LETTER

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Butterfly genome reveals promiscuous exchange of mimicry adaptations among species

The *Heliconius* Genome Consortium*

The evolutionary importance of hybridization and introgression has long been debated[1]. Hybrids are usually rare and unfit, but even infrequent hybridization can aid adaptation by transferring beneficial traits between species. Here we use genomic tools to investigate introgression in *Heliconius*, a rapidly radiating genus of neotropical butterflies widely used in studies of ecology, behaviour, mimicry and speciation[2–5]. We sequenced the genome of *Heliconius melpomene* and compared it with other taxa to investigate chromosomal evolution in Lepidoptera and gene flow among multiple *Heliconius* species and races. Among 12,669 predicted genes, biologically important expansions of families of chemosensory and *Hox* genes are particularly noteworthy. Chromosomal organization has remained broadly conserved since the Cretaceous period, when butterflies split from the *Bombyx* (silkmoth) lineage. Using genomic resequencing, we show hybrid exchange of genes between three co-mimics, *Heliconius melpomene*, *Heliconius timareta* and *Heliconius elevatus*, especially at two genomic regions that control mimicry pattern. We infer that closely related *Heliconius* species exchange protective colour-pattern genes promiscuously, implying that hybridization has an important role in adaptive radiation.

The butterfly genus *Heliconius* (Nymphalidae: Heliconiinae) is associated with a suite of derived life-history and ecological traits, including pollen feeding, extended lifespan, augmented ultraviolet colour vision, 'trap-lining' foraging behaviour, gregarious roosting and complex mating behaviours, and provides outstanding opportunities for genomic studies of adaptive radiation and speciation[4,6]. The genus is best known for the hundreds of races with different colour patterns seen among its 43 species, with repeated examples of both convergent evolution among distantly related species and divergent evolution between closely related taxa[3]. Geographic mosaics of multiple colour-pattern races, such as in *Heliconius melpomene* (Fig. 1), converge to similar mosaics in other species, and this led to the hypothesis of mimicry[2]. *Heliconius* are unpalatable to vertebrate predators and Müllerian mimicry of warning colour patterns enables species to share the cost of educating predators[3]. As a result of its dual role in mimicry and mate selection, divergence in wing pattern is also associated with speciation and adaptive radiation[3,5]. A particularly recent radiation is the *melpomene*–silvaniform clade, in which mimetic patterns often seem to be polyphyletic (Fig. 1a). Most species in this clade occasionally hybridize in the wild with other clade members[7]. Gene genealogies at

