There follows an annotated bibliography. It is extensive, but still far from complete. I have separated the primary sources which form a less intimidating list. If I have the energy I'll add a section related to the seminar at a later date.

References

Lecture 1	
[A1]	Hudson, R. (1990). Gene genealogies and the coalescent process. Oxford Surveys in Evolutionary Biology, 7:1–44. A nice (although now somewhat out of date) account of the coalescent and some of its simple extensions.
[A2]	Kimura, M. (1953). Stepping stone model of population. Ann. Rep. Nat. Inst. Genetics Japan, 3:62–63.
[A3]	Kingman, J. F. C. (1982a). The coalescent. <i>Stochastic Process. Appl.</i> , 13(3):235–248.
[A4]	Kingman, J. F. C. (1982b). On the genealogy of large populations. <i>J. Appl. Probab.</i> , (Special Vol. 19A):27–43. Essays in statistical science.
[A5]	Shiga, T. (1988). Stepping stone models in population genetics and population dynamics. In <i>Stochastic processes in Physics and Engineering</i> , (Albeverio <i>et al.</i> Eds.), 345-355. <i>Amongst other things, Shiga establishes the duality between the stepping stone model and a system of coalescing random walks</i> .
— Supplementary references —	
[AS6]	Feller, W. (1951). Diffusion processes in genetics. <i>Proc. Second Berkeley</i> <i>Symp.</i> , pages 227–246. In this important and influential paper, Feller obtained both of our key diffusions, what we now call the Feller diffusion and the Wright-Fisher diffusion, as large population limits when time is suitably rescaled.
[AS7]	Kaj, I. and Krone, S. M. (2003). The coalescent process in a population with stochastically varying size. J. Appl. Prob., 40:33–48. This gives rather general conditions under which the genealogy of a sample from a population whose size varies stochastically in time is given by a time change of Kingman's coalescent.
[AS8]	Kimura, M., and Weiss, G. H. (1964). The stepping stone model of population structure and the decrease of genetic correlation with distance. <i>Genetics</i> 49:561–576.
[AS9]	P. J. Donnelly and T. G. Kurtz. A countable representation of the Fleming- Viot diffusion. Ann Prob, 24:698–742, 1996. This paper introduces the famous 'lookdown process'. Using exchangeability, individuals in a

Moran model are labelled so that in a reproduction event it is always the individual with the smaller label that reproduces. In this way the Moran model for population size N is embedded in that for population size N+k for every k > 0.

[AS10] J. F. Wilkins. A separation of timescales approach to the coalescent in a continuous population. *Genetics*, 168:2227–2244, 2004. *There are numerous papers showing how Kingman's coalescent emerges from spatially structured models in which migration rates are fast and one sees a 'separation of timescales'. This one happened to be in my reference list. John Wakeley is a name firmly associated with this approach.*

Lecture 2

- [B11] Griffiths, R. C. and Marjoram, P. (1997). An ancestral recombination graph. In Donnelly, P. and Tavaré, S., editors, *Progress in Population Genetics and Human Evolution*, volume 87 of *IMA Vol. Math. Appl.*, pages 257–270. Springer, New York.
- [B12] Wiuf, C. and Hein, J. (1999). Recombination as a point process along sequences. *Theor. Pop. Biol.*, 55:248–259.
- [B13] Baird, S.J.E.; Barton, N.H. & A.M. Etheridge (2003) The distribution of ancestral blocks of an ancestral genome. Theor. Pop. Biol. 64:451–471.
 Supplementary references —
- [BS14] Bellman, R. and Harris, T. (1951). Recurrence times for the Ehrenfest model. *Pacific J. Math.*, 1:179–193. *This gives us the key asymptotic estimates for the Ehrenfest model that we use to study long genomes.*
- [BS15] Derrida, B. and Jung-Muller, B. (1999). The genealogical tree of a chromosome. J. Stat. Phys., 94:277–298. This paper addresses the question that we posed at the end of the lecture, but it does not give a complete solution.
- [BS16] Ehrenfest, P. and Ehrenfest, T. (1907). Über zwei bekannte Einwände gegen das Boltzmannsche H-Theorem. *Phys. Z.*, 8:311. *Probably not the easiest place to learn about the model these days...*
- [BS17] Goodman, S. J., Barton, N. H., Swanson, G., Abernethy, K., and Pemberton, J. M. (1999). Introregression through rare hybridisation: a genetic study of a hybrid zone between red and sika deer (genus Cervus), in Argyll, Scotland. *Genetics*, 152:355–371.
- [BS18] Takacs, L. (1979). On an urn problem of Paul and Tatiana Ehrenfest. Math. Proc. Camb. Phil. Soc, 86:127–130. The first place I could find with the continuous time version of the Ehrenfest model. The application was different.
- [BS19] Mcvean G.A.V. and N. Cardin (2005) Approximating the coalescent

