

Curriculum Vitae

Ziheng Yang, FRS

R.A. Fisher Professor of Statistical Genetics

DEPARTMENT OF GENETICS, EVOLUTION AND ENVIRONMENT

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PRESENT POST: R.A. FISHER PROFESSOR OF STATISTICAL GENETICS, SINCE 2010

BIOGRAPHICAL

Date of birth: 1 November 1964.

Place of Birth: Gansu Province, P.R. China.

Citizenship: British

RESEARCH INTERESTS

Molecular evolution; molecular phylogenetics; theoretical population genetics; computational biology and bioinformatics; computational statistics.

EDUCATION

- Ph. D., 1992, agricultural science (molecular evolution), Beijing Agricultural University, P.R. China
- M. Sc., 1987, agricultural science (quantitative genetics and animal breeding), Beijing Agricultural University, China
- B. Sc., 1984, agricultural science, Gansu Agricultural University, China

PROFESSIONAL HISTORY

- 2010-date, Director, RA Fisher Centre for Computational Biology, UCL.
- 2010-date, RA Fisher Chair of Statistical Genetics, Department of Genetics, Evolution and Environment, University College London.
- 2001-2010, Professor of Statistical Genetics, Department of Biology, University College London.
- 2000-2001, Reader of Evolutionary Genetics, Department of Biology, University College London.
- 1997-2000, Lecturer, Department of Biology, University College London.
- 1995-1997, Postdoctoral research fellow, Department of Integrative Biology, University of California at Berkeley.
- 1994-1995, Postdoctoral research fellow, Institute of Molecular Evolutionary Genetics, The Pennsylvania State University.
- 1993-1994, Postdoctoral research fellow (independent researcher) at Department of Zoology, The Natural History Museum (London).
- 1992-1993, Postdoctoral research fellow at Department of Zoology, University of Cambridge.
- 1992-1997, Lecturer of Genetics at Department of Animal Science, Beijing Agricultural University.

OTHER APPOINTMENTS AND AFFILIATIONS

- 2017-2018, Radcliffe Fellow, Harvard University
- 2017-2021, Visiting Professor, Academy of Mathematics and Systems Science, Chinese Academy of Sciences, Beijing.

- 1 April 2016-31 March 2019, Visiting Professor, National Institute of Genetics, Japan.
- June 2013-2016, Visiting Professor, Centre for Computational Genomics, Beijing Institute of Genomics, Chinese Academy of Sciences, Beijing.
- February-August 2011, Visiting Professor, Computer Science, Swiss Institute of Technology (ETH), Zurich.
- November 2010-February 2011, Visiting Professor, Institute of Zoology, Chinese Academy of Sciences, Beijing.
- August-November 2010, Visiting Professor, College of Life Sciences, Peking University, Beijing, China.
- 2008-2011, Changjiang Chair Visiting Professor, Sun Yat-sen University, Guangdong, China.
- 2007-2012, Director, Centre for Computational and Evolutionary Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing.
- Oct 2007-Mar 2008, Visiting Professor, University of Tokyo, Japan.
- Oct-Nov 2004, Visiting Professor, University of Montpellier.
- 1998-1999, Research Associate, Natural History Museum.
- Nov 1997-Feb 1998, Visiting Associate Professor, Institute of Statistical Mathematics, Tokyo, Japan.

AWARDS AND OTHER HONOURS

- 2017, Honorary Professor, Beijing Normal University
- 2010, Frink Medal for British Zoologists, The Zoological Society of London.
- 2009, Royal Society Wolfson Research Merit Award
- 2008, Presidents' Award for Lifetime Achievement, Society for Systematic Biology
- 2006, Fellow of the Royal Society, The Royal Society of London
- 1995, Young Investigator's Prize from American Society of Naturalists.
- 1992 - 1993, China-EEC exchange programme, awarded as a postdoctoral fellowship in England.
- 10 January 2018, Hua Lookeng Distinguished Lecture (*Markov chain Monte Carlo: how do you propose?*), Academy of Mathematics and Systems Sciences, Chinese Academy of Sciences, Beijing, China.

GRANTS

PROJECT GRANTS

- 2022-2026 Integrating computational, phenotypic, and population-genomic approaches to reveal processes of cryptic speciation and gene flow in Madagascar's mouse lemurs. NSFDEB-NERC, 298K for the UK component (Leading investigator, Prof Anne Yoder).
- 2022-2025 The unreliable clade Deuterostomia: implications for bilaterian evolution, Leverhulme, 592K (*Co-I: Professor Max Telford*)
- 2020-2023, BB/T012951/1. Efficient Bayesian phylogenomic dating with new models of trait evolution and rich diversities of living and fossil species, BBSRC, £307k for UCL component (Co-I: Dr Mario dos Reis, Prof. Philip Donoghue).
- 2020-2023, BB/T003502/1. Bayesian implementation of the multispecies-coalescent-with-introgression (MSci) model for analysis of population genomic data, BBSRC, £438K.
- 2018-2021, BB/R016240/1. *Addressing the problem of deep coalescence in ancient radiations: Resolving the explosive radiation of the Lophotrochozoa*, BBSRC, (Co-I: Professor Max Telford)
- 2017-2020, BB/P006493/1. *Phylogeographic inference using genomic sequence data under the multispecies coalescent model*, £398K
- 2016-2020, BB/N000609/1. *Improving Bayesian methods for estimating divergence times integrating genomic and trait data*, BBSRC (co-PI with Dr Philip Donoghue of U. Bristol), £480K.
- 2016-2018, *The Origin of Plants: Genomes, rocks, and biogeochemical cycles*, 366K, NERC (co-PI. Leading PI: Harald Schneider, Natural History Museum), £366K.
- 2015-2017, *Untangling the enigmatic origins of placental mammals with fossils and genomics*, BBSRC (co-Applicant with Dr Anjali Goswami of UCL), £85K.
- 2013-2016, *Statistical methods for genomic analysis of species divergences*, BBSRC, £416K.
- 2012-2015, *Bayesian estimation of species divergence times integrating fossil and molecular information*. BBSRC (co-PI with Dr Philip Donoghue of U. Bristol), £446K.
- 2009-2014, *Meeting the challenges of population genomics and phylogenomics*. Royal Society Wolfson Research Merit Awards, £75K.
- 2009-2012, *Representation and incorporation of fossil data in molecular dating of species divergences*, BBSRC (co-PI with Dr Philip Donoghue of U. Bristol), £444K.

- 2005-2009, *Development of codon-based substitution models for detecting natural selection in protein-coding genes*, BBSRC (PI), £225K.
- 2005-2008, *Statistical methods for estimating species divergence times combining heterogeneous genetic data sets*, NERC (PI), £234K.
- 2001-2005, *From molecular adaptation to protein function: New tools for genome analysis*, Human Frontier Science Programme (co-PI with Drs Rasmus Nielsen and Karl Schmid) US\$750K.
- 2001-2004, *Development, evaluation, and application of phylogenetic methods for detecting molecular adaptation*, BBSRC (PI, with Dr Joe Bielawski as named researcher), £178K.
- 2001-2004, *Statistical and computational improvements to molecular phylogenetic estimation*, BBSRC (PI), £149K.
- 2000-2003, *Molecular phylogenetics and evolution of actinopterygian fishes as inferred from mitochondrial protein coding sequences*, BBSRC (Co-Appl, with Drs Mark Thomas (PI) and Mike Coates), £157K.
- 1998-2001, *Bayesian estimation of molecular phylogenies*, BBSRC (PI), £133K.
- 1998-2001, *Models of codon substitution and detection of adaptive molecular evolution*, BBSRC (PI), £148K.
- 1994-1996, *Molecular evolution and systematics of mammals*. National Science Foundation of China (PI).
- 1993-1994, *Reliability of phylogenetic inference*. Natural History Museum (London), Interdisciplinary research project.

TRAVEL AND EQUIPMENT GRANTS

- 2009 *Bayesian automatic clustering and its use in population genetics*, UCL CoMPLEX travel grant to collaborate with Professor Jukka Corander of Department of Mathematics, Åbo Akademi University, Finland. £1250.
- 2005-2008 *Phylogenetic analysis of large molecular data sets from multiple loci and estimation of divergence times and ancestral population sizes*. National Science Foundation of China Collaborative Grant, China (Collaborator: Professor De-Xing Zhang, Institute of Zoology, Beijing, China), RMB Yuan 250,000.
- 2000 *Combining structural and evolutionary approaches to understand protein evolution*, International Scientific Interchange Scheme (BBSRC) for collaboration with Dr Belinda Chang in Rockefeller University, BBSRC, £2,900.
- 1999-2001 *Estimation of nucleotide substitution rates to study the mechanisms of molecular evolution*, Royal Society Joint Project for collaboration with Prof. Masami Hasegawa of Institute of Statistical Mathematics, Tokyo, Japan, £11,400.
- 1999 Joint Research Equipment Initiative (Co-Appl, with Profs Linda Partridge (PI), David Goldstein, Drs. Stephen Wilson, and David Gems). £312K.

PUBLICATIONS (75K citations, $h = 101$, google scholar)

BOOKS

1. Yang, Z. 2014, *Molecular Evolution: A Statistical Approach*, Oxford University Press. 512 pages (ISBN: 9780199602612).
2. Yang, Z. 2006, *Computational Molecular Evolution*, Oxford University Press. 376 pages (ISBN: 9780198567028). (This has been translated into Chinese and Japanese.)

