Phylogenetic comparative methods  
CEB 35300, Winter 2018

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# Readings

All readings marked with an ‘\*’ are required; the remaining readings are optional, and you can pursue them if and as you see fit.

**Week 1 (9 January):** Trees, traits, and covariance: importing and visualizing comparative data   
*Lab: reading, editing, and visualizing phylogenetic data*

\* Paradis, E. 2014. An Introduction to the Phylogenetic Comparative Method. Pp. 3-18 in: Garamszegi, Z.L., (ed), Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice. Springer Berlin Heidelberg, Berlin, Heidelberg. p 3-18.

\* Pennell MW, Harmon LJ. 2013. An integrative view of phylogenetic comparative methods: connections to population genetics, community ecology, and paleobiology. Annals of the New York Academy of Sciences 1289: 90–105.

\* Revell, L.J. 2013. Two new graphical methods for mapping trait evolution on phylogenies. Methods in Ecology and Evolution 4:754-759.

\* Revell, L.J. 2014. Graphical Methods for Visualizing Comparative Data on Phylogenies. Pp. 77-103 in: Garamszegi, Z.L., (ed), Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice. Springer Berlin Heidelberg, Berlin, Heidelberg. p 77-103.

Paradis, E. 2014. Simulation of Phylogenetic Data. Pp. 335-350 in: Garamszegi, Z.L., (ed), Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice. Springer Berlin Heidelberg, Berlin, Heidelberg. p 335-350.

**Week 2 (16 January):**Independent contrasts and its extensions: addressing phylogenetic autocorrelation.

*Lab:* PIC

Helpful but optional background: https://www.khanacademy.org/math/statistics-probability/describing-relationships-quantitative-data

\* Felsenstein J. 1985. Phylogenies and the comparative method. Am Nat 125: 1-15.

\* Harvey PH, Read AF, Nee S. 1995. Further remarks on the role of phylogeny in comparative ecology. Journal of Ecology 83: 733–734.

\* Harvey PH, Read AF, Nee S. 1995. Why ecologists need to be phylogenetically challenged. Journal of Ecology 83: 535–536.

\* Westoby M, Leishman M, Lord J. 1995b. Further Remarks on Phylogenetic Correction. Journal of Ecology 83: 727–729.

\* Westoby M, Leishman MR, Lord JM. 1995a. On Misinterpreting the `Phylogenetic Correction’. Journal of Ecology 83: 531–534.

Ackerly, D.D., Schwilk, D.W., and Webb, C.O. 2006. Niche evolution and adaptive radiation: testing the order of trait divergence. Ecology 87:50-61.

Garland T, Harvey PH, Ives AR. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst Biol 41: 18-31.

Garland T, Midford PE, Ives AR. 1999. An Introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. Am Zool 39: 374-388.

**Week 3 (23 January; Volunteer center classroom):**Generalized linear models (GLS).

*Lab: GLS*

Helpful but optional background: https://www.khanacademy.org/math/precalculus/precalc-matrices

\* Garland T, Ives AR. 2000. Using the past to predict the present: Confidence intervals for regression equations in phylogenetic comparative methods. Am Nat 155: 346-364.

\* Mundry, R. 2014. Statistical Issues and Assumptions of Phylogenetic Generalized Least Squares. Pp. 131-153 in: Garamszegi, Z.L., (ed), Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice. Springer Berlin Heidelberg, Berlin, Heidelberg. p 131-153.

\* Symonds, M.R.E., and Blomberg, S.P. 2014. A Primer on Phylogenetic Generalised Least Squares. Pp. 105-130 in: Garamszegi, Z.L., (ed), Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice. Springer Berlin Heidelberg, Berlin, Heidelberg. p 105-130.

Bolker 2008, sect. 10.3 (“Correlations: time-series and spatial data” provides a fairly easy introduction to the multivariate normal distribution)

Blomberg, S.P., Lefevre, J.G., Wells, J.A., and Waterhouse, M. 2012. Independent Contrasts and PGLS Regression Estimators Are Equivalent. Syst. Biol. 61:382-391.

Revell, L.J. 2010. Phylogenetic signal and linear regression on species data. Methods in Ecology and Evolution 1:319-329.

Rohlf, F.J. 2006. A comment on phylogenetic correction. Evolution 60:1509-1515.