with recombination. *Philos. Trans. Roy. Soc. London Ser. B Biol. Sci.* 360 (1459):1387-1393 *Essentially the approximation is that the 'local trees' in the ancestral recombination graph are replaced by the Markov process in which one only takes account of coalescences back into the 'most recent' local tree.*

Lecture 3

- [C20] J. Schweinsberg and R. Durrett. Random partitions approximating the coalescence of lineages during a selective sweep. Ann Appl Probab, 15:1591–1651, 2005.
- [C21] R. Durrett and J. Schweinsberg. Approximating Selective Sweeps. *Theoretical Population Biology*, 66(2):129–138, 2004.
- [C22] A. M. Etheridge, P. Pfaffelhuber, and A. Wakolbinger. An approximate sampling formula under genetic hitchhiking. Ann Appl Probab, 16(2):685–729, 2007. Whereas Durrett & Schweinsberg let population size tend to infinity directly in their Moran model with the selection coefficient s held fixed, in this paper first population size N is sent to infinity with Ns fixed and then $Ns \rightarrow \infty$. It turns out that the calculations are much simpler in this setting.
- [C23] Barton, N. H., Etheridge A. M., and Sturm, A. K. (2004). Coalescence in a random background. Ann. Appl. Probab., 14(2):754–785. This paper is primarily concerned with establishing the effect of balancing selection on a linked neutral locus. It is closely related to Darden, Kaplan & Hudson's 1988 and 1989 papers.

— Supplementary references —

- [CS24] Kaplan, N. L., Darden, T., and Hudson, R. B. (1988). The coalescent process in models with selection. *Genetics*, 120:819–829.
- [CS25] Darden, T., Kaplan, N. L., and Hudson, R. B. (1989). A numerical method for calculating moments of coalescent times in finite populations with selection. J. Math. Biol, 27(3):355–368. This paper (and the one above) covers much of the same ground as Barton, Etheridge & Sturm (2004), but it didn't have as much influence as perhaps it would have had it appeared later when the numerical differential equations solvers became easier to find and use.
- [CS26] Barton, N. H., and Etheridge, A. M. (2004). The effect of selection on genealogies. Genetics, 166(2):1115–1131. This is the companion paper to Barton, Etheridge & Sturm (2004). It explores the biological implications more fully.
- [CS27] Navarro, A. and Barton, N. H. (2002). The effects of multilocus balancing selection on neutral variability. *Genetics*, 161:849–863.

