PERSPECTIVE

doi:10.1038/nature25750

Dynamics of body time, social time and life history at adolescence

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Recent opposing trends towards earlier physical maturation and later social maturation present a conundrum of apparent biological–social mismatch. Here we use life history analysis from evolutionary ecology to identify forces that drive these shifts. Together with findings in developmental science, our life history analysis indicates that adolescence is a distinctive period for biological embedding of culture. Ethnographic evidence shows that mass education is a novel feature of the globalizing cultural configurations of adolescence, which are driven by transformations in labour, livelihood and lifestyle. Evaluation of the life history trade-offs and sociocultural ecologies that are experienced by adolescents may offer a practical basis for enhancing their development.

For humans, the second decade of life is often described as a period of turmoil roiled by biological and sociocultural forces. This tension is captured in the linguistic distinction between puberty and adolescence, where puberty refers to the suite of physical changes comprising the transition from immaturity to maturity, juxtaposed against adolescence, which refers to the sociocultural construction of that transition. Dynamics behind these two forces are incompletely coupled, creating the potential for complex interactions generated by degrees of synchrony or dyssynchrony between them. Indeed, ongoing trends of globalization are transforming the timing of adolescence on both fronts: physical maturation has been accelerating even as sociocultural thresholds for achieving adulthood are rising[1,2].

These trends are well-recognized[3], but their origins and effects remain underexplored, hindering attempts to promote better outcomes across the board for adolescents. Recent conceptual and empirical advances in evolutionary ecology and in developmental science offer insight into factors that are driving these shifts in both biological timing and sociocultural schedules. Within evolutionary ecology, life history theory has identified trade-offs behind biological and sociocultural factors that influence timing of puberty and the configuration of adolescence[4,5]. In developmental science, ongoing identification of synergies between context and biology[6] points to adolescence as a period for biological embedding of culture, and highlights the potential impact of alterations in bio-contextual alignments[7]. These convergent insights come at a crucial time, when promotion of emerging adolescent capacities and health is vital for future economic and social prosperity, especially given global demographic ageing[2].

Here we describe human life history strategy, the determinants of physical and sociocultural timing of maturation, and the grounds for biological embedding of culture. Subsequently, we review evidence for acceleration in the timing of biological maturation, and evaluate it in the light of life history theory. Next, we delineate the changing cultural configurations of adolescence by contrasting patterns of historical ethnographic records with recent globalizing trends, and consider them in terms of life history strategy and the concept of embodied capital (see below). Lastly, we discuss the implications of these fresh insights for assumptions regarding globalizing formations of adolescence, for tracking life history trade-offs in development, and for considering social ecology as an approach to better meet the diverse developmental needs of adolescents that will help them to build viable futures. Recognition of adolescence as a critical window for the biological embedding of culture emphasizes the need for attention to interactions between pubertal maturation and ambient socioecological configurations that shape the emergent social–emotional and psychobehavioural capacities of adolescents.

Life history, puberty and adolescence

Life history theory aims to account for biodiversity, from ants to zebras, in terms of allocation of limited resources (time, energy) across the life course[8]. The challenge is to use these resources to carve out and inhabit a niche that sustains survival and reproduction[9]. A life history strategy represents an evolved, species-characteristic design for partitioning available resources among competing life demands (growth, reproduction or maintenance (metabolism and repair)) in order to optimize fitness within its ecological niche. Limited resources impose trade-offs among competing demands, and evolved life history strategies establish priorities and set trade-offs among these demands. Neuroendocrine processes negotiate trade-offs in resource allocation at the physiological and behavioural level, and scaffold the architecture of life history[10]. The schedule of trade-offs structures the timing of events, such as weaning, puberty, first birth or death, and outcomes, such as adult size, rate of reproduction or longevity.

Humans occupy a flexible niche characterized by skill-, technology- and cooperation-based extraction and sharing of high-quality resources, environmental modification and cultural complexes that support these behaviours and social arrangements[11]. The corresponding human life history strategy is slow: juvenile provisioning and other resource-intensive conditions enhance early survivorship and extend life expectancy, thus promoting protracted investment in development. Two distinctive human life history features are particularly relevant for adolescence, namely maturational delay and reliance on learning and cultural transmission. The extended juvenile period between infancy and adolescence accommodates demands for the formation of embodied capacities, including brain development, learning and socialization[12], and relies on deferring puberty. Extended childhood and delayed puberty are established by neuroendocrine mechanisms that repress the activity of the hypothalamic–pituitary–gonadal (HPG) reproductive axis a few months after birth[10].

Consequently, a coordinated set of mechanisms is required to derepress the HPG axis and permit puberty to proceed[13]. These mechanisms are sensitive to the quality of the environment (nutrition and pathogen burden), which determines trade-offs between advantages of continued growth versus gains from the onset of fertility[14]. Timing mechanisms provide adaptive flexibility to align maturation and onset of fertility with

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ambient resources and risk. Accordingly, growth rates and timing of puberty respond to resource availability and demands as well as mortality risk, accelerating under good conditions and slowing under poor ones[15]. As a result, human growth and age at puberty exhibit marked plasticity, or reaction norms, defined as the range of phenotypes that are expressed by a given genotype across disparate environmental conditions[4]. Thus, height may differ among countries by as much as 20 cm[16], and median age at menarche has been found to vary by more than six years from affluent urban to remote horticultural populations[1].

The human reliance on learning and cultural transmission underscores the importance of the large human brain and particularly the expanded human cortex, which is considered to be the basis of the cognitive and socio-emotional capacities that underlie human sociality, culture and adaptation[17]. The human brain undergoes a distinctive developmental pattern of extremely rapid growth in infancy, slower sustained growth in childhood and a final burst of growth and reorganization during the second decade of life that is initiated in puberty[18]. Infancy and childhood are recognized as important periods for learning and culture acquisition. However, accumulating imaging studies demonstrating important brain maturational changes in puberty and adolescence suggest that another learning period occurs during puberty and adolescence, when pubertal hormones are activated and cortical and subcortical structures of the brain are remodelled[19]. The pronounced structural and functional changes during this period follow sexually dimorphic trajectories[20,21]. Longitudinal studies of brain development through adolescence document not only anatomical changes[22,23], but also rapid advances in functional connectivity among brain regions[20] and emergence of individually distinctive connectivity patterns that also follow a sexually dimorphic course[24].

