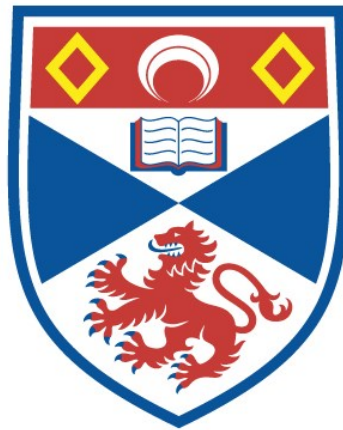


**The social evolution of religion:
modelling genetic and cultural evolution
[Redacted version]**

Kerstin Inge Stucky

A thesis submitted for the degree of PhD
at the
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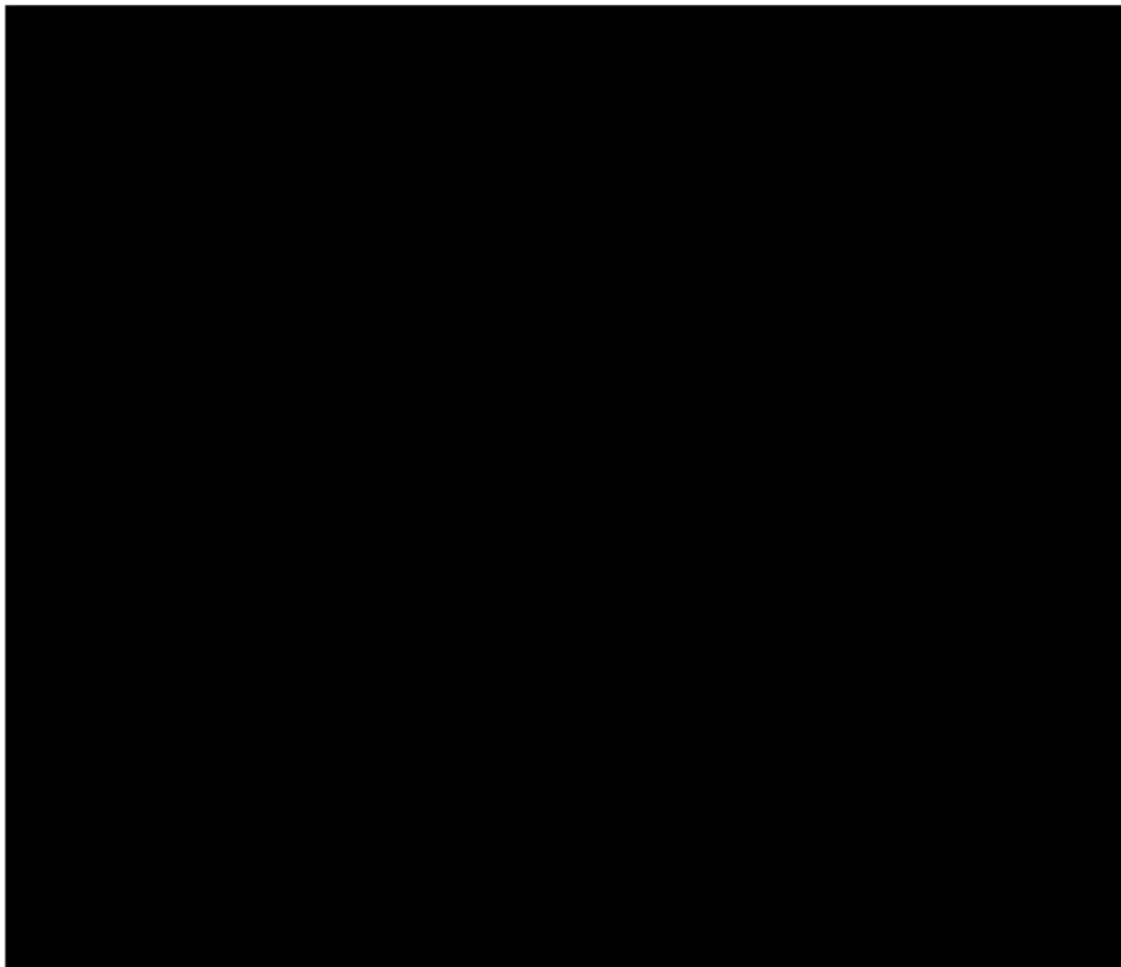
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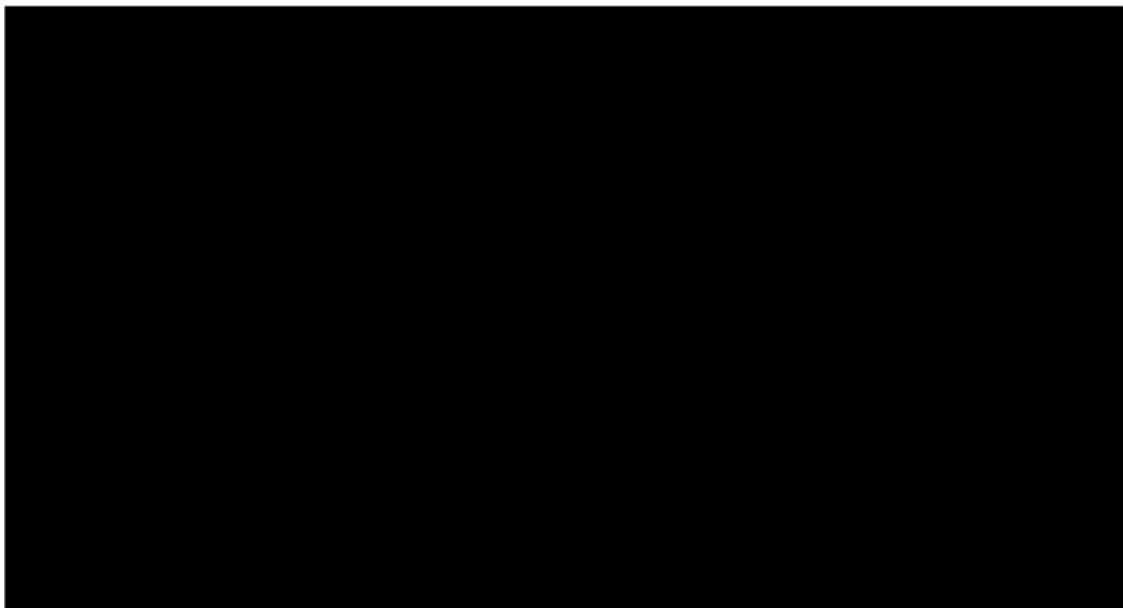
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1 Introduction

1.1 Social evolution - cooperation and conflict

The living world is a world of hierarchies. Higher levels of organisation have evolved from, and apparently dominate, the units of which they are composed. For instance, genes congregate on chromosomes to form genomes, which are contained within cell nuclei, with those cells potentially making up tissues of multi-cellular organisms, which in turn may unite to form groups of organisms and even larger units (Okasha, 2006; West *et al.*, 2015); which in the case of human societies can be structured into a myriad of complex sub-units and institutions and comprise hundreds of millions of individuals (Turchin, 2013). This is interesting from an evolutionary standpoint, since the existence of such hierarchies indicates that in many cases – during the “major evolutionary transitions” (Szathmáry and Maynard Smith, 1995) – higher-level organisation has been favoured by natural selection, i.e., the differential survival and reproduction of individuals due to phenotypic variation (Darwin, 1859; 1871). This further implies that the suppression of competition, and possibly the cooperation of sub-units has been selected for, despite the potential for conflict between units on each hierarchical level of organisation (Maynard Smith, 1988; Frank, 2003; Okasha, 2006). Cooperation is defined as a behaviour which provides a benefit to a recipient, and which has been selected for due to this beneficial effect (West *et al.*, 2007a). In this sense, an actor’s own relative fitness – all else being equal – can be expected to be reduced by cooperating with others (West *et al.*, 2007b). Why then would entities confer a fitness benefit to others in the struggle for “the survival of the fittest” (Spencer, 1864)?

		Effect on recipient	
		+	-
Effect on actor	+	Mutually beneficial	Selfish
	-	Altruistic	Spiteful

Table 1.1 Hamilton’s classification of social behaviours – according to their average fitness effects on the actor and recipient (Hamilton 1964; 1970; see also West *et al.*, 2007a).

Inclusive fitness theory provides a powerful means of analysing such social evolutionary problems and has first been formalised to explain individual level adaptations by Hamilton (1964). ‘Hamilton’s rule’ states that a behaviour will be favoured by natural selection if:

$$-c + rb > 0, \tag{1.1}$$

where $-c$ is the direct fitness effect to the actor as a result of the respective behaviour, b is the indirect fitness effect to the recipient as a result of the behaviour, and r represents the genetic relatedness between the interacting individuals, relative to the population average (Hamilton, 1964; 1970; Charnov, 1977; Gardner *et al.*, 2011). Hamilton’s rule can be applied to any kind of social behaviour, i.e., a behaviour that “has fitness consequences for both the individual that performs that behaviour (the actor) and another individual (the recipient)” (West *et al.*, 2007a: p. 418). Social behaviours can therefore comprise acts that are beneficial for both the actor and recipient, i.e., mutually beneficial, acts that are costly to the actor and beneficial for the recipient, i.e., altruistic, acts that are beneficial for the actor and costly to the recipient, i.e., selfish, and acts that are costly to both the actor and recipient, i.e., spiteful (see **Table 1.1**).

Cooperation, which according to West *et al.*’s (2007a) definition and Hamilton’s (1964; 1970) classification encompasses altruistic and mutually beneficial behaviours, can thus evolve due to indirect fitness benefits (i.e., $rb > 0$) and direct fitness benefits

(i.e., $c < 0$). Indirect fitness benefits can arise from social interactions between related individuals (i.e., $r > 0$). Mechanisms such as limited dispersal or kin discrimination can lead to the positive assortment of relatives, and thus cooperative acts are predominantly directed at individuals who with a greater probability share alleles with the actor, which thereby increase in frequency (termed “kin selection”, Maynard Smith, 1964; Birch, 2017; West *et al.*, 2011). Direct fitness benefits can arise from social interactions with related or unrelated individuals, via mechanisms such as group augmentation (Kingma *et al.*, 2014; Kokko *et al.*, 2001), direct or indirect reciprocity (Barta *et al.*, 2011; Pfeiffer *et al.*, 2005; Panchanathan and Boyd, 2004; Trivers, 1971), punishment of non-cooperators (Birch, 2017; Gardner and West, 2004; Singh and Boomsma, 2015), signalling of cooperation (Martinez-Vaquero *et al.*, 2020; Pacheco *et al.*, 2015), and intergroup competition (Richerson *et al.*, 2016). Note that, since inclusive fitness covers both indirect and direct fitness effects, cooperative behaviours can evolve due to a combination of both. For example, it has been suggested that some cooperative behaviours might have originally evolved mainly via kin selection and have been maintained, at higher levels and in groups of unrelated individuals, predominantly via the effects of punishment (Gardner and West, 2004), group augmentation (Kokko *et al.*, 2001), or intergroup competition (Tomasello *et al.*, 2012).