- [CS28] Barton, N. H. and Navarro, A. (2002). Extending the coalescent to multilocus systems: the case of balancing selection. Genetical Research, 79:129–139. We didn't talk about this, but in these two papers Barton and Navarro examine the effect of balancing selection acting on multiple linked loci on variation at a linked neutral locus. The intriguing numerical results here have not been understood analytically.
- [CS29] Donnelly, P. J. and Kurtz, T. G. (1999). Genealogical processes for Fleming-Viot models with selection and recombination. Ann. Appl. Probab., 9:1091–1148. A modification of their 1996 'lookdown process' (which applied to infinite population limits of neutral Moran models) allowed Donnelly & Kurtz to provide 'particle representations' for the infinite population limit in the presence of selection and recombination.
- [CS30] Neuhauser, C and Krone, S.M. (1997). Genealogy of samples in models with selection. *Genetics*, 145:519–534.
- [CS31] Krone, S. M. and Neuhauser, C. (1997). Ancestral processes with selection. Theor. Pop. Biol., 51:210–237. These papers show how one can use a branching-coalescing system to construct the genealogy of a sample from a population subject to selection. A modification allows a similar construction for a population subject to balancing selection.
- [CS32] J. Gillespie. Genetic drift in an infinite population: the pseudohitchhiking model. *Genetics*, 155:909–919, 2000.
- [CS33] R. Durrett and J. Schweinsberg. A coalescent model for the effect of advantageous mutations on the genealogy of a population. Stoch. Proc. Appl., 115(10):1628–1657, 2005. This paper considers the effect of recurrent (non-overlapping) selective sweeps on a linked neutral locus and approximates the resulting genealogy via a Ξ-coalescent (a coalescent describing the genealogy in an exchangeable population model in which, because in the forwards in time population model a small number of individuals in the population can give rise to a large portion of the next generation, we see simultaneous multiple coalescences. Here a multiple coalescence is one in which three or more lineages come together into a common ancestor). The forwards in time model is Gillespie's pseudohitchhiking model.
- [CS34] J. Maynard Smith and J. Haigh. The hitch-hiking effect of a favourable allele. Genet. Res., 23:23–35, 1974. This paper could equally have appeared under supplementary references for lecture 5. This is where the term 'genetic hitch-hiking' was coined and the paper provides the first mathematical analysis of its effect.
- [CS35] Kim, Y. and Stephan, W. (2002). Detecting a local signature of genetic hitchhiking along a recombining chromosome. *Genetics*, 160:765–777.

Lecture 4

- [D36] Etheridge, A. M. (2004). Survival and Extinction in a Locally Regulated Population. Ann. Appl. Probab. 14(1):188–214. Influenced by Bolker & Pacala (1997), two different models are introduced, one in discrete space and one in a continuum, that describe a branching population in which the reproductive success is determined by the local population density. For such a population to survive for all time, individuals must migrate quickly enough that they move on to colonise vacant areas before they are killed by overcrowding caused by their own close relatives.
- [D37] J Blath, A M Etheridge, and M E Meredith. Coexistence in locally regulated competing populations and survival of branching annihilating random walk. *Ann Appl Probab*, In Press, 2007. *Various results and conjectures on coexistence of competing populations following models analogous to the single population models in Etheridge (2004) are laid out in detail here.*
- [D38] Cardy, J. L. and Täuber, U. C. (1996). Theory of branching and annihilating random walks. *Phys. Rev. Lett.*, 77:4780–4783.
- [D39] Cardy, J. L. and Täuber, U. C. (1998). Field theory of branching and annihilating random walks. J. Stat. Phys., 90(1-2):1–56. These two papers by Cardy and Täuber lie behind our conjectures for Model II in Blath, Etheridge & Meredith (2007). It is a real mathematical challenge to try to prove these results rigorously because of the lack of monotonicity in the model. Our results on the coexisting models give partial answers, but, in spite of very considerable efforts, we haven't be able to prove that the branching annihilating walk (with 'delayed' annihilation) with offspring number two dies out for small branching rate in one dimension.
- [D40] Murrell, D. J. and Law, R. (2003). Heteromyopia and the spatial coexistence of similar competitors. *Ecology Letters*, 6:48–59.
- [D41] Barton, N. H., Depaulis, F., and Etheridge, A. M. (2002). Neutral evolution in spatially continuous populations. *Theor. Pop. Biol.*, 61:31–48. *This paper extends formulae of Wright and Malécot for the probability of identity of two individuals sampled from a population dispersed in a twodimensional continuum to models which incorporate some local structure. The difficulty is the lack of explicit models for which the assumptions can be validated and the 'effective parameters' appearing in the formula calculated.*

— Supplementary references —

[DS42] Bolker, B. M., and Pacala, S. W. (1997). Using moment equations to understand stochastically driven spatial pattern formation in ecological

systems. Theor. Pop. Biol., 52(3):179–197. The model studied here influenced the formulation of the models in Etheridge (2004). Moment closure techniques are used to examine longtime behaviour of the population.