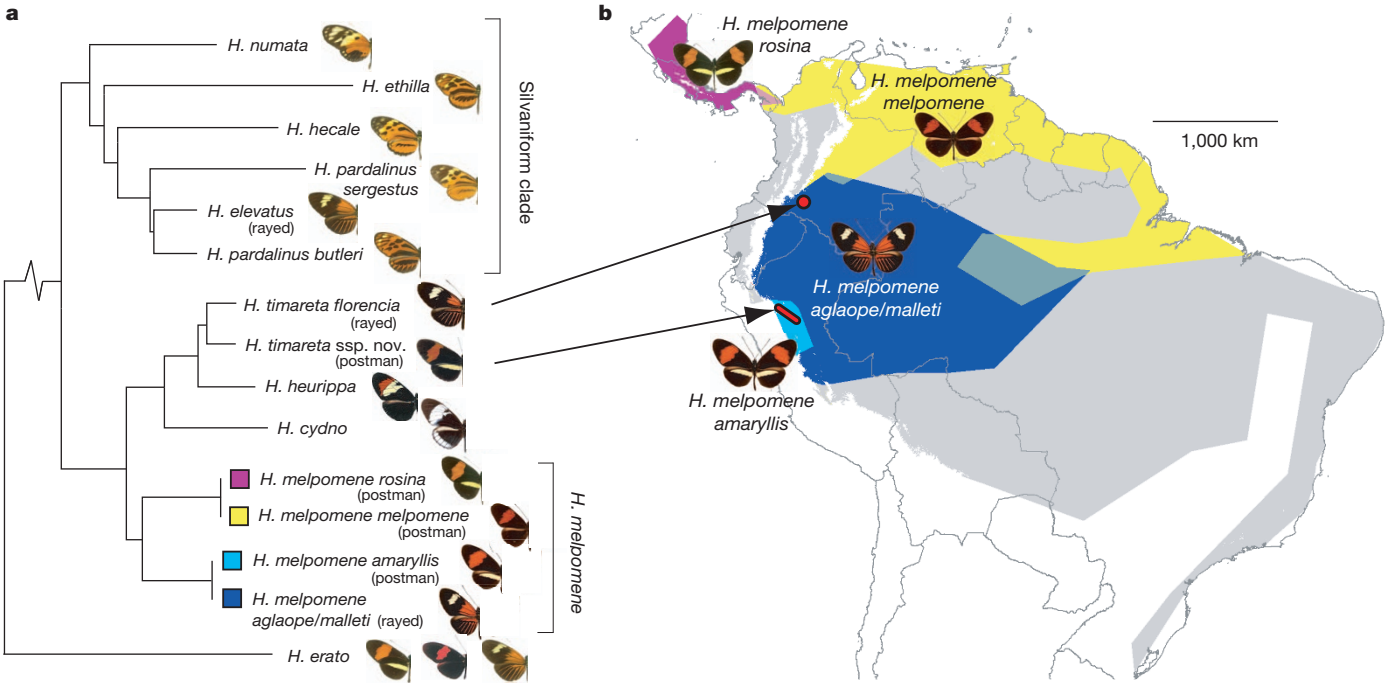

Figure 1 | Distribution, mimicry and phylogenetic relationships of sequenced taxa. **a**, Phylogenetic relationship of sequenced species and subspecies in the *melpomene*–silvaniform clade of *Heliconius*. *Heliconius elevatus* falls in the silvaniform clade, but it mimics colour patterns of *melpomene*–*timareta* clade taxa. Most other silvaniforms mimic unrelated ithomiine butterflies[24]. **b**, Geographic distribution of postman and rayed *H. melpomene* races studied here (blue, yellow and purple), and the entire distribution of *H. melpomene* (grey). The *H. timareta* races investigated have limited distributions (red) indicated by arrows and mimic sympatric races of *H. melpomene*. *Heliconius elevatus* and the other silvaniform species are distributed widely across the Amazon basin (Supplementary Information, section 22).

*Lists of participants and their affiliations appear at the end of the paper.

a small number of loci indicate introgression between species[8], and one non-mimetic species, *Heliconius heurippa*, has a hybrid origin[9]. Adaptive introgression of mimicry loci is therefore a plausible explanation for parallel evolution of multiple mimetic patterns in the *melpomene*–silvaniform clade.

A *Heliconius melpomene melpomene* stock from Darién, Panama (Fig. 1), was inbred through five generations of sib mating. We sequenced a single male to ×38 coverage (after quality filtering) using combined 454 and Illumina technologies (Supplementary Information, sections 1–8). The complete draft genome assembly, which is 269 megabases (Mb) in size, consists of 3,807 scaffolds with an N50 of 277 kb and contains 12,669 predicted protein-coding genes. Restriction-site-associated DNA (RAD) linkage mapping was used to assign and order 83% of the sequenced genome onto the 21 chromosomes (Supplementary Information, section 4). These data permit a considerably improved genome-wide chromosomal synteny comparison with the silkmoth *Bombyx mori*[10,11].

Using 6,010 orthologues identified between *H. melpomene* and *B. mori*, we found that 11 of 21 *H. melpomene* linkage groups show homology to single *B. mori* chromosomes and that ten linkage groups have major contributions from two *B. mori* chromosomes (Fig. 2a and Supplementary Information, section 8), revealing several previously unidentified chromosomal fusions. These fusions on the *Heliconius* lineage most probably occurred after divergence from the sister genus *Eueides*[4], which has the lepidopteran modal karyotype of $n = 31$ (ref. 12). Three chromosomal fusions are evident in *Bombyx* (*B. mori* chromosomes 11, 23 and 24; Fig. 2a), as required for evolution of the *Bombyx* $n = 28$ karyotype from the ancestral $n = 31$ karyotype. *Heliconius* and *Bombyx* lineages diverged in the Cretaceous, more than 100 million years ago[11], so the gross chromosomal structures of Lepidoptera genomes have remained highly conserved compared with those of flies or vertebrates[13,14]. By contrast, small-scale rearrangements were frequent. In the comparison with *Bombyx*, we estimate there to be 0.05–0.13 breaks per megabase per million years, and in that with *Danaus plexippus* (Monarch butterfly), we estimate there to be 0.04–0.29 breaks per megabase per million years. Although lower than previously suggested for Lepidoptera[15], these rates are comparable to those in *Drosophila* (Supplementary Information, section 8).

The origin of butterflies was associated with a switch from nocturnal to diurnal behaviour, and a corresponding increase in visual communication[16]. *Heliconius* have increased visual complexity through expression of a duplicate ultraviolet opsin[6], in addition to the long-wavelength-, blue- and ultraviolet-sensitive opsins in *Bombyx*. We might therefore predict reduced complexity of olfactory genes, but in fact *Heliconius* and *Danaus*[17] genomes have more chemosensory genes than any other insect genome: 33 and 34, respectively (Supplementary Information, section 9). For comparison, there are 24 in *Bombyx* and 3–4 in *Drosophila*[18]. Lineage-specific expansions of chemosensory genes were evident in both *Danaus* and *Heliconius* (Fig. 2b). By contrast, all three lepidopteran genomes have similar numbers of odorant binding proteins and olfactory receptors (Supplementary Information, section 9). *Hox* genes are involved in body plan development and show strong conservation across animals. We identified four additional *Hox* genes located between the canonical *Hox* genes *pb* and *zen*, orthologous to *shx* genes in *B. mori*[19] (Supplementary Information, section 10). These *Hox* gene duplications in the butterflies and *Bombyx* have a common origin and are independent of the two tandem duplications known in dipterans (*zen2* and *bcd*). Immunity-related gene families are similar across all three lepidopterans (Supplementary Information, section 11), whereas there are extensive duplications and losses within dipterans[20].

