. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Tsuboi MW, Van der B, Kopperud BT, Erritzøe J, Voje KL, Kotrschal A, Yopak KE, Collin SP, Iwaniuk AN, Kolm N. 2018. Breakdown of brain–body allometry and the encephalization of birds and mammals. *Nature Ecology and Evolution* **2:** 1492–1500 DOI:10.1038/s41559-018-0632-1.

van der Bijl W. 2018. phylopath: Easy phylogenetic path analysis in R. *PeerJ* **6**: e4718 DOI:10.7717/peerj.4718.

Vinogradov AE. 1997. Nucleotypic effect in homeotherms: body-mass independent resting metabolic rate of passerine birds is related to genome size. *Evolution* **51:** 220–225 DOI: 10.1111/j.1558-5646.1995.tb04451.x.

Vinogradov AE. 1998. Genome size and GC-percent in vertebrates as determined by flow cytometry: the triangular relationship. *Cytometry* **31:** 100–109 DOI:10.1002/(sici)1097-0320(19980201)31:2<100::aid-cyto5>3.0.co;2-q.

von Hardenberg A, Gonzalez-Voyer A. 2013. Disentangling evolutionary cause-effect relationships with phylogenetic confirmatory path analysis. *Evolution* **67:** 378–387 DOI:10.1111/j.1558-5646.2012.01790.x.

Warchałowska-Śliwa E, Maryańska-Nadachowska A, Grzywacz B, Karamysheva T, Lehmann AW, Lehmann GUC, et al. 2011. Changes in the numbers of chromosomes and sex determination system in bushcrickets of the genus *Odontura* (Orthoptera, Tettigoniidae, Phaneropterinae). *European Journal of Entomology* **108:** 183–195 DOI:10.14411/eje.2011.025.

Wilman H, Belmaker J, Simpson J, de la Rosa C, Rivadeneira M.M, Jetz W. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* **95:** 2027 DOI:10.1890/13-1917.1.

Wyngaard GA, Rasch EM, Manning NM, Gasser K, Domangue R. 2005. The relationship between genome size, development rate, and body size in copepods. *Hydrobiologia* **532:** 123–137 DOI:10.1007/s10750-004-9521-5.

Xia X. 1995. Body temperature, rate of biosynthesis, and evolution of genome size. *Molecular Biology and Evolution* **12:** 834–842 DOI:10.1093/oxfordjournals.molbev.a040260.

Yu JP, Liu W, Mai CL, Liao WB. 2019. Genome size variation is associated with life-history traits in birds. *Journal of Zoology* **310**: 255–260 DOI:10.1111/jzo.12755.

Zamudio KR, Bell RC, Mason NA. 2016. Phenotypes in phylogeography: species’ traits, environmental variation, and vertebrate diversification. *Proceedings of the National Academy of Sciences USA* **113:** 8041–8048

Zhang G, Li C, Li O, Li B, Larkin DM, Lee C, Storz JF, et al. 2014. Comparative Genomics Reveals Insights into Avian Genome Evolution and Adaptation. *Science* **346:** 1311–1320 DOI:10.1126/science.1251385.

Table 1(on next page)

Phylogenetic generalized least squares models testing association among geographic species ranges in birds and genome size, chromosome number, body mass and brain mass.

Three models differed by available sample size for each explanatory variable. Statistically significant effects have emboldened P-values.

Table 1.

Model 1st (N = 637 species)				
Effect	*estimate*	*SE*	*t*	*P*
(Intercept)	5289443.1	13829566.4	0.382	0.702
Genome size	11091038.8	3804045.0	2.916	**0.004**
Body mass	-1633966.4	795215.3	-2.055	**0.040**
Model 2nd (N = 311)				
Effect	*estimate*	*SE*	*t*	*P*
(Intercept)	1376343.2	17699071.3	0.078	0.938
Genome size	16948814.5	5833707.1	2.905	**0.004**
Body mass	-2279812.5	1122943.7	-2.030	**0.043**
Brain mass (residual)	-907984.9	5189134.3	-0.175	0.861
Model 3rd (N = 65)				
Effect	*estimate*	*SE*	*t*	*P*
(Intercept)	24592890.8	31740891.8	0.775	0.441
Genome size	31354218.3	11017812.5	2.846	**0.006**
Chromosome number	-345892.5	279420.0	-1.238	0.221
Body mass	-4052065.1	1673309.7	-2.422	**0.018**
Brain mass (residual)	474102.4	9059940.2	0.052	0.958

Table 2(on next page)

The results of phylogenetic path analysis.

