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Review

Phenotypic signatures of incomplete lineage sorting in hominids

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Incomplete lineage sorting (ILS) generates widespread genomic discordance in rapidly radiating lineages, yet its phenotypic impacts remain poorly understood. Among hominids, over 30% of the human genome supports conflicting phylogenetic trees due to ILS, affecting numerous genes with morphological functions. We present a trait-based approach integrating comparative morphology, population genomics, and functional experiments to identify and validate ILS-affected traits in hominids, often interpreted as convergent adaptations. Phylogenetically incongruent traits are frequent in the craniofacial and appendicular skeletons, highlighting priority areas for ILS investigation and ascertainment bias. This approach requires collaborative models bridging morphological and genomic data gaps in non-human hominid research, illuminating the forces shaping great ape evolution and establishing a roadmap for exploring ILS consequences in diverse taxonomic groups.

Highlights

Incomplete lineage sorting (ILS) occurs when ancestral genetic variation is randomly sorted into descendant lineages, causing conflicts between gene trees and species trees.

Over one-third of the human genome is affected by ILS, yet its impacts on morphology remain unknown.

Identification of ILS-affected traits offers insights into the historical processes shaping modern diversity, including speciation, population dynamics, and selective versus neutral evolution.

Numerous hominid traits exhibit phylogenetic incongruence, suggesting that shared morphological features historically interpreted as convergent adaptations may reflect ILS events.

Integration of comparative morphology with population genomics and functional validation will allow us to quantify the relative contributions of these processes, resolving trait-species tree conflicts and revealing the complex history of hominid evolution.

Hominid relationships – a history of phylogenetic conflict

> 'Man still bears in his bodily frame the indelible stamp of his lowly origin.' – Charles Darwin, *The Descent of Man, and Selection in Relation to Sex*

Little could Darwin have imagined while writing *The Descent of Man* that human's connection to 'some extinct ape-like creature' would be written not only in our physical appearance, but in our DNA. Both Darwin [1] and Huxley [2] hypothesised shared ancestry of modern humans and African apes based on comparative anatomy, embryology, and behaviour, although a century would pass before they were validated by molecular studies. Immunological, protein, and chromosome-based analyses confirmed a trichotomy between human (*Homo*), chimpanzee (*Pan*), and gorilla (*Gorilla*), later resolved by DNA sequence and gene expression data as a *Homo–Pan* clade, leaving gorillas instead of humans as 'the odd ape out' (see [3] for a review of molecular anthropology). Overwhelming evidence has since accumulated to support a monophyletic **Hominidae** (see Glossary) comprising the **great apes** and their most recent common ancestor [4], with numerous fossils, **synapomorphies** and artifacts linking us to our African origins, as well as to other archaic humans, or **hominins** [5]. Throughout this review, unless otherwise noted, we use the common name 'human' to refer to modern *Homo sapiens*, 'chimpanzee' to refer to both the common chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*), 'gorilla' to the eastern gorilla (*Gorilla gorilla*) and western gorilla (*Gorilla beringei*), and 'orangutan' to the Bornean (*Pongo pygmaeus*), Sumatran (*Pongo abelii*), and Tapanuli (*Pongo tapanuliensis*) orangutan. With the extant family tree now resolved by whole-genome data as (((HC)G)O) for human [6], chimpanzee [7], gorilla [8], and orangutan [9], a new mystery emerged – that about 17% of the human genome is more similar to gorilla than to our closest living relative, the chimpanzee, while another ~17% supports a *Pan–Gorilla* clade [4,8,10–12]. These contradictory topologies

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of individual gene trees are caused by ILS, defined as the random fixation of ancestral alleles among descent species.

Evolutionary processes such as ILS (Box 1) are known to complicate reconstructions of lineage diversification, by causing **phylogenetic discordance** between gene trees and species trees. However, empirical evidence connecting ILS-affected genes to morphological variation remains elusive, largely due to the lack of **comparative genomic analyses** associating specific DNA changes to their phenotypic end-products [13,14]. This gap is particularly acute for non-human primates, for which little is known about the functional consequences of gene expression except for species used in biomedical research, for example Rhesus macaque (*Macaca mulatta*). In this review, we provide a trait-based approach towards identifying the impacts of ILS on hominid morphology and propose a roadmap for functionally validating putative underlying ILS-affected genes using experimental systems. Implementing this conceptual framework will require addressing several methodological challenges, including development of standardised protocols for trait validation, efficient methods for linking phenotypic and genomic data, and rigorous approaches to distinguish ILS from other evolutionary processes (see Outstanding questions).

Post-genomic era brings expanded awareness of ILS

While ILS has long been recognised in hominid evolution [15], the extent to which it impacts extant variation was only recently appreciated with the application of **coalescent theory** to comparisons of reference genomes across the phylogeny [9,10]. Coalescent theory predicts that the frequency of ILS on each locus is associated with the local **effective population size (N_e)** and natural selection acting on those loci [11,16]. Because genomic regions with higher N_e normally carry higher levels of genetic diversity, these regions tend to coalesce in deeper time, thus increasing the likelihood of ILS. Since both positive and negative selection in ancient populations is expected to reduce local N_e, the proportion of ILS is reduced in genomic regions under that selection. By contrast, regions targeted by balancing selection will be more variable in the population, resulting in a longer coalescence time and occurrence of ILS. ILS therefore occurs in particularly high frequency during adaptive and/or rapid radiations [17] and has been recorded in diverse taxonomic groups, including plants [18], insects [19], birds [20,21], fish [22], marine mammals [23], marsupials [13], and primates [24].

Beyond complicating species tree estimation, ILS has substantial implications for the interpretation of morphological evolution. Because ILS results in discordant genomic regions, traits controlled by genes located within these regions may not exhibit a simple correspondence with the species tree, leading to situations where phenotypic similarities are observed among species due to the retention and differential fixation of ancestral variants – a phenomenon described as **hemiplasy** [25]. In other words, traits that appear to have evolved convergently or as a result of **homoplasy** may instead be the product of **ancestral polymorphisms** that persist through ILS [25,26]. This is particularly critical for studies that attempt to map genetic changes directly onto traits; if the underlying gene trees are discordant, the inference of trait evolution can be confounded, thus misrepresenting the true evolutionary history. ILS not only alters the phylogenetic signal across the genome, but also directly influences phenotypic variation by affecting genes that contribute to specific morphological traits [13]. Functional experiments have established causal relationships between ILS-derived genetic variation and morphological diversity, further substantiating the idea that trait evolution may not adhere strictly to the bifurcating pattern implied by a simple species tree [13].