The *Heliconius* reference genome allowed us to perform rigorous tests for introgression among *melpomene*–silvaniform clade species. We used RAD resequencing to reconstruct a robust phylogenetic tree based on 84 individuals of *H. melpomene* and its relatives, sampling on average 12 Mb, or 4%, of the genome (Fig. 1a and Supplementary Information, sections 12–18). We then tested for introgression between the sympatric co-mimetic postman butterfly races of *Heliconius melpomene amaryllis* and *H. timareta* ssp. nov. (Fig. 1) in Peru, using 'ABBA/BABA' single nucleotide sites and Patterson's *D*-statistics (Fig. 3a), originally developed to test for admixture between Neanderthals and modern humans[21,22] (Supplementary Information, section 12). Genome-wide, we found an excess of ABBA sites, giving a significantly positive Patterson's D of 0.037 ± 0.003 (two-tailed Z-test for $D = 0$, $P = 1 \times 10^{-40}$), indicating greater genome-wide introgression between the sympatric mimetic taxa *H. melpomene amaryllis* and

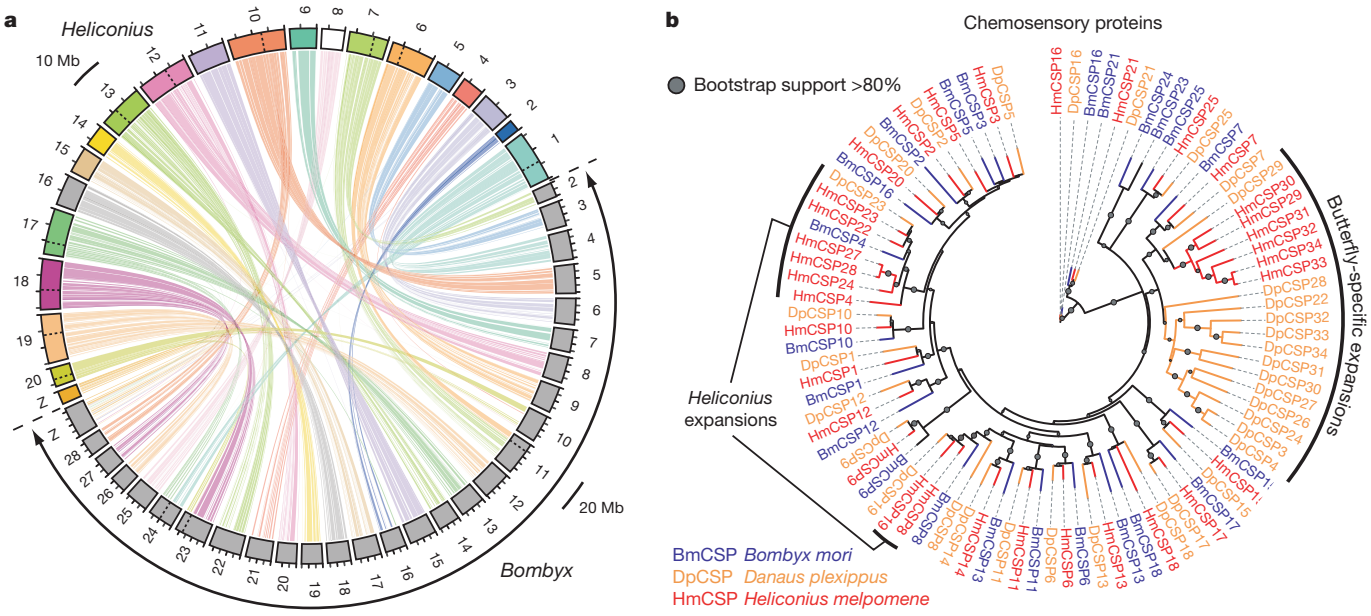

Figure 2 | Comparative analysis of synteny and expansion of the chemosensory genes. a, Maps of the 21 *Heliconius* chromosomes (colour) and of the 28 *Bombyx* chromosomes (grey) based on positions of 6,010 orthologue pairs demonstrate highly conserved synteny and a shared $n = 31$ ancestor (Supplementary Information, section 8). Dotted lines within chromosomes indicate major chromosomal fusions. **b**, Maximum-likelihood tree showing expansions of chemosensory protein (CSP) genes in the two butterfly genomes.