- [DS43] Bolker, B. M., and Pacala, S. W. (1999). Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. American Naturalist, 153(6):575–602. This was part of the motivation for the models studied in Blath, Etheridge & Meredith (2007).
- [DS44] Durrett, R. (1995). Ten lectures on particle systems. In *Ecole d'été* de probabilités de Saint Flour XXIII:1993, Lecture Notes in Mathematics Vol. 1608. Springer-Verlag. We won't present the proofs in detail, but comparison with oriented percolation lies at the heart of the proof of survival of the locally regulated population studied in Etheridge (2004) and also the proof of coexistence of the populations studied in Blath, Etheridge & Meredith (2007). These notes provide the necessary results from the particle systems literature.
- [DS45] Sawyer, S., and Fleischmann, J. (1978) The maximal geographical range of a mutant allele considered as a subtype of a Brownian branching random field. *Proc. Nat. Acad. Sci. USA* 76:872–875.
- [DS46] Felsenstein, J. (1975). A pain in the torus: some difficulties with the model of isolation by distance. *Amer. Nat.*, 109:359–368. *Felsenstein and Sawyer & Fleischmann independently uncovered the clumping and extinction phenomenon for branching Brownian motion in low dimensions. It is this that compels us to look for models in which the clumping is suppressed.*
- [DS47] Hutzenthaler, M. and Wakolbinger, A. (2007). Ergodic behaviour of locally regulated branching populations. Ann. Appl. Probab., 17(2):474– 501. This paper examines a special case of the models in Etheridge (2004) and provides conditions for long term survival in addition to an ergodic theorem.
- [DS48] Law, R., Murrell, D. J., and Dieckmann, U. (2003). Population growth in space and time: spatial logistic equations. *Ecology*, 84(2):252–262. *These authors study models very similar to those in Etheridge (2004) through numerical methods and moment closure. They draw the same conclusion, that individuals must spread out fast enough not to be killed by overcrowding caused by their own close relatives if the population is to survive over arbitrarily long timescales.*
- [DS49] Malécot, G. (1948). Les Mathématiques de l'hérédité. Masson et Cie, Paris. The calculation here for the probability of identity of a sample of size two from a population evolving in a spatial continuum was mimicked in Barton, Depaulis & Etheridge. Malécot assumes that a population

evolving in a two dimensional continuum is at constant local density. He incorrectly believed that this was compatible with the forwards in time model in which each individual leaves a Poisson number of offspring in a Gaussian distribution around themselves in the next generation.

- [DS50] Malécot, G. (1969). Mathematics of Heredity. Freeman, San Francisco. *English translation of the one above.*
- [DS51] Nagylaki, T. (1978a). A diffusion model for geographically structured populations. *J. Math. Biol.* 6:375–382.
- [DS52] Nagylaki, T. (1978b). Random genetic drift in a cline. *Proc. Nat. Acad. Sci. USA* 75:423–426. *Nagylaki effectively shows in these papers that rescaling the stepping stone model in two dimensions does not result in what one might call a continuum stepping stone model.*
- [DS53] Neuhauser, C. and Pacala, S. W. (1999). An explicitly spatial version of the Lotka-Volterra model with interspecific competition. Ann. Appl. Probab., 9(4):1226–1259. This paper is concerned with models for competing populations which allow exactly one individual to occupy each site of the integer lattice. What is surprising is that the range of parameters for which the two populations coexist is then smaller than in the mean field limit. This contrasts with the intuition that spatial structure should aid coexistence because each population can exploit 'gaps' in the range of the other. For this model the population forms clusters and the interactions at the cluster boundaries dominate.
- [DS54] Sudbury, A. (1990). The branching annihilating process: an interacting particle system. Ann. Probab. 18(2):581–601. Amongst other things, his paper considers branching annihilating random walk with offspring number two and instant annihilation in one spatial dimension. In contrast to the case with delayed annihilation, no matter how big the branching rate if one starts from an even number of particles then the process will die out. This is most easily seen through the duality with the voter model with 'swapping'.
- [DS55] J Blath, A M Meredith, and M E Meredith. Coexistence in locally regulated competing populations and survival of branching annihilating random walk (full version). *Technical University of Berlin Preprint*, 2007. *This is the full version of Blath, Etheridge & Meredith (2007) including all the details of the proofs.*
- [DS56] J.B. Walsh. An introduction to stochastic partial differential equations. *École d'été de probabilités de Saint Flour*, Lecture Notes in Mathematics, vol. 1180, 1986. *Still the clearest place to start learning about spde*. *Sadly, in two dimensions spde's driven by white noise often don't have a solution. For example if one formally writes down the spde corresponding to a continuum version of the Kimura stepping stone model, one obtains a*

'Fisher-Wright' noise driven by white noise. In one dimension this is what comes out of applying the diffusive rescaling to the stepping stone model. In two dimensions the corresponding model has no solution. In fact it is also not what comes out of the diffusive rescaling. Moreover, one's first guess is that one might replace white noise by 'coloured' noise. The equation does then have a solution, but this is not the equation that one obtains by rescaling the obvious individual based models with correlated reproduction. If you want to use an spde you have to derive it to make sure you really have the right one.