REFEREED JOURNAL ARTICLES (*CORRESPONDING AUTHOR)

3. Huang J, Thawornwattana Y, Flour T, Mallet J, Yang Z. 2022. Inference of gene flow between species under misspecified models. *Mol Biol Evol*.
4. Ji J, Jackson DJ, Leache AD, Yang Z. 2022. Power of Bayesian and heuristic tests to detect cross-species introgression with reference to gene flow in the *Tamias quadrivittatus* group of North American chipmunks. *Syst Biol*.
5. Flour T, Huang J, Jiao X, Kapli P, Rannala B, Yang Z.* 2022. Bayesian phylogenetic inference using relaxed-clocks and the multispecies coalescent. *Mol Biol Evol* 39:msac161.
6. Thawornwattana Y*, Seixas FA, Mallet J*, Yang Z*. 2022. Full-likelihood genomic analysis clarifies a complex history of species divergence and introgression: the example of the erato-sara group of *Heliconius* butterflies. *Systematic Biology* 71:1159-1177 (DOI: 10.1093/sysbio/syac009).
7. Poelstra J, Montero BK, Lüdemann J, Yang Z, Rakotondranary SJ, Hohenlohe P, Stetter N, Ganzhorn JU, Yoder AD.* 2022. RADseq data reveal a lack of admixture in a mouse lemur contact zone contrary to previous microsatellite results. *Proc Ro Soc B Biol Sci*. 289: 20220596.
8. Yang Z, Flour T. 2022. Estimation of cross-species introgression rates using genomic data despite model unidentifiability. *Molecular Biology and Evolution* 39(5): msac083. DOI: 10.1093/molbev/msac083.

9. Zhu T, Flouri T, Yang Z. 2022. A simulation study to examine the impact of recombination on phylogenomic inferences under the multispecies coalescent model. *Molecular Ecology* 31:2814-2829 (10.1111/mec.16433).
10. Huang J, Bennett J, Flouri T, Yang Z. 2022. Phase resolution of heterozygous sites in diploid genomes is important to phylogenomic analysis under the multispecies coalescent model. *Systematic Biology* 71:334-352. (DOI:10.1093/sysbio/syab047)
11. Finger N, Farleigh K, Bracken JT, Leache AD, Francois O, Yang Z, Flour T, Charran T, Jezkova T, Williams DA et al. 2022. Genome-scale data reveal deep lineage divergence and a complex demographic history in the Texas horned lizard (*Phrynosoma cornutum*) throughout the southwestern and central USA. *Genome Biology and Evolution* DOI: 10.1093/gbe/evab260.
12. Álvarez-Carretero S, Tamuri AU, Battini M, Nascimento FF, Carlisle E, Asher RJ, Yang Z, Donoghue PCJ, dos Reis M. 2022. A species-level timeline of mammal evolution integrating phylogenomic data. *Nature* 602: 263-267 (10.1038/s41586-41021-04341-41581)
13. Jiao X, Flouri T, Yang Z. 2021. Multispecies coalescent and its applications to infer species phylogenies and cross-species gene flow. *National Science Review*: 8: nwab127 (DOI: 110.1093/nsr/nwab127).
14. Feng Y, Xu H, Liu J, Xie N, Gao L, He Y, Yao Y, Lv F, Zhang Y, Lu J, ..., Hu X.*, Yang, Z.*, Xiao R-P. 2021. Functional and adaptive significance of promoter mutations that affect divergent myocardial expressions of TRIM72 in primates. *Molecular Biology and Evolution*, 38: 2930-2945 (10.1093/molbev/msab083).
15. Huang J, Liu Y, Zhu T, Yang Z.* 2021. The asymptotic behavior of bootstrap support values in molecular phylogenetics. *Systematic Biology* 70: 774-785 (10.1093/sysbio/syaa100).
16. Zhu T, Yang Z.* 2021. Complexity of the simplest species tree problem. *Molecular Biology and Evolution*, 39: 3993-4009 (10.1093/molbev/msab009).
17. Jiao X, Yang Z. 2021. Defining species when there is gene flow. *Systematic Biology* 70(1): 108-119. 10.1093/sysbio/syaa052
18. Huang J, Flouri T, Yang Z.* 2020. A simulation study to examine the information content in phylogenomic datasets under the multispecies coalescent model. *Molecular Biology and Evolution* 32: 3211-3224.
19. Tiley GP, Poelstra JP, dos Reis M, Yang Z, Yoder AD. 2020. Molecular clocks without rocks: new solutions for old problems. *Trends in Genetics* 36:845-856 (10.1016/j.tig.2020.06.002)
20. Kapli P, Telford M, Yang Z. 2020. Phylogenetic tree building in the genomic age, *Nature Reviews Genetics* 21: 428-444 (10.1038/s41576-020-0233-0)
21. Weber C., Yang Z., Goldman N. 2020. Ambiguity coding allows accurate inference of evolutionary parameters from alignments in an aggregated state-space. *Systematic Biology* 70(1): 21-32.
22. Jiao X, Flouri T, Rannala B, Yang Z.* 2020. The impact of cross-species gene flow on species tree estimation. *Systematic Biology* 69(5): 830-847. 10.1093/sysbio/syaa001.
23. Flouri T, Jiao X, Rannala B, Yang Z.* 2020. A Bayesian implementation of the multispecies coalescent model with introgression for phylogenomic analysis. *Molecular Biology and Evolution*, 37: 1211-1223. 10.1093/molbev/mst012.
24. Dos Reis M, Yang Z. 2019. Bayesian molecular clock dating using genome-scale datasets in Anisimova M, ed. *Evolutionary Genomics: Volume 2, Statistical and Computational Methods*. Springer, New York.
25. Halliday TJD, Dos Reis M, Tamuri AU, Ferguson-Gow H, Yang Z, Goswami A. 2019. Rapid morphological evolution in placental mammals post-dates the origin of the crown group. *Proc Biol Sci* 286:20182418.
26. Alvarez-Carretero, S., A. Goswami, Z. Yang, and M. dos Reis. 2019. Bayesian estimation of species divergence times using correlated quantitative characters. *Systematic Biology* 68:967-986 DOI:10.1093/sysbio/syz015.
27. Leaché A.D., Zhu T., Rannala B., Yang Z.* 2019. The spectre of too many species. *Systematic Biology* 68: 168-181.
28. Ostrander EA, Wang GD, et al. 2019. Dog10K: an international sequencing effort to advance studies of canine domestication, phenotypes and health. *National Science Review* 6:810-824.
29. Morris JL, Puttick MN, Clark J, Edwards D, Kenrick P, Pressel S, Wellman CH, Yang Z, Schneider H, Donoghue PCJ. 2018. Accurate timetrees do indeed require accurate calibrations. Response to comment by Hedges et al. *Proc Nat Acad Sci USA* 115: E9512-E9513.
30. Liu Z, Chen G, Zhu T, Zeng Z, Lyu Z, Wang J, Messenger K, Greenberg AJ, Guo Z, Yang Z et al. 2018. Prevalence of cryptic species in morphologically uniform taxa - Fast speciation and evolutionary radiation in Asian frogs. *Molecular Phylogenetics and Evolution* 127:723-731.
31. Flouri T, Jiao X, Rannala B, Yang Z.* 2018. Species tree inference with BPP using genomic sequences and the multispecies coalescent. *Molecular Biology and Evolution* 35 (10): 2585-2593.