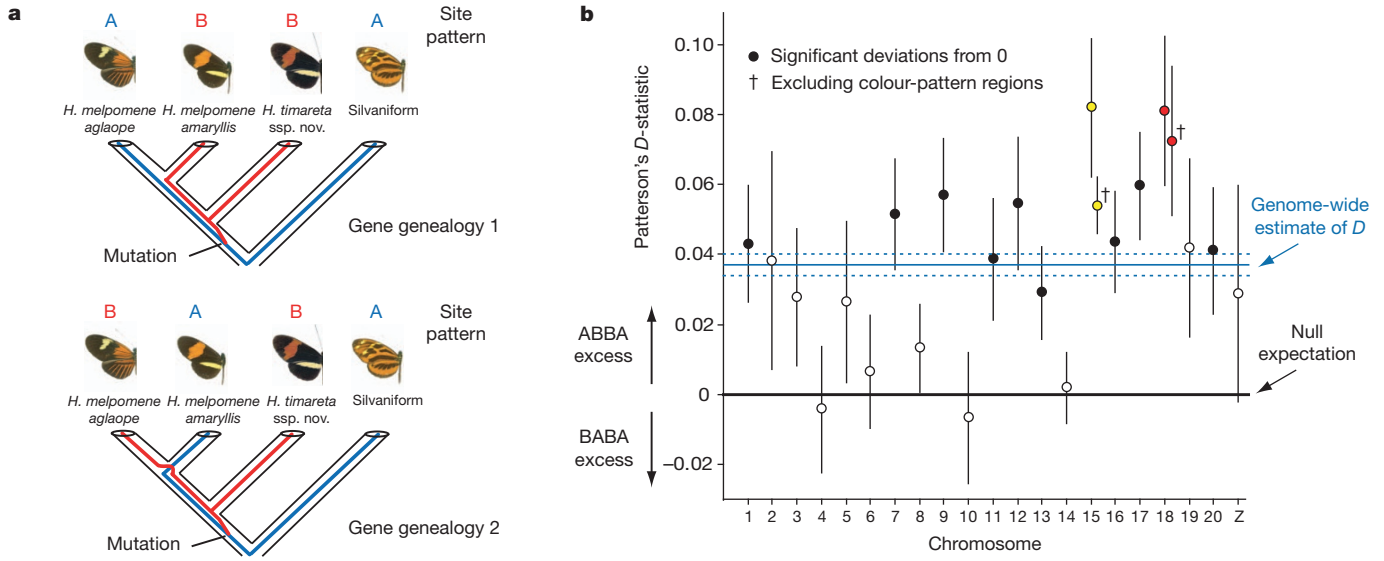

Figure 3 | Four-taxon ABBA/BABA test of introgression. **a**, ABBA and BABA nucleotide sites employed in the test are derived (– – **B** –) in *H. timareta* compared with the silvaniform outgroup (– – – **A**), but differ among *H. melpomene amaryllis* and *H. melpomene aglaope* (either **AB**BA or **BA**BA). As this almost exclusively restricts attention to sites polymorphic in the ancestor of *H. timareta* and *H. melpomene*, equal numbers of ABBA and BABA sites are expected under a null hypothesis of no introgression[22], as depicted in the two gene genealogies. **b**, Distribution among chromosomes of Patterson's *D*-statistic (±s.e.), which measures excess of ABBA sites over BABA sites[22], here for the comparison: *H. m. aglaope*, *H. m. amaryllis*, *H. timareta* ssp. nov., silvaniform. Chromosomes containing the two colour-pattern regions (*B/D*, red; *N/Yb*, yellow) have the two highest *D*-statistics; the combinatorial probability of this occurring by chance is 0.005. The excess of ABBA sites ($0 < D < 1$) indicates introgression between sympatric *H. timareta* and *H. m. amaryllis*.

H. timareta ssp. nov. than between *H. melpomene aglaope* and *H. timareta* ssp. nov., which do not overlap spatially (Fig. 1b). On the basis of these *D*-statistics, we estimate that 2–5% of the genome was exchanged[21] between *H. timareta* and *H. melpomene amaryllis*, to the exclusion of *H. melpomene aglaope*. (Supplementary Information, section 12). Exchange was not random. Of the 21 chromosomes, 11 have significantly positive *D*-statistics, and the strongest signals of introgression were found on the two chromosomes containing known mimicry loci *B/D* and *N/Yb* (Fig. 3b and Supplementary Information, section 15).