Different sets of models are compared (see Figure 3) Explanations: *k* - independence claims made by the model, *q* - the number of parameters, *C*- the C statistic, *P* - p-value for *C*, *CICc* - the *C*-statistic information criterion corrected for small sample sizes, Δ*CICc* - the difference in *CICc* with the top model, *l* - the associated relative likelihoods, *w* - *CICc* weights (w). A significant *p* indicates that the available evidence rejects the model.

Table 2.

Model	*k*	*q*	*C*	*p*	*CICc*	*ΔCICc*	*l*	*w*
indirect simple	3	12	4.027	0.673	34.027	0.000	1.000	0.811
indirect complex	1	14	0.537	0.764	36.937	2.910	0.233	0.189
direct	6	9	83.671	0.000	104.944	70.917	0.000	0.000
null	10	5	102.454	0.000	113.471	79.444	0.000	0.000

Figure 1

Consensus phylogenetic trees that were used in the analyses.

Phylogenetic tree for all studied species (A) and a subset of 65 species (B) which had all explanatory variables (bars). Colors are in agreement with bird orders.

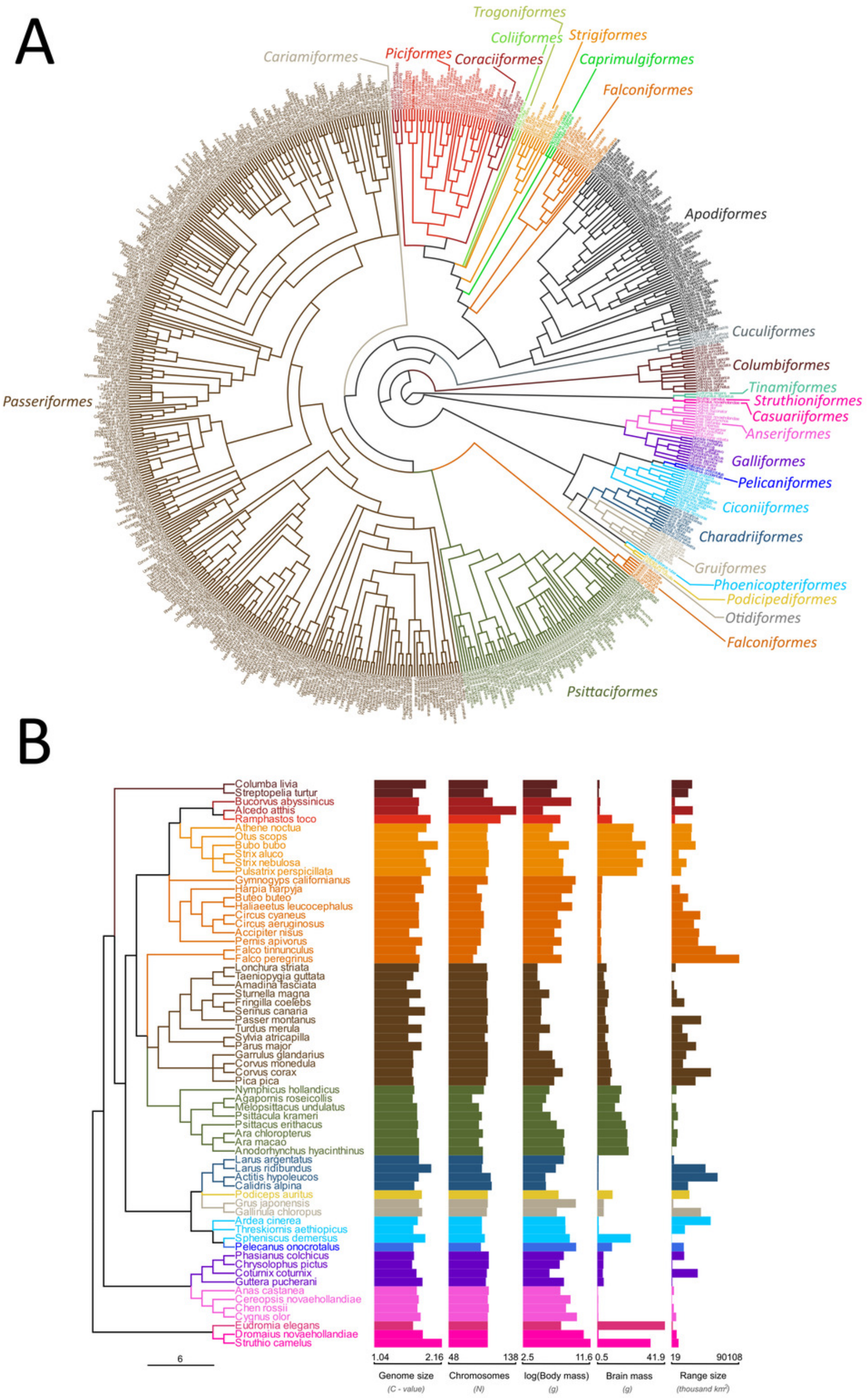

A
Trogoniformes
Coliiformes
Strigiformes
Cariamiformes
Piciformes
Coraciiformes
Caprimulgiformes
Falconiformes
Apodiformes
Cuculiformes
Columbiformes
Passeriformes
Tinamiformes
Struthioniformes
Casuariiformes
Anseriformes
Galliformes
Pelicaniformes
Ciconiiformes
Charadriiformes
Gruiformes
Phoenicopteriformes
Podicipediformes
Otidiformes
Falconiformes
Psittaciformes
B
Columba livia
Streptopelia turtur
Bucorvus abyssinicus
Alcedo atthis
Ramphastos toco
Athene noctua