32. Thawornwattana Y, Dalquen DA, Yang Z.* 2018. Coalescent analysis of phylogenomic data confidently resolves the species relationships in the *Anopheles gambiae* species complex. *Molecular Biology and Evolution* **35**:2512-2527.
33. Thawornwattana Y, Dalquen DA, Yang Z.* 2018. Designing simple and efficient Markov chain Monte Carlo proposal kernels. *Bayesian Analysis* **13**: 1033-1059.
34. Morris J.L., Puttick M.N., Clark J., Edwards D., Kenrick P., Pressel S., Wellman C.H., Yang Z., Schneider H., Donoghue P.C.J. 2018. The timescale of early land plant evolution. *Proc. Nat. Acad. Sci. USA*.
35. Yang, Z.* 2018. AWF Edwards and the origin of Bayesian phylogenetics, pp. 352-362 in *AWF Edwards* (R. G. Winther, ed.) Cambridge University Press, Cambridge, England.
36. dos Reis M., Gunnell G.F., Barba-Montoya J., Wilkins A., Yang Z., Yoder A.D. 2018. Using phylogenomic data to explore the effects of relaxed clocks and calibration strategies on divergence time estimation: Primates as a test case. *Systematic Biology* **67**(4): 594-615.
37. Yang Z*, Zhu T. 2018. Bayesian selection of misspecified models is overconfident and may cause spurious posterior probabilities for phylogenetic trees. *Proc. Nat. Acad. Sci. USA* **115**:1854-1859.
38. Barba-Montoyaa J, dos Reisa M, Schneider H, Donoghue PCJ, Yang Z.* 2018. Constraining uncertainty in the timescale of angiosperm evolution and the veracity of a Cretaceous terrestrial revolution. *New Phytologist*. **218**: 819-834.
39. Angelis K, Álvarez-Carretero S, dos Reis M, Yang Z.* 2018. An evaluation of different partitioning strategies for Bayesian estimation of species divergence times. *Systematic Biology* **67**:61-77. [Best student paper for *Systematic Biology* 2018]
40. Shi, C.-M., and Z. Yang*. 2018. Coalescent-based analyses of genomic sequence data provide a robust resolution of phylogenetic relationships among major groups of gibbons. *Molecular Biology and Evolution* **35**: 159-179.
41. Zeng, L, et al. ..., Yang, Z., ..., Zhong, Y. 2017. Evolution of a high altitude ecotype of *Arabidopsis thaliana* from the Himalayas. *Sci. Bull.* **62**: 1628-1630.
42. Barba-Montoya, J., M. dos Reis, and Z. Yang*. 2017. Comparison of different strategies for using fossil calibrations to generate the time prior in Bayesian molecular clock dating. *Mol. Phylogenet. Evol.* **114**: 386-400.
43. Nascimento, F. F., M. dos Reis, and Z. Yang*. 2017. A biologist's guide to Bayesian phylogenetic analysis. *Nature Ecology and Evolution* **1**: 1446-1454.
44. Warnock, R. C., Z. Yang, and P. C. Donoghue. 2017. Testing the molecular clock using mechanistic models of both fossil preservation and molecular evolution. *Proc. R. Soc. Lond. B.* **284**: 20170227.
45. Rannala, B., and Z. Yang*. 2017. Efficient Bayesian species tree inference under the multispecies coalescent. *Systematic Biology* **66**: 823-842.
46. Yang, Z., and B. Rannala. 2017. Bayesian species identification under the multispecies coalescent provides significant improvements to DNA barcoding analyses. *Molecular Ecology* **26**: 3028-3036.
47. Dalquen, D., Zhu, T., Yang, Z.* 2017. Maximum likelihood implementation of an isolation-with-migration model for three species. *Systematic Biology*, **66**: 379-398.
48. Xu, B. and Z. Yang*. 2016. Challenges in species tree estimation under the multispecies coalescent model. *Genetics* **204**: 1353-1368
49. Yang, Z. and P.C. Donoghue, 2016. Dating species divergences using rocks and clocks. *Phil. Trans. R. Soc. B: Biol. Sci.*, **371**: 20150126.
50. Donoghue, P.C. and Z. Yang, 2016. The evolution of methods for establishing evolutionary timescales. *Phil. Trans. R. Soc. B: Biol. Sci.*, **371**:20160020
51. dos Reis, M.*, P.C.J. Donoghue and Z. Yang*, 2016. Bayesian molecular clock dating of species divergences in the genomics era. *Nature Reviews Genetics* **17**: 71-80.
52. dos Reis, M., Y. Thawornwattana, K. Angelis, M. J. Telford, P. C. J. Donoghue*, and Z. Yang*. 2015. Uncertainty in the timing of origin of animals and the limits of precision in molecular timescales. *Current Biology* **25**:2939-2950.
53. Yang, Z.* 2015. The BPP program for species tree estimation and species delimitation. *Current Zoology* **61**: 854-865.
54. Matsumoto T., Akashi H., Yang Z.* 2015. Evaluation of ancestral sequence reconstruction methods to infer nonstationary patterns of nucleotide substitution. *Genetics* **200**: 873-890. [Genetics highlight]
55. Liu, J., Zhang, D.-X., Yang, Z.* 2015. A discrete-beta model for testing gene flow after speciation, *Methods in Ecology and Evolution*, 10.1111/2041-210X.12356.

56. Zhu T, dos Reis M, Yang Z.* 2015. Characterization of the uncertainty of divergence time estimation under relaxed molecular clock models using multiple loci. *Systematic Biology* **64**: 267-280.
57. Yang, Z., and B. Rannala*. 2014. Unguided species delimitation using DNA sequence data from multiple loci. *Mol. Biol. Evol.* **31**: 3125-3135
58. Zhang C, Rannala B, Yang Z.* 2014. Bayesian species delimitation can be robust to guide tree inference errors. *Systematic Biology* **63**: 993-1004
59. Angelis K, dos Reis M, Yang Z.* 2014. Bayesian estimation of nonsynonymous/synonymous rate ratios for pairwise sequence comparisons. *Molecular Biology and Evolution* **31**(7): 1902-1913.
60. dos Reis, M., T. Zhu, and Z. Yang*. 2014. The impact of the rate prior on Bayesian estimation of divergence times with multiple loci. *Systematic Biology* **63**(4): 555-565.
61. dos Reis, M.*, M. J. Donoghue, and Z. Yang. 2014. Neither phylogenomic nor palaeontological data support a Paleogene origin of placental mammals. *Biological Letters* **10**: 20131003 [reported in *Discovery*, *The Scientist*, *Nature*, and *Times of India*.]
62. Yoder, A. D., L. M. Chan, M. dos Reis, P. A. Larsen, C. R. Campbell, R. Rasolarison, M. Barrett, C. Roos, P. Kappeler, J. P. Bielawski, and Z. Yang. 2014. Molecular evolutionary characterization of a V1R subfamily unique to Strepsirrhine primates. *Genome Biology and Evolution* **6**: 213-227.
63. Leaché, A. D.*, R. B. Harris, B. Rannala, and Z. Yang. 2014. The influence of gene flow on Bayesian species tree estimation: A simulation study. *Systematic Biology* **63**: 17-30.
64. Yang Z.*, Rodríguez C.E. 2013. Searching for efficient Markov chain Monte Carlo proposal kernels. *Proc Natl Acad Sci USA* **110**: 19307-19312.
65. Xu B, Yang Z.* 2013. PamlX: A graphical user interface for PAML. *Molecular Biology and Evolution* **30**: 2723-2724.
66. dos Reis, M., and Z. Yang*. 2013. Why do more divergent sequences produce smaller nonsynonymous/synonymous rate ratios in pairwise sequence comparisons? *Genetics* **195**:195-204.
67. Stadler T, Yang Z* 2013. Dating phylogenies with sequentially sampled tips. *Systematic Biology* **62**: 674-688.
68. Zou X-H, Yang Z, Doyle JJ & Ge S.* 2013. Multilocus estimation of divergence times and ancestral effective population sizes of *Oryza* species and implications for the rapid diversification of the genus. *New Phytologist* **198**: 1155-1164.
69. Rannala, B., and Yang Z.* 2013. Improved reversible jump algorithms for Bayesian species delimitation. *Genetics* **194**: 245-253.
70. dos Reis M, and Yang Z.* 2013. The unbearable uncertainty of Bayesian divergence time estimation. *Journal of Systematics and Evolution* **51**: 30-43.
71. Schabauer H, Valley M, Pacher C, Stockinger H, Stamatakis A, Robinson-Rechavi M, Yang Z, Salamin N. 2012. SlimCodeML: An optimized version of CodeML for the branch-site model. Pp. 700-708. 11th International Workshop on High Performance Computational Biology (HiCOMB). IEEE.
72. dos Reis M., Inoue J., Hasegawa M., Asher R., Donoghue P.C.*, Yang Z.* 2012. Phylogenomic data sets provide both precision and accuracy in estimating the timescale of placental mammal evolution. *Proc. R. Soc. Lond. B.* **279**: 3491-3500.
73. Zhai W, Nielsen R, Goldman N, Yang Z.* 2012. Looking for Darwin in genomic sequences - validity and success of statistical methods. *Molecular Biology and Evolution* **29**: 2889-2893.
74. Zhu T, Yang Z.* 2012. Maximum likelihood implementation of an isolation-with-migration model with three species for testing speciation with gene flow. *Molecular Biology and Evolution* **29**: 3131-3142.
75. Zhang C, Rannala B, Yang Z.* 2012. Robustness of compound Dirichlet priors for Bayesian inference of branch lengths. *Systematic Biology* **61**: 779-784.
76. Yang Z.*, Rannala B. 2012. Molecular phylogenetics: principles and practice. *Nature Review Genetics* **13**: 303-314.
77. Parham, J.*, Donoghue, P, Bell, C, Calway, T, Head, J, Holroyd, P, Inoue, J, Irmis, R, Joyce, W, Ksepka, D, Patane, J, Smith, N, Tarver, J, van Tuinen, M, Yang, Z, Angielczyk, K, Greenwood, J, Hipsley, C, Louis, J, Makovicky, P, Mueller, J, Smith, K, Theodor, J, Warnock, R and Benton, M, 2012. Best practices for applying paleontological data to molecular divergence dating analyses. *Systematic Biology* **61**: 346-359.
78. Warnock, R.C.M., Z. Yang, and P.C.J. Donoghue*. 2012. Exploring uncertainty in the calibration of the molecular clock. *Biological Letters* **8**: 156-159.
79. Rannala B., Zhu T., Yang Z.* 2012. Tail paradox, partial identifiability and influential priors in Bayesian branch length inference. *Molecular Biology and Evolution* **29**: 325-335.
80. Zhang C., Zhang D.-X., Yang Z.* 2011. Evaluation of a Bayesian coalescent method of species delimitation. *Systematic Biology* **60**: 747-761.

