

Allen, Benjamin; Rosenbloom, Daniel I. Scholes

Mutation rate evolution in replicator dynamics. (English) Zbl 1362.92047
Bull. Math. Biol. 74, No. 11, 2650-2675 (2012).

Summary: The mutation rate of an organism is itself evolvable. In stable environments, if faithful replication is costless, theory predicts that mutation rates will evolve to zero. However, positive mutation rates can evolve in novel or fluctuating environments, as analytical and empirical studies have shown. Previous work on this question has focused on environments that fluctuate independently of the evolving population. Here we consider fluctuations that arise from frequency-dependent selection in the evolving population itself. We investigate how the dynamics of competing traits can induce selective pressure on the rates of mutation between these traits. To address this question, we introduce a theoretical framework combining replicator dynamics and adaptive dynamics. We suppose that changes in mutation rates are rare, compared to changes in the traits under direct selection, so that the expected evolutionary trajectories of mutation rates can be obtained from analysis of pairwise competition between strains of different rates. Depending on the nature of frequency-dependent trait dynamics, we demonstrate three possible outcomes of this competition. First, if trait frequencies are at a mutation-selection equilibrium, lower mutation rates can displace higher ones. Second, if trait dynamics converge to a heteroclinic cycle – arising, for example, from “rock-paper-scissors” interactions – mutator strains succeed against non-mutators. Third, in cases where selection alone maintains all traits at positive frequencies, zero and nonzero mutation rates can coexist indefinitely. Our second result suggests that relatively high mutation rates may be observed for traits subject to cyclical frequency-dependent dynamics.

MSC:

92D15 Problems related to evolution
37N25 Dynamical systems in biology
91A22 Evolutionary games

Cited in 4 Documents

Keywords:

mutation rate; evolution; replicator dynamics; adaptive dynamics; evolvability

Full Text: [DOI](#)

References:

- [1] Aharoni, A., Gaidukov, L., Khersonsky, O., Gould, S. M. Q., Roodveldt, C., & Tawfik, D. S. (2005). The 'evolvability' of promiscuous protein functions. *Nat. Genet.*, 37(1), 73–76.
- [2] André, J.-B., & Godelle, B. (2006). The evolution of mutation rate in finite asexual populations. *Genetics*, 172(1), 611–626. · [doi:10.1534/genetics.105.046680](#)
- [3] Bonneuil, N. (1992). Attractors and confiners in demography. *Ann. Oper. Res.*, 37, 17–32. · [Zbl 0751.92007](#) · [doi:10.1007/BF02071046](#)
- [4] Brandstrom, M., & Ellegren, H. (2007). The genomic landscape of short insertion and deletion polymorphisms in the chicken (*Gallus gallus*) genome: a high frequency of deletions in tandem duplicates. *Genetics*, 176, 1691–1701. · [doi:10.1534/genetics.107.070805](#)
- [5] Buss, L. W., & Jackson, J. B. C. (1979). Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *Am. Nat.*, 113(2), 223–234. · [doi:10.1086/283381](#)
- [6] Chen, J. Q., Wu, Y., Yang, H., Bergelson, J., Kreitman, M., & Tian, D. (2009). Variation in the ratio of nucleotide substitution and indel rates across genomes in mammals and bacteria. *Mol. Biol. Evol.*, 26, 1523–1531. · [doi:10.1093/molbev/msp063](#)
- [7] Chen, F., Liu, W.-Q., Eisenstark, A., Johnston, R., Liu, G.-R., & Liu, S.-L. (2010). Multiple genetic switches spontaneously modulating bacterial mutability. *BMC Evol. Biol.*, 10(1), 277. · [doi:10.1186/1471-2148-10-277](#)
- [8] Chicone, C. C. (2006). Ordinary differential equations with applications. Berlin: Springer. · [Zbl 1120.34001](#)
- [9] Cortez, M. H., & Ellner, S. P. (2010). Understanding rapid evolution in predator–prey interactions using the theory of fast–slow dynamical systems. *Am. Nat.*, 176(5), e109–e127. · [doi:10.1086/656485](#)
- [10] Dercole, F. (2002). Evolutionary dynamics through bifurcation analysis: methods and applications. Ph.D. thesis, Department of Electronics and Information, Politecnico di Milano, Milano, Italy. · [Zbl 1102.92038](#)
- [11] Dercole, F., & Rinaldi, S. (2008). Analysis of evolutionary processes: the adaptive dynamics approach and its applica-