Perhaps the best-known case of Müllerian mimicry is the geographic mosaic of ~30 bold postman and rayed colour-pattern races of *H. melpomene* (Fig. 1b and Supplementary Information, section 22), which mimic a near-identical colour-pattern mosaic in *Heliconius erato* (Fig. 1a), among other *Heliconius* species. Mimicry variation is mostly controlled by a few loci with strong effects. Mimetic pattern differences between the postman *H. m. amaryllis* and the rayed *H. m. aglaope* races studied here (Fig. 1a) are controlled by the *B/D* (red pattern) and *N/Yb* (yellow pattern) loci[23,24]. These loci are located on the two chromosomes that show the highest *D*-statistics in our RAD analysis (Fig. 3b). To test whether mimicry loci might be introgressed between co-mimetic *H. timareta* and *H. melpomene*[7] (Fig. 1a), we resequenced the colour-pattern regions *B/D* (0.7 Mb) and *N/Yb* (1.2 Mb), and 1.8 Mb of unlinked regions across the genome, from both postman and ray-patterned *H. melpomene* and *H. timareta* from Peru and Colombia, and six silvaniform outgroup taxa (Fig. 1a and Supplementary Information, section 12). To test for introgression at the *B/D* mimicry locus, we compared rayed *H. m. aglaope* and postman *H. m. amaryllis* as the ingroup with postman *H. timareta* ssp. nov. (Fig. 3a) and found large, significant peaks of shared, fixed ABBA nucleotide sites combined with an almost complete lack of BABA sites (Fig. 4b). This provides evidence that blocks of shared sequence variation in the *B/D* region were exchanged between postman *H. timareta* and postman *H. melpomene* in the genomic region known to determine red mimicry patterns between races of *H. melpomene*[23,24] (Fig. 4a).

For a reciprocal test, we used the same *H. melpomene* races as the ingroup to compare with rayed *Heliconius timareta florencia* at the *B/D* region. In this case, correspondingly large and significant peaks of BABA nucleotide sites are accompanied by an almost complete absence of ABBA sites (Fig. 4c), indicating that variation at the same mimicry locus was also shared between rayed *H. timareta* and rayed *H. melpomene*. Equivalent results in the *N/Yb* colour-pattern region, controlling yellow colour-pattern differences, are in the expected directions for introgression and are highly significant for the test using postman *H. timareta* ssp. nov. ($P = 6 \times 10^{-34}$), but are not significant in rayed *H. t. florencia* ($P = 0.13$; Supplementary Information, section 17). By contrast, hardly any ABBA or BABA sites are present in either comparison across 1.8 Mb in 55 genomic scaffolds that are unlinked to the colour-pattern regions (Supplementary Information, section 21). These concordant but reciprocal patterns of fixed ABBA and BABA substitutions occur almost exclusively within large genomic blocks at two different colour-pattern loci (449 and 99 sites for *B/D* and *N/Yb*, respectively; Fig. 4b, c and Supplementary Information, section 17). These patterns would be very hard to explain in terms of convergent functional-site evolution or random coalescent fluctuations. Instead, our results imply that derived colour-pattern elements have introgressed recently between both rayed and postman forms of *H. timareta* and *H. melpomene*.

To test whether colour-pattern loci might be shared more broadly across the clade, we used sliding-window phylogenetic analyses along the colour-pattern regions. For regions flanking and unlinked to colour-pattern loci, tree topologies are similar to the predominant signal recovered from the genome as a whole (Supplementary Information, section 18). Races of *H. melpomene* and *H. timareta* each form separate monophyletic sister groups and both are separated from the more distantly related silvaniform species (Fig. 4d). By contrast, topologies within the region of peak ABBA/BABA differences group individuals by colour pattern, and the species themselves become polyphyletic (Fig. 4e, f and Supplementary Information, sections 19 and 20). Remarkably, the rayed *H. elevatus*, a member of the silvaniform clade according to genome average relationships (Fig. 1a and Supplementary Information, section 18), groups with rayed races of unrelated *H. melpomene* and *H. timareta* in small sections within both *B/D* and *N/Yb* colour-pattern loci (Fig. 4e and Supplementary