The evolutionary history of great apes exhibits conditions that are ideal for the persistence of ancestral polymorphisms, including rapid speciation events and large ancestral effective population

Glossary

Ancestral polymorphisms: gene variants that mutated before the divergence of the lineages in which the variants have segregated.
Appendicular skeleton: the skeleton of the limbs (i.e., the arms and legs) and the shoulder and pelvic girdles.
Bulk RNA-seq: a sequencing method that measures gene expression across cells or tissues, providing an averaged transcriptomic profile.
Coalescent hidden Markov model (CoalHMM): a method using hidden Markov models on genomic data to infer demographic history, divergence times, and ancestry.
Coalescent theory: a mathematical model that traces alleles back to a most recent common ancestor under parameters such as population size and divergence time.
Comparative genomic analyses: comparisons of genome sequences across species to identify differences in gene content and structure.
Convergent evolution: the independent emergence of similar traits in distantly related lineages due to similar selective pressures.
Craniofacial: pertains to the skull, jaw, and face.
Effective population size (N_e): the size of an ideal population experiencing the same genetic drift or inbreeding as the observed population.
Gene introgression: transfer of genetic material from one species to another through hybridisation and repeated backcrossing.
Genome-wide association studies (GWAS): analysis for mapping gene variants to associated traits or diseases.
Great apes: a primate family (*Hominidae*) comprising humans (*Homo*), chimpanzees and bonobos (*Pan*), gorillas (*Gorilla*), and orangutans (*Pongo*).
Hemiplasy: a pattern where shared traits result from ILS rather than convergent evolution or introgression.
Hominidae: the family of great apes including humans, chimpanzees, gorillas, and orangutans.
Hominins: extinct and extant human lineages after the split from the common ancestor with chimpanzees.
Homoplasy: the presence of similar traits in lineages not inherited from a common ancestor, but through convergent or parallel evolution.

sizes [10]. Additionally, their long generation times further exacerbate ILS by extending the period during which these polymorphisms can persist before allelic sorting is completed [12]. Genomic tools such as the **coalescent hidden Markov model** (**CoalHMM,** [27]) enable accurate quantification of such events at single-base-pair resolution, demonstrating extensive evidence of ILS across the human, chimpanzee, and gorilla lineages [12]. In the human genome, this approach revealed 7905 genes with coding regions that overlap with ILS-affected sites, supporting the ((HG)C) topology [12,28]. Of these, 2715 genes (34%) share at least one amino acid between human and gorilla that differs from chimpanzee. When examining noncoding regions within 10 kb of coding genes, up to 10 942 genes may be influenced by ILS. These genes are involved in various biological pathways that serve as substrates for phenotypic variation, likely generating conflicting evolutionary signals. Indeed, research indicated that genes with more ILS-affected sites tend to have similar expression patterns between human and gorilla, for example, loci involved in pathogen interactions like the major histocompatibility complex (MHC) and ABO blood group system [8,12]. However, immunity loci like the MHC region present a particular analytical challenge, as they are also a well-documented target of balancing selection across mammalian lineages which can maintain ancestral polymorphisms and produce phylogenetic patterns similar to those generated by ILS. Therefore, distinguishing between these processes requires careful integration of demographic modelling with tests for selection signatures.

Previous functional studies have focused on human-specific traits, revealing a wealth of similarities and differences with our closest living relatives including genetic, cellular, behavioural, musculoskeletal, and physiological modifications (see [14] for a review). These findings are often interpreted as signatures of adaptive selection to past conditions (e.g., [29]), with potential trade-offs in the modern world such as increased disease risk or osteoarthritis. Fewer studies have attempted to identify hominid **phenotypes** derived from other (non-adaptive) evolutionary scenarios, making now an ideal time to revisit phylogenetic discordance between morphological and molecular data within an ILS framework. Recent work has demonstrated the utility of simulation-based methods for evaluating the relative probability of hemiplasy versus homoplasy in specific trait systems [30], providing a quantitative foundation for distinguishing between these evolutionary scenarios.

The search for phenotypic patterns of ILS in hominids

Linking ILS-affected genes to hominid phenotypes has so far been challenging due to limited access to non-human tissue samples for functional studies [14,31]. In lieu of gene expression data for (non-human) hominid cell types, we present a trait-guided approach to explore the genetic basis of discrepancies between morphological variation and the speciation process. As a first step, we surveyed published studies of hominid phenotypes for the potential presence of ILS-affected traits, meaning those supporting divergence patterns other than (((HC)G)O) (see Box 2 for methods). We focus on African great apes given the low ILS found between humans and orangutans [10], although we acknowledge instances of hemiplasy between these lineages. We then propose a framework for validating potential ILS-affected traits that integrates comparative morphology, population genomics, and functional validation approaches. Finally, we illustrate how traits showing signatures of morphological hemiplasy may be aligned with candidate genes affected by ILS based on the highly annotated human genome. Following a similar approach, evidence of ILS in biological functions was recently shown for marsupials, in which hemiplasious morphologies (e.g., humerus curvature, vertebral shape, incisor pattern) established during rapid speciation were regulated by ILS-affected genes [13]. For example, ILS was identified in the locus *WFIKKN1*, controlling the activity of skeletal growth factor and vertebral patterning [32]. Stochastic sorting of the ancestral gene variant produced similar spinous process

