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**Supplementary Information** is available in the online version of the paper.

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**Author Contributions** R.C. conceived the study, performed experiments, and wrote the manuscript. J.C.L. and T.Y. purified Pol $\theta$  fragments from insect cells and performed ATPase and gel shift assays. R.A. performed D-loop formation assays. I.H. and S.J.E. performed the DNA fibres assay. B.P. performed mice work and analysed *in vivo* data. M.I.R.P. and S.J.B. performed the Pol $\theta$  peptide array and the RAD51–ssDNA filament assembly and release assays. K.W.O. scored RAD51 foci. P.A.K. curated TCGA datasets for Figure 3a and Extended Data Figures 5h and 9e and provided clinical perspectives. A.D.D. conceived the study and wrote the manuscript. All authors approved the final version of the manuscript.

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