Lecture 5

- [E57] J. Haigh. The accumulation of deleterious genes in a population–Muller's Ratchet. *Theor. Popul. Biol.*, 14(2):251–267, 1978.
- [E58] Etheridge, A. M., Pfaffelhuber, P. and Wakolbinger, A. How often does the ratchet click? Facts, heuristics, asymptotics. *To appear in* Trends in Stochastic Analysis, J. Blath, P. Mörters and M. Scheutzow Eds, Cambridge University Press (2007).
- [E59] C Cuthbertson, A M Etheridge, and F Yu. Asymptotic behaviour of the rate of adaptation. Preprint (on the ArXiv), 2007. This complements the heuristic argument of the lecture with a rigorous proof that if selective advantage is additive, genomes are arbitrarily long and at least some proportion of mutations are advantageous then the rate of adaptation grows faster than any fractional power of $\log N$ (where N is population size) as $N \to \infty$.

— Supplementary references —

- [ES60] H. J. Muller. The relation of recombination and mutational advance. *Mutat. Res*, 106:2–9, 1964.
- [ES61] Maynard Smith, J. M. (1990). The evolution of prokaryotes does sex matter? *Ann Rev Ecol and Syst*, 21:1–12.
- [ES62] W. Stephan, L. Chao, and J. Smale. The advance of Muller's ratchet in a haploid asexual population: approximate solutions based on diffusion theory. *Genet. Res.*, 61(3):225–231, 1993.
- [ES63] I Gordo and B CharlesWorth. On the speed of mullers ratchet. *Genetics*, 156:2137–2140, 2000.
- [ES64] I. Gordo and B. Charlesworth. The degeneration of asexual haploid populations and the speed of Muller's ratchet. *Genetics*, 154(3):1379– 1387, 2000.
- [ES65] D. D. Gessler. The constraints of finite size in asexual populations and the rate of the ratchet. *Genet. Res.*, 66(3):241–253, 1995. *Gessler considers the case where the ratchet clicks very fast (in evolutionary time units).*

This corresponds to our parameter $\theta = \mu/s$ being large. In the Poisson equilibrium, the proportion of individuals in the best class is very small and, in particular, when multiplied by population size yields a number less than one. As a result, the dynamical system, in trying to reach equilibrium, will push the best class to zero even in the absence of the random resampling.

- [ES66] J. Maynard Smith. *The Evolution of Sex.* Cambridge University Press, 1978.
- [ES67] J. Felsenstein. The evolutionary advantage of recombination. *Genetics*, 78(2):737–756, 1974. *This is the paper that first uses the term 'Muller's ratchet'*.
- [ES68] L. Loewe. Quantifying the genomic decay paradox due to muller's ratchet in human mitochondrial dna. Genet. Res., 87:133–159, 2006. The length of the bibliography in this paper gives an idea of the size of the literature devoted to the ratchet.
- [ES69] N.H. Barton. Linkage and the limits to natural selection. Genetics, 140:821–841, 1995. This paper examines just two overlapping selective sweeps, a case which is itself not fully understood. For example Barton assumes that the second of the two sweeps to arise has the smaller selection coefficient. The opposite case is much harder (see Cuthbertson, Etheridge & Yu 2007) below.
- [ES70] C. Cuthbertson, A.M. Etheridge and F. Yu (2007). The probability of fixation of two competing advantageous alleles. *Preprint*.
- [ES71] N.H. Barton and J.B. Coe. An upper limit to the rate of adaptation. Unpublished manuscript, 2007. The simulations reported here suggested that there was a limit to the rate of adaptation. In fact we expect it to increase, but no faster than logarithmically in population size.
- [ES72] E. Brunet, B. Derrida, A.H. Muller, and S Munier. Noisy travelling waves: effect of selection on genealogies. *Europhys. Lett.*, 76:1–7, 2006.
- [ES73] I. Rouzine, J. Wakeley, and J. M. Coffin. The solitary wave of asexual evolution. Proceedings of the National Academy of Sciences, 100(2):587– 592, 2003. This paper and the one above are similar in flavour to Cuthbertson, Etheridge & Yu. Both approximate the behaviour of the 'bulk' of the population by a deterministic travelling wave and use stochasticity at the extreme points of the distribution to identify the appropriate wave speed. In contrast to Cuthbertson et al., neither paper is wholly mathematically rigorous.
- [ES74] R. A Fisher. The Genetical Theory of Natural Selection. Clarendon Press, Oxford, 1930. That the rate of adaptation depends on the variance of the fitness in the population is a rewording of Fisher's fundamental theorem of natural selection which originally read 'The rate of increase