81. Brown RP, Yang Z. 2011. Rate variation and estimation of divergence times using strict and relaxed clocks. *BMC Evolutionary Biology* **11**: 271.
82. Zang, L.-L., X.-H. Zou, F.-M. Zhang, Z. Yang, S. Ge*, 2011 Phylogeny and species delimitation of the C-genome diploid species in *Oryza*. *Journal of Systematics and Evolution* **49**: 386-395.
83. Groussin M., Pawlowski J., Yang Z.* 2011. Bayesian relaxed clock estimation of divergence times in Foraminifera. *Molecular Phylogenetics and Evolution*, **61**: 157-166.
84. Yoshida I., Sugiura W., Shibata J., Ren F.*, Yang Z., Tanaka H. 2011. Change of positive selection pressure on HIV-1 envelope gene inferred by early and recent samples. *PLOS One* **6**:e18630.
85. dos Reis M, Yang Z.* 2011. Approximate likelihood calculation for Bayesian estimation of divergence times. *Molecular Biology and Evolution* **28**:2161–2172.
86. Zhu T., Hu, Y., Ma, Z., Zhang, D.-X., Li, T. and Yang, Z.* 2011. Efficient simulation under a population genetics model of carcinogenesis. *Bioinformatics* **27**: 837-843.
87. Yang Z.*, dos Reis M. 2011. Statistical properties of the branch-site test of positive selection. *Molecular Biology and Evolution*, **28**: 1217-1228.
88. Wilkinson R.D.*, M.E. Steiper, C. Soligo, R.D. Martin, Z. Yang, S. Tavaré. 2011. Dating primate divergences through an integrated analysis of palaeontological and molecular data. *Systematic Biology*, **60**: 16-31.
89. Chen M.-S.*, X. Liu, Z. Yang, H. Zhao, R. Shukle, J. Stuart, S. Hulbert. 2010. Unusual conservation among genes encoding small secreted salivary gland proteins from a gall midge. *BMC Evolutionary Biology* **10**:296.
90. Fletcher W. and Z. Yang* 2010. The effect of insertions, deletions and alignment errors on the branch-site test of positive selection. *Molecular Biology and Evolution* **27**: 2257-2267.
91. Yang Z. and B. Rannala *. 2010. Bayesian species delimitation using multilocus sequence data. *Proc. Natl. Acad. Sci. USA*. **107**: 9264-9269.
92. Yang Z.* 2010. A likelihood ratio test of parapatric speciation using genomic data from three species. *Genome Biology and Evolution* **2**: 200-211.
93. Beaumont, M.*, R. Nielsen, C. Robert, J. Hey, O. Gaggiotti, L. Knowles, A. Estoup, M. Panchal, J. Corander, M. Hickerson, S. Sisson, N. Fagundes, L. Chikhi, P. Beerli, R. Vitalis, J.-M. Cornuet, J. Huelsenbeck, J. Novembre, M. Foll, Z. Yang, F. Rousset, D. Balding And L. Excoffier. 2010. In defence of model-based inference in phylogeography. *Molecular Ecology* **19**: 436-446.
94. Brown, R.P.* and Z. Yang. 2010. Bayesian dating of shallow phylogenies with a relaxed clock. *Systematic Biology* **59**: 119-131.
95. Inoue, J., P. C. H. Donoghue, and Z. Yang*. 2010. The impact of the representation of fossil calibrations on Bayesian estimation of species divergence times. *Systematic Biology* **59**: 74-89.
96. Yang, Z.*, R. Nielsen, and N. Goldman, 2009 In defense of statistical methods for detecting positive selection. *Proceedings of the National Academy of Sciences of U.S.A.* **106**:E95-E95.
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50. Yang, Z. 1998 *Bayesian estimation of molecular evolutionary trees*. European Mathematical Genetics Meeting, Reading, England, April 2–4, 1998.
51. Yang, Z. 1996 *Among-site rate heterogeneity in phylogenetic analysis*. The 4th Annual meeting of the Society for Molecular Biology and Evolution. Tucson, Arizona, June 8–11, 1996.
52. Yang, Z. 1993 *Models of nucleotide substitution and maximum likelihood estimation of phylogeny*. Workshop on Mathematical and Statistical Aspects of Molecular Biology, University of Oxford, Oxford, January 4–5, 1993.

SOFTWARE PACKAGE

- *PAML (for Phylogenetic Analysis by Maximum Likelihood)*, 1993-date, is a package of phylogenetic programs for maximum likelihood analyses of nucleotide, amino acid and codon sequences. It has been widely used in a range of fields such as molecular evolution, phylogenetics, molecular biology, bacteriology, etc. It has attracted >6000 citations (June 2013).

- *BPP (for Bayesian phylogenetics and phylogeography)*, 2010-date, implements a Bayesian MCMC algorithm for species delimitation and inference under the multispecies coalescent model.

PROFESSIONAL SERVICE

SOCIETY MEMBERSHIPS

- American Association for the Advancement of Sciences (1997-2008)
- International Society for Molecular Evolution (1997-2004)
- Society for Molecular Biology and Evolution (1997-date)
- Society for Systematic Biology (1998-date)

SERVICE ON INTERNATIONAL COMMITTEES

- Royal Society Sectional Committee 9: Patterns in Populations, 1 November 2022 - 31 October 2025.
- International Strategy Advisor for Research Organization of Information and Systems, an umbrella Organization consisting of five national research institutes in Japan (National Institute of Polar Research, National Institute of Informatics, Institute of Statistical Mathematics, National Institute of Genetics, Database Center for Life Science). 2016-2019.
- Member of Academic Board, Biology and Medicine Branch, National Centre for Mathematics and Interdisciplinary Sciences, Chinese Academy of Sciences, Beijing, 2011-2016
- Non-North American Vice President of the Society for the Study of Evolution, 2010-2013.
- Councillor of Society for Molecular Biology and Evolution, 2008-2010
- Member, Academic Board of State Key Laboratory of Systematic and Evolutionary Botany (LSEB), Beijing, The Chinese Academy of Sciences, since 2005
- Vice Chair, Academic Board, Institute of Zoology, Chinese Academy of Sciences, Beijing, 2008-date
- Member of the Academic Board, National Key Laboratory of Cellular and Molecular Evolution, Kunming Institute of Zoology, Chinese Academy of Sciences. 2002-2007.
- Member of International Evaluation Committee for Kunming Institute of Zoology, Chinese Academy of Sciences. October 2003.
- Member of International Review Committee for the Molecular Evolution Group, Institute of Statistical Mathematics, Tokyo, Japan, November 1998

SERVICE ON UCL COMMITTEES

- Biosciences MRes Stream Tutor, UCL, since 2008
- Computational Biology Steering Group, UCL.
- Member of Scientific Advisory Board, UCL Genetics Institute (UGI), since 2007
- Steering Committee Member of Bloomsbury Centre of Bioinformatics, London, since 2004.
- Board Member of London Bioinformatics Forum, since 2003
- Management Board Member for Centre for Computational Science, UCL, since 2003.
- Steering Committee Member, BSc/MSci programme in Mathematics with Biology, Mathematics, UCL, since 2003.
- Member of Bioinformatics Advisory Board, UCL, since 2001.
- Graduate adviser for the CoMPLEX Centre, UCL, since 1998.

EXTERNAL EXAMINATION

External Examiner for Ph. D. thesis

- 2013 Carina Mugal, Evolutionary Biology Center, Uppsala University, Sweden.
- 2012 Jukka Sirén, Department of Mathematics, University of Helsinki, Finland.
- 2008 Boussau Bastien, devant L'Université Claude Bernard - Lyon 1, France
- 2005 Lachlan James Murray Coin, University of Cambridge.
- 2003 Howsun Jow, Department of Computer Science, University of Manchester.
- 2000 Simon Whelan, Department of Genetics, University of Cambridge.
- 1999 Anne-Mette Pedersen, Department of Ecology and Genetics, University of Århus, Denmark.

Committee member for Ph. D. students

- 2001-2007 Karen Cranston, University of Alberta (Supervisor: Professor Bruce Rannala);
- 2001-2007 Ligia M. Mateiu, University of Alberta (Supervisor: Professor Bruce Rannala).

EDITORIAL AND REFEREEING SERVICE

- Member of Statistics Review Board, Cell Press, since 2019
- Editorial Board Member for
 - *Philosophical Transactions of the Royal Society B*, 2014-2016.
 - *Biological Letters*, 2011-2013
- Associate Editor for
 - *Molecular Biology and Evolution*, 2006-2008
 - *Evolutionary Bioinformatics*, 2005-
 - *Genetics*, 2002-2007
 - *Systematic Biology*, 2001-2004, 2021-date
 - *Journal of Molecular Evolution*, 1998-2002
- Referee for funding agencies
BBSRC, Human Frontier Science Program (HFSP), Israel Science Foundation, NERC, The Leverhulme Trust, National Science Foundation (USA), The Wellcome Trust.
- Referee for scientific journals
Annals of Human Genetics, Bioinformatics, Biological Reviews, Briefings in Bioinformatics, Computer Application in BioSciences, Current Biology, Genetical Research, Genetics, Genome Research, Genomics, Journal of American Statistical Association, Journal of Molecular Biology, Journal of Molecular Evolution, Journal of Theoretical Biology, Mathematical BioSciences, Molecular Biology and Evolution, Molecular Phylogenetics and Evolution, Nature, Nature Genetics, Nature Reviews Genetics, Proceedings of National Academy of Sciences U.S.A., Proceedings of the Royal Society Series B, Science, Systematic Biology, Trends in Biochemical Sciences, Trends in Genetics, Trends in Ecology and Evolution.
- Faculty member of *FACULTY OF 1000*, a “revolutionary online service whose principal aim is to organize and evaluate the life sciences literature”.