Discovery of these processes has stimulated intense investigation of how pubertal changes interact with life circumstances to shape social, emotional and behavioural development. Notably, they also create the conditions for biological embedding of cultural ecologies. Structural reorganization of the brain has been tied to functional changes in cognitive, affective and social processing in adolescence, although regional differences in cortical maturation rates may lead to temporal asynchronies in maturation of cognitive capacities. Crone and Dahl[25] have argued that dynamic asynchrony enables flexible engagement of cognitive control that is attuned to the motivational importance of contextual cues, including the presence of peers, perceived awards and threats, and task priority. Attunement to social context creates the basis for local socio-emotional development and learning. For instance, brain-imaging studies show that, relative to adults, adolescents have a stronger central neural response to threat and reward stimuli[26], to social exclusion[27,28] and to peer-observed task performance[29]. They also have an enhanced capacity to process evaluative feedback and modify behaviour accordingly[30]. Pubertal hormones (particularly testosterone) have been linked to these shifts in attention and motivation[31]. The heightened sensitivity to context and social evaluation, particularly by peers[32], supports the idea that adolescence is a sensitive period for specific forms of sociocultural learning and the acquisition of skillsets that are needed to transition successfully towards adult roles[33]. Heightened contextual sensitivity enhances responsiveness to cultural constructions of the second decade that strongly shape the contexts in which neurodevelopment and learning take place.

These dynamics modulate the continuous acquisition of cultural competence. Learning from others is the principal means for culture acquisition, however, some people are better sources than others[34,35]. How can learners decide with and from whom to learn? Infants swiftly assimilate huge chunks of the dominant culture (language, gestures and social behaviours) in everyday settings, but expanding mobility and social contacts with age raise options for selective updating. Puberty initiates an intense period of updating cultural information as maturational processes open up new domains and capacities (for example, romantic love, sexuality, moral logics and self-identity), triggering acute quests for relevant models and guides for direction and navigation as new skills are built and possible selves explored. Anthropological studies of cultural transmission have identified selective attention as a potent mediator of differential learning or biased transmission[36]. Learning may be frequency-dependent, biased towards normative (conformist bias) or rare (novelty bias) features: the former favours risk reduction and cultural stability, and the latter facilitates niche construction[9,37]. Learning may also be person-dependent, and sensitive to prestige markers of social status or success. People with perceived prestige or dominance, for instance, command more visual attention in experimental and naturalistic settings[36,38].

Adolescent attunement to social contexts, sensitivity to feedback and peer learning biases all suggest that maturational processes equip and motivate selective social learning and culture acquisition by adolescents. Reciprocally, cultural regulation of learning opportunities, such as assignment to gender- or class-based roles and settings, powerfully shapes development and acquisition of cultural competence[39]. These dynamics tailor the fit of adolescents to local social realities, such as performance of gender or occupational roles, yet may generate or perpetuate disparities and constrain life chances at adulthood.

Analyses of human life history have also identified embodied capital as a key developmental outcome[40]. Mere physical growth and maturation are insufficient for viability. Functional capacities are required, such as strength, immune function or resilience, as well as knowledge and skills that include linguistic, social and productive skills that are essential for subsistence and cultural competence[5]. Therefore, embodied or somatic capital comprises both physical and functional capabilities, the bases for meeting life challenges and opportunities. Humans invest heavily in embodied capital, both through prolonged growth and maturation, and through intensive concomitant investments in acquiring the functional capabilities that are necessary for productive, reproductive and social viability (knowledge, emotion regulation, executive function and social skills)[11]. Parents, and society as a whole, track the forms of embodied capital that will be needed for future success, and accordingly adjust their investments as well as the constructions of adolescence, including timing and criteria for adulthood[41]. Notably, cultural allocation of opportunities to build embodied capital both support access to life chances and may foster inequality, on the basis of gender, class, geographic or other grounds.

In summary, adolescence represents a pivotal point in life history when somatic investments in growth and maturation are completed and resources are reallocated to reproduction. Reproduction, however, entails not only the production of offspring, but also requires years of skilled investments in parenting, and the creation of contexts for the survival and nurturance of the young (ecological inheritance)[9]. Therefore, adolescence is a crucial period for generating embodied capital and not only in terms of reproductive or productive capacities, but also via pubertal processes that promote cultural embedding by preparing adolescents for context-sensitive formation or honing of socio-emotional skills and networks that are essential for their own and their future offsprings' survival.

Changes in the timing of physical maturation

Recent population changes match life history predictions, attest to wide reaction norms for growth rates and timing of puberty, and support their potential adaptive life history role in adjusting maturational timing to current environmental conditions[10]. In contrast to the obvious physical manifestations of puberty, such as growth or menarche, the underlying physiological processes are not easily analysed. Physiologically, puberty comprises a suite of changes that are orchestrated not only by the reproductive axis via gonadal steroids but also by adrenal, metabolic and other contributory factors[42]. Both casual and scientific assessments of pubertal timing and progress commonly rely on observable phenomena such as breast development, accelerated height gain or voice change[43–45]. Detectable signs of puberty can cue social and personal responses, whereas invisible albeit 'real' underlying conditions, such as gamete production, cannot. Menarche exemplifies this disjunction: an arresting and memorable event, it commonly acts as a marker of reproductive maturation, yet does not correspond to the first ovulation much less to established ovarian cyclicity[46]. Conversely, the absence of an equivalent

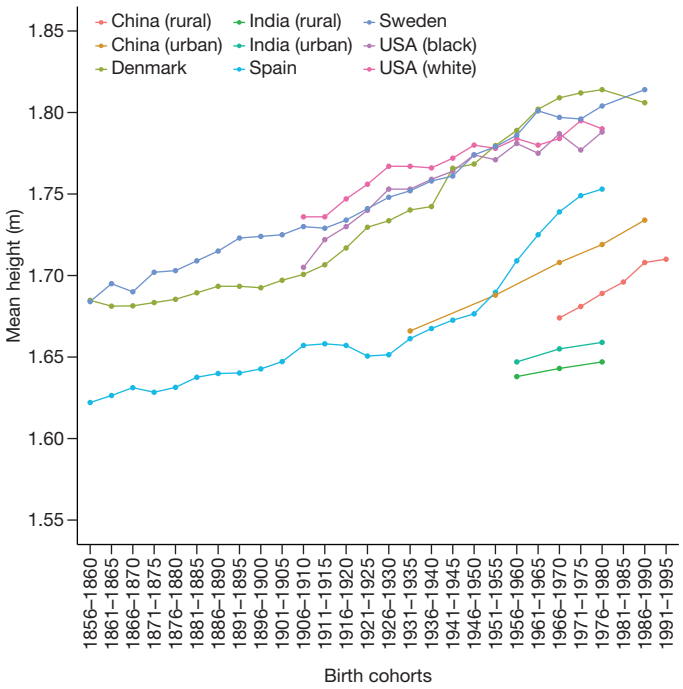

Figure 1 | Secular trends in male height. Drawn from data in ref. 97.