- tions. Princeton: Princeton University Press. · [Zbl 1305.92001](#)
- [12] Dercole, F., Ferrière, R., Gagnani, A., & Rinaldi, S. (2006). Coevolution of slow–fast populations: evolutionary sliding, evolutionary pseudo-equilibria and complex Red Queen dynamics. *Proc. R. Soc. B, Biol. Sci.*, 273, 983–990. 1589. · [doi:10.1098/rspb.2005.3398](#)
- [13] Desai, M. M., & Fisher, D. S. (2011). The balance between mutators and nonmutators in asexual populations. *Genetics*, 188(4), 997–1014. · [doi:10.1534/genetics.111.128116](#)
- [14] Dieckmann, U., & Law, R. (1996). The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.*, 34(5), 579–612. · [Zbl 0845.92013](#) · [doi:10.1007/BF02409751](#)
- [15] Dieckmann, U., Marrow, P., & Law, R. (1995). Evolutionary cycling in predator–prey interactions: population dynamics and the Red Queen. *J. Theor. Biol.*, 176(1), 91–102. · [doi:10.1006/jtbi.1995.0179](#)
- [16] Doebeli, M. (1995). Evolutionary predictions from invariant physical measures of dynamic processes. *J. Theor. Biol.*, 173(4), 377–387. · [doi:10.1006/jtbi.1995.0070](#)
- [17] Doebeli, M., & Koella, J. C. (1995). Evolution of simple population dynamics. *Proc. R. Soc. B, Biol. Sci.*, 260(1358), 119–125. · [doi:10.1098/rspb.1995.0068](#)
- [18] Duret, L. (2009). Mutation patterns in the human genome: more variable than expected. *PLoS Biol.*, 7, e1000028. · [doi:10.1371/journal.pbio.1000028](#)
- [19] Earl, D. J., & Deem, M. W. (2004). Evolvability is a selectable trait. *Proc. Natl. Acad. Sci.*, 101(32), 11531–11536. · [doi:10.1073/pnas.0404656101](#)
- [20] Eckmann, J. P., & Ruelle, D. (1985). Ergodic theory of chaos and strange attractors. *Rev. Mod. Phys.*, 57(3), 617–656. · [Zbl 0989.37516](#) · [doi:10.1103/RevModPhys.57.617](#)
- [21] Elango, N., Kim, S. H., Program, N. C. S., Vigoda, E., & Soojin, V. Y. (2008). Mutations of different molecular origins exhibit contrasting patterns of regional substitution rate variation. *PLoS Comput. Biol.*, 4, e1000015. · [doi:10.1371/journal.pcbi.1000015](#)
- [22] Fryxell, K. J., & Moon, W. J. (2005). CpG mutation rates in the human genome are highly dependent on local GC content. *Mol. Biol. Evol.*, 22, 650–658. · [doi:10.1093/molbev/msi043](#)
- [23] Gaunersdorfer, A. (1992). Time averages for heteroclinic attractors. *SIAM J. Appl. Math.*, 52(5), 1476–1489. · [Zbl 0755.34040](#) · [doi:10.1137/0152085](#)
- [24] Geritz, S. A. H. (2005). Resident–invader dynamics and the coexistence of similar strategies. *J. Math. Biol.*, 50(1), 67–82. · [Zbl 1055.92042](#) · [doi:10.1007/s00285-004-0280-8](#)
- [25] Geritz, S. A. H., Kisdi, E., Meszeña, G., & Metz, J. A. J. (1997). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, 12(1), 35–57. · [doi:10.1023/A:1006554906681](#)