CONFERENCE AND WORKSHOP ORGANIZATION

- *Preparing for a Changing Climate and an Altered Landscape: A Workshop for Uniting Theoretical and Empirical Approaches to Biodiversity Science*, Duke Kunshan University, 7 June 2019 (Co-Organizer: Dr Anne Yoder).
- *Wellcome Trust Advanced Workshop on Computational Molecular Evolution*, Hinxton, 10-21 May 2019 (Co-Organizers: Drs Adam Leache, Alexandros Stamatakis, Cilia Antoniou).
- *EMBO Practical Course on Computational Molecular Evolution*, Heraklion, Crete, 6-17 May 2018 (Co-Organizers: Drs Alexandros Stamatakis, Nick Goldman, Adam Leache).
- *Wellcome Trust Advanced Workshop on Computational Molecular Evolution*, Hinxton, 8-19 May 2017 (Co-Organizers: Drs Nick Goldman, Adam Leache, & Alexandros Stamatakis).
- *EMBO Practical Course on Computational Molecular Evolution*, Heraklion, Crete, 8-19 May 2016 (Co-Organizers: Drs Nick Goldman, Aidan Budd, & Alexandros Stamatakis).
- Royal Society Discussion Meeting *Dating species divergence using rocks and clocks*, 9-10 November 2015, The Royal Society, London (co-organizer Dr Phil Donoghue).
- *Mathematics in population genetics and evolution*, Mini-symposium at International Congress on Industrial and Applied Mathematics (ICIAM 2015), Beijing, 10-14 August 2015 (co-Organiser: Professor Zhi-Ming Ma).
- *Bayesian Methods to Estimate Species Divergence Times*, University of Bristol, 30 - 31 July 2015 (co-Organisers: Drs Mario dos Reis and Philip Donoghue).
- *Workshop on Molecular Evolution and Systematics*, Beijing Institute of Genomics, Chinese Academy of Sciences, Beijing, China, 17-23 August 2014 (Co-Organizer: Professor De-Xing Zhang).
- *EMBO Practical Course on Computational Molecular Evolution*, Heraklion, Crete, 4-15 May 2014 (Co-Organizers: Drs Nick Goldman, Aidan Budd, Alexandros Stamatakis, & Georgios Kotoulas).
- *Wellcome Trust Advanced Workshop on Computational Molecular Evolution*, Hinxton, 29 April-10 May 2013 (Co-Organizers: Drs Nick Goldman, Aidan Budd, & Alexandros Stamatakis).
- *EMBO Practical Course on Computational Molecular Evolution*, Heraklion, Crete, 29 April-10 May 2012 (Co-Organizers: Drs Nick Goldman, Aidan Budd, Alexandros Stamatakis, & Georgios Kotoulas).
- *Society for Molecular Biology and Evolution 2011 Annual Meeting*, 26-30 July 2011, Tokyo Japan, Global Organizing Committee Member.
- *Wellcome Trust Advanced Workshop on Computational Molecular Evolution*, Hinxton, 10-21 April 2011 (Co-Organizers: Drs Nick Goldman, Aidan Budd, & Alexandros Stamatakis).
- *Workshop on Molecular Evolution and Systematics*, Institute of Zoology, Chinese Academy of Sciences, Beijing, China, 12-17 June 2010 (Co-Organizer: Professor De-Xing Zhang).

- *EMBO Practical Course on Computational Molecular Evolution*, Heraklion, Crete, 3-12 May 2010 (Co-Organizers: Drs Nick Goldman, Aidan Budd, Alexandros Stamatakis, & Georgios Kotoulas).
- *Wellcome Trust Advanced Course on Molecular Evolution*, Hinxton, 30 March - 8 April 2009 (Co-Organizers: Drs Nick Goldman and Aidan Budd).
- *Workshop on Molecular Evolution and Systematics*, Institute of Zoology, Chinese Academy of Sciences, Beijing, China, 12-16 May 2008 (Co-Organizer: Professor De-Xing Zhang).
- Royal Society Discussion Meeting *Statistical and computational challenges in molecular phylogenetics and evolution*, 28-29 April 2008, The Royal Society, London (co-organizer Dr Nick Goldman).
- *PhyloGroup Meeting VII*, 28 September 2007, Cambridge (Co-Organizer Dr Nick Goldman)
- *PhyloGroup Meeting VI*, 12 January 2007, EBI, Hinxton (Co-Organizer Dr Nick Goldman)
- *PhyloGroup Meeting V*, 28 April 2006, UCL, London
- *PhyloGroup Meeting IV*, 21 October 2005, UCL, London
- *PhyloGroup Meeting III*, 5 October 2004, University College London, London
- *Workshop on Molecular Evolution and Systematics*, Institute of Zoology, Chinese Academy of Sciences, Beijing, China, 19-22 August 2004 (Co-Organizer: Professor De-Xing Zhang).
- Symposium on *Methodological advances in estimation of species divergence dates using molecular data*, International Congress of Zoology, 23-27 August 2004, Beijing, China (Co-Organizer: Dr Bruce Rannala).
- Symposium on "Exploring clade divergence age estimation: why are fossil and molecular data in conflict regarding the age of crown placental mammals?" (Co-Organizer: Dr Anne Yoder), Fort Collins, Colorado, 26-30 June 2004
- Organising Committee Member of the series *Mathematics of Evolution and Phylogeny*, Institut Henri Poincare, Paris, since 2004.
- *PhyloGroup Meeting II*, 18 February 2004, UCL, London
- *PhyloGroup Meeting I*, 16 September 2003, UCL, London
- *Proteins, Structure, Function and Evolution*. 3-8 January 2002 at Lihue, Kauai, Hawaii, (co-organizers: Drs Peter Clote and Gavin Naylor).
- *Adaptive molecular evolution*. 27 April 2000 at Zoology Society of London, London, Centre for Ecology and Evolution workshop (co-organizer Dr Bill Jordan).

ACADEMIC SUPERVISION AND HOSTING OF VISITORS

POSTDOCS SUPERVISED

- Dr Tomas Flouri, 2017-2021.
- Dr Paschalia Kapli, 2017-2021.
- Dr Xiyun Jiao, 2017-2020.
- Dr Daniel Dalquen (Researcher co-I), 2013-2017.
- Dr Mario dos Reis, BBSRC Research Fellow (Researcher co-I), 2010-2016.
- Dr Adam Leache, NSF fellowship, 2010
- Dr Jun Inoue, BBSRC Research Fellow (RA1A), 2008-2010 (currently Lecturer, Okinawa Institute of Technology)
- Dr Maria Anisimova, BBSRC Research Fellow (RA1A), 2005-2008 (now Zurich U. Applied Sciences)
- Dr Rick Desper, NERC Research Fellow (RA1A), 2005-2007
- Dr Samit Kundu, BBSRC Research Fellow (RA1A), 2003-2004
- Dr Becky Furlong, BBSRC Research Fellow (RA1A), 2003-2004 (Editor, *Genome Medicine*)
- Dr Paul Michael-Agapow, BBSRC Research Fellow (RA1A), 2002-2004 (currently Dept Biology, Imperial College)
- Dr Lounes Chikhi, BBSRC Research Fellow (RA1A), 2001-2002 (currently Group Leader, Population and Conservation Genetics Group, Instituto Gulbenkian de Ciência in Oeiras, Portugal)
- Dr Paul Taylor, Wellcome Research Fellow, 2000-2002
- Dr Joe Bielawski, BBSRC Research Fellow (RA1A), 1999-2003 (currently Associate Professor, Dept Maths and Stats, Dalhousie University, Canada)
- Dr Kathy Dunn, BBSRC Research Fellow (RA1A), 1999-2003

PH. D. STUDENTS SUPERVISED

- Jose Barba-Montoya, Department of Genetics, UCL, 2014-2017.
- Konstantinos Angelis, Department of Genetics, UCL, 2014-2016
- Rachel Warnock, Department of Earth Sciences, University of Bristol, joint supervision with Prof. Philip Donoghue (2009-date).
- John Ambrose, Royal Free Medical School (2010-, joint supervision with Anna Geretti)

- Will Fletcher (2006-2010), Quantitative Analyst, Smartodds Ltd.
- Yuval Itan (2005-2009, joint supervision with Dr Mark Thomas).
- Jessica Vamathevan (2005-2008), Senior Scientific Investigator, Computational Biology, GlaxoSmithKline, Stevenage, UK
- Dave Dale (2002-2006).
- Daniel White (2001-2004, joint supervision with Dr Andres Ruiz-Linares).
- Sarah Darwin (2001-2007, joint supervision with Professor Jim Mallet).
- Giselle Walker, Natural History Museum (2001-2004, joint supervision with Dr Martin Embley) "Eukaryote evolution and the systematics of amoeboid flagellates". (currently Lecturer, Dept Botany, University of Otago, New Zealand)
- Gabriela Estrada (2000-2004) "The evolution of the vertebrate beta-globin gene family". (currently postdoc in Comparative Genomics Group, CRG-Centre for Genomic Regulation, Barcelona, Spain)
- Maria Anisimova (2000-2003) "Detecting positive selection in protein-coding genes". (currently Junior Group Leader, Dept Computer Science, ETH Zurich)
- Wa Yang (1999-2003) "The evolution of human AIDs viruses".
- Stephane Aris-Brosou (1999-2002) "*Bayes molecular phylogenetics: estimation of divergence dates and hypothesis testing*". (currently Associate Professor, Director of Bioinformatics, Dept Biology, University of Ottawa, Canada)