Irrespective of whether such benefits arise from dyadic interactions or from long-term enhanced group productivity, however, there remains the threat of exploitation by so-called free riders or cheaters, i.e., individuals who gain from the “social good” (Rankin *et al.*, 2007) of cooperation by others without contributing to it themselves, or to a lesser degree (termed the “tragedy of the commons”, Hardin, 1968; Rankin *et al.*, 2007). For instance, variation in relatedness can result in conflict even

within close circles of kin. For example, in humans a mother is equally related to each of her biological offspring and is therefore selected to maximise her inclusive fitness by investing equally in said offspring. Siblings, though, are more related to themselves than to each other, even more so if different fathers were involved, and are therefore selected to solicit relatively more investment from their mother (termed “parent-offspring conflict”, Trivers, 1974). Furthermore, this variation in relatedness of mother to offspring and offspring to other offspring may have led to maternally and paternally inherited gene copies at specific loci expressing different optimal levels due to their phenotypic effects, e.g., regarding fitness-related demands on the mother by her offspring (termed “intragenomic conflict”, Burt and Trivers, 2006; Gardner and Úbeda, 2017; Haig, 1997). The potential for conflict is expected to be even more pronounced in larger groups of unrelated or even unfamiliar individuals, as is often the case in human societies, and which build the foundation of Hardin’s (1968) original essay on the tragedy of the commons. Yet, humans cooperate to a degree which is unusual compared to other species (Melis and Semmann, 2010), which raises the question of whether distinct mechanisms to suppress intra-group competition have evolved in humans.

What distinguishes humans from other species, even from our close primate relatives, is “the massive degree to which the human species altered and constructed their own environments through cumulative cultural evolution of technology and social normative systems” (Kendal and Walters, 2015: p. 147). Evolved complex cognitive mechanisms allow for a high flexibility in human behaviour in response to particular cues in the ecological and social environment and provide for special modes of social learning which accrue to “cumulative adaptive change in extrasomatically stored information” (Hill *et al.*, 2009: p. 188; Boyd *et al.*, 2011, Dean *et al.*, 2013, Henrich and

McElreath, 2003). Such changes have potential feedback effects for the genetic evolution of humans by altering existing social and physical environments and constructing new ones (termed “niche construction”, Laland *et al.*, 1996; 2000), and the selection pressures along with it (termed “gene-culture coevolution”, Feldman and Laland, 1996). Regarding cooperation, this means that more complex and interrelated enforcement mechanisms could evolve, e.g., in the form of cultural institutions which generate direct fitness benefits for cooperating individuals, thereby reducing the potential for free riding which would be expected in species with a less distinct social cognition (West *et al.*, 2011), and thus suppressing intra-group competition.

Furthermore, cumulative cultural change occurs more rapidly than changes via genetic evolution, with different, local pathways potentially leading to multiple stable equilibria (Silk and House, 2016). Accordingly, it has been suggested that group-level variation in cultural traits promoting cooperation has led to the cultural group selection of such traits, with potential consequences for the selection of genes underlying our social cognition (Boyd and Richerson, 2009; Boyd and Richerson, 2010; Richerson *et al.*, 2016). A promising candidate for such a product of gene-culture coevolution in humans and specifically as a cultural promoter of cooperation might be religion (e.g., Boyd and Richerson, 2008; Ferretti and Adornetti, 2014; Fieder and Huber, 2021; Henrich, 2004; Lo and Sasaki, 2017).

1.2 Religion – a cultural promoter of human cooperation

Religion is considered to be a “human universal”, as some kind of belief system with regulated practices regarding supernatural agency appears to occur in nearly every human population, past and present (Brown, 2000). At the same time, religious systems

are as diverse in their shape as cultures and languages. In the social sciences, religion has therefore been a subject of interest for a long time, whereas researchers of evolution have only comparatively recently started to systematically investigate the nature of religion in human societies (Bendixen *et al.*, 2023; Wilson, 2002). Consequently, there is not yet a consensus on the definition of the term ‘religion’, but numerous explanations of what religion entails, available in the literature. Most of these are very similar but differ in some details according to the focus of the respective analysis. As Sosis (2009) puts it, religion is “an inherently fuzzy category with unclear boundaries” (p. 319). Still, most authors can agree on one form or the other of the following rather broad definition, which will be used here: religion is “a shared system of beliefs and actions concerning superhuman agency” (Barrett, 2000: p. 29). There are two major approaches to the emergence and functionality of religion from an evolutionary standpoint, both of which reflect the disciplines involved, and which at first were seen as opposing explanations but have been reconciled in an integrated framework recently: so-called by-product hypotheses which explore the cognitive foundations, i.e., the proximate mechanisms, of religious beliefs and behaviours, and so-called adaptationist explanations trying to uncover the ultimate function(s) of religious systems (Powell and Clarke, 2012; Purzycki and Sosis, 2022).

1.2.1 *Proximate mechanisms of religious beliefs and behaviours*

Scholars of the cognitive sciences, and Evolutionary Psychology in particular, have applied the theory of the modularity of mind in their approach to explain the underlying mechanisms of religious beliefs and behaviours as well as the dissemination of those. Domain-specific modules are suggested to have evolved in order to deal with recurrent

cognitive tasks, which have produced a variety of biases that in turn have enabled and constrained the evolution of specific cultural traits, religious systems being one of them (for an overview see, e.g., Czachesz, 2018; McKay and Whitehouse, 2014).

For instance, ethnographic evidence indicates that humans, as social beings *per se*, are preoccupied with their own species in a way that activity in ambiguous situations is dominantly associated with human agency (Guthrie, 1980). Accordingly, researchers have proposed that our cognition produced a “hyperactive agent-detection device” (Barrett, 2000) which is easily triggered to suspect the presence of another human being and therefore susceptible to concepts of supernatural human actors, since false positives are less costly than false negatives (Guthrie, 1980; Barrett, 2000; Atran and Norenzayan, 2004; McKay and Whitehouse, 2014; Bulbulia and Slingerland, 2012). Furthermore, our mentalistic cognition, also known as “theory of mind” (Premack and Woodruff, 1978), enables us to infer the mental states of our conspecifics which serves to facilitate interactions within our social environment (Premack and Woodruff, 1978). This ability, however, is not constrained by the presence of the person whose state of mind one tries to predict. Humans can apply this capacity towards physically absent people as well as deceased individuals. Even though adults are aware of and accept the discontinuity of physical functions of a deceased person, they tend to imagine that this person’s mental properties will continue to exist, which might play into the emergence of afterlife beliefs (e.g., Crespi, 2016; Gervais, 2013; McKay and Whitehouse, 2014.). This mind-body dualism supposedly derives from the two cognitive systems that have evolved to cope with the physical sphere on the one hand, and the social sphere on the other hand (Bloom, 2007). Indeed, studies on mental disorders with impaired or hyperdeveloped mentalising capabilities such as autism and psychosis, indicate that

inter-individual differences in mentalistic cognition can relate to different degrees in religiosity (e.g., Barnes and Gibson, 2013; Breslin and Lewis, 2015; Iyassu *et al.*, 2014; Lindeman and Lipsanen, 2016; Norenzayan *et al.*, 2012), with implications for the underlying genetic mechanisms (Crespi and Badcock, 2008). In addition, children have been found to regard features of their natural surroundings as purposeful, i.e., designed by an agent, and therefore tend to readily accept creationist explanations (Kelemen and DiYanni, 2005). Although this effect diminishes with age, adults seem to be able to resist this teleological tendency only through effort (Kelemen and Rosset, 2009). In combination with the tendency to over-attribute human-like agency in unclear situations, this could contribute to the emergence of concepts about supernatural interference (McKay and Whitehouse, 2014).

Furthermore, content-dependent transmission biases in human cognition may have played a role in the successful dissemination of similar religious beliefs. For example, people tend to memorise narratives with elements which minimally violate the expectations of our intuitive knowledge about our environment (Sperber and Hirschfeld, 2004). Some studies found that simple concepts with “minimally counterintuitive” (Barrett, 2000) content exhibited a delayed memory advantage in subjects compared to purely intuitive concepts, especially when human agents were involved (Atran and Norenzayan, 2004; Porubanova-Norquist *et al.*, 2013), but others did not (Willard *et al.*, 2016). Besides, as Willard and colleagues (2016) demonstrated, memorability does not necessarily imply belief. However, when concepts were conferred via “credibility-enhancing displays” (CREDS, Henrich, 2009), subjects were more likely to believe narratives with minimally counterintuitive content (Willard *et al.*, 2016). Credibility-enhancing displays serve to demonstrate commitment to the contents of an individual’s

statement which would seem too costly to the actor, were they not to believe in their own testimony. A social learning bias supposedly predisposes humans to accept information more easily when accompanied by a CRED (Henrich, 2009). Lanman and Buhrmester (2017) found evidence for the hypothesis that the exposure to credibility-enhancing displays significantly accounts for inter-individual variation in religiosity in their two studies on 216, and 100, Americans respectively.

Additionally, our capacity for social learning has produced a variety of context-dependent transmission biases which enable the fast adoption of cultural traits not only vertically, i.e., from parents to offspring, but also horizontally and oblique, i.e., between related as well as non-related individuals across all ages (Mesoudi and Danielson, 2008), and which might have been particularly relevant in the context of the dissemination of religious beliefs and behaviours (Gervais *et al.*, 2011; White *et al.*, 2021). For instance, humans tend to disproportionately imitate behaviour already prevalent in a population (termed “conformity” bias, Henrich and McElreath, 2003) as well as behaviour expressed by ostensibly successful individuals (termed “prestige” bias, Henrich and Gil-White, 2001), regardless of a connection between the demonstrated behaviour and the reasons for their success. Moreover, the human tendency to imitate even causally opaque behaviour (termed “overimitation”, Whiten *et al.*, 2009), either for the purpose to enable children to acquire skills from an early age or to the effect of integration into a social group, enhances such effects (McKay and Whitehouse, 2014). These social learning processes can result in the accumulation of stable between-group differences in, e.g., social norms and values (Boyd and Richerson, 2009).

Although it has been widely acknowledged that humans are predisposed to imagine and accept supernatural concepts possibly as by-products of our normal cognition, the question of how, and more importantly, why these propensities were maintained and resulted in today's cross-culturally diverse belief systems, remains debated. Answering these questions becomes even more difficult as some of the components that are usually viewed as core elements of religious systems, such as rituals, myths, music, and taboos are not unique to religion and may have primarily evolved due to other selection pressures (Sosis, 2009). By-product hypotheses state that religion simply persists as a costly side-effect of the aforementioned cognitive processes but is being outweighed by their general benefits, as well as exploited for the relief of existential anxieties, which in turn are presumed by-products of evolved emotions (e.g., Barrett, 2000; Boyer, 2003; Atran and Norenzayan, 2004). Similarly, Dawkins (2008) argues that religion is a by-product with harmful effects which acts like a cultural pathogen virus, 'infecting' children at a young age, when their social learning mechanisms make them 'vulnerable' to adopting cultural traits. These hypotheses have their roots in the traditional approach of Evolutionary Psychology, which regards various cultural traits in modern human societies as the result of a mismatch between cognitive adaptations that arose during the formative period of the evolution of *H. sapiens*, approximately between 2.5 million and 12,000 years ago, and today's environment(s) (Czachesz, 2018). For religious belief systems to be a simple aggregation of cognitive by-products or even maladaptations, however, it would be expected that natural selection had produced less costly mechanisms with similar overall beneficial effects during the evolution of human cognition. Furthermore, the cross-culturally recurrent integration of the single elements in religious systems is not

sufficiently explained by the by-product hypothesis (Crespi and Summers, 2014; Powell and Clarke, 2012; Sosis, 2009). It can therefore be assumed that the aforementioned cognitive mechanisms have been subject to natural selection in the course of the evolution of religion.