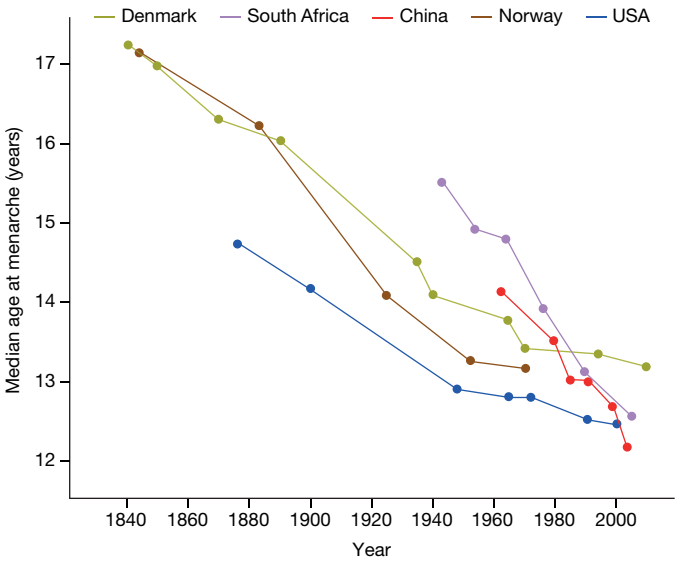

Figure 2 | Secular trends in age at menarche from first year of survey collection. Drawn from data in refs 50 and 98.

marker contributes to the more limited understanding of pubertal timing and variation among males.

Secular trends to increasing height and decreasing ages at menarche were first detected among European populations in the early nineteenth century[47] (Figs 1, 2). Declines were pronounced: median age at menarche decreased from over 17 to under 14 years among Norwegians from 1840 to 1940, for example. Subsequently, decreasing ages at menarche have been widely observed, but the timing and pace have varied among populations: decreases have proceeded more swiftly where they have occurred more recently[48,49], and appear to plateau around a median age of 12.5–13.5 years[50,51]. Continuing widespread acceleration in the onset of breast development (thelarche) contributes to perceptions that age at puberty continues to decrease, but appears to be dissociated from HPG activation and menarche, and may respond to environmental disruptors[52].

Tracking secular trends in male pubertal development has been complicated by the paucity of equivalent population studies and the use of indirect indicators, such as growth velocity, first seminal emission, voice break and risk-taking behaviour, that represent different aspects of puberty[44,45,53,54]. Studies that specifically examined pubic hair (pubarche) and testicular (gonadarche) development in boys have produced mixed results[55,56]. Nevertheless, clear secular trends to earlier peak height velocity in puberty and increased height for age are reliably documented among males and females[57,58]. Gonadal steroid hormones have crucial roles in accelerated growth at puberty, suggesting that the secular growth trends observed in boys, and girls, correspond to secular trends in gonadal activity that stimulate height gains[59].

Causes of accelerated growth and maturation have been intensely investigated. The speed of change rules out genetic bases; rather, the quality of early environments (and in particular nutrition), health and, to a lesser degree, psychosocial stress consistently emerge as major factors[60]. Accelerated growth and timing of puberty have followed the rise of public health measures, improved nutrition and effective maternal–child health care as they have (or have not) spread through populations around the globe[61,62]. Indeed, so tight is this association, that height for age is widely used as a cumulative indicator of environmental conditions[63], including socioeconomic disparities within populations that are commonly reflected by urban–rural differences[64].

Factors that influence the pace and timing of maturation act cumulatively. The greatest sensitivity to resource availability occurs during the period of very rapid growth and development in gestation and the first two years, when poor nutrition and effects of illness have the highest impact. Poor conditions influence body mass and metabolic rate, which determine energetic resources that are available for future growth and reproduction. They also signal poor future conditions and increased mortality risk, acting as cues to adjust life history strategy towards later maturation[65]. For instance, among Filipino men in the Cebu longitudinal health and nutrition survey, weight velocity in the first six months after birth, a proxy for nutritional and growth environment, predicted ages of sexual maturity and initial sexual activity as well as markers of physical embodied capital, such as height at age 22[66]. Moreover, intervention can shift life history outcomes: a controlled study in Guatemalan villages found that supplementation of undernourished infants increased growth and accelerated reproductive milestones, while also improving later function and health, educational and cognitive outcomes, and adult income[67].

Such adjustments in life history are mediated by neuroendocrine processes that bring about trade-offs in resource partitioning. Timing of puberty is the most obvious example, and the psycho-behavioural dimensions of the hormonal changes associated with differences in pubertal timing merit attention. For example, Filipino men with higher infant weight velocity in the above study also had higher testosterone levels as young adults[66]. Testosterone variation among these men was, in turn, associated with mating effort, marital status and parenthood[68]. Increased production of gonadal steroids and adrenal androgens is a consistent, but frequently overlooked, correlate of accelerated maturation, and is associated with good early health and nutrition[10,15]. Therefore, the exposure to steroids of early maturing individuals is both earlier and more intense, adding to the potential impact of secular trends to earlier puberty. Although the reproductive health consequences have been widely discussed[15], current studies that relate pubertal hormones to brain development and behaviour would benefit from exploring those possible correlates in cognitive outcomes through comparative work[69].

Given human sociality and interdependency, psychosocial stress also signals poor environmental quality and informs life history via a neuroendocrine signature that alters stress vulnerability and reactions[70]. The hypothalamic–pituitary–adrenal (HPA) axis regulates stress responses and appears to antagonize HPG activity in healthy adults (stress signals the need to invest in survival, rather than in reproduction). It also partially regulates adrenal androgen production, which undergoes distinctive changes across the life course, including increases that are integral to puberty[10]. Nevertheless, emerging evidence suggests that the conditional coupling of HPA and HPG activity shifts during development[42,68]. Exposure to early life stress may perturb the developmental course of

HPG and HPA coupling[71] and contribute to early sexual maturation and accelerated life histories (that is, early maturation and early reproduction) observed among females exposed to high psychosocial stress[72]. Whether there are secular trends in HPA reactivity or HPA–HPG coupling is not known.

To summarize thus far, adolescence reflects the distinctive life history strategy of humans that includes a long childhood and delayed puberty. Moreover, growth and pubertal timing are sensitive to environmental quality (nutrition, health, socioeconomic status and psychosocial stress), displaying developmental reaction norms that are reflective of adaptive capacities for adjustment to current and anticipated resources. Recently, human populations have undergone marked shifts or secular trends in maturational milestones and, by inference, their underlying physiology. These secular trends are uneven within and across populations, and are related to the changing material and social conditions under which development occurs. Such changes illustrate biological embedding in which conditions experienced during development are embodied in both physical and functional outcomes. Next, we discuss the patterns in the cultural configurations of adolescence that shape those conditions.