Horizontal gene transfer (HGT): genetic transfer independently of reproduction.
Induced pluripotent stem cells (iPSCs): somatic cells reprogrammed to an embryonic stem cell-like state.
MorphoSource.org: an open-access repository of 3D biological data.
Organogenesis: the formation of organs during embryonic growth.
Phenotypes: observable traits of an organism shaped by genetic and environmental factors.
Phylogenetic discordance: disparities between gene trees and species trees due to processes such as ILS, convergence, or hybridisation.
Phylogenetic distance: a measure of evolutionary divergence between taxa based on genetic or morphological data.
Physical anthropology: the study of human biological evolution, variation, and adaptation.
Plesiomorphy: an ancestral character state retained in descendant lineages.
Single-cell RNA-seq: RNA sequencing performed on individual cells to study expression heterogeneity.
Single-nucleotide polymorphisms (SNPs): variants defined by a single base substitution at a specific genomic position.
Soft tissues: non-skeletal tissues, including muscles, tendons, ligaments, adipose tissue, fibrous tissue, and internal organs.
Solid tissues: dense, mineralised tissues such as cortical (the dense exterior layer) and cancellous (also known as trabecular bone, a porous, less dense type on the interior) bone types.
Synapomorphy: a derived trait shared by two or more taxa from a common ancestor.
Transgenic mice: laboratory mice engineered to carry inserted genetic material.

lengths of the thoracic vertebrae in Microbiotheria (monito del monte, *Dromiciops gliroides*) and phylogenetically distant diprotodontid marsupials, further validated by consistent phenotypic changes in **transgenic mice** [13].

Hominid morphological literature: new perspectives on old data

Hominid traits displaying signatures of phylogenetic incongruence occur throughout the body but tend to concentrate in bone and muscle tissue of the head, shoulders, hands, and feet (Box 2). Starting with the **craniofacial** region, hominid brains and eyes have been the focus of numerous studies. While humans have uniquely uniform white sclera (depigmented from the iris edge to eye corner), we share similar lens and corneal thickness with gorillas, as well as anterior chamber (lens to cornea) depth and globe dimensions [33,34]. Gorillas, bonobos, and orangutans exhibit similar iridoscleral contrast to humans [35,36], whereas chimpanzees resemble gibbons (family Hylobatidae, the outgroup to great apes) in ocular contrast and relative iris luminance (Figure 1, [37]). Greater exposure of white sclera is thought to have evolved in humans to amplify gaze direction; however, gorillas have been shown to display similar amounts of visible sclera but differ in external eye shape – humans' eyes are more horizontally elongated [38]. These studies question the uniqueness of the human eye and challenge the gaze-camouflaging hypothesis in non-human primates with darkly pigmented sclera, who may avoid potential aggression or conflict by concealing their gaze from dominant individuals or predators [39].

Moving to the **appendicular skeleton**, human shoulder blades appear closer to orangutans than chimpanzees, having broader and longer scapulae [40] (Figure 1), and similar glenohumeral abduction (arm raising) potential [41]. Humans and gorillas share extrinsic hand (thumb-to-fourth digit) proportions [42] (Figure 1) and morphology of the first metacarpal (hand bone leading to the thumb), which is significantly broader, straighter, and more robust than that of chimpanzees [43]. The first metacarpal is furthermore integrated with the trapezium (wrist bone) in humans and gorillas [44], while the wrist shows patterns of covariation between the capitate (wrist bone below middle finger) and lunate (central wrist bone) [45]. As with forelimbs, hindlimbs are one of the most researched areas in hominid comparative anatomy, with foot characters constituting

Box 1. Evolutionary events contributing to phylogenetic discordance

Several evolutionary scenarios can generate phylogenetic discordance with the speciation process (Figure I), with **convergent evolution**, **gene introgression** followed by hybridisation, **horizontal gene transfer (HGT)**, and ILS being frequently reported across taxonomic groups [13]. While the former three events are known to contribute to trait evolution and can lead to similar morphologies or biological functions in distantly related species [17], the phenotypic roles of ILS have so far been neglected.

As opposed to 'complete' lineage sorting in which ancestral polymorphisms neatly segregate into descendent lineages, 'incomplete' lineage sorting means that alleles assort randomly across successive evolutionary nodes. These polymorphisms may later be lost by genetic drift in some lineages and fixed in others, producing gene trees that do not accurately reflect species relationships [17]. If ILS occurs in coding or regulatory regions of the genome, the traits they encode are likely to be affected, resulting in conflicting evolutionary patterns. This stochastic fixation of alternative character states among descendent lineages, termed hemiplasy [25], can give the illusion of convergence or homoplasy in phylogenetic reconstructions, appearing as independently derived traits.

Genomic tools are being developed to distinguish these processes, including D-statistics and ABBA-BABA tests for detecting introgression, coalescent simulations for modelling ILS expectations, and phylogenetic network analyses for identifying reticulate evolutionary patterns [30,75]. For example, ILS can be distinguished from introgression through demographic modelling that incorporates migration rates, with introgression typically showing localised genomic signatures and deviation from neutral coalescent expectations; by contrast, ILS affects genome-wide patterns consistent with ancestral population structure. Convergent evolution produces similar phenotypes through independent mutations at different genomic locations, distinguishable from ILS by examining whether discordant gene trees involve homologous versus analogous genetic changes. HGT, while rare in mammals, typically affects single genes rather than genomic regions [25]. Balancing selection can be distinguished from ILS through signatures of elevated nucleotide diversity, reduced linkage disequilibrium, and skewed allele frequency spectra at affected loci, contrasting with the neutral patterns expected under ILS [76]. We note that these processes are not mutually exclusive – even highly adaptive traits may be influenced by the initial substrate of genetic variation that ILS provides for natural selection to act upon. Distinguishing between these scenarios in hominids will require large sample sizes to quantify intraspecific variation and rigorously test competing hypotheses underlying discordant trait patterns.