1.2.2 *Ultimate explanations for religious beliefs and behaviours*

Many adaptationist approaches to the evolution of religion have in common that they portray religious systems as a function of group living. Prosocial effects between members of the same religious community facilitate cooperation and therefore promote collective action, with associated benefits for those members (for an overview see, e.g., Bendixen *et al.*, 2023; Szocik, 2017). However, researchers have produced different hypotheses about the origins of these effects, focusing on different aspects of religion and on different, spatial and temporal, levels. For instance, some scholars focus on explaining the origin of religious systems within the context of small-scale, ancestral hunter-gatherer societies, which have been characterised by infrequent, intense, and potentially traumatic rituals and the lack of hierarchical structures – the “imagistic mode” of religion (Whitehouse *et al.*, 2012; Whitehouse, 2021) or “religions of experience” (Dunbar, 2017). Others focus on the role that religious systems might have played in the rise of large-scale, more modern societies, including the present world religions, which are characterised by codified knowledge, hierarchical structures, and frequent repetitive rituals – the “doctrinal mode” of religion (Whitehouse *et al.*, 2012; Whitehouse, 2021).

For example, Crespi (2016) and Crespi and Summers (2014) have drawn on inclusive fitness theory in order to explain the origin of cooperative effects of religion in

ancestral, small-scale societies. In light of the aforementioned parent-offspring conflict, they argue that features of human social cognition such as mentalising capacities have been exploited by the introduction of moralising supernatural agents, which a mother might employ to increase cooperativeness in her offspring and consequently reduce “the degree to which copies of her genes interfere with their own transmission” (Crespi, 2016: p. 9). In extension, they argue that such religious manipulation could have promoted cooperation within the wider context of groups, which are assumed to have consisted predominantly of kin, due to indirect fitness benefits. In addition, kin recognition in humans evidently depends on ecological cues which can easily be manipulated, e.g., via verbally transmitted traditions or shared experiences (Crespi, 2016; Crespi and Summers, 2014). For instance, religiously motivated traditions such as ancestor worship have been suggested to promote cooperation among distant kin via the manipulation of perceived relatedness, thereby maximising the inclusive fitness of such ancestors (e.g., Clark and Coe, 2021; Coe *et al.*, 2010; Steadman and Palmer, 2008). Furthermore, synchronic movement and ‘arousal’ induced by religious rituals can create bonds of psychological or fictive kinship and consequently increase group cohesion (McKay and Whitehouse, 2014), e.g., via the release of oxytocin (Crespi, 2016) or other endorphins (Dunbar, 2017).

Accordingly, ritual behaviours have been put forward as one of the relevant factors in the ongoing selection of religious belief systems in both small- and large-scale societies, as a result of their direct fitness benefits. Ritual behaviours which can be found in other mammalian species as well, have been hypothesised to serve in a religious context as “hard-to-fake” (Irons, 2001) signals of commitment to an individual’s group and the respective belief system, thereby leading to the positive

assortment of cooperators and associated direct benefits (e.g., Irons, 2001; Brusse, 2020; Bulbulia and Sosis, 2011; Lang and Kundt, 2023; Sosis, 2003). A signal is defined as a display “which alters the behaviour of other organisms, which evolved because of that effect, and which is effective because the receiver’s response has also evolved” (Maynard Smith and Harper, 2003: p. 3). Moreover, empirical evidence suggests a positive relationship between costs of such religious displays and the degree of cooperativeness (e.g., Lang *et al.*, 2023; Sosis and Bressler, 2003; Sosis and Ruffle, 2003; Sosis *et al.*, 2007; Xygalatas *et al.*, 2013). For example, Sosis and Alcorta (2003) found a positive relationship between the quantity of costly requirements and longevity of 19th century American religious communities. Soler (2012) demonstrated in her study of an Afro-Brazilian religious community that religious commitment and willingness to cooperate within the group was reflected by the amount participants donated in a public goods economic game. In addition, Chavja *et al.* (2023) found that pilgrims to Santiago de Compostela positively associated the degree of physical effort involved with a ‘real’ pilgrim’s identity and that long-distance compared to short-distance and to non-pilgrimage was associated with higher perceived trustworthiness of pilgrims by study participants. Importantly, these effects were more pronounced in a religious compared to a secular setting, which might be due to the fact that religious rituals often serve to express commitment to belief systems concerning moralising deities (Chavja *et al.*, 2023).

Indeed, several hypotheses about the cooperative effects of religious systems emphasise the importance of concepts of omniscient, moralizing deities as effective means to discourage free riders, via the exploitation of cognitive biases concerned with punishment avoidance, for example (e.g., Johnson, 2005; Norenzayan *et al.*, 2016; Potz,

2022). Moreover, it has been argued that cultural ‘packages’ containing such moralizing deities together with practices utilizing costly displays, cultural learning biases, and other self-regulatory mechanisms may have spread more effectively than other concepts and produced a cultural survival advantage in light of strong intergroup competition. Favoured by cultural group selection, such packages might therefore have played an important role in the rise of cooperative, anonymous, large-scale societies (Atran and Henrich, 2010; Norenzayan *et al.*, 2016). Similarly, Wilson (2002) refers to religion as a group-level adaptation and religious groups as culturally competing “trait groups”. In this view, which is rooted in multi-level selection theory, evolved moral systems have generated mechanisms such as conformity, detection and punishment of cheating, and docility which serve to suppress within-group selection to a degree that allows for between-group selection. Supernatural beliefs can generate a strong motivation to adopt a particular set of adaptive, normative behaviours which supposedly led to the proliferation of certain religious systems, as opposed to others, in the past and present. Wilson provides a variety of examples to prove his point, emphasising the context-sensitivity and flexibility of cultural traits in different times and locations as the product of the open-ended character of cultural evolutionary mechanisms, which is reflected in the variety of different religious systems, temporally and cross-culturally.

1.3 Thesis outline

In this thesis, I investigate the genetic and cultural evolution of religion using mathematical methods derived from the theory of social evolution. By formalising some of the ideas presented above, I explore the diverse selection pressures which might have produced and shaped the evolution of religious beliefs and behaviours. More

specifically, in **Chapter 2 “The evolution of religiosity by kin selection”**, I explore Crespi and Summers’ (2014) idea that parent-offspring conflict has driven the evolution of religious beliefs to investigate how kin selection may mould an individual’s propensity for religiosity and corresponding patterns of gene expression, i.e., the potential for intragenomic conflict. In **Chapter 3 “Kin selection favours religious traditions: Ancestor worship as a cultural descendant-leaving strategy”**, I examine the evolutionary feasibility of religiously motivated, cultural norms that promote altruism among co-descendants via the manipulation of kin recognition, i.e., whether ancestor worship might have originated as a “descendant-leaving strategy” despite the potential for “ancestor-descendant conflict”, an idea put forward by Coe and colleagues (2010).

In **Chapter 5 “Discussion”**, I synthesise my findings and give a brief outlook on potential research questions in need of mathematical modelling.

2 The evolution of religiosity by kin selection

Abstract

Despite religion's apparent ubiquity, hypotheses about the selection pressures that may have shaped its cognitive foundations remain controversial. Here, we develop and analyse a mathematical model inspired by Crespi and Summers' suggestion that parent-offspring conflict has driven the evolution of religious beliefs to explore the causes and consequences of these selection pressures. To this end, we employ kin selection methodology to investigate how selection may mould an individual's propensity for religiosity and corresponding patterns of gene expression, revealing that the evolution of religiosity is modulated by genetic relatedness between social partners, that selection in relation to religiosity may depend on an individual's age and sex, and that religiosity can foment intragenomic conflicts of interest that give rise to parent-of-origin specific patterns of gene expression and concomitant clinical disorders. More generally, we develop a formal, theoretical framework that enables the derivation of clear-cut, comparative predictions about adaptive as well as maladaptive phenotypes.

2.1 Introduction

Religion is regarded as a “human universal”, meaning that it has been found in all known contemporary and historical human societies (Brown, 2000). It appears to have existed from at least the Upper Palaeolithic (Sterelny, 2018) and has evolved into a complex and culturally diverse phenomenon (Wilson 2002). This variety has led to a lack of consensus on how to even define religion, but a useful working definition is that religion represents a shared system of beliefs and actions concerning supernatural agency (Barrett, 2000: p. 29). It is widely acknowledged that humans are predisposed to imagine and accept supernatural concepts as products of our normal cognition but – given its counterintuitive contents, associated costly commitments and other seemingly maladaptive effects – understanding why religion should feature so prominently in human populations remains a substantial problem for evolutionary biology and allied disciplines (Powell and Clarke, 2012; Sosis, 2009).

There are two major approaches to explaining religion from an evolutionary standpoint (**Table 2.1**). Proponents of “by-product” hypotheses suggest that religion arises as an incidental consequence of cognitive processes that have themselves been evolutionarily favoured for reasons having nothing to do with religion (Atran, 2005; Atran and Henrich, 2010; Barrett, 2000; Barrett and Lanman, 2008; Boyer, 2003; Guthrie, 1980; Hinde, 1999). A potential candidate for one of these cognitive processes underlying religiosity is “theory of mind” (e.g., Crespi, 2016; Gervais, 2013; McKay and Whitehouse, 2014), which enables humans to infer the mental states of others and therefore serves to facilitate interactions in one’s social environment. This capacity usefully applies even to social partners who are not physically present, and by extension – without requiring the invocation of further, special adaptations – it is easy to see how

By-Product/ Adaptation	Inheritance mode	Unit of adaptation	Adaptive function	References
By-Product	Genetic	Individual	None beyond primary functions of ordinary cognitive features	e.g., Atran, 2005; Atran & Henrich, 2010; Barrett, 2000; Barrett & Lanman, 2008; Boyer, 2001; Boyer, 2003; Dawkins, 2006; Dennet, 2006; Guthrie, 1980; Hinde, 1999.
Adaptation	Genetic	Individual	Fostering intra- family cooperation	e.g., Crespi, 2016; Crespi & Summers, 2014.
			Fostering (large- scale) intra-group cooperation	e.g., Alcorta & Sosis, 2005; Bulbulia, 2008; Bulbulia & Freaan, 2010; Kiper & Sosis, 2014; Norenzayan <i>et al.</i> , 2016; Powell & Clarke, 2012; Purzycki & Sosis, 2009; Purzycki & Sosis, 2013; Sosis, 2005; Sosis & Alcorta, 2003; Wilson, 2002.
	Cultural	Group/ Institution	Fostering (large- scale) intra-group cooperation	e.g., Atran & Henrich, 2010; Bulbulia, 2008; Bulbulia & Freaan, 2010; Crespi, 2016; Crespi & Summers, 2014; Kiper & Sosis, 2014; Norenzayan <i>et al.</i> , 2016; Powell & Clarke, 2012; Szocik, 2017; Wilson, 2002.
		Meme	Dissemination via appealing to human cognition	e.g., Boyer, 2001; Dawkins, 2006; Dennet, 2006.