Cultural constructions of adolescence

Societal changes over the last 200 years have not only altered the conditions for physical development and thus shifted the timing of maturation, but also moved from localized to globalized constructions of adolescence that have redefined the experience of the adolescents. Effects of the rise in schooling and the related globalization of life course schedules are often discussed, but the longer history of diverse, localized cultural formations of adolescence receives less attention. Both are important for the present discussion about relative shifts in biological and cultural timing in life history during the second decade. The cross-cultural comparative literature provides systematic analyses of primary ethnographies to derive general patterns in now mostly historical cultures[73], offering a comprehensive overview with historical depth for considering contemporary formations of adolescence.

Here we draw on descriptive statistics derived from the standard cross-cultural sample (SCCS), comprising ethnographies of 186 preindustrial societies representing optimally independent culture regions (details can be found in refs 74 and 75). Ethnographic material in the SCCS has been rigorously coded on hundreds of variables, including many related to adolescence[76]. Limitations of ethnographic literature for comparative analysis are widely debated[77]. However, our present purposes are not comparative but descriptive, concerned with the distribution of practices that are documented in the record. Although most ethnographies are not focused on adolescence per se, two factors have prompted systematic documentation of this period of life: firstly, the interest of anthropologists in cultural configurations of the life course[78]; secondly, the emphasis on comprehensive description. Consequently, information using nominal coding (present or absent) of defining features of adolescence is sufficient for nearly the entire sample. Establishing the chronology of life events is confounded by the unavailability of chronological age, but as noted previously, in these settings societal responses are cued by the physical signs of puberty. Thus, ethnographic data have been coded for timing of intervention in relation to recognition of initial signs of puberty[79].

Social adolescence appears to have been prevalent, yet both differentiated by gender and widely varied in importance and content among preindustrial societies in the SCCS[80] (Table 1). Unsurprisingly, entry into adolescence in most societies coincided with recognition of puberty, and the transition was often ritually marked in some manner. Over half (56%) held formal initiation ceremonies for either or both sexes, which ritually effected the transition from childhood and instigated a total social transformation encompassing most to all aspects of social life, rather than targeting single aspects (for example, graduation or confirmation)[81]. Initiation ceremonies universally were gender-segregated for initiates, and generally coordinated more closely with physical maturation (onset of menarche) in girls than in boys, who lack a similarly distinct marker. Notably, construction of adolescence as a social condition does not require a specific term for 'adolescence', which was present in only a minority of the relatively small number of societies for which specific information is available. Markers distinguishing adolescents from children need not be linguistic; rather, most societies had distinctive visual markers of adolescence in hairstyle, dress, painting or tattoos, or adornments, whether or not a ritual was held. Visible markers distinguishing adults from adolescents were less common, albeit not rare, suggesting a greater social salience for demarcating childhood from the maturational cascade initiated by puberty[79].

Table 1 | Cultural constructions of adolescence

	Females	Males
Start of adolescence relative to puberty*	Percentage of societies	
Before	17	28
At	82	72
After	1	0
Transition ritualized†	79	68
Formal initiation ritual‡	46	36
Term for adolescent§	41	35
Markers child versus adolescent‖	88	86
Markers adolescent versus adult¶	35	32
Partner choice#	50	57
End of adolescence relative to puberty**		
Early (<2 years)	63	31
Medium (2–4 years)	25	35
Late (>4 year)	12	35
Young-adult stage present††	20	25

Data are from the standard cross-cultural sample ($n = 186$). Puberty is defined as menarche for females (14 if age unspecified); spermarche for males (16 if age unspecified). Number of societies for which the variable could be coded are given in parentheses. Sum of percentages may differ from 100% owing to rounding.
*In societies marking adolescence, onset is based on changes in behaviour or treatment relative to puberty ($n = 182$)[79].
†Ritualized behaviour (formal/public or other) that signifies the childhood–adolescence transition ($n = 130$)[81].
‡Adolescent initiation ceremony ($n = 182$)[99].
§Presence of term for adolescence that is applied to all young people ($n = 41$)[79].
‖Adolescents are differentiated from children by visual markers (dress or ornamentation) ($n = 118$)[79].
¶Adolescents are differentiated from adults by visual markers (dress or ornamentation) ($n = 118$)[79].
#Adolescent has some say as to whether marriage choice occurs in adolescence.
**End of social adolescence, relative to puberty. Girls: early indicates early–mid teens; mid indicates mid–late teens; late indicates late teens–age 20. Boys: early indicates around mid-teens; mid indicate late teens, late indicate early 20s. ($n = 178$)[79].
††Move from adolescence to full adulthood is not direct; a youth phase is included ($n = 168$)[79].

Daily lives of adolescents in these societies were fully integrated into ongoing subsistence activities, and same sex adults commonly dominated their everyday social worlds (66% of SCCS societies for males, 86% for females in 160 and 161 cases, respectively)[79]. Learning occurred informally, mostly through observation and participation with adults, from infancy onward[82], although initiation rituals often included instruction[78]. Therefore, very few societies practiced formal schooling[80], although parents and high-skill mentors might engage in active teaching[83]. Marriage, or socially recognized partnering, usually occurred fairly early, within two years after menarche for girls in their mid to late teens and slightly later for boys, and brought closure to adolescence, with an even distribution as to whether young people had a say in partner choice. Although rapid passage through adolescence to marriage and adulthood was most common, some societies recognized a stage of young adulthood between adolescence and adulthood.

Viewed comprehensively, evidence from preindustrial societies suggests continuities and contrasts with the globalizing contemporary configurations of adolescence. Social adolescence is not a modern innovation, although contemporary formations may be novel; adolescents then and now display distinctive visual markers, and transitions into and out of this period are culturally marked and managed. The radical innovation is compulsory universal schooling[84] (Fig. 3a). Schooling arose along with reliance on chronological age, a shift to peer-dominated settings, and adoption of an education-based wage labour economy, with a concomitant reduction in adolescent productive roles and subsistence activities, and of society-wide initiation rituals[85]. Moreover, schedules