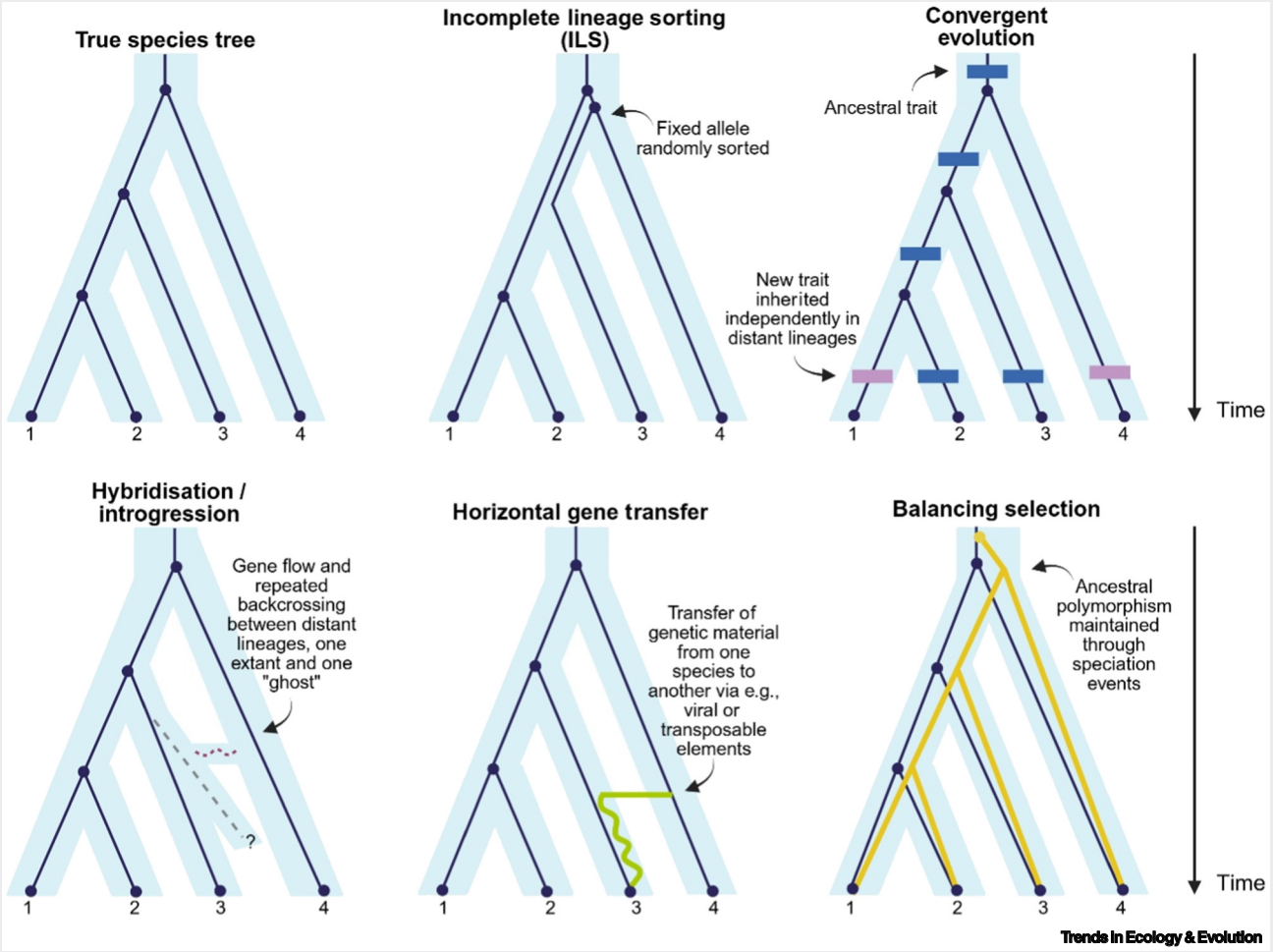

Figure I. Distinguishing patterns of phylogenetic discordance. In contrast to incomplete lineage sorting (ILS) which happens during species divergence, convergent evolution and gene flow via introgression or hybridisation occur after speciation, giving rise to superficially similar traits in distantly (convergence) or closely (hybridisation) related species. Introgression from contemporary or extinct 'ghost' lineages can reintroduce ancestral variation, inflating apparent ILS signatures. Horizontal gene transfer also differs from ILS in causing a gene tree that differs dramatically from the consensus phylogeny. Balancing selection preserves ancestral polymorphisms over extended periods, producing discordance that mimics ILS but reflects ongoing selective pressures rather than neutral drift. Figure created in BioRender.com.

one-fifth of all appendicular skeleton-related studies (Box 1 and Table S1 in the supplemental information online). The shape of the calcaneal, or heel bone, displays conflicting phylogenetic signals among great ape species, being more similar among humans and gorillas, or humans, chimpanzees, and orangutans, depending on size standardisation [46]. The fifth metatarsal, or foot bone leading to the outermost toe, overlaps in shape of the articular surface among humans, gorillas, and hylobatids [47], although there is substantial interspecific variation in the overall curvature of the toe bones. Notably, humans and gorillas share larger foot muscle dimensions (measured across 24 muscles), with less difference between bipedal humans and quadrupedal African apes than between the African apes and orangutans [48]. Similar phylogenetic conflicts are reported for features of the hip bones, in which the relative height of the human lower ilium overlaps with that of *Gorilla*, *P. paniscus*, and other primates, but not with *P. troglodytes* or *Pongo* [49]. Limbs, and especially feet, are heavily studied in hominid morphology as they are

key to understanding the evolution of bipedalism, as well as evolutionary trade-offs between grasping and walking [50,51].

Phenotypic comparisons of limb and girdle elements are commonly linked to locomotion, with non-human primates adapted to arboreal environments not shared by humans. Although adult gorillas have several features interpreted as adaptations to forelimb (hanging) suspension [41], active arboreal locomotion is exclusively restricted to juveniles, who, by age four, transition from placing the whole hand on the ground (palmigrade quadrupedalism) to predominantly knuckle-walking [52]. Orangutan suspensory (hanging) behaviour is also different from that of African apes, being fundamentally quadrumanous (all four feet acting as hands) climbers in the rainforest canopy, seldom walking on the ground [53]. By contrast, humans are the only hominid species to adopt habitual bipedalism, accompanied by increased precision gripping in the hand and loss of gripping capacity in the foot [48]. This variation in positional and locomotor behaviour often forms the basis of discussions on hominid traits, with unexpected patterns commonly explained as functional trade-offs, convergent adaptation, or **plesiomorphic** conditions. In fact, we found only one mention of ILS as a potential driver of phenotypic patterns (shape of the semicircular canals – fluid-filled tubes in the inner ear [54]), emphasising the novelty of this perspective in hominid morphological research.