M.SC. STUDENTS SUPERVISED

- Yuttapong Thawornwattana, Department of Genetics, UCL, 2014-2018.
- Rhiju Das (MRes. 2000) *Systematics of Phylogeny Reconstruction*
- Maria Anisimova (MRes. 2000) *The power of the likelihood ratio test to detect adaptive molecular evolution*
- Jonathan Wald (MRes. 2001) *A molecular genetic investigation into selection and gene flow in the Heliconius melpomene species complex*
- Christian Bottomley (MRes. 2002) *An investigation into the role of diversifying selection in the evolution of the merozoite surface protein (MSP1) of Plasmodium falciparum*
- Chris Mullaley (MRes. 2002) *Molecular evolutionary analysis of a set of sequenced rhinovirus genes*

HOSTS TO COLLABORATORS (1 WEEK OR LONGER)

- (1 year August 2021-August 2022) Dr Eyal Privman, University of Haifa, Israel
- (7 days in 2012) Professor Bruce Rannala, University of California Davis.
- (5 months in 2012) Professor Anne Yoder, Duke University
- (10 days in 2011) Professor Bruce Rannala, University of California Davis.
- (1.5 months in 2008) Dr Fengrong Ren, Associate Professor, Tokyo Medical and Dental University.
- (2 weeks in 2008) Dr Richard Brown, Reader, School of Biological & Earth Sciences, Liverpool John Moores University, Liverpool.
- (2 months in 2006) Dr Fengrong Ren, Associate Professor, Tokyo Medical and Dental University.
- (1 week in 2005) Professor Bruce Rannala, University of California, Davis, California.
- (2 weeks in 2005) Dr Fengrong Ren, Associate Professor, Tokyo Medical and Dental University.
- (2 weeks in 2004) Dr Fengrong Ren, Associate Professor, Tokyo Medical and Dental University.
- (6 months in 2004) Carlos Shrago, Universidade Federal Do Rio de Janeiro, Brazil.
- (2 months in 2004) Dr Ying Cao, Assistant Professor, Institute of Statistical Mathematics, Tokyo.
- (4 weeks in 2003) Dr Fengrong Ren, Assistant Professor, Tokyo Medical and Dental University.
- (2 weeks in 2003) Dr Bruce Rannala, Associate Professor, University of Alberta, Edmonton, Canada.
- (1 week in 2002) Dr Bruce Rannala, Assistant Professor, University of Alberta, Edmonton, Canada.
- (1 week in 2002) Dr Karl Schmid, Assistant Professor, Max-Planck Institute of Molecular Ecology, Jena, Germany.
- (8 weeks in 2001) Mr Raazesh Sainudiin, Graduate Student, Cornell University.
- (6 weeks in 2000) Dr Fengrong Ren, Assistant Professor, Tokyo Medical and Dental University.
- (2 weeks in 2000) Dr Hidetoshi Shimodaira, Assistant Professor, Institute of Statistical Mathematics, Tokyo.
- (1 week 1999) Dr Belinda Chang, Rockefeller University.
- (2 weeks in 1999) Dr Rasmus Nielsen, Harvard University
- (3 weeks in 1999) Dr Hidetoshi Shimodaira, Assistant Professor, Institute of Statistical Mathematics, Tokyo.

INVITED LECTURES AND SEMINARS

PLENARY, KEYNOTE OR NAMED LECTURES

- “Inferring cross-species gene flow using genomic sequence data under the multispecies coalescent model”, International Symposium on Biodiversity and Comparative Genomics, Jiangsu Normal University, China, 15-17 September 2021.
- “Species delimitation using genomic data under the multispecies coalescent model: BPP demo”, Smithsonian Species Delimitation Workshop, 16-20 August, 2021, National Museum of Natural History (NMNH).
- *Species tree inference under the multispecies coalescent model*, keynote talk at *Mathematical, inferential and computational phylogenomics (MIC-Phy 2021)*, Vienna, Austria, 15-17 February 2021.
- *The multispecies coalescent and its applications in phylogenomics*, Bioinformatics Boot Camp for Ecology and Evolution, New York, 3-6 August, 2020.
- *Inference of cross-species introgression using genomic sequence data*, Kunming Institute of Zoology, Kunming, Yunnan, 13 June 2019.
- *Inferring the history of species divergences using genomic sequence data under the multispecies coalescent model*, Beijing Jiaotong University, Beijing, 11 June 2019.
- *Coalescent-based models and methods for inferring gene flow between species using genomic data*. Duke Kunshan University, 7 June 2019.
- *Inference in genomics under the multispecies coalescent*, Invited Lecture, Konstanz, 8 May, 2019.
- *Multispecies coalescent: an overview*, Plenary Lecture at First Asian Evolution Meeting (AsiaEvo 2018), 18-20 April, 2018, Shenzhen, China
- *Markov chain Monte Carlo: how do you propose?* Hua Lookeng Distinguished Lecture, Academy of Mathematics and Systems Sciences, Chinese Academy of Sciences, Beijing, China, 10 January 2018.
- *Bayesian MCMC computation in comparative genomics*, 2nd Conference of International Society for Bayesian Analysis Eastern Asia Chapter (ISBA-EAC), 6-7 July, 2017, Changchun, China
- *Bayesian inference from genomic sequence data under the multispecies coalescent*, Mathematical Approaches to Evolutionary Trees and Networks, Banff International Research Station, 12-17 February 2017.
- *Multispecies coalescent model and its applications in analysis of genomic sequence data*. International Congress on Industrial and Applied Mathematics (ICIAM 2015), Beijing, 10-14 August 2015.
- *Estimation of species divergence times incorporating fossil and molecular information*. Keynote lecture at JOBIM 2015, Annual French Bioinformatics Meeting, Clermont-Ferrand, France, 6-9 June 2015.
- *The limit of species divergence time estimation*. SAMSI Fall Course 2014-5 on *Statistical and Mathematical Challenges in Molecular Evolution*, North Carolina, 16 September 2014.
- *MCMC: how would you propose?* Department of Statistics and Operations Research. University of North Carolina, Chapel Hill, 15 September 2014.
- *Multispecies coalescent and its use in population genetics inference from genomic data*. Bioinformatics Opening Workshop for Program on Beyond Bioinformatics: Statistical and Mathematical Challenges, SAMSI, North Carolina, 8-12 September 2014.
- *The impact of the prior on Bayesian molecular clock dating*. Workshop on Methods for Biodiversity Research, Fudan University, Shanghai, China, 10-12 March 2014.
- *Bayesian delimitation of species using genomic sequence data*. Keynote lecture, Symposium on Computational Biology, Institute of Genomics, Chinese Academy of Sciences, Beijing, 27-28 November 2011.
- *Bayesian estimation of species divergence times*, Plenary speech, Annual Congress of Brazilian Society of Genetics, 30 August - 3 September 2011, Aguas de Lindoia, Sao Paulo, Brazil.
- *Bayesian estimation of species divergence times*, 2011 Journal of Systematics and Evolution Symposium, Linzhi, Tibet, China, 6-9 August 2011.
- *Species delimitation using genomic sequence data*. Advanced Seminar Series, Institute of Biological Sciences, Chinese Academy of Sciences, Beijing, 26 November 2010.
- *Over-confident Bayesian and molecular phylogenetics*. Keynote lecture, ComBi Symposium 18 December 2009, Turku Castle, Finland
- *Detecting adaptive molecular evolution in protein-coding DNA sequences*, Centro de Ciencias Genomicas-UNAM, Cuernavaca, 20 October 2008.

- *Bayesian estimation of hominoid ancestral population sizes*, Keynote speech at The 2008 LASR workshop "The Art and Science of Statistical Bioinformatics". University of Leeds, 16-17 July 2008.
- *Detecting Darwinian selection in DNA sequences*. Keynote speech, The University of Tokyo 130th Anniversary International Symposium on "Frontier of Microbial and Plant Biotechnology in Environmental and Life Sciences". University of Toyo, Japan, 5-6 December 2007.
- *Estimation of species divergence times*. Keynote speech, Asia-Africa Evolution Meeting, Chiba, Japan, 4-6 December 2007.
- *Estimation of species divergence times by incorporating uncertainties in fossils*, Keynote speech, International symposium on "Evolutionary Biology in the 21st Century - Tracing Patterns of Evolution through the Tree of Life", 3-7 June 2007, Beijing
- *Markov chain Monte Carlo in genetics*, Keynote lecture at Summer Symposium in Bioinformatics, International Centre of Excellence for Education in Mathematics (ICE-EM), Australian National University, 6-10 December 2004, Canberra, Australia
- *Detecting adaptive protein evolution*, keynote lecture at Summer Symposium in Bioinformatics, International Centre of Excellence for Education in Mathematics (ICE-EM), Australian National University, 6-10 December 2004, Canberra, Australia
- *Dating techniques*, Xiangshan Science Symposium on Genomics and Evolution, Beijing, 28-30 October 2003.
- *Markov-process models of codon substitution and their use to detect adaptive molecular evolution*. Keynote lecture at Workshop on Computational Evolutionary Biology and Ecology, May 6–8, 1999. Tallahassee, Florida State University.