Otus scops
Bubo bubo
Strix aluco
Strix nebulosa
Pulsatrix perspicillata
Gymnogyps californianus
Harpia harpyja
Buteo buteo
Haliaeetus leucocephalus
Circus cyaneus
Circus aeruginosus
Accipiter nisus
Pernis apivorus
Falco tinnunculus
Falco peregrinus
Lonchura striata
Taeniopygia guttata
Amadina fasciata
Sturnella magna
Fringilla coelebs
Serinus canaria
Passer montanus
Turdus merula
Sylvia atricapilla
Parus major
Garrulus glandarius
Corvus monedula
Corvus corax
Pica pica
Nymphicus hollandicus
Agapornis roseicollis
Melopsittacus undulatus
Psittacula krameri
Psittacus erithacus
Ara chloropterus
Ara macao
Anodorhynchus hyacinthinus
Larus argentatus
Larus ridibundus
Actitis hypoleucos
Calidris alpina
Podiceps auritus
Grus japonensis
Gallinula chloropus
Ardea cinerea
Threskiornis aethiopicus
Spheniscus demersus
Pelecanus onocrotalus
Phasianus colchicus
Chrysolophus pictus
Coturnix coturnix
Guttera pucherani
Anas castanea
Cereopsis novaehollandiae
Chen rossii
Cygnus olor
Eudromia elegans
Dromaius novaehollandiae
Struthio camelus
6
1.04
2.16
48
138
2.5
11.6
0.5
41.9
19
90108
Genome size
(C - value)
Chromosomes
(N)
log(Body mass)
(g)
Brain mass
(g)
Range size
(thousand km²)

Figure 2

The associations among the explanatory variables revealed by phylogenetic generalized least squares (fitted red line).

The size of dots is scaled according to geographic range size. Dots are transparent for better visibility of overlapping data. Statistical significance is given together with sample size.