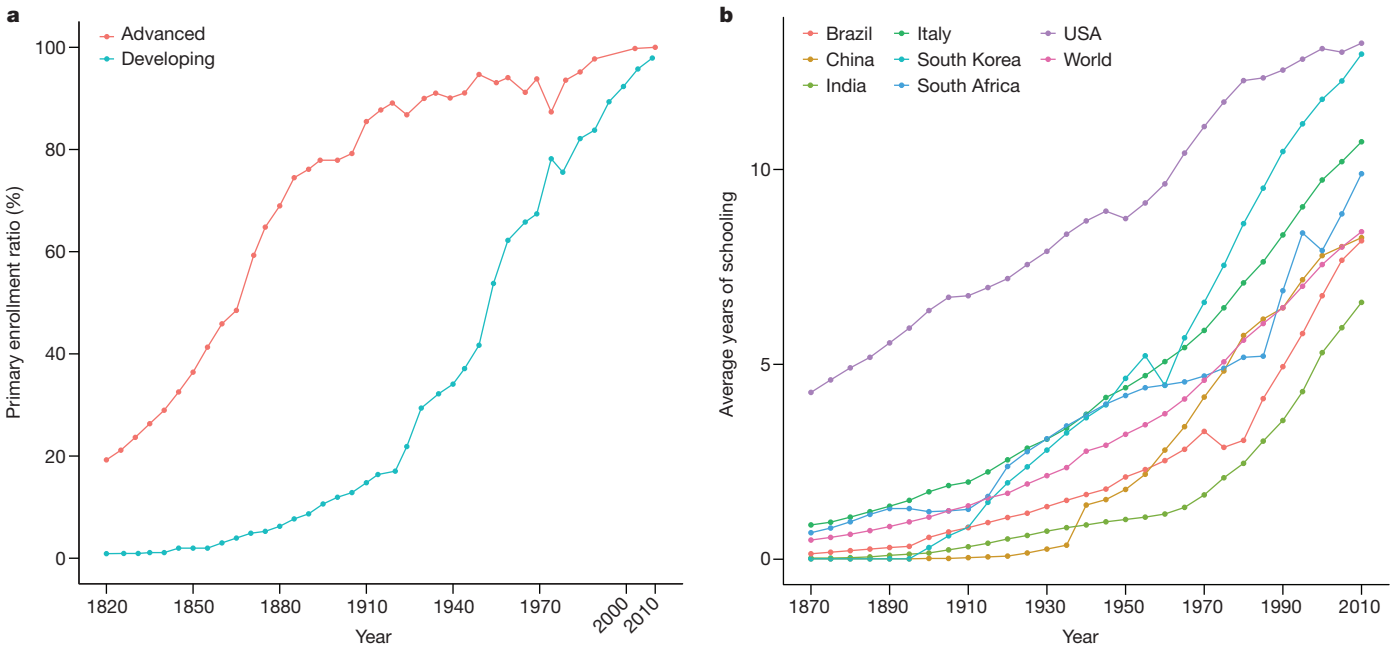

Figure 3 | Trends in education for 1820–2010. a, Trends in primary enrolment ratios (percentage of students enrolled in primary school relative to total primary school-aged population), by 'advanced' and 'developing' economies for 1820–2010. Advanced economies include: Austria, Canada, Japan, Oceania, Turkey, United States and Western Europe. Developing economies include: Asia and the Pacific, excluding Japan; Eastern Europe; Latin America and the Caribbean; the Middle East and North Africa, excluding Turkey; and Sub-Saharan Africa. **b**, Trends in total years of schooling. Drawn from data compiled in ref. 84.

of adolescence have been standardized to progression through school, and prolonged by expanding prerequisites for adulthood that include school completion, gaining employment or an economic foothold, and establishing independence, with a consequent delay in marriage. Unemployment, absent as a category in the preindustrial sample, today affects one in eight youths (over 73 million, three times the number of adults)[86]. Between the years 1970 and 2005, global age at first marriage increased by nearly 6 years in women and 5 years in men[87]. Recognition of a young adult stage (roughly between the age of 18 and 25) has become widespread along with rising thresholds of social criteria for adulthood and uncertainty of attaining them[88].

Why did the global, unprecedented adoption of mass schooling occur? Although abundant social, political and economic rationales motivate mass schooling projects[89], from a life history perspective, formal education represents intensifying investments in functional embodied capital. Changes in survivorship, health and forms of production and prestige prompt facultative adjustments in life history that propel sharply escalating investments in specific forms of functional embodied capital encouraged by schooling[40]. Reduced early mortality and greater life expectancy have increased potential returns from education as labour markets track changing modes of production that reward education- and skill-based embodied capital[5,90]. Accelerated growth and maturation from availability of increased resources for physical embodied capital have converged with pressure for increased investment in functional capacities to greatly expand the window for embodied capital formation at adolescence indexed by an increase in the number of years of schooling[40] (Fig. 3b). The vicissitudes of economic development combined with rising numbers of educated adolescents reinforce competition for employment and a qualifications arms race[91]. Escalating employer demands for labour with novel skills and an education-based capacity for flexibility exacerbate youth unemployment rates, strengthen competition and expand uncertainty and inequality[92,93]. Furthermore, the perception of spiralling demands for investments in embodied capital and related cost of children has been linked to ongoing changes in reproduction and parenting that contribute to widespread fertility declines in the demographic transition[94,95]. These dynamics have remodelled childhood, adolescence and early adulthood.

In summary, cultural formations of adolescence in preindustrial societies differed widely but commonly recognized an adolescent phase that began with signs of puberty and concluded with partnering or marriage. Adolescents usually experienced rites of passage, frequently bore distinctive markers, pursued subsistence tasks in adult-dominated domestic settings, and passed on to marriage and/or adulthood fairly promptly. The rise of compulsory formal education recast adolescent cultural ecology, as defined by chronological age, removed from cooperative domestic productive tasks, installed in competitive peer-dominated settings, and prolonged by educational demands. In life history terms, this considerable shift represents intensifying investment in specific forms of functional embodied capital that education aims to instil. Motivating these changes are structural transformations in labour, livelihood and lifestyle that require specific attitudes, capacities and skills that the young will need for viable futures.

Outlook on strengthening adolescent outcomes

Recent much-discussed shifts in the pace of physical maturation and the cultural formation of adolescence can be explained in life history terms as responses to improved environmental quality on the one hand, and intensifying investments in embodied capital on the other. An apparent discrepancy between biological and cultural processes turns out to represent responses from a shared suite of evolved life history adaptations. Although we describe adolescence from a broad perspective, focusing on population trends that omit variation within and between them, the reality is more complicated. Environmental factors that drive secular trends for physical development also drive within-population variation along urban–rural, socioeconomic, regional or ethnic lines[1]. The well-recognized sources of these differences in physical growth and maturation are targets for policy and intervention from local to global levels that are aimed primarily at infancy and childhood. Yet the distinctive needs of adolescents for promoting their crucial maturational agendas, including growth, reproduction, immune function, cognition and emotion regulation, are only just coming into focus and represent important windows of opportunity to enhance physical embodied capital[2]. As policy and intervention take up this challenge, adolescents as a whole should benefit and inequalities in physical embodied capital should be reduced.

Concurrently, uptake of schooling as a primary means for formation of functional embodied capital aims to foster life chances and mobility to opportunity, yet it also opens new sources of inequality and marginalization that erode the value of this strategy for many[8]. The great gains in average years of schooling (Fig. 3b) still show persistent regional differences, and mask underlying disparities in access (costs and barriers) and quality (teachers, facilities and schooling systems) that generate educational inequality in both years attained and benefits obtained[96]. Furthermore, the relationship between such inequality and gender gaps in education has strengthened with time. Family resources and capacities interact with schooling access and quality to reinforce existing local inequalities in life chances.