OTHER INVITED LECTURES

- *Inference of cross-species gene flow using genomic data under the multispecies coalescent model*, International Symposium on Biodiversity and Comparative Genomics, 15-17 September, 2021, Jiangsu Normal University, China
- *Inference of species tree and cross-species gene flow under the multispecies coalescent model*, in "Models of Genome Evolution from Populations to Species", A symposium hosted by the Swedish Collegium for Advanced Study (SCAS), Uppsala University, 19 - 21 May, 2021
- *The good, the bad, and the ugly: overconfident Bayesian model selection in molecular phylogenetics*, Bayesian Model Comparison at CMStatistics2020 in Kings College London, 19-21 December 2020.
- *Phylogeny and introgression in African mosquitoes Anopheles gambiae species complex*, Department of Biology, York University, 31 October 2019.
- *The good, the bad, and the ugly: Bayesian model selection when all models are wrong*, Department of Statistics, Dalhousie University, 22 August 2019.
- *Inferring the history of species divergences using genomic sequence data under the multispecies coalescent model*, School of Sciences, Beijing Jiaotong University, 11 June 2019.
- *Coalescent-based models and methods for inferring gene flow between species using genomic data*, Duke Kunshan University, 7 June 2019.
- *Bayesian species tree estimation under the multispecies coalescent*, Society for Molecular Biology and Evolution Annual Meeting, Yokohama, Japan, 8-12 July 2018.
- *Coalescent analysis of phylogenomic data resolves the species relationships in the Anopheles gambiae species complex*, Symposium on Evolutionary Genetics and Omics, National Institute of Genetics, Mishima, Japan, 13-14 July 2018.
- *Bayesian inference using genomic sequence data under the multispecies coalescent model*, Department of Statistics, University of Georgia, 18 January 2018.
- *Bayesian inference under the multispecies coalescent model*. Department of Statistics, Rice University, 20 November 2017.
- *Bayesian inference from genomic sequence data under the multispecies coalescent*, Mathematical Approaches to Evolutionary Trees and Networks, Banff International Research Station, 12-17 February 2017.
- *Statistical inference using genomic sequence data from multiple closely related species*, Kunming Institute of Zoology, 12 October 2016.
- *Learning about population history using genomic sequence data*, Gansu Agricultural University, 10 October 2016.
- *Bayesian inference under the multispecies coalescent model from genomic sequence data*. Dog10k conference, Beijing, 17-19 June 2016.
- *Bayesian estimation of species trees under the multispecies coalescent*. 10-12 December 2015, University of California at Berkeley.

- *Some species tree methods are more equal than others.* Mathematical Approaches to Evolutionary Trees, 16-18 September 2015, Imperial College, London.
- *Bayesian molecular clock dating*, Workshop on “Bayesian methods to estimate species divergence times”, University of Bristol, 30 - 31 July 2015.
- *Estimation of species divergence times integrating molecules and fossils.* 28 May 2015, Imperial College, Silwood Park.
- *Bayesian estimation of species divergence times.* 17 February 2014, University of Ferrara, Italy.
- *Bayesian species delimitation using multilocus genomic sequence data.* Phylogenetics workshop, Swedish Natural History Museum, Stockholm, 14 June 2013.
- *The uncertainty of Bayesian divergence time estimation.* Swedish Natural History Museum, Stockholm, 14 June 2013.
- *The uncertainty of Bayesian divergence time estimation.* Institute of Zoology, Chinese Academy of Sciences, Beijing, 15 March 2013.
- *Maximum likelihood implementation of an isolation with migration model for three species*, College of Life Sciences, Sun-Yatsen University, Guangzhou, China, 11 December 2012
- *Species delimitation using genomic sequence data*, in Symposium on *Computational and Statistical Phylogenetics*, Vigo, Spain, 13-14 September 2012.
- *The impact of prior on Bayesian estimation of branch lengths*, College of Life Sciences, Sun-Yatsen University, Guangzhou, China, 31 December 2011.
- *Bayesian estimation of species divergence times.* Workshop on Molecular Evolution and Phylogenetics, Institute of Zoology, Chinese Academy of Sciences, Beijing, 26-29 December 2011.
- *Bayesian estimation of species divergence times*, Segunda Escuela Latinoamericana de Evolution, 7-18 November 2011, Universidad Austral de Chile, Valdivia, Chile.
- *Species delimitation using genomic sequence data.* National Institute of Genetics, Mishima, Japan, 28 January 2011.
- *Species delimitation using genomic sequence data.* China Agricultural University, Beijing, 10 January 2011.
- *Species delimitation using genomic sequence data.* College of Life Sciences, Sun Yat-sen University, Guangzhou, China, 8 December 2010.
- *Detection of positive selection in protein-coding DNA sequences.* Workshop on Molecular Evolution and Phylogenetics, Institute of Zoology, Chinese Academy of Sciences, Beijing, 12-17 June 2010.
- *Adaptive molecular evolution.* EMBO Practical Workshop on Molecular Evolution, 3-15 May 2010.
- *Population genomics and human-chimpanzee speciation*, Symposium on comparative genomics, University of St. Andrews, 18 August 2009.
- *Detection of Darwinian selection from genomic comparisons*, Bioinformatics and Comparative Genomics Summer School, University of St. Andrews, 15-17 August 2009.
- *Coalescent and human-chimpanzee speciation*, Peking University, China, 5 May 2009.
- Wellcome Trust Advanced Workshop on Molecular Evolution, 29 March-9 April 2009, Wellcome Trust Genome Campus, Hinxton, Cambridge, UK (co-organizer, with Drs Nick Goldman and Aidan Budd, and lecturer).
- *Lecture 1: Comparison between two protein-coding gene sequences;*
Lecture 2: Codon models and positive selection in protein evolution;
Lecture 3: PAML demo.
Graduate Course on Population Genetics, University of Helsinki, 10 November 2008.
- *Estimation of hominoid ancestral population sizes*, Centro de Ciencias Genómicas-UNAM, Cuernavaca, 20 October 2008.
- *Detecting adaptive evolution in protein-coding DNA sequences*, University of Nebraska at Lincoln, 15 October 2008.
- *Estimation of hominoid ancestral population size and complex speciation of humans and chimpanzees*, Institut für Tierzucht und Genetik, Veterinärmedizinische Universität, Wien. 15 September 2008.
- *Bayesian estimation of hominoid ancestral population*, Department of Integrative Biology, University of California at Berkeley. 12 September 2008.
- *Coalescent and estimation of hominoid ancestral population*, College of Life Sciences, Sun Yat-sen University, Guangzhou, China. 18 August 2008.
- *Estimation of hominoid ancestral population sizes*, Institut fuer Genetik, Universitaet zu Koeln, Germany, 9-11 June 2008.
- *Detection of positive selection in protein-coding DNA sequences.* Workshop on Molecular Evolution and Phylogenetics, Institute of Zoology, Chinese Academy of Sciences, Beijing, 12-16 May 2008.
- *Empirical evaluation of a prior for Bayesian phylogenetic inference*, Royal Society Discussion Meeting, London, 28-29 April 2008

- *Estimation of hominoid ancestral population sizes*, 6 March 2008, Kyushu University, Fukuoka, Japan.
- *Training Workshop on Computational Molecular Evolution*, four-day course including lectures and computer demonstrations at Taiwan National University, 29 December 2007 - 1 January 2008.
- *Estimation of species divergence times by incorporating uncertainties in fossils*. Gordon Conference on Structural, Functional & Evolutionary Genomics, Hinxton, Cambridge, 30 July - 4 August 2007.
- *Statistics in Genetics*, 15 June 2007, Institute of Applied Mathematics, Chinese Academy of Sciences, Beijing, China.
- *Biodiversity and Conservation Biology in the Tibet Plateau*, keynote speech in "2007 International Workshop on Biodiversity", 8 June 2007, University of Tibet.
- *Detecting selective pressures from comparative analysis of protein-coding sequences*, Institute of Zoology, Beijing, China, 30 April 2007.
- *The star-tree paradox and Bayesian phylogenetics*, Institute of Statistical Mathematics, Tokyo, Japan, 27 March, 2007.
- *The star-tree paradox and Bayesian phylogenetics*, Zhongshan University, Guangdong, China, 2 January, 2007.
- *Lindley's paradox, star-tree paradox, and Bayesian phylogenetics*, Newton Institute of Mathematical Sciences, Cambridge, 15 December, 2006.
- *Detecting adaptive protein evolution*, University of Groningen, Centre for Ecological and Evolutionary Studies, 26 October 2006.
- *Training Course in Molecular Phylogenetics*, two-day course including lectures and computer demonstrations at Rothamsted Research Institute, 18-19 October 2006.
- *Phylogenetic methods for detecting adaptive protein evolution*, University of Lausanne, 8 June 2006.
- *Codon substitution models and adaptive protein evolution*, University of Bern, 9 June 2006.
- *Phylogenetic methods for detecting adaptive protein evolution*, Workshop on "Statistical methods for identification of genes under natural selection", Helsinki, 15-19 May 2006.
- *Detecting molecular adaptation from genomic sequences: near the horizon of unknowables*, Workshop on Chicken Genomics & Development, Cold Spring Harbor Laboratory, New York, 7-10 May 2006.
- *Estimation of species divergence times*, Zhongshan University, Guangdong, China, 24 April 2006.
- *Models in molecular evolution*, Fudan University, Shanghai, 19 April 2006.
- *Bayesian methods in genetics*, Teaching course in Bioinformatics, Tokyo Dental and Medical University, 24 & 27 March 2006.
- *Detecting molecular adaptation from genomic sequences*, Omix Informatics Symposium, Tokyo Dental and Medical University, 20 March 2006.
- *Detection of molecular adaptation in protein-coding genes*, University of York, 9 February 2006.
- *Phylogenetic methods to detect adaptive protein evolution*, Max Planck Institute of Chemical Ecology, Jena, Germany, 17 November 2005.
- *Adaptive evolution in viral genomes*, Windeyer Institute of Medical Sciences, UCL, 28 June 2005.
- *Introduction to molecular phylogenetics*, two-day course at Institute of Zoology, Chinese Academy of Sciences, Beijing, China, 2-3 May 2005.
- *Detecting molecular adaptation through phylogenetic sequence comparison*, Fudan University, Shanghai, China, 27 April 2005.
- *Phylogenetic analysis in the post-genomic age*, Novartis Foundation/Royal Society Discussion Meeting on *Insights into evolution from post-genomic data*. London, 6 April 2005.
- *Workshop in Molecular Phylogenetics*, two-day course (lectures and computer demonstrations) at Rothamsted Research Institute, 17-18 March 2005.
- *Markov chain Monte Carlo in genetics & phylogenetics: 3-hour lecture*, University of Montpellier II, 25 October 2004.
- *Detecting adaptive protein evolution*, University of Montpellier II, 12 October 2004.
- *Bayes empirical Bayes inference of sites under positive selection*. PhyloGroup meeting III, 5 October 2004, University College London.
- *Adaptive protein evolution*, Workshop in Molecular Evolution and phylogenetics, Institute of Zoology, Beijing, China, 19-22 August 2004.
- *The effects of prior models in Bayesian MCMC estimation of divergence times*, International Congress of Zoology, Beijing, 23-27 August 2004.
- *Markov chain Monte Carlo methods for integrated analysis of heterogeneous genetic data sets*, University of California, San Diego 1 December 2003.
- *Estimation of species divergence times from molecular sequence data*, Institute of Zoology, Chinese Academy of Sciences, Beijing, 31 October 2003.