Given the pervasiveness of ILS across hominid genomes (including bonobo [55]), these cases present a valuable opportunity to revisit comparative analyses for signatures of ILS-affected traits. While we acknowledge that the aforementioned studies were conducted in the context of other functional or evolutionary hypotheses (e.g., manipulation vs. locomotion capabilities), they provide tantalising evidence of phylogenetic discord warranting further investigation (see the later section 'The way forward in ILS research'). At the same time, they highlight outstanding gaps in hominid sampling, indicating areas where a more complete phylogenetic picture may be captured with little effort. In the following we discuss species contrasts and phenotypic regions that have received less attention in hominid comparative literature, with the hope that targeted sampling (and by extension, data sharing) will fill important gaps needed to distinguish between evolutionary processes underlying trait-species tree conflict.

Systematic biases in hominid morphological research

Comparative analyses of hominid morphology have historically focused on hard (skeletal, dental) tissues of the head and limbs, that is, craniofacial and appendicular skeletons, rather than the

Box 2. Interrogating the hominid morphological literature for signatures of ILS

To collect information on the comparative phenotypes of modern humans and their closest living relatives, we searched the Web of Science (WOS) database for all combinations of *Homo*, *Pan*, and *Gorilla* generic and common names (human, chimpanzee, bonobo, and gorilla), using the 'Search within results' option to return papers containing the terms anato*, morpho*, and/or shape*. We further restricted 'Document Types' to articles, review articles, and proceeding papers within the WOS categories: Anthropology; Evolutionary Biology; Anatomy Morphology; Multidisciplinary Sciences; Zoology; Genetics Hereditary; Biology; Biochemistry Molecular Biology; Geosciences Multidisciplinary; Paleontology; Behavioral Sciences; Archeology; Ecology; Geography Physical; Neurosciences; Physiology; Pediatrics; Imaging Science; Photographic Technology; Orthopedics; Biodiversity Conservation; Veterinary Sciences; Developmental Biology; Biophysics. This resulted in 2081 unique papers published from 1976 to 2025, which after assessing for relevance (i.e., qualitative and/or quantitative comparisons of two or more living hominid species), left 571 articles for evaluation of possible ILS-affected traits. Of those, we found 62 instances of morphological traits showing phylogenetic incongruence with the species tree reported over the past 50 years. See Tables S1 and S2 in the supplemental information online for the full literature list.

We identified systematic biases in hominid morphological analyses, regarding studied body regions, tissue types, taxonomic comparisons and sample sizes (Figure I). Over two-thirds (68%) of the 571 studies comparing two or more hominid species examined **solid tissues** (teeth and bone), while 29% focused on soft tissues like brains, muscles, and eyes (Figure IA). The remaining 3% examined both. Studies of both tissue types are increasing steadily over time studies, although soft tissue analyses are still under-represented (Figure IB). Roughly half (300 or 53%) of the papers compared all three African great ape genera, 216 (38%) compared *Pan* and *Homo*, while only 44 (8%) compared *Pan–Gorilla*, and 8 (1%) *Gorilla–Homo* (Figure IC). Studies also varied dramatically in sample sizes for each genus (Figure ID). For example, analyses ranged from musculoskeletal modelling of a single gorilla individual [41] or eye anatomy of two gorillas [33], to ~900 dried atlases (the topmost vertebra of the backbone [77]) and >1000 vertebrae of living hominids and other primates [78].