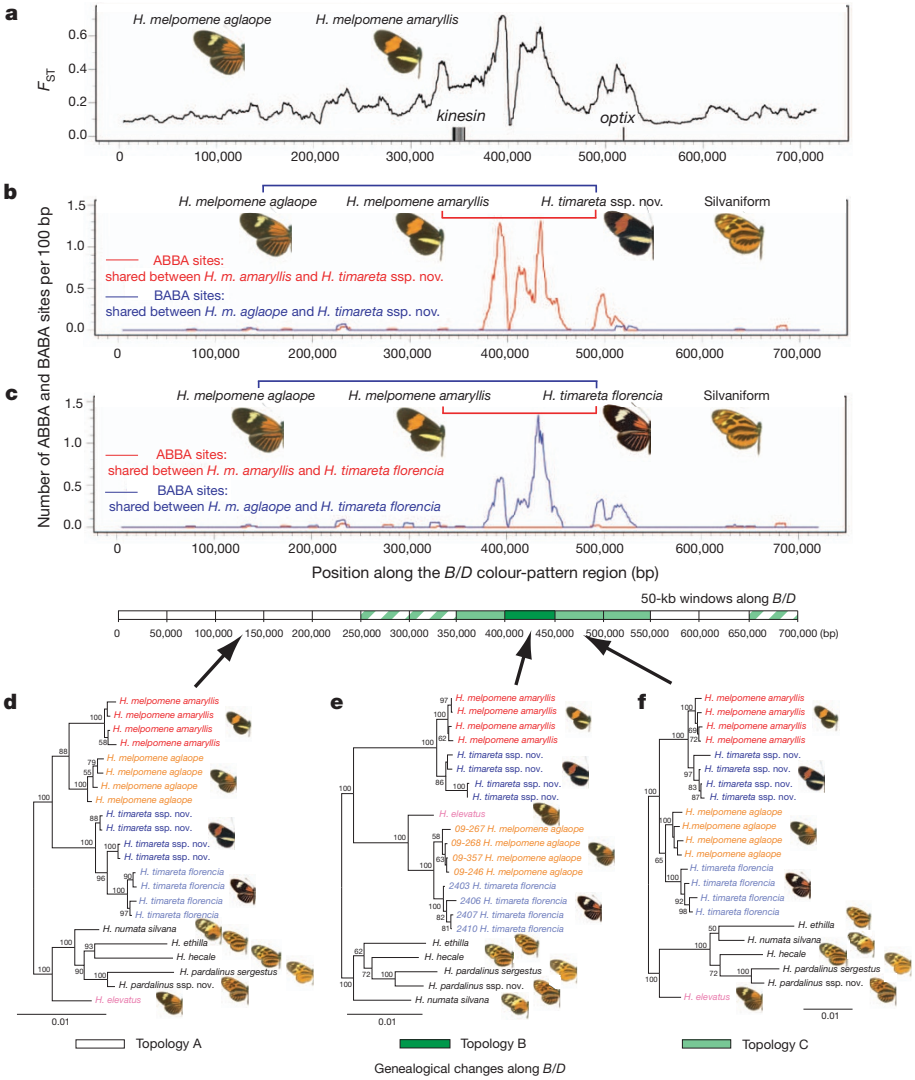

Figure 4 | Evidence for adaptive introgression at the *B/D* mimicry locus. **a**, Genetic divergence between *H. melpomene* races *aglaope* (rayed) and *amaryllis* (postman) across a hybrid zone in northeast Peru. Divergence, F_{ST}, is measured along the *B/D* region (Supplementary Information 14) and peaks in the region known to control red wing pattern elements between the genes *kinesin* and *optix*[23]. **b**, **c**, Distribution of fixed ABBA and BABA sites (see Fig. 3a) along *B/D* for two comparisons. Excesses of ABBA in **b** and BABA in **c** are highly significant (two-tailed *Z*-tests for $D = 0$; $D = 0.90 \pm 0.13$, $P = 5 \times 10^{-14}$ and $D = -0.91 \pm 0.10$, $P = 9 \times 10^{-24}$, respectively), indicating introgression. **d**, **e**, **f**, Genealogical change along *B/D* investigated with maximum likelihood based on 50-kb windows. Three representative tree topologies are shown. Topology A, the species tree, is found within the white windows. In topologies B (dark green window) and C (light green windows) taxa group by colour pattern rather than by species. Within striped windows, *H. melpomene* and/or *H. timareta* are paraphyletic but the taxa do not group by colour pattern. Support is shown for nodes with >50% bootstrap support (Supplementary Information, section 19). bp, base pair.

Information, sections 19 and 20). These results are again most readily explained by introgression and fixation of mimicry genes.

We have developed a *de novo* reference genome sequence that will facilitate evolutionary and ecological studies in this key group of butterflies. We have demonstrated repeated exchange of large (~100-kb) adaptive regions among multiple species in a recent radiation. Our genome-scale analysis provides considerably greater power than previous tests of introgression[8,25–27]. Our evidence suggests that *H. elevatus*, like *H. heurippa*[9], was formed during a hybrid speciation event. The main genomic signal from this rayed species places it closest to *Heliconius pardalinus butleri* (Fig. 1a), but colour-pattern genomic regions resemble those of rayed races of *H. melpomene* (Fig. 4e and Supplementary Information, sections 18–21). Colour pattern is important in mating behaviour in *Heliconius*[5], and the transfer of mimetic pattern may have enabled the divergent sibling species *H. elevatus* to coexist with *H. pardalinus* across the Amazon basin. Although it was long suspected that introgression might be important in evolutionary radiations[1], our results from the most diverse terrestrial biome on the planet suggest that adaptive introgression is more pervasive than previously realized.