**Week 4 (30 January):**Fitting and evaluating alternative models (including multimodel inference)  
*Lab: AIC, parametric bootstrapping, model-averaging*

Helpful but optional background: https://en.wikipedia.org/wiki/Akaike\_information\_criterion

\* Boettiger, C., G. Coop, and P. Ralph. 2012. Is your phylogeny informative? Measuring the power of comparative methods. Evolution doi: 10.1111/j.1558-5646.2011.01574.x

\* Burnham K, Anderson D, Huyvaert K. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65(1): 23-35

\* Freckleton, R. P. 2009. The seven deadly sins of comparative analysis. J Evol Biol 22:1367-1375.

\* Pennell MW, FitzJohn RG, Cornwell WK, Harmon LJ. 2015. Model Adequacy and the Macroevolution of Angiosperm Functional Traits. *The American Naturalist* 186: E33–E50.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York: Springer.

Garamszegi, L.Z., and Mundry, R. 2014. Multimodel-Inference in Comparative Analyses. Pp. 305-331 in: Garamszegi, Z.L., (ed), Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice. Springer Berlin Heidelberg, Berlin, Heidelberg. p 305-331.

Slater GJ, Pennell MW. 2014. Robust Regression and Posterior Predictive Simulation Increase Power to Detect Early Bursts of Trait Evolution. *Systematic Biology* 63: 293–308.

**Week 5 (6 February):** Stretching the tree: evolutionary rates and models of continuous trait evolution  
*Lab: stretching the tree and modifying the covariance matrix*

\* Blomberg, S., Garland, T. and Ives, A., 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. Evolution, 57(4), p.717-745.

\* O'Meara, B. et al., 2006. Testing for different rates of continuous trait evolution using likelihood. Evolution, 60(5), p.922-933.

\* Pagel, M. 1997. Inferring evolutionary processes from phylogenies. Zoologica Scripta, 26(4), p.331-348.

\* Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature (Lond) 401(6756): 877-884.

Duchen P, Leuenberger C, Szilágyi SM, Harmon L, Eastman J, Schweizer M, Wegmann D. 2017. Inference of Evolutionary Jumps in Large Phylogenies using Lévy Processes. Systematic Biology 66: 950–963.

Eastman JM, Alfaro ME, Joyce P, Hipp AL, Harmon LJ (2011) A novel comparative method for modeling shifts in the rate of character evolution on trees. Evolution 65, 3578–3589.

Elliot MG, Mooers AØ. 2014. Inferring ancestral states without assuming neutrality or gradualism using a stable model of continuous character evolution. BMC Evolutionary Biology 14: 226.

Freckleton RP, Harvey PH, Pagel M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. American Naturalist 160(6): 712-726.

Freckleton, R. P., and P. H. Harvey. 2006. Detecting Non-Brownian Trait Evolution in Adaptive Radiations. PLoS Biology 4:e373.

Harmon LJ, Losos JB, Jonathan Davies T, et al. (2010) Early bursts of body size and shape evolution are rare in comparative data. Evolution 64, 2385-2396.

Harmon LJ, Schulte JAI, Larson A, Losos JB (2003) Tempo and Mode of Evolutionary Radiation in Iguanian Lizards. Nature (London) 301, 961-964.

Pagel M (1999) Inferring the historical patterns of biological evolution. Nature (London) 401, 877-884.

Revell LJ, Harmon LJ, Collar DC (2008) Phylogenetic Signal, Evolutionary Process, and Rate. Systematic Biology 57, 591-601.

Revell, L. J., D. L. Mahler, P. R. Peres-Neto, and B. D. Redelings. 2012. A new phylogenetic method for identifying exceptional phenotypic diversification. Evolution 66:135-146.

Slater GJ, Harmon LJ, Wegmann D, Joyce P, Revell LJ, Alfaro ME. 2012. Fitting models of continuous trait evolution to incompletely sampled comparative data using approximate Bayesian computation. Evolution 66(3): 752–762.

Venditti, C., A. Meade, and M. Pagel. 2011. Multiple routes to mammalian diversity. Nature 479:393-396.

**Week 6 (13 February):** Ornstein-Uhlenbeck models. *Lab: fitting O-U models*

\* Butler M, King AA. 2004. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. Am Nat 164: 683-695.

\* Cooper N, Thomas GH, Venditti C, Meade A, Freckleton RP. 2016. A cautionary note on the use of Ornstein Uhlenbeck models in macroevolutionary studies. Biological Journal of the Linnean Society 118: 64–77.

\* Hansen TF, Pienaar J, Orzack SH. 2008. A Comparative Method for Studying Adaptation to a Randomly Evolving Environment. Evolution 62(8): 1965-1977.

\* Hansen, T.F. 2014. Use and Misuse of Comparative Methods in the Study of Adaptation. Pp. 351-379 in: Garamszegi, Z.L., (ed), Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice. Springer Berlin Heidelberg, Berlin, Heidelberg. p 351-379.