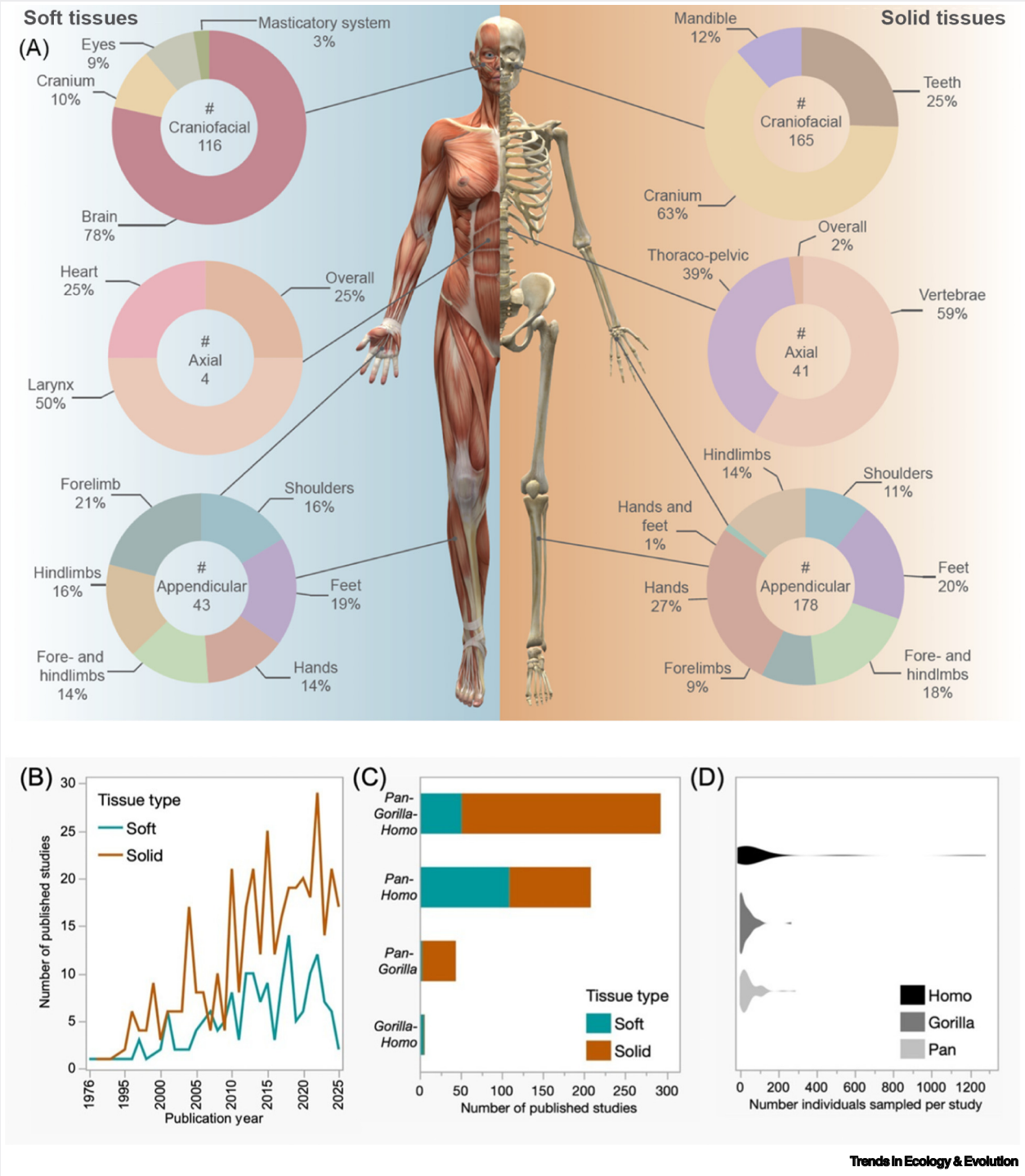

Figure I. Trends in hominid comparative morphological analyses. (A) Hominid studies have mainly focused on the craniofacial and appendicular skeletons while largely ignoring soft tissues of the trunk and head, except for the brain – which has been investigated increasingly during recent years. In both solid and soft tissues, the trunk region has been studied the least. Systematic biases were also recovered in (B) examined tissue types over time, (C) genus-level comparisons, and (D) sample sizes.

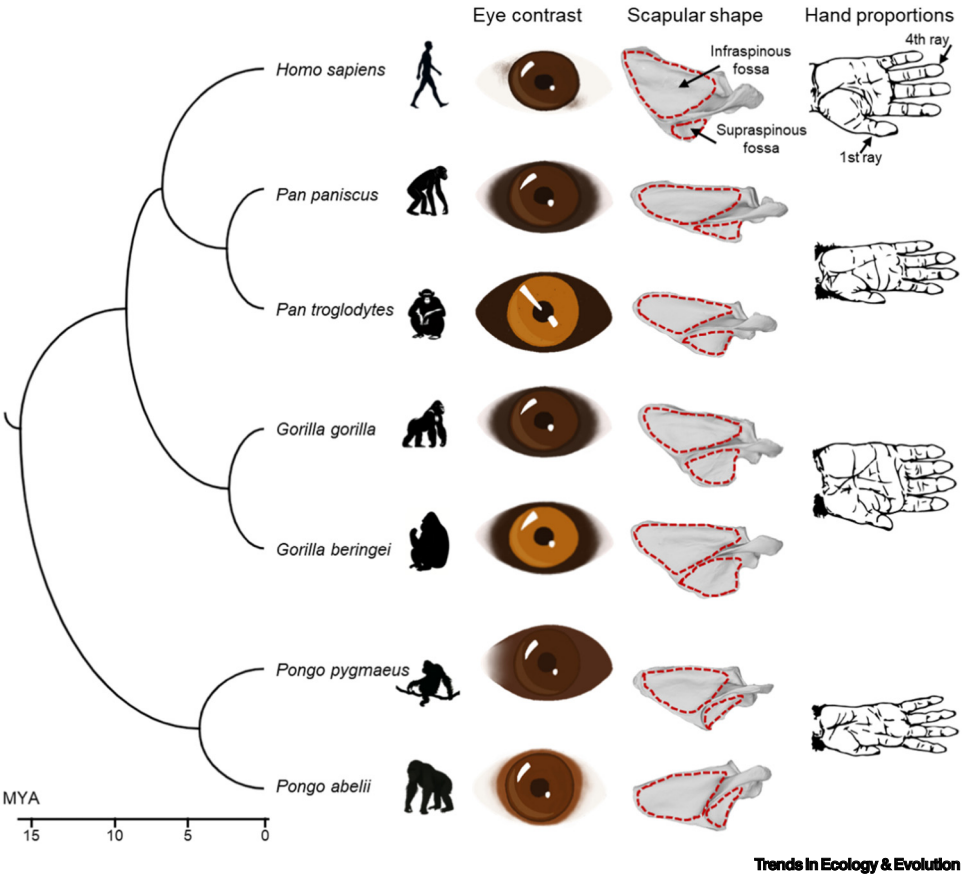

Figure 1. Examples of hominid traits in conflict with the species tree. Comparative studies have emphasised eye contrast, scapular (shoulder blade) shape, and hand proportions in hominids, with discordant patterns often interpreted as adaptations. For example, Sumatran orangutans (*Pongo abelii*), bonobos (*Pan paniscus*), and western gorilla (*Gorilla gorilla*) display similar patterns of ocular contrast to humans, although note that even pairs of species can have remarkably different eye colouration [35]. In the shoulder blade, scapular spine orientation and infraspinous fossa shape groups humans and orangutans, while whole scapular shape is more similar between humans and gorillas [40,79]. Likewise, human thumb-to-ring finger proportions most closely resemble those of gorillas, instead of our closest living relatives [42]. Eye drawings: Anupama Prakash [35]. Hand drawings: Sergio Almécija, redrawn from Schultz (1968) [80]. Tree generated by Timetree.org, note absence of *Pongo tapanuliensis*, for whom no data were available. Abbreviation: MYA, million years ago.

vertebral skeleton or **soft tissues** (Box 2, [56]). This disparity in focal traits is due to differences in preservation, as bones and teeth are easier to handle as dry, disarticulated material than 'wet' or intact specimens. That hominid teeth preserve exceptionally well also makes them frequent subjects in paleoanthropological comparisons because the enamel that covers the tooth surface is the hardest and most mineralised substance in the body. In addition to substantial regional biases favouring the head, hands, and feet, we found a strong bias towards species comparisons including human and chimpanzee.

Despite a rise in studies of both tissue types since the late 1990s, soft-tissue analyses remain less than half the number of those performed on the skeleton (Box 2), even within the same region (e.g., appendicular). The most frequent soft-tissue studies focus on the brain, facial muscles, and eyes, while the tongue, larynx, pectoral and upper limb muscles receive less attention (Table S1). These trends reflect the meta-analysis of Gibbs *et al*. [56], in which only 9% of the

1783 soft-tissue structures in great apes were found to be useful for phylogenetic analyses (i.e., with published data for all species, more than one character state per structure, and one state present in two or more taxa), themselves being biased towards the muscles and limbs. Most non-human hominoid soft-tissue studies target single organs or structures, or a single taxon – most commonly *Pan*, followed by *Gorilla* and *Pongo* [57].