in fitness of any organism at any time is equal to its genetic variance in fitness at that time'. The key point is that natural selection requires variation to act.

- [ES75] P. J. Gerrish and R.E. Lenski. The fate of competing beneficial mutations in an asexual population. *Genetica*, 102/103:127–144, 1998.
- [ES76] M. Hegreness, N. Shoresh, D. Hartl, and R. Kishony. An equivalence principle for the incorporation of favourable mutations in asexual populations. Science, 311:1615–1617, 2006. A weakness of our model is that it assumes the same absolute value for the selection coefficient associated with each new mutation. The work in this paper suggests that this is not too bad an approximation.
- [ES77] Claus O. Wilke. The speed of adaptation in large asexual populations. *Genetics*, 167:2045–2054, 2004.

Miscellaneous

- [M78] Dawson, D. A. (1993). Measure-valued Markov processes. In Ecole d'été de probabilités de Saint Flour XXI, Lecture Notes in Mathematics Vol. 1541. Springer-Verlag. A comprehensive introduction to superprocesses from the person many of us consider to be the father of the subject.
- [M79] Etheridge, A. M. (2000). An introduction to superprocesses, volume 20 of University lecture notes. A.M.S. What it says on the box.
- [M80] Ethier, S. N. and Kurtz, T. G. (1986). *Markov processes: characterization and convergence*. Wiley. *An essential reference for proving weak convergence results*.
- [M81] Wright, S. (1938). Size of population and breeding structure in relation to evolution. *Science*, 87:430–431.
- [M82] Wright, S. (1940). Breeding structure of populations in relation to speciation. *American Naturalist*, 74:232–248.
- [M83] Wright, S. (1943) Isolation by distance *Genetics*, 28:114–138. *Wright's* papers are an excellent read and are now available online.
- [M84] A. M. Etheridge. Evolution in fluctuating populations. In A Bovier, F Dunlop, A van Enter, F den Hollander, and J Dalibard, editors, Mathematical Statistical Physics. Lecture notes of the Les Houches summer school 2005. Elsevier, 2006. These notes cover much of the material from lectures 1 and 4 and the balancing selection example from lecture 3.
- [M85] Etheridge, A.M. (2007) Drift, draft and structure: mathematical models of evolution. To appear in Banach Center Publications. *These lecture notes also provide a complete description of the new model discussed in the seminar.*
- [M86] Warren Ewens (2004). Mathematical Population Genetics vol. 1: theo-

retical introduction. Springer. *This is an update of his highly influential* 1979 book. It is an excellent reference for the applications of diffusion processes in genetics.

- [M87] John H Gillespie 1994. The Causes of Molecular Evolution. Oxford series in ecology and evolution. Oxford University Press. *This contains some important and fascinating material that is not very extensively covered elsewhere (for example the sections on fluctuating selection).*
- [M88] John H. Gillespie (2004). Population Genetics a concise guide (2nd edition). Johns Hopkins University Press. *Not aimed at mathematicians, but a good way to learn some basic genetics and a bit about the underlying models.*
- [M89] Etheridge, A.M. (2006). Diffusion Process Models in Mathematical Genetics. Available from my home page, these notes cover some of the material from Ewens. They are notes from a final year undergraduate course in Oxford.