Table 2.1 Religion as adaptation versus by-product. A classification of hypotheses on the evolution of religion according to mode of inheritance, unit of adaptation, and adaptive function – if any.

humans might also apply this capacity to deceased individuals and even non-animate entities, forming a basis for religiosity (see McKay and Whitehouse, 2014). However, the role of mentalizing in the expression of religiosity remains unclear (Di Dio *et al.*, 2018; Ishii and Watanabe, 2021; Jack *et al.*, 2016; Kapiogiannis *et al.*, 2009; Lindeman *et al.* 2015; Maji *et al.*, 2017; Norenzayan *et al.*, 2012; Reddish *et al.*, 2016; Willard and Norenzayan, 2013).

In contrast, “adaptationist” hypotheses posit the existence of a “religious phenotype” that has emerged as an adaptation in its own right (Purzycki and Sosis, 2013). Adaptationist hypotheses subdivide into those which view religion as a product of genetical evolution, and representing an adaptation on the part of the individual for the purpose of fostering cooperation within families and/or within wider society (Alcorta and Sosis, 2005; Bulbulia, 2008; Bulbulia and Freat, 2010; Crespi and Summers, 2014; Crespi, 2016; Purzycki and Sosis, 2009; Purzycki and Sosis, 2013; Sosis and Alcorta, 2003; Sosis, 2009), versus those which view religion as a product of cultural evolution, and representing an adaptation of the social group/cultural institution (Atran and Henrich, 2010; Bulbulia, 2008; Bulbulia and Freat, 2010; Crespi and Summers, 2014; Crespi, 2016; Kiper and Sosis, 2014; Norenzayan *et al.*, 2016; Powell and Clarke, 2012; Szocik, 2017; Wilson, 2002) or else the meme (Boyer, 2001; Dawkins, 2006; Dennet, 2006). The multifaceted nature of religion means that these hypotheses are not mutually exclusive with, for example, some seeing the biological capacity for religion as a simple by-product which has subsequently been hijacked by a cultural process driven by the evolutionary interests of memes (Dawkins, 2006).

Recently, it has been suggested that religion may have originated as a means to suppress intra-family conflict via parental manipulation. Crespi and Summers (Crespi,

2016; Crespi and Summers, 2014) – building upon and synthesizing the work of Alexander (2006), Lahti (2009), Coe and Palmer (2008; 2013), Palmer *et al.* (2008), Steadman and Palmer (2008), amongst others – have proposed that during human evolutionary history a mother may have been able to increase her inclusive fitness by instilling her children with beliefs in moralising supernatural agents (e.g., deceased ancestors), thereby encouraging them to increase their cooperativeness with her and each other. They argue that children, owing to their strong dependence upon social learning, a tendency to readily adopt divine explanations and a pre-existing moral propensity, are predisposed to accept such manipulation. They have further suggested that religion may have subsequently been elaborated – both genetically and culturally – within and beyond the intra-family context as a means for social control and the establishment of cooperative relationships more generally. Following from this, they have predicted a tight linkage between the proximate mechanisms of religious and social bonding traits, placing a particular emphasis on the role of the neuropeptide oxytocin, which is understood to play a key part in the formation and maintenance of human social relationships, and which has been implicated in behaviours and cognitive features identified as important aspects of religion (Crespi, 2016; Crespi and Summers, 2014; and references therein). Crespi and Summers have also highlighted the possibility for developing comparative predictions linking inter-individual and inter-group variation in religious cognition and behaviours with variation in the strength and nature of within-group versus between-group competition, and variation in the benefits and costs of religious, i.e., mentalistic, versus mechanistic cognition.

This is a compelling origin story for religion. However, Crespi and Summers’ hypothesis remains underdeveloped. First, their argument has been developed in purely

verbal terms, rather than formally in mathematical terms. Second, their parent-offspring conflict scenario applies very broadly, implying that maternal manipulation would be straightforwardly favoured across a wide range of demographic and ecological contexts, such that it is difficult to see why quantitative variation in demographic and ecological factors would translate into variation in the intensity of religious beliefs and behaviour, which limits the extent to which clear-cut, comparative predictions can be derived from their hypothesis. Third, although it is plausible that children would initially be susceptible to their mothers' religious indoctrination it is unclear that this susceptibility would be evolutionarily maintained in the face of potentially strong selection to reduce their receptiveness for supernatural ideas, so as to avoid being manipulated.

Here, we undertake a formal treatment of the evolution of religion, building upon the verbal framework of Crespi and Summers. In contrast to Crespi and Summers, we focus our attention on the manipulated party – in the first instance, a child being exposed to supernatural ideas by their mother, and in the second instance, an adult being exposed to similar religious manipulation by their social partners – in order to investigate how natural selection shapes the individual's susceptibility to such indoctrination. This involves describing the three-way tension between the direct-fitness theory-of-mind (and/or other) benefits associated with a cognition that predisposes the individual to supernatural ideas, the direct-fitness costs of being thereby more prone to manipulation, and the indirect-fitness (i.e., kin-selected) benefits arising from allowing oneself to be manipulated into being more cooperative with genetically related social partners. The analysis enables the derivation of a suite of novel, concrete, comparative predictions concerning differences in religiosity in relation to age and sex, and also with respect to different elements of the genome, all modulated by variation in demographic

and ecological factors. Consideration of intragenomic conflict with respect to religiosity further yields novel predictions concerning parent-of-origin specific patterns of expression in relation to genetic loci that affect religiosity and the maladaptive and clinical consequences of concomitant disorders of genomic imprinting. More generally, we intend our mathematical treatment to help connect a large and exciting literature on the possible evolutionary drivers of religion to current concepts and methodologies of social evolution theory.

2.2 Methods

We consider a large population divided into social groups, each containing women and men who are producing and raising children, with their success in this activity being modulated by religiosity – that is, an individual’s susceptibility to supernatural concepts. On the one hand, we assume that individuals with higher religiosity enjoy basic benefits of improved theory-of-mind and/or other abilities, which allow them to navigate through their social lives more successfully. On the other hand, we assume that individuals with higher religiosity tend to be less competitive with their social partners for resources – insofar as supernatural agents are invoked to manipulate one to behave more selflessly with social partners – which results in both a direct-fitness cost for themselves and an indirect-fitness benefit for their social partners, in line with the classic “tragedy of the commons” model (Hardin, 1968; Frank, 1998). For children, we assume that individuals compete with their maternal siblings for resources that improve their survival to adulthood. For adults, we assume that individuals compete with same-sex group mates for resources that improve their fecundity and investment into their children. That is, religiosity is associated with inclusive-fitness costs and benefits which

we expect to balance out at equilibrium. For simplicity, we assume non-overlapping generations, with groups undergoing fission at the end of each generation and with daughter groups moving off to compete with other, unrelated groups for reproductive resources (Haldane, 1932; Gardner and West, 2006). Following density-dependent regulation that maintains the total number of groups in the population at a fixed level, adults disperse with sex-specific rates to other groups or else remain in their native group. Mating then occurs at random within each group, with some adults potentially achieving more reproductive success than their same-sex group mates, according to sex-specific degrees of reproductive skew. We perform a kin-selection analysis (Frank, 1998; Hamilton, 1964; Taylor, 1996; Taylor and Frank, 1996) to investigate how natural selection may act upon religiosity as a function of the individual's age and sex, and under different assumptions of the genetic architecture of the trait (see **2.5 Extended methods** for full details).

2.3 Results

2.3.1 *Kin selection favours religiosity*

Our model involves a three-way tension that modulates the evolution of religiosity. First, there is a direct-fitness benefit associated with greater predisposition to religious ideas owing to the cognitive processes that give rise to religiosity more generally, underpinning theory of mind and/or other abilities that are important for an individual's success in navigating their social life. Second, a higher degree of religiosity is also associated with a greater susceptibility to manipulation by social partners, which makes the focal individual less competitive in competition for resources. Third, this loss of competitiveness leads to an indirect-fitness (i.e., kin-selected) benefit owing to the

increased success of the focal individual's competitors, to the extent that they are their genetic relatives. Accordingly, in the absence of genetic relatedness the individual is favoured to exhibit a degree of religiosity that exactly balances the direct-fitness theory-of-mind benefit against the direct-fitness cost due to loss of competitiveness, i.e., that which maximizes their direct fitness overall. And as social partners increasingly share genes in common with each other (higher relatedness), the individual is favoured to exhibit a higher degree of religiosity than this baseline, resulting in an overall reduction in their direct fitness and an overall increase in the fitness of their social partners (**Fig. 2.1; Table 2.2**, Prediction 1).

In line with Crespi and Summers (2014), we assume that religiosity in childhood modulates the individual's cooperativeness towards – and, in turn, their competitiveness against – maternal siblings for maternal resources. Here, we consider that maternal siblings may or may not share the same father, and by varying the degree of their paternal sibship we are able to vary the degree of relatedness between them in order to investigate its impact on the evolution of religiosity in childhood. In accordance with the general prediction given above, we find that higher relatedness – owing to higher paternal sibship – leads to a greater level of religiosity being favoured (**Fig. 2.1a**). Note that, owing to the symmetrical inheritance of autosomal genes in relation to the two sexes, we do not expect there to be sex differences in the relatedness of maternal siblings. Hence, in the absence of sex differences in the costs and benefits of religiosity we expect there to be no sex differences in religiosity during childhood, with girls and boys being equally receptive to maternal religious manipulation (**Table 2.2**, Prediction 2).