Reasons for the aforementioned biases are well recognised in **physical anthropology** [58], in which restricted access to specimens, and the expertise and technology to study them, still presents major challenges. This is made more difficult for large, whole-bodied animals with preserved connective tissues such as muscle, fat, organs, and nerves. Advanced bioimaging techniques, such as magnetic resonance Imaging (MRI) or staining prior to X-ray computed tomography (CT) scanning, will therefore be required to visualise, quantify, and compare complex phenotypes related to these structures.

Filling the gaps – targeted sampling of endangered hominid phenotypes

Because we are unlikely to acquire new material from (critically) endangered hominids, we advocate for the nondestructive imaging of existing museum specimens, followed by open access to their digital data. Based on our literature review, we recommend that future digitisation efforts focus on filling persistent gaps in phenotypic sampling of non-human hominids, particularly in published analyses where one or more taxa are absent. Data sharing at this level (up to 100 GB per scan, with whole bodies often requiring multiple scans) was previously considered a technological limitation [59]. However open data frameworks and repositories (e.g., **MorphoSource.org**) now aim to democratise the process, aligning with increased attention in the anthropological sciences to CARE [Collective benefit, Authority to control, Responsibility, and Ethics (www.gida-global.org/)] and FAIR (Findable, Accessible, Interoperable, and Reusable [60]) data principles.

Fortunately, recent initiatives to curate open-access digital archives of hominid phenotypes are paving the way for this endeavour. For example, Almécija *et al*. [61] published 3D morphology data on MorphoSource for over 90 primate species (and their subspecies), representing all skeletal regions of the body with laser and structured light (surface) scans or CT. Human-fossil-record.org provides digital resources for the study of fossil and extant primate teeth and bones, including digital photographs, 3D surface models, and CT data for ancient humans and hominins. For modern humans, the New Mexico Decendent Image Database (NMDID) hosts whole-body CT scans and their associated metadata for over 15 000 individuals who died between 2010 and 2017. Together, these databases enable targeted searches for specific taxa, sexes, age groups, and body parts, facilitating designed experiments for explicit hypothesis testing.

In addition to reducing observed biases in hominid morphological research, improved attitudes towards open data serve to alleviate growing pressures on museum collections to host visitors and/or loan protected materials for study. While concerns about data access are frequent in fields where researchers compete over limited specimens, studies indicate substantial benefits to data sharing, even in physical anthropology [58]. The fossil *Homo naledi* discovered in 2013 is a prime example of open-access advantages, with over 30 publications based on its digital images receiving nearly 600 citations in 5 years – more than any other recently discovered hominin at the time [62]. Such global access to digitisation results is critical for local stakeholders in developing countries where hominid species originate (i.e., Borneo and Malaysia for *Pongo*, equatorial and West Africa for *Gorilla* and *Pan*), as they often lack the resources for digital imaging. Ideally, we can support research in these countries by

donating equipment such as portable CT and surface scanners and transferring the skills to use them.

As well as increasing sample sizes for understudied regions of the hominid body (see Box 2 for suggestions), we advocate for increased digitisation of outgroups beyond *Hylobates*, which is itself highly under-represented in soft-tissue data [56]. This digitisation may encompass various technologies (e.g., structured light, photogrammetry, MRI, CT) and downstream analyses, allowing systematic exploration of hominid phenotypes and their underlying evolutionary processes, including ILS. Only recently has it become possible to evaluate intraspecific variation in complex traits using explicit evolutionary models (e.g., extended phylogenetic generalised least squares, [63]), making now the ideal time to invest in expanded sampling. Following CARE and FAIR principles of data management for open-access will further ensure that the benefits to science, and society, outweigh the costs.

The way forward in ILS research – experimental validation

As mentioned earlier, approximately 2715 human genes comprise amino acids shared with gorilla to the exclusion of chimpanzee, and 10 492 human genes contain similar regulatory components as gorilla due to ILS. Understanding the phenotypic effects of these ILS-affected sites requires combination of multi-level data with cross-disciplinary approaches. Functional annotations for ILS genes and substitutions based on existing knowledge can help to narrow the search for potential candidate sites with significant effects on the phenotypes of interest. Several databases provide rich information related to gene function for select (model) species, including tissue expression patterns and their underlying molecular processes. **Genome-wide association studies (GWAS)** have identified numerous genes and **single-nucleotide polymorphisms (SNPs)** that are statistically associated with specific phenotypes in humans, such as physical traits, diseases and behaviours [64–66]. ClinVar [67] hosts data on the clinical significance of genetic variants, including loci in noncoding regions, while Online Mendelian Inheritance in Man (OMIM) [68] catalogues known human diseases related to genetic components. Similarly, the Mouse Genome Informatics (MGI) [69] database compiles extensive data for mouse mutant strains with phenotypic descriptions, providing valuable guidelines for phenotypic measurements in transgenic experiments. Recent advances in deep learning have significantly advanced the predictions of noncoding sequence functions, enabling systematic comparative analyses of gene regulatory elements across species [70,71]. Integration of these resources may help to infer the tissues or functions impacted by ILS through testable hypotheses on their phenotypic consequences.

In Figure 2 we present a roadmap towards validating candidate ILS-affected traits in hominids. We note that restricted access to tissues of endangered hominid species will require the use of experimental systems such as **induced pluripotent stem cells (iPSCs)** to study the *in vitro* formation of organs and tissues affected by ILS. Many studies have showed that the organoids derived from iPSCs produce structures and gene activity patterns that resemble the modelled organs [72,73], opening possibilities for investigating potential hemiplasy effects of ILS genes on organ development of great apes. For example, recent studies comparing cerebral organoids from humans and chimpanzees demonstrated proof-of-concept that these organoids represent a promising platform for a comprehensive examination of molecular alterations influencing human brain development and evolution [73,74]. Together, these approaches offer new avenues to experimentally test the contribution of genetic variants to complex traits and physiological processes. Despite the various limitations that *in vitro* organoid systems still face, tracing and comparing the **organogenesis** expressed by ancestral alleles may provide valuable insights into the phenotypic roles of ILS, and by extension offer renewed understanding of the evolution of many human, and hominid, traits.