- [26] Geritz, S. A. H., Gyllenberg, M., Jacobs, F. J. A., & Parvinen, K. (2002). Invasion dynamics and attractor inheritance. *J. Math. Biol.*, 44, 548–560. · [Zbl 0990.92029](#) · [doi:10.1007/s002850100136](#)
- [27] Giraud, A., Matic, I., Tenaillon, O., Clara, A., Radman, M., Fons, M., & Taddei, F. (2001). Costs and benefits of high mutation rates: adaptive evolution of bacteria in the mouse gut. *Science*, 291(5513), 2606–2608. · [doi:10.1126/science.1056421](#)
- [28] Gore, J., Youk, H., & Van Oudenaarden, A. (2009). Snowdrift game dynamics and facultative cheating in yeast. *Nature*, 458(7244), 253–256. · [doi:10.1038/nature07921](#)
- [29] Gyllenberg, M., Osipov, A., & Söderbacka, G. (1996). Bifurcation analysis of a metapopulation model with sources and sinks. *J. Nonlinear Sci.*, 6, 329–366. · [Zbl 0927.37028](#) · [doi:10.1007/BF02433474](#)
- [30] Hader, K. P. (1981). Stable polymorphisms in a selection model with mutation. *SIAM J. Appl. Math.*, 41(1), 1–7. · [Zbl 0456.34023](#) · [doi:10.1137/0141001](#)
- [31] Heino, M., Metz, J. A. J., & Kaitala, V. (1998). The enigma of frequency-dependent selection. *Trends Ecol. Evol.*, 13(9), 367–370. · [doi:10.1016/S0169-5347\(98\)01380-9](#)
- [32] Hodgkinson, A., Ladoukakis, E., & Eyre-Walker, A. (2009). Cryptic variation in the human mutation rate. *PLoS Biol.*, 7, e1000027. · [doi:10.1371/journal.pbio.1000027](#)
- [33] Hofbauer, J. (1985). The selection mutation equation. *J. Math. Biol.*, 23(1), 41–53. · [Zbl 0582.92017](#) · [doi:10.1007/BF00276557](#)
- [34] Hofbauer, J. (1994). Heteroclinic cycles in ecological differential equations. *Tatra Mt. Math. Publ.*, 4, 105–116. · [Zbl 0811.34035](#)
- [35] Hofbauer, J., & Sigmund, K. (1990). Adaptive dynamics and evolutionary stability. *Appl. Math. Lett.*, 3(4), 75–79. · [Zbl 0709.92015](#) · [doi:10.1016/0893-9659\(90\)90051-C](#)
- [36] Hofbauer, J., & Sigmund, K. (1998). Evolutionary games and replicator dynamics. Cambridge: Cambridge University Press. · [Zbl 0914.90287](#)
- [37] Hofbauer, J., & Sigmund, K. (2003). Evolutionary game dynamics. *Bull. Am. Math. Soc.*, 40(4), 479–520. · [Zbl 1049.91025](#) · [doi:10.1090/S0273-0979-03-00988-1](#)
- [38] Hofbauer, J., Schuster, P., & Sigmund, K. (1979). A note on evolutionary stable strategies and game dynamics. *J. Theor. Biol.*, 81(3), 609–612. · [doi:10.1016/0022-5193\(79\)90058-4](#)
- [39] Horn, R. A., & Johnson, C. R. (1990). Matrix analysis. Cambridge: Cambridge University Press. · [Zbl 0704.15002](#)
- [40] Ishii, K., Matsuda, H., Iwasa, Y., & Sasaki, A. (1989). Evolutionarily stable mutation rate in a periodically changing environment. *Genetics*, 121, 163–174.
- [41] Johnson, T. (1999a). Beneficial mutations, hitchhiking and the evolution of mutation rates in sexual populations. *Genetics*, 151(4), 1621–1631.
- [42] Johnson, T. (1999b). The approach to mutation–selection balance in an infinite asexual population, and the evolution of