- *Detection of molecular adaptation from comparison of protein-coding DNA sequences*, Workshop on Mathematics of Evolution and Phylogeny", Paris, France, 15 – 19 June 2003.
- *Statistical methods for detecting molecular adaptation*, Symposium on "Relating molecular evolution and protein function", Valencia, Spain, 13-14 June 2003.
- *Phylogenetic analysis of protein coding DNA sequences*, Woods Hole Workshop on Molecular Evolution, 27 July – 9 August 2003, Woods Hole, MA (one 3-hour lecture and one computer demonstration).
- *Phylogenetic methods for detecting adaptive molecular evolution*, Laboratoire d'Ecologie Alpine, Université Joseph Fourier, Grenoble, France, 16 May 2003.
- *Evolutionary comparison of gene sequences to help understand protein function*. School of Biosciences, University of Birmingham, 13 November 2002.
- *Phylogenetic methods for detecting adaptive molecular evolution*, Department of Ecology and Evolutionary Biology, Yale University, 20 March 2002.
- *Phylogenetic methods for detecting adaptive molecular evolution*, Symposium on Molecular Evolutionary Genetics, Annual Meeting of American Genetics Association, 22-24 March 2002, Tempe, Arizona.
- *Statistical methods for detecting molecular adaptation*, Symposium on Molecular Evolution and Systematics, 26-28 December 2001, Academia Sinica, Taipei, Taiwan (lecture and computer demonstration).
- *Statistical methods for detecting molecular adaptation*, 31 December 2001, Department of Biology, National Tsinghua University, Taiwan.
- *Use of phylogenies to detect adaptive molecular evolution*, Symposium on Systematics: the foundation of biology? 28 November 2001, Natural History Museum, London.
- *Markov models of codon substitution for detecting adaptive molecular evolution*, 13 November, 2001, Department of Statistics, University of Oxford.
- *Phylogenetic methods to detect adaptive molecular evolution*, 5th Anton Dohrn Workshop Natural Selection and the Neutral Theory, 24-27 October 2001, Ischia, Italy.
- *Codon substitution models and phylogenetic analysis of protein coding genes*, Woods Hole Workshop on Molecular Evolution, 27 July – 10 August 2001, Woods Hole, MA (one lecture and one computer demonstration).
- *Models of codon substitution to detect adaptive molecular evolution*, 16 July 2001, Department of Medical Genetics, University of Alberta, Edmonton, Canada.
- *Estimation of synonymous and nonsynonymous substitution rates and the evolution of mammalian nuclear genes*, 3 July 2001, Department of Biometrics, Cornell University, USA.
- *Detecting adaptive evolution in viral genes*, 27 – 29 April 2001, VIIIth International Meeting on HIV Dynamics and Evolution, Paris, France.
- *Estimation of synonymous and nonsynonymous substitution rates and the evolution of mammalian and Drosophila genes*, Workshop on Population Genetics at the Molecular Level, Montreal, Canada, 8-11 March 2001.
- *Maximum likelihood analysis of adaptive evolution in HIV-1 gp120 env gene*. Pacific Symposium on BioComputing 2001, Kona, Hawaii, 4-9 January 2001.
- *Dating speciation events using local molecular clocks*. The 26th CIB Seminar, Center for Information Biology, National Institute of Genetics, Mishima, Japan. 6 December 2000.
- *Molecular clocks*, Department of Systematics and Animal Biology, University of Geneva, 24 November 2000.
- *Detecting molecular adaptation to study protein function*, Stockholm Bioinformatics Center, University of Stockholm, 9 November 2000.
- *Maximum likelihood calculation on large phylogenies and analysis of adaptive evolution in human influenza virus A*, Department of Statistics, University of Reading. 6 July 2000.
- *Phylogenetic methods for detecting adaptive molecular evolution*. University of Edinburgh, 31 May 2000.
- *Statistical methods for detecting molecular adaptation*. College of Life Sciences, Peking University, 27 March 2000.
- *Dating speciation events using local molecular clocks*. Institute of Statistical Mathematics, Tokyo, 9 March 2000.
- *Statistical methods for detecting adaptive molecular evolution*. Evolution 2000, Tokyo, 5-7 March 2000.
- *Relating physicochemical properties of amino acids to variable nucleotide substitution patterns among sites*. Pacific Symposium on Computational Biology 2000, Honolulu, Hawaii, 4-9 January 2000.
- *Statistical methods for detecting molecular adaptation*. Department of Genetics, Queen's Medical School, University of Nottingham. November 24, 1999.
- *Models of codon substitution and adaptive evolution in abalone sperm lysin*. School of Biological Sciences, University of Manchester. September 15, 1999.
- *Models of codon substitution and their use to detect adaptive molecular evolution*. VIIth Conference of European Society of Evolutionary Biology, August 23-28, 1999, Barcelona, Spain.
- *Detecting adaptive molecular evolution*. BBSRC Workshop on Molecular Evolution and Diversity, May 10–11, 1999, Warwick, England.

- *Models of amino acid substitution*, Natural History Museum Systematics Discussion Group, October 1, 1998.
- *On the estimation of ancestral population sizes*. Newton Institute Program on *Biomolecular structure and function in the context of genome projects*, Population genetics week organised by Profs Simon Tavare and Peter Donnelly, Cambridge (England), September 25, 1998.
- *Statistical tests in molecular phylogenetics*. Prof Joe. Felsenstein's EC Summer School on *Phylogenetic Methods*, Cambridge, UK, August 13, 1998 (lecture and computer demonstration)
- *Bayesian estimation of molecular evolutionary trees*, Department of Statistics, UCL, May 11, 1998.
- *Bayesian estimation of molecular evolutionary trees*, CoMPLEX workshop on Population Biology, UCL, April 29, 1998.
- *Bayesian estimation of molecular evolutionary trees*, Institute of Statistical Mathematics, Tokyo, Japan, February 25, 1998.
- *Models of codon substitution and their use to understand the evolutionary process of protein-coding DNA sequences*, National Institute of Genetics, Mishima, Japan, February 11, 1998.
- *Models of DNA sequence evolution and their use in phylogenetic analysis*. Department of Genetics, University of Cambridge, January 23, 1997.
- *Models of DNA sequence evolution and their use in phylogenetic analysis*. Natural History Museum (London) Systematics Discussion Group, January 20, 1997.
- *Modelling the variation of substitution rates among sites in a DNA sequence*. Departments of Statistics and Genetics, North Carolina State University, November 15, 1995.
- *Reconstruction of ancestral nucleotide or amino acid sequences by the likelihood approach*. American Society of Naturalists Young Investigators Prize Symposium. McGill University, Montreal, Quebec, July 8–12, 1995.
- *Evolutionary trees from DNA sequences: a peculiar statistical estimation problem*. International Biometrics Society British Region Meeting, February 14, 1994.
- *Variation of substitution rates across nucleotide sites*. Computer Users Group Symposium at the 126th Meeting of the Society for General Microbiology. University of Exeter, Exeter, England, September 7–9, 1993.
- *Maximum likelihood phylogenetic estimation with variable rates among sites*, Natural History Museum (London) Systematics Discussion Group. April 20, 1993.
- *Statistical properties of maximum likelihood and distance-based methods of phylogenetic estimation*, Queen Mary and Westfield College, London, March 17, 1993.

COURSES TAUGHT

- 2001-date. Molecular Evolution, BSc, MSc and MSci course, UCL.
- 2016-date, Advanced Computational Biology, MSci/MSc course, UCL
- 2011. Probability modelling in molecular evolution, graduate course, ETH Zurich, Zurich.
- 2010. Computational Molecular evolution, graduate course, Peking University, Beijing
- 1999-2008. Quantitative Biology, first-year undergraduate course at UCL.
- 1998-2007. Molecular Evolution and Systematics, MSc. course in CoMPLEX, UCL.
- 1992, Biostatistics, undergraduate course at Beijing Agricultural University, China
- 1988, Quantitative Genetics and Animal Breeding, undergraduate course at Gansu Agricultural University, China.
- 1987, Biostatistics, undergraduate course at Gansu Agricultural University, China.