The annotated genome version 1.1 is available on the *Heliconius* Genome Consortium's genome browser at http://butterflygenome.org/ and this version will also be included in the next release of ENSEMBL Genomes. A full description of methods can be found in Supplementary Information.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions Consortium leaders: C.D.J., W.O.M. Heliconius Genome Consortium Principal Investigators: R.H.f.-C., M.R.K., M.J., J.M., S.M., R.D.R, M.L.B., L.E.G., M.L., G.L. Introgression study leader: J.M. Lead investigators: K.K.D., J.R.W., N.J.N., A.W., J.W.D., A.D.B., L.C.F., D.S.T.H., S.M., C.S., J.J.L., A.V.Z. Sequencing: S.R., S.E.S., A.L.B., M.T., K. Gharbi, C.E., M.L.B., R.A.G., Y.H., J.C.J., C.K., T.M., D.M.M., F.O., L.-L.P., J.Q., R.L.T., K.C.W., Y.-Q.W. Assembly: A.V.Z., J.A.Y., S.L.S., A.P., K. Gordon. RAD map and assembly verification: J.W.D., S.W.B., M.L.B., L.S.M., D.D.K., J.R.W., P.A.W. Geographic distribution map: N.R. Annotation: J.R.W., D.S.T.H., D.W., D.L., K.J.H., S.A., P.A.W., P.K. Genome browser and databases: D.S.T.H., J.J.L. Manual annotation and evolutionary analyses: A.D.B., E.J.-J., F.Y. (olfactory proteins); L.C.F., P.W.H.H., J.R.W. (*Hox* genes); A.S., T.D., D.M., S.M. (microRNAs); W.J.P., F.M.J. (immune genes); R.T.J., R.C. (P450 genes); H.V., S.-J.A., D.G.H. (uridine diphosphate glucuronosyltransferase genes); Y.P. (ribosomal proteins); S.W.B., M.L.B., A.D.B., N.L.C., B.A.C., L.C.F., H.M.H., C.D.J., F.M.J., M.J., D.D.K., M.R.K., J.M., A.M., S.P.M., N.J.N., W.J.P, R.P., M.A.S., A.T.-T., A.W., F.Y. (manual annotation group); B.A.C., D.A.R. (transposable elements); D.A.B. (orthologue predictions); A.W., J.W.D., D.G.H., K. Gordon (synteny); K.K.D., N.J.N., J.W.D., S.H.M., C.S., C.D.J., M.J., J.M. (introgression analysis). K.K.D. and J.R.W. contributed equally to this work.

Author Information The genome sequence has been submitted to the European Nucleotide Archive under accession numbers HE667773–HE672081. Additional short read sequences have been submitted to the European Nucleotide Archive under accession numbers ERP000993 and ERP000991. Reprints and permissions information is available at www.nature.com/reprints. This paper is distributed under the terms of the Creative Commons Attribution-Non-Commercial-Share Alike licence, and is freely available to all readers at www.nature.com/nature. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this article at www.nature.com/nature. Correspondence and requests for materials should be addressed to J.M. (jmallet@oeb.harvard.edu).

The *Heliconius* Genome Consortium Kanchon K. Dasmahapatra[1], James R. Walters[2], Adriana D. Briscoe[3], John W. Davey[4], Annabel Whibley[5], Nicola J. Nadeau[2], Aleksey V. Zimin[6], Daniel S. T. Hughes[7], Laura C. Ferguson[8], Simon H. Martin[2], Camilo Salazar[2,9], James J. Lewis[3], Sebastian Adler[10], Seung-Joon Ahn[11], Dean A. Baker[12], Simon W. Baxter[2], Nicola L. Chamberlain[13], Ritika Chauhan[14], Brian A. Counterman[15], Tamas Dalmay[16], Lawrence E. Gilbert[17], Karl Gordon[18], David G. Heckel[11], Heather M. Hines[19], Katharina J. Hoff[10], Peter W. H. Holland[8], Emmanuelle Jacquin-Joly[20], Francis M. Jiggins[21], Robert T. Jones[5], Durrell D. Kapan[22,23], Paul Kersey[7], Gerardo Lamas[24], Daniel Lawson[7], Daniel Mapleson[25], Luana S. Maroja[26], Arnaud Martin[3], Simon Moxon[27], William J. Palmer[21], Riccardo Papa[28], Alexie Papanicolaou[18], Yannick Pauchet[11], David A. Ray[29,30], Neil Rosser[1], Steven L. Salzberg[31], Megan A. Supple[32], Alison Surridge[2], Ayse Tenger-Trolander[13], Heiko Vogel[11], Paul A. Wilkinson[33], Derek Wilson[7], James A. Yorke[6], Furong Yuan[3], Alexi L. Balmuth[34], Cathlene Eland[34], Karim Gharbi[34], Marian Thomson[34], Richard A. Gibbs[35], Yi Han[35], Joy C. Jayaseelan[35], Christie Kovar[35], Tittu Mathew[35], Donna M. Muzny[35], Fiona Ongeri[35], Ling-Ling Pu[35], Jiaxin Qu[35], Rebecca L. Thornton[35], Kim C. Worley[35], Yuan-Qing Wu[35], Mauricio Linares[36], Mark L. Blaxter[4,34], Richard H. ffrench-Constant[14], Mathieu Joron[5], Marcus R. Kronforst[13], Sean P. Mullen[37], Robert D. Reed[3], Steven E. Scherer[35], Stephen Richards[35], James Mallet[1,38], W. Owen McMillan[9], Chris D. Jiggins[2,9]