In adults, we assume that religiosity modulates the individual's competitiveness

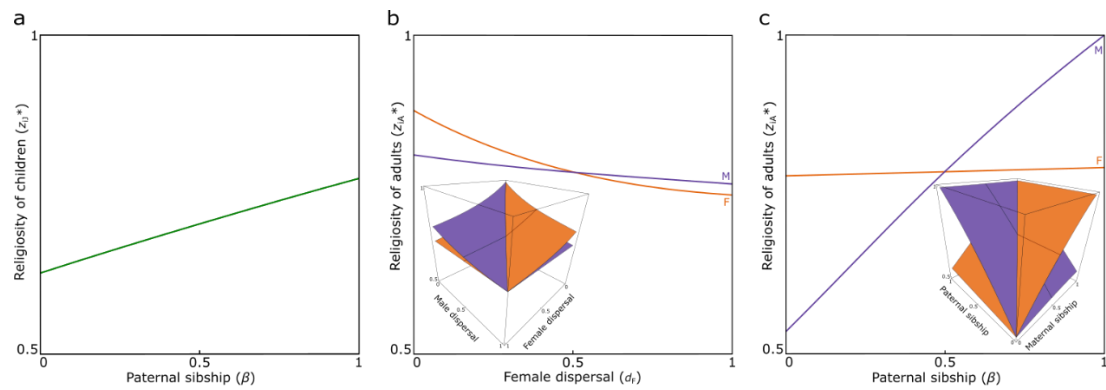


Fig. 2.1 Kin selection favours religiosity. (a) In children, a higher degree of relatedness among maternal siblings (owing to greater probability of having the same father, β) favours a greater level of religiosity. **(b)** In adults, women (orange) favour a higher degree of religiosity due to higher within-group relatedness for women in scenarios with male-biased dispersal ($d_M > d_F$), and men (purple) favour a higher degree of religiosity due to higher within-group relatedness for men in scenarios with female-biased dispersal ($d_F > d_M$). **(c)** Women (orange) favour a higher degree of religiosity in scenarios with higher female reproductive variance ($\alpha > \beta$), and men (purple) favour a higher degree of religiosity in scenarios with higher male reproductive variance ($\beta > \alpha$).

for reproductive resources against same-sex groupmates extending beyond the nuclear family. Accordingly, demographic and ecological factors that influence the degree of relatedness between groupmates are expected to impact upon the evolution of religiosity. We find that lower rates of dispersal and higher maternal and paternal sibship between group mates leads to a higher degree of within-group relatedness and hence a greater level of religiosity (**Fig. 2.1b & 2.1c; Table 2.2**, Predictions 3 & 4). Moreover, we find that sex differences in dispersal rate and/or unequal degrees of maternal and paternal sibship lead to sex differences in relatedness to group mates and hence to different levels of religiosity being favoured in women and men, even if the basic costs and benefits of religiosity are exactly the same for both sexes. Specifically, because adults of the less-dispersing sex are, on average, more related to their group mates, then – all else being equal – in populations characterised by male-biased

#	Prediction
1	Higher relatedness promotes religiosity.
2	In children, full (as opposed to half) sibship promotes religiosity, equally for both sexes.
3	Lower dispersal promotes religiosity in adulthood.
4	Higher sibship within social groups promotes religiosity in adulthood.
5	The least-dispersing sex has a higher potential for religiosity.
6	The sex with greater reproductive variance has a higher potential for religiosity.
7	Genomic imprinting will be favoured at loci affecting religiosity.
8	In children, religiosity-promoter loci will be maternally expressed and paternally silenced, whereas religiosity-inhibitor loci will be paternally silenced and maternally expressed.
9	All else being equal, in adults, religiosity-promoter loci will be: paternally expressed and maternally silenced if dispersal is female-biased, and the reverse if dispersal is male-biased; paternally expressed and maternally silenced if reproductive variance is male-biased, and the reverse if reproductive variance is female-biased; and the opposite patterns will be true of religiosity-inhibiter loci.
10	Mutations and epimutations at religiosity loci will be associated with parent-of-origin specific maladaptive phenotypes in predictable directions, as detailed in Fig. 2.3 .

Table 2.2 Predictions emerging from our analysis. All predictions are based on relatedness considerations and assume no sex differences in fitness costs and benefits of religiosity.

dispersal (e.g., matrilocality) religiosity is expected to be higher among women than among men, whereas in populations characterised by female-biased dispersal (e.g., patrilocality) religiosity is expected to be higher among men than among women (**Fig. 2.1b**; **Table 2.2**, Prediction 5). Also, if reproduction by one of the sexes is dominated by a smaller number of individuals, then they will be more inclined towards religiosity because any group benefit will largely accrue to their own reproductive success, and accordingly – all else being equal – we would expect populations characterised by a higher degree of maternal sibship (e.g., polyandry) to favour higher religiosity among

women than among men, whereas populations characterised by a higher degree of paternal sibship (e.g., polygyny) would favour higher religiosity among men than among women (**Fig. 2.1c**; **Table 2.2**, Prediction 6).

2.3.2 Kin selection drives intragenomic conflict over religiosity

Above, we have shown that the evolution of religiosity is modulated by the degree of genetic relatedness between social partners. However, different parts of an individual's genome may differ in the extent to which they share genes in common with the individual's social partners. Crucially, individuals carry two genes at every one of their autosomal loci, one derived from the individual's mother and one derived from the individual's father, and these two genes are liable to be differently related to the individual's social partners owing to sex differences in demographic and ecological factors (Haig, 1997). This means that genes deriving from the individual's mother are liable to experience selection pressures in relation to the individual's religiosity phenotype that are different from those experienced by the genes deriving from the individual's father, and hence there is expected to be an intragenomic conflict (Burt and Trivers, 2006; Gardner and Úbeda, 2017; Haig, 1997) with each set of genes having a different optimum with regard to the individual's level of religiosity (**Fig. 2.2**).

Such differences in gene interests are understood to drive the evolution of parent-of-origin specific gene expression, or "genomic imprinting" (Haig, 1997). Specifically, if a locus encodes a gene product that increases the individual's religiosity (a 'religiosity promoter'), then the gene with the higher optimum is expected to favour a greater degree of gene expression and its homologue is expected to favour a lower degree of gene expression, culminating in the silencing of the latter gene and the

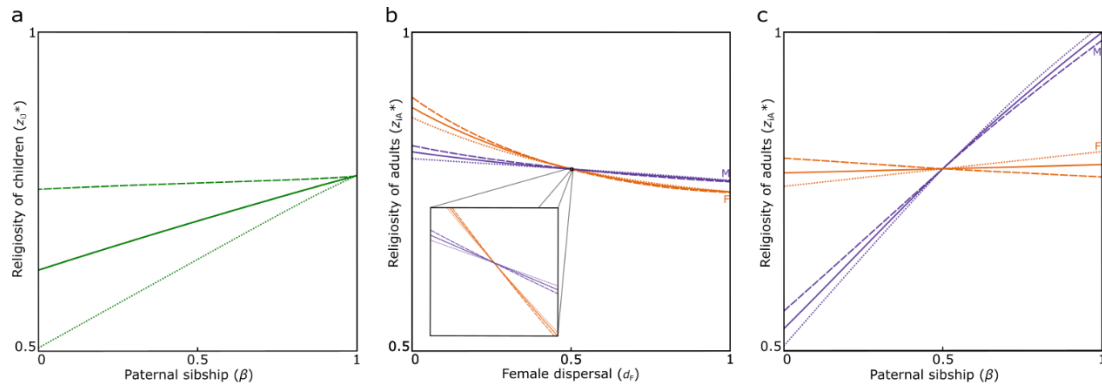


Fig. 2.2 Kin selection drives intragenomic conflict over religiosity. (a) In children (green), maternal-origin genes (dashed) always favour a higher degree of religiosity than paternal-origin genes (dotted) and genes that are ignorant of their origin (solid), except for in the special case whereby maternal offspring are guaranteed to have the same father. **(b)** In women (orange) and men (purple), maternal-origin genes (dashed) favour a higher degree of religiosity than paternal-origin genes (dotted) and genes that are ignorant of their origin (solid) in scenarios with male-biased dispersal ($d_M > d_F$), and the opposite pattern arises in scenarios with female-biased dispersal ($d_F > d_M$). **(c)** Maternal-origin genes (dashed) favour a higher degree of religiosity than paternal-origin genes (dotted) and genes that are ignorant of their origin (solid) in scenarios with higher female reproductive variance ($\alpha > \beta$) and the opposite pattern arises in scenarios with higher male reproductive variance ($\beta > \alpha$).

expression of the former gene at its optimal level, in what has been termed the “loudest voice prevails” principle (Haig, 1996). Conversely, if the gene product decreases the individual’s religiosity (a ‘religiosity inhibitor’) then the reverse pattern of gene expression is predicted. Accordingly, if kin selection has been a driver of the evolution of religiosity, we would expect religiosity loci to show a greater tendency towards parent-of-origin specific gene expression (Table 2.2, Prediction 7).

During childhood, the salient social partners are the individual’s maternal siblings, who may or may not be paternal siblings. This means that, except for in populations where all maternal siblings are guaranteed to share the same father, relatedness will generally be higher with respect to maternal-origin genes than with respect to paternal-origin genes, and hence we expect a child’s maternal-origin genes will favour a greater level of religiosity than will the paternal-origin genes (Fig. 2.2a).

Accordingly, during childhood, religiosity-promoter loci are expected to be maternally-expressed and paternally-silenced, whereas religiosity-inhibitor loci are expected to be paternally-expressed and maternally-silenced (**Fig. 2.3**; **Table 2.2**, Prediction 8).

In adults, we also find potential for intragenomic conflict over religiosity. As in children, maternal-origin genes and paternal-origin genes in adults can favour different optimal levels of religiosity. During adulthood, however, relatedness between group members may depend upon dispersal as well as mating patterns and can therefore vary significantly across different populations. All else being equal, in populations with male-biased dispersal, relatedness will generally be higher with respect to maternal-origin genes than with respect to paternal-origin genes, and as a consequence we again expect an individual's maternal-origin genes to favour a greater level of religiosity than will their paternal-origin genes (see left half of **Fig. 2.2b**), such that religiosity-promoter loci are expected to be maternally-expressed and paternally-silenced and religiosity-inhibitor loci are expected to be maternally-silenced and paternally-expressed.

Conversely, all else being equal, in populations with female-biased dispersal, we expect paternal-origin genes will favour a greater level of religiosity than will maternal-origin genes (see right half of **Fig. 2.2b**), such that religiosity-promoter loci are expected to be maternally-silenced and paternally-expressed and religiosity-inhibitor loci are expected to be maternally-expressed and paternally-silenced (**Fig. 2.3**).

All else being equal, in polyandrous populations (with higher maternal than paternal sibship) we expect an adult's maternal-origin genes to favour a greater level of religiosity than will their paternal-origin genes (see left half of **Fig. 2.2c**), such that religiosity-promoter loci are expected to be maternally-expressed and paternally-silenced and religiosity-inhibitor loci are expected to be maternally-silenced and

paternally-expressed, and in polygynous populations (with higher paternal than maternal sibship) we expect an adult's paternal-origin genes to favour a greater level of religiosity than their maternal-origin genes (see right half of **Fig. 2.2c**), such that religiosity-promoter loci are expected to be maternally-silenced and paternally-expressed and religiosity-inhibitor loci are expected to be maternally-expressed and paternally-silenced (**Fig. 2.3**). Interestingly, in those scenarios involving within-group relatedness being higher via paternal-origin genes, we expect the pattern of imprinting of religiosity loci to reverse between childhood and adulthood, from maternally-expressed and paternally-silenced to maternally-silenced and paternally-expressed at promoter loci and the other way round at inhibitor loci (**Fig. 2.3**; **Table 2.2**, Prediction 9).