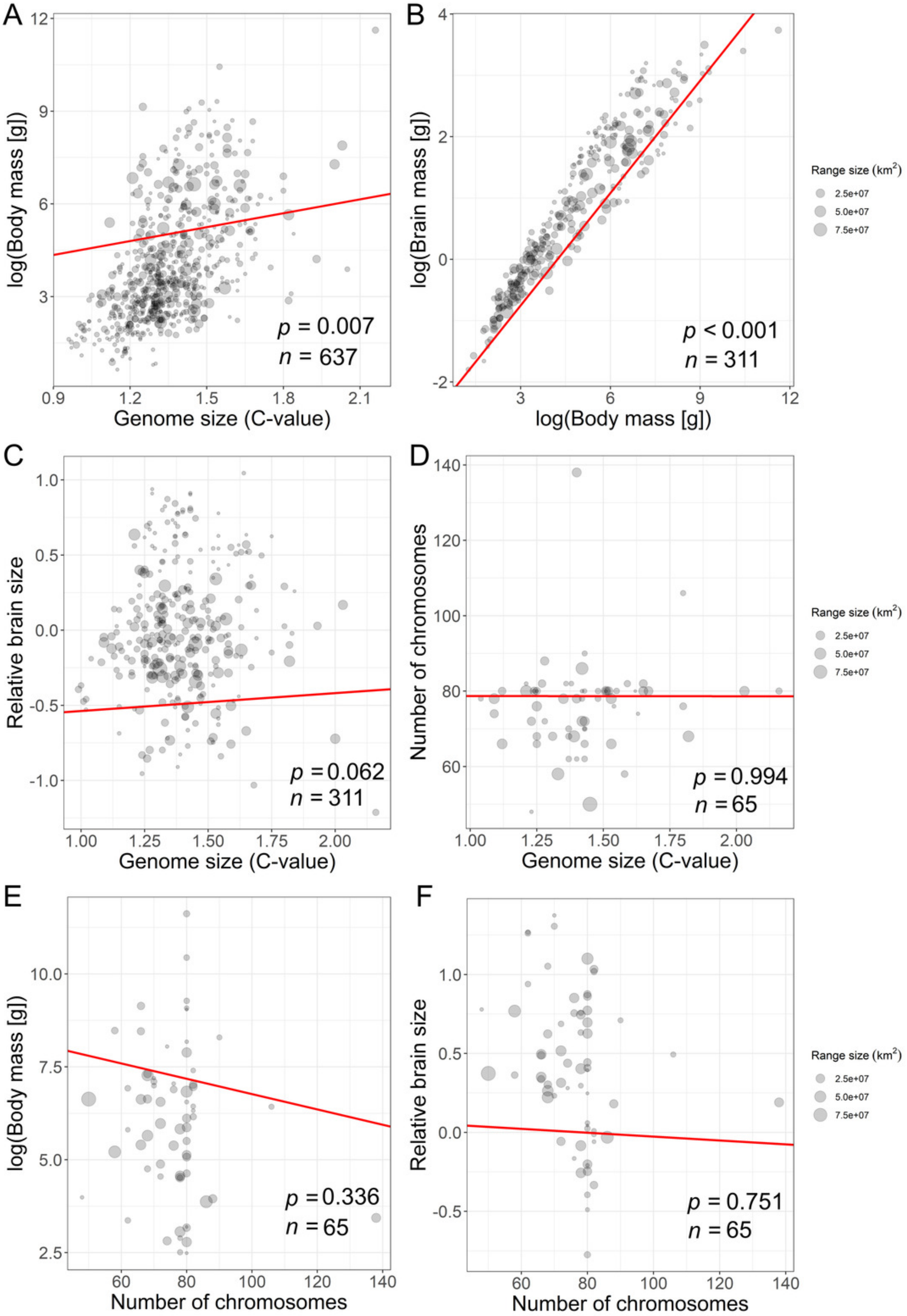

A
log(Body mass [g])
Genome size (C-value)
0.9
1.2
1.5
1.8
2.1
3
6
9
12
p = 0.007
n = 637
B
log(Brain mass [g])
log(Body mass [g])
-2
0
2
4
3
6
9
12
p < 0.001
n = 311
Range size (km^2)
2.5e+07
5.0e+07
7.5e+07
C
Relative brain size
Genome size (C-value)
1.0
0.5
0.0
-0.5
-1.0
1.00
1.25
1.50
1.75
2.00
p = 0.062
n = 311
D
Number of chromosomes
Genome size (C-value)
140
120
100
80
60
1.00
1.25
1.50
1.75
2.00
p = 0.994
n = 65
Range size (km^2)
2.5e+07
5.0e+07
7.5e+07
E
log(Body mass [g])
Number of chromosomes
10.0
7.5
5.0
2.5
60
80
100
120
140
p = 0.336
n = 65
F
Relative brain size
Number of chromosomes
1.0
0.5
0.0
-0.5
60
80
100
120
140
p = 0.751
n = 65
Range size (km^2)
2.5e+07
5.0e+07
7.5e+07

Figure 3

Competing models testing the association among geographic range size in birds (Range), and genome size, number of chromosomes (Chromosomes), body mass and brain mass.