Beaulieu, J.M., Jhwueng, D.-C., Boettiger, C., and O’Meara, B.C. 2012. Modeling stabilizing selection: expanding the Ornstein-Uhlenbeck model of adaptive evolution. Evolution 66:2369-2383.

Blomberg SP. 2017. Beyond Brownian motion and the Ornstein-Uhlenbeck process: Stochastic diffusion models for the evolution of quantitative characters. bioRxiv: 067363.

Boucher FC, Démery V, Conti E, Harmon LJ, Uyeda J. 2018. A General Model for Estimating Macroevolutionary Landscapes. Systematic Biology.

Cressler, C.E., Butler, M.A., King, A.A., 2015. Detecting adaptive evolution in phylogenetic comparative analysis using the Ornstein-Uhlenbeck model. Syst Biol syv043. doi:10.1093/sysbio/syv043

Hansen TF, Martins EP. 1996. Translating between microevolutionary process and macroevolutionary patterns: the correlation structure of interspecific data. Evolution 50: 1404-1417.

Hansen TF, Orzack SH. 2005. Assessing current adaptation and phylogenetic inertia as explanations of trait evolution: The need for controlled comparisons. Evolution 59(10): 2063-2072.

Hansen TF. 1997. Stabilizing selection and the comparative analysis of adaptation. Evolution 51(5): 1341-1351.

Ho, L.S.T., Ané, C., 2014. Intrinsic inference difficulties for trait evolution with Ornstein-Uhlenbeck models. Methods Ecol Evol 5, 1133–1146. doi:10.1111/2041-210X.12285

Khabbazian, M., Kriebel, R., Rohe, K., Ané, C., 2016. Fast and accurate detection of evolutionary shifts in Ornstein–Uhlenbeck models. Methods Ecol Evol n/a–n/a. doi:10.1111/2041-210X.12534

Mahler, D.L., and Ingram, T. 2014. Phylogenetic Comparative Methods for Studying Clade-Wide Convergence. Pp. 425-450 in: Garamszegi, Z.L., (ed), Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice. Springer Berlin Heidelberg, Berlin, Heidelberg. p 425-450.

Martins EP, Hansen TF. 1997. Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into analysis of interspecific data. Am Nat 149: 646-667.

O’Meara, B.C., and Beaulieu, J.M. 2014. Modelling Stabilizing Selection: The Attraction of Ornstein–Uhlenbeck Models. Pp. 381-393 in: Garamszegi, Z.L., (ed), Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice. Springer Berlin Heidelberg, Berlin, Heidelberg. p 381-393.

**Week 7 (20 February):**Multivariate vs univariate; and accounting for intraspecific variation and error. *Lab: incorporating phylogenetic error and measurement error in analysis*

\* Felsenstein, J. 2008. Comparative Methods with Sampling Error and Within-Species Variation: Contrasts Revisited and Revised. The American Naturalist 171:713-725.

\* Harmon, L.J. and J.B. Losos. 2005. The effect of intraspecific sample size on Type I and Type II error rates in comparative studies. Evolution 59: 2705-2710.

\* Ives, A.R., Midford, P.E., and Garland, J., Theodore. 2007. Within-Species variation and measurement error in phylogenetic comparative methods. Syst. Biol. 56:252-270.

\* Silvestro D, Kostikova A, Litsios G, Pearman PB, Salamin N. 2015. Measurement errors should always be incorporated in phylogenetic comparative analysis. Methods in Ecology and Evolution 6: 340–346.

\* Uyeda JC, Caetano DS, Pennell MW. 2015. Comparative analysis of principal components can be misleading. Systematic Biology 64: 677–689.

Adams DC, Collyer ML. 2018. Multivariate Phylogenetic Comparative Methods: Evaluations, Comparisons, and Recommendations. Systematic Biology 67: 14–31.

Bartoszek, K., Pienaar, J., Mostad, P., Andersson, S., and Hansen, T.F. 2012. A phylogenetic comparative method for studying multivariate adaptation. J. Theor. Biol. 314:204-215.

Felsenstein, J. 2002. Contrasts for a within-species comparative method. Pp. 118-129 in: Slatkin, M., and Veuille, M., (eds), Modern Developments in Theoretical Population Genetics. Oxford University Press, Oxford, UK. p 118-129.

Garamszegi, L.Z. 2014. Uncertainties Due to Within-Species Variation in Comparative Studies: Measurement Errors and Statistical Weights. Pp. 157-199 in: Garamszegi, Z.L., (ed), Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice. Springer Berlin Heidelberg, Berlin, Heidelberg. p 157-199.