Since only one of the two gene copies at an imprinted locus is expressed, the individual is functionally haploid at this locus and therefore potentially more vulnerable to the detrimental effects of mutation (Wilkins and Haig, 2003). For example, a loss-of-function mutation in the expressed gene would result in the complete absence of the functional gene product at the imprinted locus, with possibly drastic phenotypic consequences, as opposed to a mere halving of the functional gene product that would be expected at a non-imprinted locus. Moreover, imprinting may result in mutations having different phenotypic effects according to their parent of origin. For example, the above loss-of-function mutation would be expected to have no impact upon the phenotype if it occurred in the non-expressed gene at the same locus. We can therefore generate additional predictions about patterns concerning maladaptive phenotypes resulting from the evolution of religiosity (**Fig. 2.3**). For instance, if we consider a promoter locus for religiosity in children, we expect the paternal-origin gene to be

		Children		Adults	
		Religiosity promoter	Religiosity inhibitor	Religiosity promoter	Religiosity inhibitor
Normal					
Gene deletion	Maternal				
	Paternal				
Uniparental disomy	Maternal				
	Paternal				
Gene duplication	Maternal				
	Paternal				
Epimutation	Hypomethylation				
	Hypermethylation				

Fig. 2.3 Genomic imprinting and maladaptation in relation to religiosity. Genomic imprinting is predicted to arise as a result of intragenomic conflict over religiosity, and to be associated with maladapted phenotypes including in relation to four classes of mutational perturbation (gene deletions, gene duplications, epimutations, and uniparental disomies). The patterns predicted for adult religiosity phenotypes in this table are for scenarios in which relatedness is higher for the paternal-origin gene rather than for the maternal-origin gene (as in children interacting socially with maternal siblings).

silenced and the maternal-origin gene to be expressed at a level associated with a “normal” religiosity phenotype. Accordingly, mutational deletion of the maternal-origin gene is expected to result in the complete absence of the religiosity-promoting gene product, and therefore a “hyporeligious” phenotype. In contrast, deletion of the paternal-origin gene is expected to have no effect, i.e., giving rise to a “normal” phenotype. The parent-of-origin specific phenotypic consequences of a suite of other mutational and epimutational perturbations can be similarly determined (**Fig. 2.3; Table 2.2**, Prediction 10).

2.4 Discussion

Despite the apparent ubiquity of religion across human populations, the selection pressures that have shaped its cognitive foundations have remained obscure. Crespi and Summers (2014; see also Crespi, 2016) have suggested that the origins of religion might lie in parent-offspring conflict, whereby mothers employed religious indoctrination as a means of manipulating their children into more cooperative behaviour, and that religion has subsequently spread to become a manipulative tool employed more generally in the context of social conflict. We have developed and analysed a mathematical, kin-selection model inspired by this hypothesis. By refocusing attention on the manipulated party, we have derived a suite of new comparative predictions concerning variation in religiosity as a function of sex, age and ecological context, and also parent-of-origin specific patterns of gene expression for loci underpinning religiosity and concomitant maladaptive phenotypes associated with a range of mutational perturbations, which present novel avenues for empirical testing across multiple disciplinary domains.

Our analysis has revealed that kin selection can promote the evolution of religiosity, with an individual's predisposition to religious ideas being an increasing function of relatedness to social partners, on account of the benefits to kin offsetting some of the personal costs of religious manipulation. This strengthens the plausibility of Crespi and Summers' (2014) hypothesis, by helping to explain why individuals would not be favoured to reduce their vulnerability to indoctrination, and also yields new comparative predictions concerning how variation in religiosity across populations is characterised by different demographics. In relation to maternal manipulation, we have found that children should be more readily accepting of religious indoctrination that promotes cooperation with their maternal siblings as the likelihood of their sharing the same father increases, on account of this being associated with greater relatedness between siblings. Following from this, we would expect that children in traditionally more monogamous and polygynous populations to be more predisposed to religiosity than children in polyandrous populations. Similarly, we have found that the susceptibility of adults to religious indoctrination should also be higher when they are more related to their social partners, as for example in populations characterised by lower rates of dispersal and higher degrees of reproductive skew.

Our analysis also yields new comparative predictions concerning how religiosity varies within populations – in particular, between the sexes. In the context of our model there are no relatedness differences between girls and boys with respect to their maternal siblings, which gives no basis for expecting sex differences in religiosity to manifest in childhood. However, if the sexes disperse at different rates, then we expect them to experience different degrees of relatedness to social partners in adulthood, with individuals of the least-dispersing sex tending to interact with more highly related social

partners and hence being favoured to have a greater predisposition to religiosity. For example, if men predominantly move to other groups in order to live with their spouse and the latter's kin (matrilocal), as has been suggested for ancestral Austronesian societies (Jordan *et al.*, 2009), we would expect women, who tend to stay in their natal groups, to be more related to each other than are men, and hence that religiosity would be higher in women. In a population with a polyandrous mating system, we would expect that this effect would be even stronger. Phylogenetic analyses from contemporary hunter-gatherer societies, however, indicate that serial monogamy or low-level polygyny are more likely mating systems for ancestral populations (Walker *et al.*, 2011). If this was the case for ancestral Austronesian societies, reproductive variance would be higher for men than women with the consequence that we would expect that men would favour a higher degree of religiosity compared to women.

In addition, we have found potential for within-individual, intragenomic conflict between maternal-origin and paternal-origin genes in both children and adults, to the extent that there is parent-of-origin information available. Differential within-group relatedness via maternal-origin versus paternal-origin genes leads to these genes favouring different levels of religiosity and may consequently lead to the evolution of parent-of-origin specific gene expression, i.e., “genomic imprinting” (Haig, 1997). By considering loci that either promote or inhibit the expression of traits associated with religiosity, our predictions regarding imprinting status for different phenotypes (see **Fig. 2.3**) can be tested directly and furthermore, may give us insight into historical dispersal and mating patterns. In populations in which children are raised alongside maternal siblings who need not be paternal siblings, their maternal-origin genes are expected to favour a higher degree of religiosity than their paternal-origin genes, such that

religiosity-promoter loci are expected to be maternally-expressed and paternally-silenced and religiosity-inhibitor loci are expected to be maternally-silenced and paternally-expressed, except in the complete absence of female promiscuity (i.e., maternal siblings always have the same father). In contrast, we expect patterns of genomic imprinting in adults to be more dependent on sex-specific patterns of dispersal and reproductive skew. Indeed, in populations characterised by female-biased dispersal (i.e., patrilocality) and/or male-biased reproductive skew (i.e., polygyny) we expect an adult's paternal-origin genes to favour a higher level of religiosity than their maternal-origin genes, and hence a pattern of genomic imprinting exactly opposite to that for children in the same population. This implies that, for any locus whose action influences religiosity both in children and in adults, the pattern of imprint will reverse as the individual ages from childhood to adulthood.

Our analysis also yields new predictions concerning maladaptive phenotypes arising from a range of mutational perturbations. These predictions provide an avenue for improved understanding of clinical disorders manifesting a religiosity dimension. For instance, mis-expression of imprinted genes can lead to phenotypically diametric disorders such as Beckwith-Wiedemann and Silver-Russell Syndromes, or Prader-Willi and Angelman Syndromes, with profound effects on pre- and post-natal growth, adult metabolism, and social cognition (Ishida and Moore, 2013; Kalish *et al.*, 2014; Millership *et al.*, 2019; Peters, 2014; Plasschaert and Bartolomei, 2014; Wilkinson *et al.*, 2007). To the extent that religiosity is associated with mentalistic cognition, it is worth considering disorders that affect theory-of-mind and related capabilities, such as autism and psychosis (e.g., Gray *et al.*, 2011; also see Hill and Frith, 2003): whilst there is evidence of a positive association between schizotypal traits and aspects of religiosity

(e.g., Barnes and Gibson, 2013; Breslin and Lewis, 2015; Iyassu *et al.*, 2014; Lindeman and Lipsanen, 2016), the relationship between autistic traits and religiosity appears more complex (Jack *et al.*, 2016; Lindeman and Lipsanen, 2016; Norenzayan *et al.*, 2012; Reddish *et al.*, 2016). Crespi and Badcock (2008) have argued that autism and psychosis represent opposite extremes of mentalistic-mechanistic cognition (see e.g., Thakkar *et al.*, 2008, for an opposing view), and that this has a bearing on the clinical consequences of genomic-imprinting disorders. This “imprinted-brain” theory holds that negative symptoms in autism-spectrum disorders, and positive symptoms in psychotic-spectrum conditions, represent hypo-mentalistic, or paternally biased, and hyper-mentalistic, or maternally biased cognition, respectively, resulting from dysregulated imprinting. For example: lack of expression of the maternally expressed gene *UBE3A* in the 15q11-q13 chromosomal region is implicated in the pathogenesis of Angelman Syndrome, which exhibits autism-spectrum characteristics; overexpression of *UBE3A* is implicated in the pathogenesis of Prader-Willi Syndrome, which exhibits psychosis-related characteristics; and genetic variation in *UBE3A* architecture is associated with variation in total schizotypy, i.e., degree of psychosis-related characteristics (Salminen *et al.*, 2019). Since religious delusions are prevalent in psychosis-spectrum disorders (Anderson-Schmidt, 2019), the 15q11-q13 chromosomal region presents a possible focus for future investigation into genetic influences upon religiosity and – combined with data on ancestral mating and dispersal patterns – empirical testing of our predictions.

Our aim has been to investigate how patterns of genetic relatedness translate into clear-cut, comparative predictions that may serve to illuminate the selective forces that have modulated the evolution of religiosity. To this end, we have not explicitly

considered the consequences of individual variation in the costs and benefits. This shortcoming is particularly acute in relation to our predictions concerning sex differences in religiosity, as women and men are liable to experience different personal-fitness consequences of their own and their social partners' religiosity phenotypes, and such effects are liable to confound the patterns we have described here. A general driver of sex differences in costs and benefits is sexual selection, which across many species – including humans – is expected to operate differently between females and males (Andersson, 1994; Darwin, 1871), and indeed sexual selection has been suggested to be a key driver of the evolution of religion itself (Miller, 2007; see also Soler and Lenfesty, 2016; for an in depth summary of hypotheses see Czachesz, 2018). An exploration of sex-specific costs and benefits represents a major avenue for future exploration on this topic. In contrast, our predictions concerning intragenomic conflicts and concomitant patterns of imprinting and associated clinical disorders are expected to be robust to sex differences in cost and benefit as they hinge upon inclusive-fitness differences between genes that reside in the very same bodies, and thereby naturally control for such confounding variables (cf. Rautiala and Gardner, 2016).