Affiliations for participants: [1]Department of Genetics, Evolution and Environment, University College London, Gower Street, London WC1E 6BT, UK. [2]Department of Zoology, Downing Street, University of Cambridge, Cambridge CB2 3EJ, UK. [3]Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92697, USA. [4]Institute of Evolutionary Biology, Ashworth Laboratories, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, UK. [5]CNRS UMR 7205, Muséum National d'Histoire Naturelle, 45 rue Buffon, Paris 75005, France. [6]Institute for Physical Science and Technology, University of Maryland, College Park, Maryland 20742, USA. [7]European Bioinformatics Institute, Hinxton CB10 1SD, UK. [8]Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK. [9]Smithsonian Tropical Research Institute, Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Panamá, República de Panamá. [10]Institut für Mathematik und Informatik, Universität Greifswald, 17487 Greifswald, Germany. [11]Max Planck Institute for Chemical Ecology, D-07745 Jena, Germany. [12]Ecology and Evolution, Imperial College London, London SW7 2AZ, UK. [13]FAS Center for Systems Biology, Harvard University, Cambridge, Massachusetts 02138, USA. [14]Centre for Ecology and Conservation, School of Biosciences, University of Exeter, Penryn TR10 9EZ, UK. [15]Department of Biology, Mississippi State University, Mississippi State, Mississippi 39762, USA. [16]School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich NR4 7TJ, UK. [17]Section of Integrative Biology and Brackenridge Field Laboratory, University of Texas, Austin, Texas 78712, USA. [18]Black Mountain Laboratories, CSIRO Ecosystem Sciences, Clunies Ross Street, Canberra, Australian Capital Territory 2601, Australia. [19]Department of Genetics, North Carolina State University, Raleigh, North Carolina 27695, USA. [20]UMR-A 1272 INRA-Université Pierre et Marie Curie, Physiologie de l'Insecte: Signalisation et Communication, Route de Saint-Cyr, Versailles Cedex 78026, France. [21]Department of Genetics, Downing Street, University of Cambridge, Cambridge CB2 3EH, UK. [22]Department of Entomology, Center for Comparative Genomics, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, California 94118, USA. [23]Center for Conservation and Research Training, Pacific Biosciences Research Center, University of Hawaii at Manoa, 3050 Maile Way, Gilmore 406, Honolulu, Hawaii 96822, USA. [24]Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Apartado 14-0434, Lima, Peru. [25]School of Computing Sciences, University of East Anglia, Norwich Research Park, Norwich NR4 7TJ, UK. [26]Department of Biology, Williams College, Williamstown, Massachusetts 01267, USA. [27]Department of Genetics, Yale University School of Medicine, 333 Cedar Street, New Haven, Connecticut 06520, USA. [28]Department of Biology, University of Puerto Rico, PO Box 23360, Río Piedras, 00931-3360 Puerto Rico. [29]Department of Biochemistry, Molecular Biology, Entomology and Plant Pathology, Mississippi State University, Mississippi State, Mississippi 39762, USA. [30]Institute for Genomics, Biocomputing and Biotechnology, Mississippi State University, Mississippi State, Mississippi 39759, USA. [31]McKusick-Nathans Institute of Genetic Medicine, Johns Hopkins University, Baltimore, Maryland 21205, USA. [32]Biomathematics Program, North Carolina State University, Raleigh, North Carolina 27695, USA. [33]School of Biological Sciences, University of Bristol, Bristol BS8 1UG, UK. [34]The GenePool, Ashworth Laboratories, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, UK. [35]Human Genome Sequencing Center, Baylor College of Medicine, One Baylor Plaza, Houston, Texas 77030, USA. [36]Facultad de Ciencias Naturales y Matemáticas, Universidad del Rosario and Instituto de Genética, Universidad de los Andes, Bogotá, Colombia. [37]Department of Biology, Boston University, 5 Cummington Street, Boston, Massachusetts 02215, USA. [38]Department of Organismic and Evolutionary Biology, Harvard University, 16 Divinity Avenue, Cambridge, Massachusetts 02138, USA.