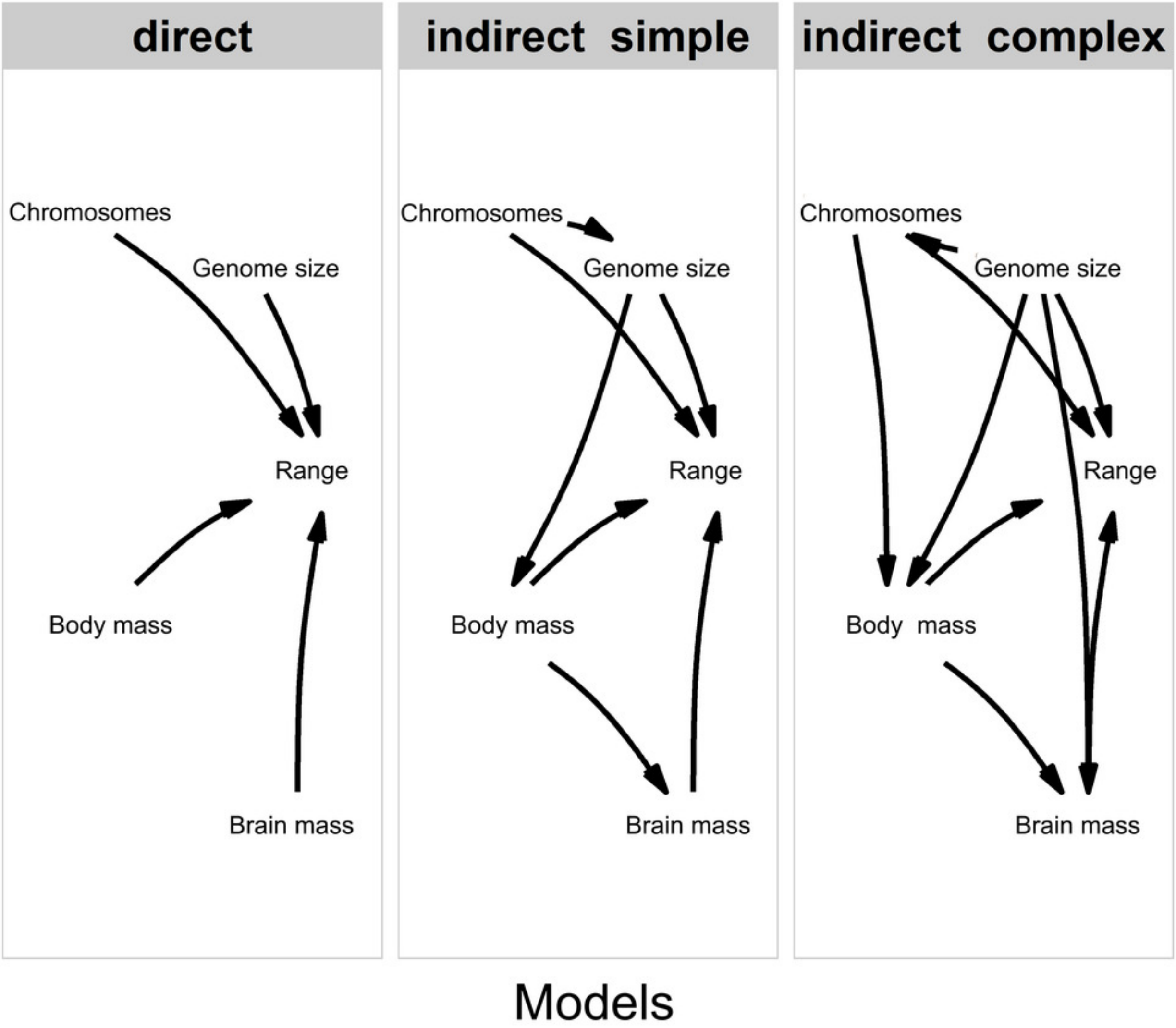


Figure 4

The association among geographic range size in birds and (A) genome size, and (B) body mass.

Fitted lines (red) are from the phylogenetic generalized least squares models. The effect of body mass is depicted on residual range sizes (residuals not explained by the genome size).