- mutation rates. *Proc. R. Soc. B, Biol. Sci.*, 266(1436), 2389–2397. · doi:10.1098/rspb.1999.0936
- [43] Kerr, B., Riley, M. A., Feldman, M. W., & Bohannan, B. J. M. (2002). Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature*, 418(6894), 171–174. · doi:10.1038/nature00823
- [44] Kessler, D. A., & Levine, H. (1998). Mutator dynamics on a smooth evolutionary landscape. *Phys. Rev. Lett.*, 80, 2012–2015. · doi:10.1103/PhysRevLett.80.2012
- [45] Khibnik, A. I., & Kondrashov, A. S. (1997). Three mechanisms of red queen dynamics. *Proc. R. Soc. Lond. B, Biol. Sci.*, 264(1384), 1049–1056. · doi:10.1098/rspb.1997.0145
- [46] Kimura, M. (1967). On the evolutionary adjustment of spontaneous mutation rates. *Genet. Res.*, 9, 23–34. · doi:10.1017/S0016672300010284
- [47] King, D. G., Soller, M., & Kashi, Y. (1997). Evolutionary tuning knobs. *Endeavour*, 21, 36–40. · doi:10.1016/S0160-9327(97)01005-3
- [48] Kirkup, B. C., & Riley, M. A. (2004). Antibiotic-mediated antagonism leads to a bacterial game of rock-paper-scissors in vivo. *Nature*, 428(6981), 412–414. · doi:10.1038/nature02429
- [49] Kirschner, M., & Gerhart, J. (1998). Evolvability. *Proc. Natl. Acad. Sci. USA*, 95(15), 8420–8427. · doi:10.1073/pnas.95.15.8420
- [50] Krivan, V., & Cressman, R. (2009). On evolutionary stability in prey–predator models with fast behavioral dynamics. *Evol. Ecol. Res.*, 11, 227–251.
- [51] Leigh, E. G. (1970). Natural selection and mutability. *Am. Nat.*, 104, 301–305. · doi:10.1086/282663
- [52] Leigh, E. G. (1973). The evolution of mutation rates. *Genetics*, 73, 1–18.
- [53] Levinson, G., & Gutman, G. A. (1987a). High frequencies of short frameshifts in poly-CA/TG tandem repeats borne by bacteriophage M13 in *Escherichia coli* K-12. *Nucleic Acids Res.*, 15, 5323–5338. · Zbl 05436166 · doi:10.1093/nar/15.13.5323
- [54] Levinson, G., & Gutman, G. A. (1987b). Slipped-strand mispairing: a major mechanism for DNA evolution. *Mol. Biol. Evol.*, 4, 203–221.
- [55] Lynch, M. (2007). *The origins of genome architecture*. Sunderland: Sinauer Associates.
- [56] Magnus, J. R., & Neudecker, H. (1988). *Matrix differential calculus with applications in statistics and econometrics*. New York: Wiley. · Zbl 0651.15001
- [57] Marrow, P., Law, R., & Cannings, C. (1992). The coevolution of predator–prey interactions: ESSs and red queen dynamics. *Proc. R. Soc. Lond. B, Biol. Sci.*, 250(1328), 133–141. · doi:10.1098/rspb.1992.0141
- [58] May, R. M. (1972). Limit cycles in predator–prey communities. *Science*, 177(4052), 900–902. · doi:10.1126/science.177.4052.900
- [59] May, R. M. (2001). *Stability and complexity in model ecosystems*. Princeton: Princeton University Press. · Zbl 1044.92047
- [60] May, R. M., & Leonard, W. J. (1975). Nonlinear aspects of competition between three species. *SIAM J. Appl. Math.*, 29(2), 243–253. · Zbl 0314.92008 · doi:10.1137/0129022