Similarly, although the scenario described by Crespi and Summers (2014) and investigated here involves a flow of ideas concerning supernatural agents from mother to child, and between group mates more generally, our explicit focus has been on the genetical moulding of the religiosity phenotype and accordingly the cultural dynamics of these religious beliefs have remained implicit. Our analysis seeks to understand the consequences of there being at least some genetic variation in religiosity, and it does not require that all – or even most – of the variation in such traits has a genetic basis. In combination with research into ancestral ecologies, our predictions as to the

relationships between religiosity and ecological parameters yield insights not only into the selective origins of religion, but also into the demographic circumstances that influenced its expression. Nonetheless, we anticipate cultural transmission dynamics to also play a crucial role in determining these traits and systems, including in relation to gene-culture co-evolution (e.g., Bulbulia, 2008; Czachesz, 2018; Ferretti and Adornetti, 2014; Norenzayan *et al.*, 2016; Rowthorn, 2011; Szocik, 2017). For example, it has been suggested that ancestor worship has evolved as a descendant-leaving strategy with culturally learned, cross-generationally transmitted cooperation among descendants – incentivised by supernatural concepts – leading to greater success for one’s lineage (Clark and Coe, 2021; Coe *et al.*, 2010). Such an approach could represent a bridge between our kin-selection approach and more culturally focused approaches to investigating the evolution of religious systems. Moreover, the possible role for religion to modulate how individuals from different backgrounds with different religious systems interact with each other might also have had a major impact upon population demography and genetic evolution. These represent exciting avenues for future exploration.

2.5 Extended methods

2.5.1 *General analysis of religiosity*

We can express a focal juvenile’s relative fitness W in terms of their own investment into religiosity (x_{FJ} if they are female and x_{MJ} if they are male), their siblings’ average investment into religiosity (y_{FJ} for their sisters and y_{MJ} for brothers), their parents’ investment into religiosity (x_{FA} for their mother and x_{MA} for their father), their parents’ social partners’ average investment into religiosity (y_{FA} for women and y_{MA} for men), as

well as the population averages of these quantities (z_{FJ} , z_{MJ} , and z_{FA} , z_{MA}), where F and M denote female and male, and J and A denote juvenile and adult, respectively. We assume that the fitness function is symmetrical with respect to the sex of actor and recipient, such that the only possible sex differences are with respect to the phenotypes that individuals express.

We consider an autosomal locus G_{ij} which influences the degree of religiosity of a class- ij individual, where $i \in \{F, M\}$ and $j \in \{J, A\}$. Drawing one of the focal individual's two genes at random from this locus and denoting its genic value by g_{ij} , then natural selection acts to increase the population average genic value – and hence the average investment made by class- ij individuals into religiosity – if $dW/dg_{ij} > 0$, where the derivative is evaluated at the population average (Taylor and Frank, 1996). Since a given carrier may be female or male, relative fitness is given as a weighted average taken across female and male juveniles, i.e., $W = c_F W_F + c_M W_M$ (Taylor, 1996), where $c_F = c_M = 1/2$ are the class reproductive values of female and male juveniles, respectively (Fisher, 1930; Price, 1970; Taylor, 1996). Assuming that a gene's impact on the phenotype does not depend on its parent of origin, we can rewrite the left-hand side of the above condition, using the chain rule, as:

$$\frac{dW}{dg_{ij}} = \sum_{k \in \{F, M\}} c_k \sum_{\substack{l \in \{F, M\} \\ m \in \{J, A\}}} \left(\frac{\partial W_k}{\partial x_{lm}} \frac{\partial x_{lm}}{\partial G_{lm}} \frac{dG_{lm}}{dg_{kij}} + \frac{\partial W_k}{\partial y_{lm}} \frac{\partial y_{lm}}{\partial G_{lm'}} \frac{dG_{lm'}}{dg_{kij}} \right), \quad (2.1)$$

where: G_{lm} is the focal individual's genetic value (if $m = J$) or the focal individual's sex- l parent's genetic value (if $m = A$), for the class- lm investment into religiosity; G_{lm}' is the average genetic value of the focal individual's sex- l siblings (if $m = J$) or the focal individual's parents' sex- l social partners (if $m = A$), for the class- lm investment into religiosity; $\partial x_{lm}/\partial G_{lm} = \partial y_{lm}/\partial G_{lm}' = \gamma_{lm}$ represents the mapping of class- lm religiosity

genetic value to class- lm religiosity phenotype; dG_{lm}/dg_{kij} represents the genetic association between a sex- k juvenile's class- ij religiosity genic value and either their own (if $m = J$) or their sex- l parent's (if $m = A$) class- lm religiosity genetic value; and dG_{lm}'/dg_{kij} represents the genetic association between a sex- k juvenile's class- ij religiosity genic value and either their sex- l siblings' (if $m = J$) or their parents' sex- l social partners' (if $m = A$) class- lm religiosity genetic value, where $l \in \{F, M\}$ and $m \in \{J, A\}$. Note that $\partial W_k/\partial x_{lm} = 0$ if $l \neq k$ and $m = J$, as the focal juvenile's fitness is not a function of the phenotype it would have expressed had it been a member of the opposite sex. Also note that if $l = i$ and $m = j$ then $dG_{lm}/dg_{kij} = p_{kij}$ represents the consanguinity of a sex- k juvenile to themselves (if $m = j = J$) or to their sex- l parent (if $m = j = A$) and $dG_{lm}'/dg_{kij} = p_{kij}'$ represents the consanguinity of a sex- k juvenile to their sex- l siblings (if $m = j = J$) or to their parents' sex- l social partners (if $m = j = A$), and if $l \neq i$ and/or $m \neq j$ then $dG_{lm}/dg_{kij} = dG_{lm}'/dg_{kij} = 0$ upon the assumption that there is no pleiotropy or linkage disequilibrium between the different classes' religiosity traits. Further note that, owing to the symmetries of diploid inheritance, $p_{kij} = p_{ij}$ and $p_{kij}' = p_{ij}'$ for all $k \in \{F, M\}$. Accordingly, natural selection favours an increase in religiosity, if:

$$-C(z_{ij}) + B(z_{ij}) r_{ij} > 0, \quad (2.2)$$

where: $r_{ij} = p_{ij}'/p_{ij}$ is the kin-selection coefficient of relatedness between the actor and recipient, which is determined by the respective consanguinities which may differ according to dispersal patterns and mating system (see below; Bulmer, 1994); $-C(z_{ij}) = c_F \partial W_F/\partial x_{lm} + c_M \partial W_M/\partial x_{lm}$ is the marginal direct fitness effect of increased investment into the trait by the focal individual during childhood or by the parents during adulthood respectively; and $B(z_{ij}) = c_F \partial W_F/\partial y_{lm} + c_M \partial W_M/\partial y_{lm}$ is the marginal indirect fitness cost

or benefit of increased investment into the trait by the juvenile maternal siblings or by the adult group members, respectively.

Note that p_{ij} and p_{ij}' are strictly speaking the consanguinities of the recipient to the part of the relevant actor's genotype that controls the actor's phenotype. If both genes at a locus share equal control over the actor's phenotype, then we have $p_{ij} = p_{ij|I} = 1/2 p_{ij|M} + 1/2 p_{ij|P}$ and $p_{ij}' = p_{ij|I}' = 1/2 p_{ij|M}' + 1/2 p_{ij|P}'$, where $p_{ij|I}$ represents the consanguinity of a juvenile to themselves (if $j = J$) or to their sex-I parent (if $j = A$), $p_{ij|M}$ represents the juvenile's consanguinity to this individual's maternal-origin gene, $p_{ij|P}$ represents the juvenile's consanguinity to this individual's paternal-origin gene, $p_{ij|I}'$ represents the consanguinity of the juvenile to their sex-i siblings (if $j = J$) or to their parents' sex-i social partners (if $j = A$), $p_{ij|M}'$ represents the juvenile's consanguinity to these individuals' maternal-origin genes, $p_{ij|P}'$ represents the juvenile's consanguinity to these individuals' paternal-origin genes, and relatedness is given by $r_{ij} = r_{ij|I} = p_{ij|I}'/p_{ij|I}$. If instead the actor's phenotype is fully controlled by only their maternal-origin gene, then we have $p_{ij} = p_{ij|M}$ and $p_{ij}' = p_{ij|M}'$, and relatedness is given by $r_{ij} = r_{ij|M} = p_{ij|M}'/p_{ij|M}$. And if the actor's phenotype is fully controlled by only their paternal-origin gene, then we have $p_{ij} = p_{ij|P}$ and $p_{ij}' = p_{ij|P}'$, and relatedness is given by $r_{ij} = r_{ij|P} = p_{ij|P}'/p_{ij|P}$.

The condition for increase takes the form $-C(z_{ij}) + B(z_{ij})\rho > 0$, where $\rho = r_{ij|M}$ for maternal-origin control, $\rho = r_{ij|P}$ for paternal-origin control, and $\rho = r_{ij|I}$ for equal control. Assuming that an intermediate, convergence-stable equilibrium z_{ij}^* exists, then we can define a function $J(z_{ij}^*, \rho) = -C(z_{ij}^*) + B(z_{ij}^*)\rho$ such that $J(z_{ij}^*, \rho) = 0$ and $\partial J/\partial z_{ij}^* < 0$ (Christiansen 1991, Taylor 1996). Using the chain rule, we can write $dJ/d\rho = (\partial J/\partial \rho) + (\partial J/\partial z_{ij}^*)(dz_{ij}^*/d\rho) = 0$, which rearranges as $dz_{ij}^*/d\rho = -(\partial J/\partial \rho)/(\partial J/\partial z_{ij}^*)$, and hence $S(dz_{ij}^*/d\rho) = S(\partial J/\partial \rho) = S(B(z_{ij}^*))$ where the function S returns the sign of its

argument (positive, negative or zero) (Pen, 2000; Farrell *et al.*, 2015). Consequently, if the religiosity of social partners improves the focal individual's fitness ($B > 0$), then higher relatedness is associated with a higher religiosity optimum ($dz_{ij}^*/d\rho > 0$); if the religiosity of social partners decreases the focal individual's fitness ($B < 0$), then higher relatedness is associated with a lower religiosity optimum ($dz_{ij}^*/d\rho < 0$); and if the religiosity of social partners does not affect the focal individual's fitness ($B = 0$), then higher relatedness is not associated with a higher or lower religiosity optimum ($dz_{ij}^*/d\rho = 0$).

Therefore, assuming that the religiosity of social partners improves the focal individual's fitness ($B > 0$), then: higher relatedness is associated with a higher religiosity optimum ($dz_{ij}^*/d\rho > 0$), recovering results 1-4 of the main text; the religiosity optimum is higher for women than it is for men ($z_{FA}^* > z_{MA}^*$) if relatedness is higher for women than men ($r_{FA} > r_{MA}$), and the religiosity optimum is lower for women than for men ($z_{FA}^* < z_{MA}^*$) if relatedness is lower for women than men ($r_{FA} < r_{MA}$), recovering results 5 and 6 of the main text; maternal-origin genes will favour a higher religiosity optimum than paternal-origin genes ($z_{ij|M}^* > z_{ij|I}^* > z_{ij|P}^*$) when relatedness is higher for the former than the latter ($r_{ij|M} > r_{ij|I} > r_{ij|P}$) and maternal-origin genes will favour a lower religiosity optimum than paternal-origin genes ($z_{ij|M}^* < z_{ij|I}^* < z_{ij|P}^*$) when relatedness is lower for the former than for the latter ($r_{ij|M} < r_{ij|I} < r_{ij|P}$), recovering results 7-9 of the main text. If the religiosity of social partners decreases the focal individual's fitness ($B < 0$) then our predictions are exactly reversed, and if the religiosity of social partners does not affect the fitness of the focal individual ($B = 0$), then the religiosity optimum for females is equal to that for males ($z_{FA}^* = z_{MA}^*$), and the religiosity optimum for maternal-origin genes is equal to that for genes ignorant of their

origin as well as paternal-origin genes ($z_{ij|M}^* = z_{ij|I}^* = z_{ij|P}^*$), with none of these quantities being dependent upon relatedness.