Hansen, T.F., and Bartoszek, K. 2012. Interpreting the Evolutionary Regression: The Interplay between Observational and Biological Errors in Phylogenetic Comparative Studies. Syst. Biol. doi: 10.1093/sysbio/syr122.

Revell, L.J. and R.G. Reynolds. 2012. A new Bayesian method for fitting evolutionary modelst to comparative data with intraspecific variation. Evolution 66: 2697-2707.

Slater GJ, Harmon LJ, Wegmann D, Joyce P, Revell LJ, Alfaro ME. 2012. Fitting models of continuous trait evolution to incompletely sampled comparative data using approximate Bayesian computation. Evolution 66: 752–762.

Stone, G.N., Nee, S., and Felsenstein, J. 2011. Controlling for non-independence in comparative analysis ueydaof patterns across populations within species. Philosophical Transactions of the Royal Society B: Biological Sciences 366:1410-1424.

**Week 8 (27 February; Zoology classroom):**Phylogenetic diversity and phylogenetic methods in community ecology part I. *Lab: metrics and permutation tests*

\* Cadotte, M. W., Davies, T. J. and Peres-Neto, P. R. (2017), Why phylogenies do not always predict ecological differences. Ecol Monogr, 87: 535–551. doi:10.1002/ecm.1267

\* Cavender-Bares J, Ackerly D, Baum D, Bazzaz F. 2004. Phylogenetic overdispersion in Floridian oak communities. Am Nat 163(6): 823-843.

\* Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW. 2009. The merging of community ecology and phylogenetic biology. Ecol Lett 12(7): 693-715.

\* Pearse, W.D., Purvis, A., Cavender-Bares, J., and Helmus, M.R. 2014. Metrics and Models of Community Phylogenetics. Pp. 451-464 in: Garamszegi, Z.L., (ed), Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice. Springer Berlin Heidelberg, Berlin, Heidelberg. p 451-464.

Cavender-Bares J, Keen A, Miles B. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology 87(7 Suppl): S109-122.

Faith DP. 2008. Threatened species and the potential loss of phylogenetic diversity: conservation scenarios based on estimated extinction probabilities and phylogenetic risk analysis. Conserv Biol 22(6): 1461-1470.

Graham CH, Fine PVA. 2008. Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. Ecol Lett 11(12): 1265-1277.

Helmus MR, Bland TJ, Williams CK, Ives AR. 2007. Phylogenetic measures of biodiversity. The American Naturalist 169(3): E68-E83.

Kembel SW. 2009. Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. Ecol Lett 12(9): 949-960.

Losos JB. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecol Lett 11(10): 995-1003.

Vamosi SM, Heard SB, Vamosi JC, Webb CO. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. Mol Ecol 18(4): 572-592.

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ. 2002. Phylogenies and community ecology. Annu Rev Ecol Syst 33: 475-505.

**Week 9 (6 March):** Phylogenetic diversity and phylogenetic methods in community ecology part II.  
*Lab: PGLMM*

\* Ives, A.R., and Garland, T. 2014. Phylogenetic Regression for Binary Dependent Variables. Pp. 231-261 in: Garamszegi, Z.L., (ed), Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice. Springer Berlin Heidelberg, Berlin, Heidelberg. p 231-261.

\* Ives, A.R., and Helmus, M.R. 2011. Generalized linear mixed models for phylogenetic analyses of community structure. Ecol. Monogr. 81:511-525.

**Week 10 (13 March):** Effects of traits on lineage diversification.   
*Lab: lineage diversification methods*

\* O’Meara BC, Beaulieu JM. 2016. Past, future, and present of state-dependent models of diversification. American Journal of Botany 103: 792–795.

\* Beaulieu JM, O’Meara BC. 2016. Detecting Hidden Diversification Shifts in Models of Trait-Dependent Speciation and Extinction. Systematic Biology 65: 583–601.

\* Uyeda JC, Zenil-Ferguson R, Pennell MW. 2017. Rethinking phylogenetic comparative methods. bioRxiv: 222729.

FitzJohn, R.G. 2010. Quantitative Traits and Diversification. Syst. Biol. 59:619-633.

Goldberg EE, Lancaster LT, Ree RH. 2011. Phylogenetic Inference of Reciprocal Effects between Geographic Range Evolution and Diversification. Systematic Biology 60: 451–465.

Rabosky DL, Goldberg EE. 2015. Model Inadequacy and Mistaken Inferences of Trait-Dependent Speciation. Systematic Biology 64: 340–355.