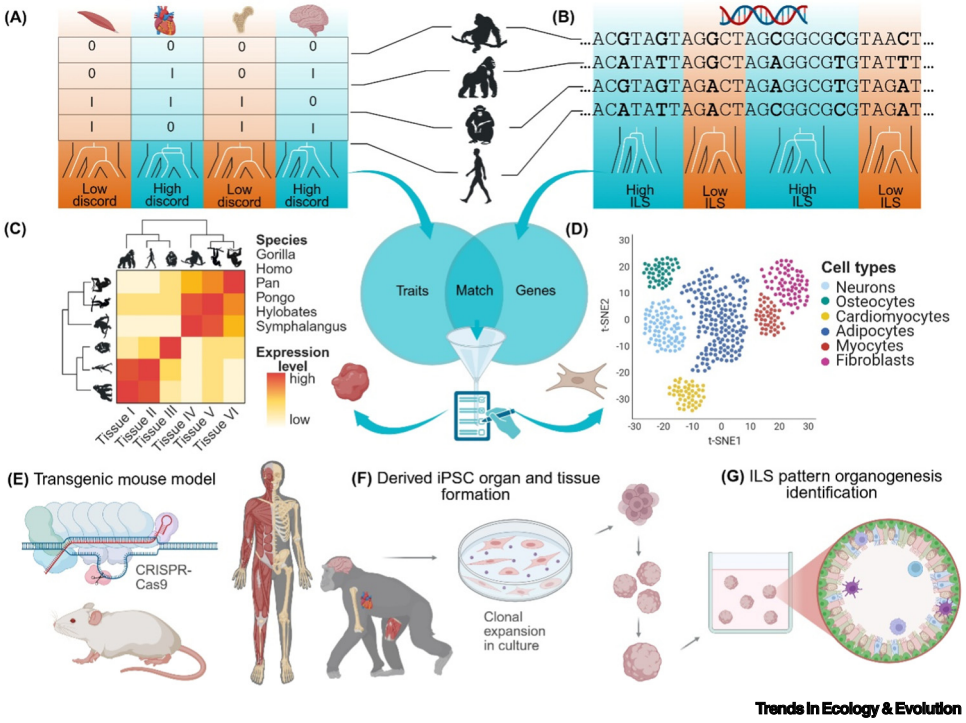

Figure 2. Theoretical roadmap for identification and validation of incomplete lineage sorting (ILS)-affected traits. (A) Evidence of phylogenetic discordance in hominid morphological studies guides identification of ILS-affected traits, potentially requiring additional phenotyping to fill sampling gaps. (B) In parallel, application of coalescent hidden Markov model (CoalHMM) [27] to aligned hominid genome sequences provides a list of annotated genes with high levels of ILS. Overlap between ILS-affected gene ontologies and discordant traits is used to further filter the list of candidate hemiplasies, based on matching annotations related to specific traits or tissues. (C) Comparative **bulk RNA-seq** or (D) **single-cell RNA-seq** on the tissue types enables direct inspection of evolutionary changes in orthologous gene expression patterns, providing expression profiling of the ILS-affected genes. (E) Because ILS involves ancestral alleles that stochastically persisted in descendant lineages, experimental systems like transgenic mice can be used to express phenotypes linked to the alternative ILS gene orthologs, for example, human–gorilla shared alleles versus those unique to chimpanzee. (F) **Phylogenetic distance** between mice and humans restricts this approach to conserved traits (e.g., skeleton, muscles, cardiovascular system); therefore, genetic modifications in organoids derived from induced pluripotent stem cells (iPSCs) provide necessary links between specific gene variants and complex traits, such as neural development. (G) Recent studies have established gene function comparisons in great apes using bioengineering tools like organogenesis. This approach enables *in vitro* study of organ and tissue formation, facilitating investigations of the phenotypic consequences of ILS in extant hominids. Figure created in BioRender.com.

Concluding remarks

Progress in linking ILS to hominid phenotypes depends critically on establishing collaborative models that bridge the gap between limited functional genomic data and morphological variation in non-human hominids. Priority initiatives should include international consortiums for non-destructive phenotyping using advanced imaging techniques, shared databases that integrate morphological and genomic data, standardised protocols for functional validation using model organisms, and targeted interdisciplinary collaborations between morphologists, genomicists, and computational biologists. Pilot studies of candidate loci affecting craniofacial development or limb proportions could provide proof-of-concept demonstrations, while organoids or transgenic model systems will enable mechanistic understanding. Addressing the outstanding questions will require distinguishing ILS from other evolutionary processes, developing efficient methods for linking phenotypic and genomic datasets, and determining whether ILS-maintained loci contribute to adaptive human traits (see Outstanding questions). Succeeding in these efforts will illuminate our

Outstanding questions

To what extent has ILS contributed to the phenotypic diversity observed in great apes? Additionally, how many previously identified human-unique features, when compared with chimpanzees, are also found in gorillas? While comprehensive data sets are becoming available for both phenotypic traits and the genes that encode them, we still lack methods for efficiently linking the two data types. This integration could determine the processes underlying discordance with the speciation process and facilitate the development of high-throughput pipelines (e.g., using artificial intelligence or AI) to identify the impacts of ILS in hominids and across the tree of life.

Does ILS play a role in the evolution of adaptive traits in humans, and are there ILS-affected loci that have been maintained by natural selection? For instance, immunity genes typically exhibit high genetic diversity both within and between species and are enriched in loci affected by ILS. Pathogen-driven balancing selection (e.g., heterozygote advantage) or positive selection may preserve these alleles over evolutionary time, enabling rapid adaptation to changing pathogenic threats. Identifying and characterising these ILS-maintained loci is crucial for understanding how deep-rooted genetic variation interacts with modern selective pressures to shape human health and disease.

Phenotypes are often influenced by multiple confounding factors, such as environment, epigenetics, and adaptation. How can we distinguish between the impacts of these on the phylogenetic incongruence of phenotypic traits? While these processes are not mutually exclusive, they occur during different timepoints during lineage diversification and leave distinct patterns in shallow versus deep-time phylogenies. Therefore, identifying subsets of the genome that reflect descent in the distant past can highlight regions possibly under ILS as opposed to more recent evolutionary processes.

own human history and the fundamental relationships between genomic and phenotypic evolution in closely related species.

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Declaration of interests

No interests are declared.

Supplemental information

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