- [61] Maynard Smith, J., & Price, G. R. (1973). The logic of animal conflict. *Nature*, 246(5427), 15–18. · Zbl 1369.92134 · doi:10.1038/246015a0
- [62] Metz, J. A. J., Nisbet, R. M., & Geritz, S. A. H. (1992). How should we define ‘fitness’ for general ecological scenarios? *Trends Ecol. Evol.*, 7(6), 198–202. · doi:10.1016/0169-5347(92)90073-K
- [63] Metz, J. A. J., Geritz, S. A. H., Meszéna, G., Jacobs, F. A., & van Heerwaarden, J. S. (1996). Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In S. J. van Strien & S. M. V. Lunel (Eds.), *Stochastic and spatial structures of dynamical systems* (pp. 183–231). Amsterdam: KNAW Verhandelingen, Afd. · Zbl 0972.92024
- [64] Milinski, M. (1987). Tit for tat in sticklebacks and the evolution of cooperation. *Nature*, 325(6103), 433–435. · doi:10.1038/325433a0
- [65] Murphy, G. L., Connell, T. D., Barritt, D. S., Koomey, M., & Cannon, J. G. (1989). Phase variation of gonococcal protein II: regulation of gene expression by slipped-strand mispairing of a repetitive DNA sequence. *Cell*, 56, 539–547. · doi:10.1016/0092-8674(89)90577-1
- [66] Nowak, M. A. (2006). Five rules for the evolution of cooperation. *Science*, 314(5805), 1560–1563. · doi:10.1126/science.1133755
- [67] Nowak, M. A., & Sigmund, K. (2004). Evolutionary dynamics of biological games. *Science*, 303(5659), 793–799. · doi:10.1126/science.1093411
- [68] Nowak, M. A., Komarova, N. L., & Niyogi, P. (2001). Evolution of universal grammar. *Science*, 291(5501), 114–118. · Zbl 1226.91060 · doi:10.1126/science.291.5501.114
- [69] Oliver, A., Cantón, R., Campo, P., Baquero, F., & Blázquez, J. (2000). High frequency of hypermutable *Pseudomonas aeruginosa* in cystic fibrosis lung infection. *Science*, 288(5469), 1251. · doi:10.1126/science.288.5469.1251
- [70] Orr, H. A. (2000). The rate of adaptation in asexuals. *Genetics*, 155(2), 961–968.
- [71] Paquin, C. E., & Adams, J. (1983). Relative fitness can decrease in evolving asexual populations of *S. cerevisiae*. *Nature*, 308–371.
- [72] Pigliucci, M., & Box, P. (2008). Is evolvability evolvable? *Nat. Rev. Genet.*, 9, 75–82. · doi:10.1038/nrg2278
- [73] Radman, M., Matic, I., & Taddei, F. (1999). Evolution of evolvability. *Ann. N.Y. Acad. Sci.*, 870(1), 146–155. · doi:10.1111/j.1749-6632.1999.tb08874.x
- [74] Rainey, P. B., & Rainey, K. (2003). Evolution of cooperation and conflict in experimental bacterial populations. *Nature*, 425(6953), 72–74. · Zbl 1243.76016 · doi:10.1038/nature01906
- [75] Rand, D. A., Wilson, H. B., & McGlade, J. M. (1994). Dynamics and evolution: evolutionarily stable attractors, invasion exponents and phenotype dynamics. *Philos. Trans. R. Soc. B, Biol. Sci.*, 343(1305), 261–283. · doi:10.1098/rstb.1994.0025

