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.

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.

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):** Disentangling rates of character change from rates of lineage diversification

\* Goldberg EE, Igic B. 2008. On Phylogenetic Tests of Irreversible Evolution. Evolution 62: 2727–2741.

\* Maddison WP. 2006. Confounding Asymmetries in Evolutionary Diversification and Character Change. Evolution 60: 1743–1746.

**Week 8 (27 February; Zoology classroom):**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.

\* 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.

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.

Kostikova A, Silvestro D, Pearman PB, Salamin N. 2016. Bridging Inter- and Intraspecific Trait Evolution with a Hierarchical Bayesian Approach. Systematic Biology 65: 417–431.

Revell, L.J. and R.G. Reynolds. 2012. A new Bayesian method for fitting evolutionary models 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 of patterns across populations within species. Philosophical Transactions of the Royal Society B: Biological Sciences 366:1410-1424.

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

\* Weber MG, Wagner CE, Best RJ, Harmon LJ, Matthews B. 2017. Evolution in a Community Context: On Integrating Ecological Interactions and Macroevolution. Trends in Ecology & Evolution 32: 291–304.

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

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.

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.

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.

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.

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 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.

\* Maddison WP, Midford PE, Otto SP. 2007. Estimating a binary character’s effect on speciation and extinction. Systematic Biology 56: 701–710.

\* 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.

FitzJohn RG, Maddison WP, Otto SP. 2009. Estimating Trait-Dependent Speciation and Extinction Rates from Incompletely Resolved Phylogenies. Systematic Biology 58: 595–611.

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

Monroe MJ, Bokma F. 2017. Does density-dependent diversification mirror ecological competitive exclusion? PLOS ONE 12: e0184814.

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