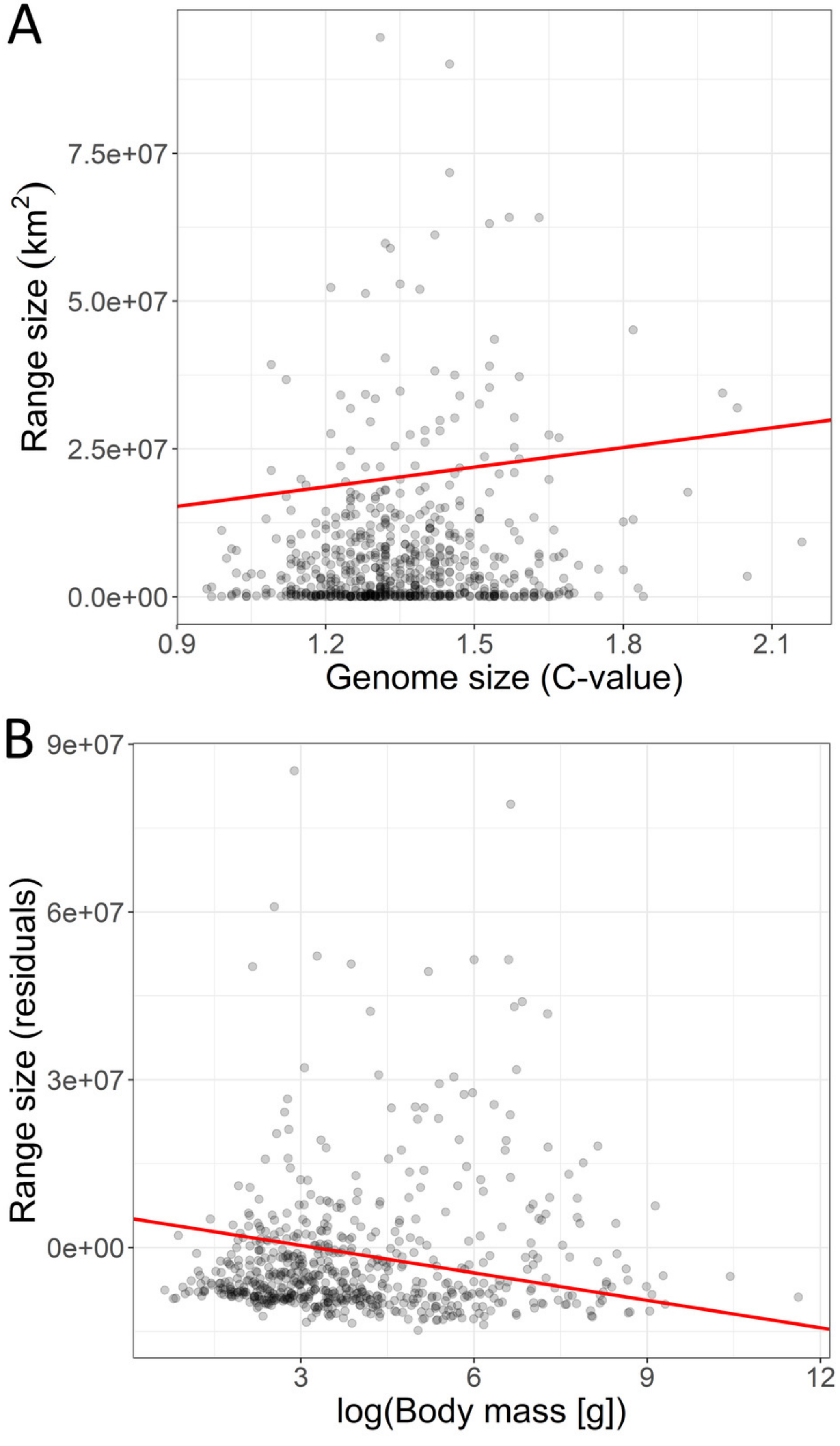
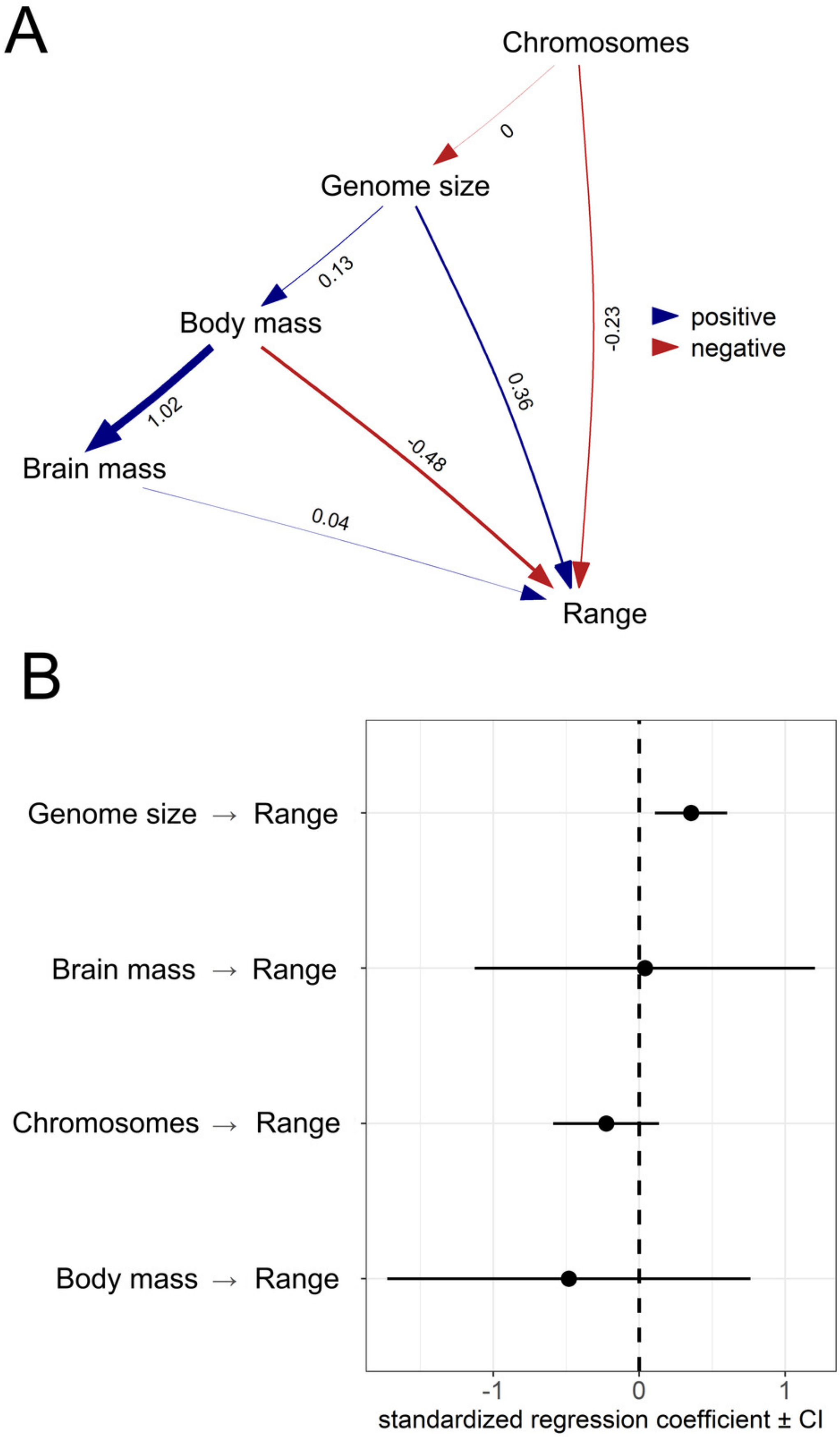

A
Range size (km^2)
7.5e+07
5.0e+07
2.5e+07
0.0e+00
0.9
1.2
1.5
1.8
2.1
Genome size (C-value)
B
Range size (residuals)
9e+07
6e+07
3e+07
0e+00
3
6
9
12
log(Body mass [g])

Figure 5

Results from the phylogenetic path analysis.

Test supporting causal model with the standardized path coefficients (A). The standardized coefficients for explanatory variables with 95 % confidence intervals (CI) associated with bird geographic range (B).


A
Chromosomes
0
Genome size
0.13
Body mass
0.36
-0.23
positive
negative
1.02
-0.48
Brain mass
0.04
Range
B
Genome size → Range
Brain mass → Range
Chromosomes → Range
Body mass → Range
-1
0
1
standardized regression coefficient ± CI