- [76] Rosche, W., Foster, P., & Cairns, J. (1999). The role of transient hypermutators in adaptive mutation in *Escherichia coli*. *Proc. Natl. Acad. Sci.*, 96, 6862–6867. · doi:10.1073/pnas.96.12.6862
- [77] Ruelle, D. (1989). *Chaotic evolution and strange attractors*. Cambridge: Cambridge University Press. · Zbl 0683.58001
- [78] Schnabl, W., Stadler, P. F., Forst, C., & Schuster, P. (1991). Full characterization of a strange attractor. *Physica D*, 48(1), 65–90. · Zbl 0717.92001 · doi:10.1016/0167-2789(91)90052-B
- [79] Schuster, P., & Sigmund, K. (1983). Replicator dynamics. *J. Theor. Biol.*, 100(533), 8. · doi:10.1016/0022-5193(83)90445-9
- [80] Seger, J., & Antonovics, J. (1988). Dynamics of some simple host–parasite models with more than two genotypes in each species [and discussion]. *Philos. Trans. R. Soc. B*, 319(1196), 541–555. · doi:10.1098/rstb.1988.0064
- [81] Shaver, A. C., & Sniegowski, P. D. (2003). Spontaneously arising mutator mutators in evolving *Escherichia coli* populations are the result of changes in repeat length. *J. Bacteriol.*, 185(20), 6076–6079. · doi:10.1128/JB.185.20.6076-6082.2003
- [82] Sigmund, K. (1992). Time averages for unpredictable orbits of deterministic systems. *Ann. Oper. Res.*, 37, 217–228. doi: 10.1007/BF02071057 · Zbl 0778.58050 · doi:10.1007/BF02071057
- [83] Sinervo, B., & Calsbeek, R. (2006). The developmental, physiological, neural, and genetical causes and consequences of frequency-dependent selection in the wild. *Annu. Rev. Ecol. Evol. Syst.*, 37, 581–610. · doi:10.1146/annurev.ecolsys.37.091305.110128
- [84] Sinervo, B., & Lively, C. M. (1996). The rock-paper-scissors game and the evolution of alternative male strategies. *Nature*, 380, 240–243. · doi:10.1038/380240a0
- [85] Sinervo, B., Miles, D. B., Frankino, W. A., Klukowski, M., & DeNardo, D. F. (1996). Testosterone, endurance, and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Horm. Behav.*, 38, 222–233. · doi:10.1006/hbeh.2000.1622
- [86] Sniegowski, P. D., Gerrish, P. J., & Lenski, R. E. (1997). Evolution of high mutation rates in experimental populations of *Escherichia coli*. *Nature*, 387(6634), 703–705. · doi:10.1038/42701
- [87] Sniegowski, P. D., Gerrish, P. J., Johnson, T., & Shaver, A. (2000). The evolution of mutation rates: separating causes from consequences. *BioEssays*, 22(12), 1057–1066. · doi:10.1002/1521-1878(200012)22:12<1057::AID-BIES3>3.0.CO;2-W
- [88] Taddei, F., Radman, M., Maynard Smith, J., Toupance, B., Gouyon, P. H., & Godelle, B. (1997). Role of mutator alleles in adaptive evolution. *Nature*, 387(6634), 700–702. · doi:10.1038/42696
- [89] Takens, F. (1985). On the numerical determination of the dimension of an attractor. In B. Braaksma, H. Broer, & F. Takens (Eds.), *Lecture notes in mathematics: Vol. 1125. Dynamical systems and bifurcations* (pp. 99–106). Berlin: Springer. · Zbl 0561.58027
- [90] Taylor, P. D., & Jonker, L. B. (1978). Evolutionary stable strategies and game dynamics. *Math. Biosci.*, 40(1–2), 145–156. · Zbl 0395.90118 · doi:10.1016/0025-5564(78)90077-9
- [91] Tenaillon, O., Toupance, B., Le Nagard, H., Taddei, F., & Godelle, B. (1999). Mutators, population size, adaptive landscape and the adaptation of asexual populations of bacteria. *Genetics*, 152(2), 485–493.
- [92] Tian, D., Wang, Q., Zhang, P., Araki, H., Yang, S., Kreitman, M., Nagylaki, T., Hudson, R., Bergelson, J., & Chen, J. Q. (2008). Single-nucleotide mutation rate increases close to insertions/deletions in eukaryotes. *Nature*, 455, 105–108. · doi:10.1038/nature07175
- [93] Travis, J. M. J., & Travis, E. R. (2002). Mutator dynamics in fluctuating environments. *Proc. R. Soc. B, Biol. Sci.*, 269(1491), 591–597. · doi:10.1098/rspb.2001.1902
- [94] Wagner, A. (2008). Robustness and evolvability: a paradox resolved. *Proc. R. Soc. B, Biol. Sci.*, 275, 91. 1630. · doi:10.1098/rspb.2007.1137
- [95] Weber, M. (1996). Evolutionary plasticity in prokaryotes: a Panglossian view. *Biol. Philos.*, 11, 67–88. · doi:10.1007/BF00127472
- [96] Woods, R. J., Barrick, J. E., Cooper, T. F., Shrestha, U., Kauth, M. R., & Lenski, R. E. (2011). Second-order selection for evolvability in a large *Escherichia coli* population. *Science*, 331(6023), 1433–1436. · doi:10.1126/science.1198914
- [97] Wylie, C. S., Ghim, C., Kessler, D., & Levine, H. (2009). The fixation probability of rare mutators in finite asexual populations. *Genetics*, 181, 1595–1612. · doi:10.1534/genetics.108.094532
- [98] Zhao, Z., & Jiang, C. (2007). Methylation-dependent transition rates are dependent on local sequence lengths and genomic regions. *Mol. Biol. Evol.*, 24, 23–25. · doi:10.1093/molbev/msl156

This reference list is based on information provided by the publisher or from digital mathematics libraries. Its items are heuristically matched to zbMATH identifiers and may contain data conversion errors. It attempts to reflect the references listed in the original paper as accurately as possible without claiming the completeness or perfect precision of the matching.