Life history analysis of how ecological factors drive cost–benefit tradeoffs that motivate parent and youth investments in embodied capital may inform approaches to these challenges[40]. Such analysis of parental behaviour has shown that inequality drives status competition and intensifies investments in locally valued markers of child quality, such as education or heritable wealth, but the effect collapses when such investments are not possible or will not benefit outcomes[95]. This finding suggests that reductions in educational and economic inequality will increase school participation and performance more effectively than the reverse, as is more commonly assumed[89,96].

In closing, we highlight that context-sensitive maturational processes at adolescence amplify effects from sociocultural ecology and generate special opportunities for biological embedding of culture. This raises the stakes for understanding the ecologies of adolescence, including formal schooling, particularly given current worldwide sociocultural shifts at local to macro levels. As knowledge about ecodevelopmental dynamics continues to accumulate, developmental science is globally expanding, as researchers take up the challenge to investigate a much wider range of human diversity. These exciting advances are stimulating a period of intensifying research and application that promises to vigorously promote adolescent welfare and capability under the diverse local realities that they inhabit within a fluid, globalized world.

Received 14 November 2017; accepted 15 January 2018.

1. Eveleth, P & Tanner, J. *Worldwide Variation in Human Growth* 2nd edn (Cambridge Univ. Press, 1990).
2. Patton, G. C. *et al.* Our future: a *Lancet* commission on adolescent health and wellbeing. *Lancet* **387,** 2423–2478 (2016).
   This comprehensive report thoroughly substantiates the need to invest in adolescents.
3. Worthman, C. M. in *Evolutionary Medicine* (eds Trevathan, W. R. *et al.*) (Oxford Univ. Press, 1999).
4. Stearns, S. C. & Koella, J. C. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* **40,** 893–913 (1986).
5. Lancaster, J. B. & Kaplan, H. S. in *Human Evolutionary Biology* (ed. Muehlenbein, M. P.) 439–455 (Cambridge Univ. Press, 2010).
6. Byrge, L., Sporns, O. & Smith, L. B. Developmental process emerges from extended brain–body–behavior networks. *Trends Cogn. Sci.* **18,** 395–403 (2014).
   This report offers a dynamic systems account of cognitive–behavioural development.
7. Sawyer, S. M. *et al.* Adolescence: a foundation for future health. *Lancet* **379,** 1630–1640 (2012).
8. Stearns, S. *The Evolution of Life Histories* (Oxford Univ. Press, 1992).
   This foundational text details principles and applications of life history theory.
9. Laland, K., Matthews, B. & Feldman, M. W. An introduction to niche construction theory. *Evol. Ecol.* **30,** 191–202 (2016).
10. Worthman, C. M. in *Hormones, Health, and Behavior: A Socio-ecological and Lifespan Perspective* (eds Panter-Brick, C. & Worthman, C. M.) 47–104 (Cambridge Univ. Press, 1999).
11. Hill, K. & Kaplan, H. Life history traits in humans: theory and empiricial studies. *Annu. Rev. Anthropol.* **28,** 397–430 (1999).
12. Kuzawa, C. W. *et al.* Metabolic costs and evolutionary implications of human brain development. *Proc. Natl Acad. Sci. USA* **111,** 13010–13015 (2014).
13. Livadas, S. & Chrousos, G. P. Control of the onset of puberty. *Curr. Opin. Pediatr.* **28,** 551–558 (2016).
14. Bateson, P. & Gluckman, P. Plasticity and robustness in development and evolution. *Int. J. Epidemiol.* **41,** 219–223 (2012).
15. Jasienska, G., Bribiescas, R. G., Furberg, A. S., Helle, S. & Núñez-de la Mora, A. Human reproduction and health: an evolutionary perspective. *Lancet* **390,** 510–520 (2017).
16. NCD Risk Factor Collaboration (NCD-RisC). A century of trends in adult human height. *eLife* **5,** e13410 (2016).
17. Stout, D. & Hecht, E. E. Evolutionary neuroscience of cumulative culture. *Proc. Natl Acad. Sci. USA* **114,** 7861–7868 (2017).
18. Silbereis, J. C., Pochareddy, S., Zhu, Y., Li, M. & Sestan, N. The cellular and molecular landscapes of the developing human central nervous system. *Neuron* **89,** 248–268 (2016).
19. Romeo, R. D. Puberty: a period of both organizational and activational effects of steroid hormones on neurobehavioural development. *J. Neuroendocrinol.* **15,** 1185–1192 (2003).
20. Paus, T. *et al.* Sexual dimorphism in the adolescent brain: role of testosterone and androgen receptor in global and local volumes of grey and white matter. *Horm. Behav.* **57,** 63–75 (2010).
21. Koolschijn, P. C. M. & Crone, E. A. Sex differences and structural brain maturation from childhood to early adulthood. *Dev. Cogn. Neurosci.* **5,** 106–118 (2013).
22. Asato, M. R., Terwilliger, R., Woo, J. & Luna, B. White matter development in adolescence: a DTI study. *Cereb. Cortex* **20,** 2122–2131 (2010).
23. Tamnes, C. K. *et al.* Brain maturation in adolescence and young adulthood: regional age-related changes in cortical thickness and white matter volume and microstructure. *Cereb. Cortex* **20,** 534–548 (2010).
24. Kaufmann, T. *et al.* Delayed stabilization and individualization in connectome development are related to psychiatric disorders. *Nat. Neurosci.* **20,** 513–515 (2017).
25. Crone, E. A & Dahl, R. E. Understanding adolescence as a period of social-affective engagement and goal flexibility. *Nat. Rev. Neurosci.* **13,** 636–650 (2012).
    This review tracks important changes in social-affective processing during adolescent neurocognitive development.
26. Galván, A. & McGlennen, K. M. Enhanced striatal sensitivity to aversive reinforcement in adolescents versus adults. *J. Cogn. Neurosci.* **25,** 284–296 (2013).
27. Silk, J. S. *et al.* Increased neural response to peer rejection associated with adolescent depression and pubertal development. *Soc. Cogn. Affect. Neurosci.* **9,** 1798–1807 (2014).
28. Gunther Moor, B. *et al.* Social exclusion and punishment of excluders: neural correlates and developmental trajectories. *Neuroimage* **59,** 708–717 (2012).
29. Chein, J., Albert, D., O'Brien, L., Uckert, K. & Steinberg, L. Peers increase adolescent risk taking by enhancing activity in the brain's reward circuitry. *Dev. Sci.* **14,** F1–F10 (2011).
30. van Duijvenvoorde, A. C. K., Zanolie, K., Rombouts, S. A. R. B., Raijmakers, M. E. J. & Crone, E. A. Evaluating the negative or valuing the positive? Neural mechanisms supporting feedback-based learning across development. *J. Neurosci.* **28,** 9495–9503 (2008).
31. Spielberg, J. M., Olino, T. M., Forbes, E. E. & Dahl, R. E. Exciting fear in adolescence: does pubertal development alter threat processing? *Dev. Cogn. Neurosci.* **8,** 86–95 (2014).
32. Rose, A. J. & Rudolph, K. D. A review of sex differences in peer relationship processes: potential trade-offs for the emotional and behavioral development of girls and boys. *Psychol. Bull.* **132,** 98–131 (2006).
33. Blakemore, S.-J. & Mills, K. L. Is adolescence a sensitive period for sociocultural processing? *Annu. Rev. Psychol.* **65,** 187–207 (2014).
    This review compiles evidence of social contextual effects on adolescent brain maturation.
34. Boyd, R., Richerson, P. J. & Henrich, J. The cultural niche: why social learning is essential for human adaptation. *Proc. Natl Acad. Sci. USA* **108** (Suppl 2), 10918–10925 (2011).
    This analysis documents the crucial role of social learning in human adaptation.
35. Chudek, M., Brosseau-Liard, P., Birch, S. & Henrich, J. in *Navigating the Social World: What Infants, Children, and other Species can teach Us* (eds Banaji, M. R. & Gelman, S. A.) 181–185 (Oxford Univ. Press, 2013).
36. Henrich, J. *et al. Foundations of Human Sociality: Economic Experiments and Ethnographic Evidence from Fifteen Small-Scale Societies* (Oxford Univ. Press, 2004).
37. Creanza, N., Kolodny, O. & Feldman, M. W. Cultural evolutionary theory: how culture evolves and why it matters. *Proc. Natl Acad. Sci. USA* **114,** 7782–7789 (2017).
38. Cheng, J. T., Tracy, J. L., Foulsham, T., Kingstone, A. & Henrich, J. Two ways to the top: evidence that dominance and prestige are distinct yet viable avenues to social rank and influence. *J. Pers. Soc. Psychol.* **104,** 103–125 (2013).
39. Whiting, B. B & Edwards, C. P. *Children of Different Worlds: The Formation of Social Behavior* (Harvard Univ. Press, 1988).
40. Kaplan, H., Lancaster, J. & Robson, A. Embodied capital and the evolutionary economics of the human life span. *Popul. Dev. Rev.* **29,** 152–182 (2003).
    This article uses the concept of embodied capital in an evolutionary account of life history.
41. Dickemann, M. in *Evolutionary Biology and Human Social Behavior* (eds Chagnon, N. & Irons, W.) 321–367 (Duxbury, 1979).
42. Shirtcliff, E. A. *et al.* A dual-axis approach to understanding neuroendocrine development. *Dev. Psychobiol.* **57,** 643–653 (2015).
43. Biro, F. M. *et al.* Pubertal assessment method and baseline characteristics in a mixed longitudinal study of girls. *Pediatrics* **126,** e583–e590 (2010).
44. Abbassi, V. Growth and normal puberty. *Pediatrics* **102,** 507–511 (1998).

45. Juul, A., Magnusdottir, S., Scheike, T., Prytz, S. & Skakkebaek, N. E. Age at voice break in Danish boys: effects of pre-pubertal body mass index and secular trend. *Int. J. Androl.* **30,** 537–542 (2007).
46. Macmahon, B. *et al.* Age at menarche, probability of ovulation and breast cancer risk. *Int. J. Cancer* **29,** 13–16 (1982).
47. Tanner, J. M. Trend towards earlier menarche in London, Olso, Copenhagen, the Netherlands and Hungary. *Nature* **243,** 95–96 (1973).
48. Atay, Z., Turan, S., Guran, T., Furman, A. & Bereket, A. Puberty and influencing factors in schoolgirls living in Istanbul: end of the secular trend? *Pediatrics* **128,** e40–e45 (2011).
49. Jones, L. L., Griffiths, P. L., Norris, S. A., Pettifor, J. M. & Cameron, N. Age at menarche and the evidence for a positive secular trend in urban South Africa. *Am. J. Hum. Biol.* **21,** 130–132 (2009).
50. Sørensen, K. *et al.* Recent secular trends in pubertal timing: implications for evaluation and diagnosis of precocious puberty. *Horm. Res. Paediatr.* **77,** 137–145 (2012).
51. Parent, A.-S. *et al.* The timing of normal puberty and the age limits of sexual precocity: variations around the world, secular trends, and changes after migration. *Endocr. Rev.* **24,** 668–693 (2003).
52. Mouritsen, A. *et al.* Hypothesis: exposure to endocrine-disrupting chemicals may interfere with timing of puberty. *Int. J. Androl.* **33,** 346–359 (2010).
53. Goldstein, J. R. A secular trend toward earlier male sexual maturity: evidence from shifting ages of male young adult mortality. *PLoS ONE* **6,** e14826 (2011).
54. Tomova, A., Lalabonova, C., Robeva, R. N. & Kumanov, P. T. Timing of pubertal maturation according to the age at first conscious ejaculation. *Andrologia* **43,** 163–166 (2011).
55. Sørensen, K., Aksglaede, L., Petersen, J. H. & Juul, A. Recent changes in pubertal timing in healthy Danish boys: associations with body mass index. *J. Clin. Endocrinol. Metab.* **95,** 263–270 (2010).
56. Papadimitriou, A. *et al.* Pubertal maturation of contemporary Greek boys: no evidence of a secular trend. *J. Adolesc. Health* **49,** 434–436 (2011).
57. Aksglaede, L., Olsen, L. W., Sørensen, T. I. & Juul, A. Forty years trends in timing of pubertal growth spurt in 157,000 Danish school children. *PLoS ONE* **3,** e2728 (2008).
58. Ali, M. A., Lestrel, P. E. & Ohtsuki, F. Secular trends for takeoff and maximum adolescent growth for eight decades of Japanese cohort data. *Am. J. Hum. Biol.* **12,** 702–712 (2000).
59. Perry, R. J., Farquharson, C. & Ahmed, S. F. The role of sex steroids in controlling pubertal growth. *Clin. Endocrinol*. **68,** 4–15 (2008).
60. Perkins, J. M., Subramanian, S. V., Davey Smith, G. & Özaltin, E. Adult height, nutrition, and population health. *Nutr. Rev.* **74,** 149–165 (2016).
61. Batty, G. D. *et al.* Height, wealth, and health: an overview with new data from three longitudinal studies. *Econ. Hum. Biol.* **7,** 137–152 (2009).
62. Moradi, A. Nutritional status and economic development in sub-Saharan Africa, 1950–1980. *Econ. Hum. Biol.* **8,** 16–29 (2010).
63. Steckel, R. H. Heights and human welfare: recent developments and new directions. *Explor. Econ. Hist.* **46,** 1–23 (2009).
64. Subramanian, S. V., Özaltin, E. & Finlay, J. E. Height of nations: a socioeconomic analysis of cohort differences and patterns among women in 54 low- to middle-income countries. *PLoS ONE* **6,** e18962 (2011).
65. Kuzawa, C. W. Developmental origins of life history: growth, productivity, and reproduction. *Am. J. Hum. Biol.* **19,** 654–661 (2007).
66. Kuzawa, C. W., McDade, T. W., Adair, L. S. & Lee, N. Rapid weight gain after birth predicts life history and reproductive strategy in Filipino males. *Proc. Natl Acad. Sci. USA* **107,** 16800–16805 (2010).
67. Martorell, R. Improved nutrition in the first 1000 days and adult human capital and health. *Am. J. Hum. Biol*. **29,** e22952 (2017).
68. Gettler, L. T., McDade, T. W. & Kuzawa, C. W. Cortisol and testosterone in Filipino young adult men: evidence for co-regulation of both hormones by fatherhood and relationship status. *Am. J. Hum. Biol.* **23,** 609–620 (2011).
69. Schulz, K. M & Sisk, C. L. The organizing actions of adolescent gonadal steroid hormones on brain and behavioral development. *Neurosci. Biobehav. Rev*. **70,** 148–158 (2016).
This review examines sex-specific effects of gonadal steroid hormones on adolescent brain and behaviour.
70. De Bellis, M. D. & Zisk, A. The biological effects of childhood trauma. *Child Adolesc. Psychiatr. Clin. N. Am.* **23,** 185–222 (2014).
71. Ruttle, P. L., Shirtcliff, E. A., Armstrong, J. M., Klein, M. H. & Essex, M. J. Neuroendocrine coupling across adolescence and the longitudinal influence of early life stress. *Dev. Psychobiol.* **57,** 688–704 (2015).
72. Belsky, J., Schlomer, G. L. & Ellis, B. J. Beyond cumulative risk: distinguishing harshness and unpredictability as determinants of parenting and early life history strategy. *Dev. Psychol.* **48,** 662–673 (2012).
73. Ember, C. R. Using the HRAF collection of ethnography in conjunction with the standard cross-cultural sample and the ethnographic atlas. *Cross Cult. Res.* **41,** 396–427 (2007).
74. Murdock, G. P. & Murdock, D. R. Standard cross-cultural sample. *Ethnology* **8,** 329–396 (1969).
75. White, D. R. Focused ethnographic bibliography: standard cross-cultural sample. *Cross Cult. Res.* **23,** 1–145 (1989).
76. Barry, H & Schlegel, A. *Cross-Cultural Samples and Codes* (Univ. Pittsburgh Press, 1980).
77. Mace, R. & Pagel, M. The comparative method in anthropology. *Curr. Anthropol.* **35,** 549–564 (1994).
78. van Gennep, A. *The Rites of Passage* (Univ. Chicago Press, 1960).
79. Schlegel, A. & Barry, H. *Adolescence: An Anthropological Inquiry* (Free Press, 1991).
On the basis of extensive ethnographic data, this work offers a detailed overview of cultural constructions of adolescence.
80. Schlegel, A. A cross-cultural approach to adolescence. *Ethos* **23,** 15–32 (1995).
81. Schlegel, A. & Barry, H. The evolutionary significance of adolescent initiation ceremonies. *Am. Ethnol*. **7,** 696–715 (1980).
82. Paradise, R. & Rogoff, B. Side by side: learning by observing and pitching in. *Ethos* **37,** 102–138 (2009).
83. Kline, M. A., Boyd, R. & Henrich, J. Teaching and the life history of cultural transmission in Fijian villages. *Hum. Nat.* **24,** 351–374 (2013).
84. Lee, J. W. & Lee, H. Human capital in the long run. *J. Dev. Econ.* **122,** 147–169 (2016).
85. Greenfield, P. M. Linking social change and developmental change: shifting pathways of human development. *Dev. Psychol.* **45,** 401–418 (2009).
86. International Labor Organization. *World Employment and Social Outlook.* http://www.ilo.org/global/research/global-reports/weso/2017/lang--en/index.htm (International Labor Office, 2017).
87. United Nations. *World Marriage Data 2012.* http://www.un.org/esa/population/publications/WMD2012/MainFrame.html (Department of Economic and Social Affairs, Population Division, 2013).
88. Lloyd, C. B. (ed.) *Growing up Global: The Changing Transitions to Adulthood in Developing Countries* (National Academies Press, 2006).
89. Hannum, E & Buchman, C. *The Consequences of Global Educational Expansion* (American Academy of Arts and Sciences, 2003).
90. Gakidou, E., Cowling, K., Lozano, R. & Murray, C. J. L. Increased educational attainment and its effect on child mortality in 175 countries between 1970 and 2009: a systematic analysis. *Lancet* **376,** 959–974 (2010).
91. Worthman, C. M. Inside-out or outside-in? Global development theory, policy, and youth. *Ethos* **39,** 432–451 (2011).
92. Johnson-Hanks, J. in *Ethnographies of Youth and Temporality* (eds Frederiksen, M. D. & Dalsgård, A. L.) 23–56 (Temple Univ. Press, 2014).
93. International Labor Organization. *Global Employment Trends for Youth 2013: A Generation at Risk.* http://www.ilo.org/global/research/global-reports/youth/2013/lang--en/index.htm (International Labor Office, 2013).
94. Bongaarts, J. Human population growth and the demographic transition. *Phil. Trans. R. Soc. B* **364,** 2985–2990 (2009).
95. Shenk, M. K., Kaplan, H. S. & Hooper, P. L. Status competition, inequality, and fertility: implications for the demographic transition. *Phil. Trans. R. Soc. B* **371,** 20150150 (2016).
96. Thomas, V., Wang, Y & Fan, X. *Measuring education inequality: Gini coefficients of education.* Policy Research Working Paper 2525 http://documents.worldbank.org/curated/en/361761468761690314/Measuring-education-inequality-Gini-coefficients-of-education (World Bank, 2001).
97. Stefan, N., Häring, H. U., Hu, F. B. & Schulze, M. B. Divergent associations of height with cardiometabolic disease and cancer: epidemiology, pathophysiology, and global implications. *Lancet Diabetes Endocrinol*. **4,** 457–467 (2016).
98. Song, Y. *et al.* Trends of age at menarche and association with body mass index in Chinese school-aged girls, 1985–2010. *J. Pediatr.* **165,** 1172–1177 (2014).
99. Schlegel, A. & Barry, H. Adolescent initiation ceremonies: a cross-cultural code. *Ethnology* **18,** 199 (1979).

Author Contributions K.T. assembled population data; C.M.W. filtered ethnographic data; C.M.W. and K.T. wrote the paper.

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Reviewer Information *Nature* thanks S. Spyrou and D. F. Lancy for their contribution to the peer review of this work.