2.5.2 Illustration

To illustrate how this general analysis applies to hypotheses about specific functions of religiosity, we construct a simple model which incorporates associated cognitive properties of religiosity in juveniles, adults, females, and males, in a variety of demographic scenarios. We assume an even sex ratio at birth, such that K girls and K boys are born in each group, where K is a large constant. We denote the probability that two juveniles born in the same group share the same mother by α and the probability that they share the same father by β , and we assume that every child is the product of an independent, random pairing of a woman and man such that the probability that two maternal siblings share the same father is also β ; this allows us to explore the effects of modulating the degree of polyandry (by varying α) and the degree of polygyny (by varying β). We denote the probability of a child's survival to adulthood by S_k , and we assume that this is a function of their own (x_{kj}), their parents' (x_{FA} and x_{MA}), their maternal siblings' (y_{FJ} and y_{MJ}) and their parents' group mates' (y_{FA} , y_{MA}) investment into religiosity. All adults of the parental generation then die, such that there is no overlapping of generations. The surviving individuals within each group organise themselves into smaller groups or 'buds' at random with some of their peers – with all buds containing the same number of individuals, and having an even sex ratio, and with any excess of individuals of one sex that are not incorporated into buds being assumed to perish – with the buds then dispersing to random locations elsewhere in the population (i.e., group fissioning; Gardner and West, 2006) and competing with the

other groups that have also dispersed there for control of the resources in that location. One group is chosen at random to survive this competition in each location to be the parents of the next generation of children to be born there. Following this density-dependent regulation that maintains the total number of groups in the population at a fixed level, adults disperse with sex-specific rates – d_F for women and d_M for men – to other groups, occupying places vacated by other dispersers, or else remain in their native group.

We assume that a juvenile's survival is given by the product of (i) a theory-of-mind benefit equal to their own level of religiosity; (ii) their share of parental resources obtained in competition with their maternal siblings; (iii) their mother's share of group reproductive resources obtained in competition with other women; and (iv) their father's share of reproductive resources obtained in competition with other men. We assume that resources are shared according to a "tragedy of the commons" (Frank, 1998) scenario, whereby the proportion of resources seized by an individual is proportional to their competitiveness and the total amount of resources is proportional to the extent that the group members refrain from outright competitiveness, and that an individual's competitiveness is equal to one unit minus their level of religiosity. Accordingly, a sex- k juvenile survives to adulthood with probability:

$$S_k = x_{kJ} \frac{1-x_{kJ}}{1-\left(\frac{1}{2}y_{FJ}+\frac{1}{2}y_{MJ}\right)} \left(\frac{1}{2}y_{FJ} + \frac{1}{2}y_{MJ}\right) x_{FA} \frac{1-x_{FA}}{1-y_{FA}} \left(\frac{1}{2}y_{FA} + \frac{1}{2}y_{MA}\right) x_{MA} \frac{1-x_{MA}}{1-y_{MA}} \left(\frac{1}{2}y_{FA} + \frac{1}{2}y_{MA}\right). \quad (2.3)$$

A sex- k juvenile's expected relative fitness is $W_k = S_k / \bar{S}_k$ if sex- k is the rarer sex and is $W_k = (S_k / S'_k) \times (S'_{-k} / \bar{S}_{-k})$ if sex- k is the more-common sex, where S'_k is the average survival of sex- k juveniles in the focal individual's group, S'_{-k} is the average survival of

non-sex-k juveniles in the focal individual's group, \bar{S}_k is the average survival of sex-k juveniles across the whole population, and \bar{S}_{-k} is the average survival of non-sex-k juveniles across the whole population. Also note that: for a juvenile trait ($j = J$) we have $p_{ij} = q_{\text{self}}$ and $p_{ij}' = q_{\text{sib}}$; for an adult trait ($j = A$) we have $p_{ij} = q_{\text{par}}$ and $p_{ij}' = q_F$ (if $i = F$) or $p_{ij}' = q_M$ (if $i = M$); and that $r_{\text{sib}} = q_{\text{sib}}/q_{\text{self}}$, $r_F = q_F/q_{\text{par}}$ and $r_M = q_M/q_{\text{par}}$, where $r_{\text{sib}} = r_{\text{sib}|I} = q_{\text{sib}|I}/q_{\text{self}|I}$, $r_F = r_F|I = q_F|I/q_{\text{par}|I}$, and $r_M = r_M|I = q_M|I/q_{\text{par}|I}$, if both genes at a locus share equal control over the actor's phenotype, $r_{\text{sib}} = r_{\text{sib}|M} = q_{\text{sib}|M}/q_{\text{self}|M}$, $r_F = r_F|M = q_F|M/q_{\text{par}|M}$, and $r_M = r_M|M = q_M|M/q_{\text{par}|M}$, if the actor's phenotype is fully controlled by only their maternal-origin gene, and $r_{\text{sib}} = r_{\text{sib}|P} = q_{\text{sib}|P}/q_{\text{self}|P}$, $r_F = r_F|P = q_F|P/q_{\text{par}|P}$, and $r_M = r_M|P = q_M|P/q_{\text{par}|P}$, if the actor's phenotype is fully controlled by only their paternal-origin gene.

Evaluating the cost and benefit terms in expression (2.2) for this illustrative fitness function, we obtain the condition for natural selection to favour an increase in the level of religiosity exhibited by female juveniles as:

$$\frac{1-2z_{FJ}}{2z_{FJ}(1-z_{FJ})} + \frac{2}{(z_{FJ}+z_{MJ})(2-z_{FJ}-z_{MJ})} r_{\text{sib}} + \varepsilon_{FJ} > 0, \quad (2.4)$$

where $\varepsilon_{FJ} = [(1-2z_{FJ})/(2z_{FJ}(1-z_{FJ}))]r_{\text{group}}$ if $z_{FJ}(1-z_{FJ}) < z_{MJ}(1-z_{MJ})$ and $\varepsilon_{FJ} = -[(1-2z_{FJ})/(2z_{FJ}(1-z_{FJ}))]r_{\text{group}}$ if $z_{FJ}(1-z_{FJ}) > z_{MJ}(1-z_{MJ})$, and where r_{group} is the relatedness of two juveniles born in the same group. Similarly, we find that the condition for natural selection to favour an increase in the level of religiosity exhibited by male juveniles is:

$$\frac{1-2z_{MJ}}{2z_{MJ}(1-z_{MJ})} + \frac{2}{(z_{FJ}+z_{MJ})(2-z_{FJ}-z_{MJ})} r_{\text{sib}} + \varepsilon_{MJ} > 0, \quad (2.5)$$

where $\varepsilon_{MJ} = -[(1-2z_{MJ})/(2z_{MJ}(1-z_{MJ}))]r_{\text{group}}$ if $z_{FJ}(1-z_{FJ}) < z_{MJ}(1-z_{MJ})$ and $\varepsilon_{MJ} = [(1-2z_{MJ})/(2z_{MJ}(1-z_{MJ}))]r_{\text{group}}$ if $z_{FJ}(1-z_{FJ}) > z_{MJ}(1-z_{MJ})$, the condition for natural selection to favour an increase in the level of religiosity exhibited by women is:

$$\frac{(z_{FA}+z_{MA})(1-2z_{FA})}{2z_{FA}(1-z_{FA})(z_{FA}+z_{MA})} + \frac{z_{FA}(2-z_{FA}+z_{MA})}{2z_{FA}(1-z_{FA})(z_{FA}+z_{MA})} r_F > 0, \quad (2.6)$$

and the condition for natural selection to favour an increase in the level of religiosity exhibited by men is:

$$\frac{(z_{FA}+z_{MA})(1-2z_{MA})}{2z_{MA}(1-z_{MA})(z_{FA}+z_{MA})} + \frac{z_{MA}(2-z_{MA}+z_{FA})}{2z_{MA}(1-z_{MA})(z_{FA}+z_{MA})} r_M > 0. \quad (2.7)$$

2.5.2.1 Relatedness

We can calculate an individual's consanguinity to any social partner (including themselves) as the probability that a gene drawn at random from the focal individual and a gene drawn at random from their social partner from the same locus (with replacement, in the event that the social partner is the focal individual themselves) are identical by descent (Bulmer, 1994).

The consanguinity of the focal individual to self is:

$$q_{\text{self}} = q_{\text{self}|I} = q_{\text{self}|M} = q_{\text{self}|P} = \frac{1}{2} + \frac{1}{2}\phi, \quad (2.8)$$

i.e., with probability $\frac{1}{2}$ the same gene is drawn twice, in which case the consanguinity is 1, and with probability $\frac{1}{2}$ the individual's two genes at this locus are both drawn, in which case the consanguinity is that of the individual's parents, Φ .

The consanguinity of an individual's parents equals that of two mating partners:

$$\phi = (1 - d_F)(1 - d_M) q_{\text{juv}|I}, \quad (2.9)$$

i.e., with probability $(1-d_F)(1-d_M)$ neither the female nor the male partner dispersed (that is they both remained in their native group), in which case their consanguinity is that of two juveniles born in the same group, $q_{juv|I}$.

The consanguinity between two juveniles born in the same group is:

$$q_{juv|I} = \frac{1}{2} q_{juv|M} + \frac{1}{2} q_{juv|P}, \quad (2.10)$$

i.e., the average of the consanguinity $q_{juv|M}$ of a focal juvenile to the maternal-origin gene of another juvenile in the same group and the consanguinity $q_{juv|P}$ of the focal juvenile to the paternal-origin gene of the other juvenile in the group.

The consanguinity of a focal juvenile to the maternal-origin gene of another juvenile in the group is:

$$q_{juv|M} = \frac{1}{2} (\alpha q_{self} + (1 - \alpha)(1 - d_F)^2 q_{juv|I}) + \frac{1}{2} \phi, \quad (2.11)$$

i.e., with probability $\frac{1}{2}$ the maternal-origin gene is drawn in the focal individual, in which case their consanguinity is determined by the probability α that both individuals have the same mother, in which case their consanguinity is equal to the consanguinity q_{self} of their mother to herself, and the probability $1-\alpha$ that they have different mothers as well as the probability $(1-d_F)^2$ that neither of the mothers dispersed, in which case their consanguinity is again that of two juveniles born in the same group $q_{juv|I}$; and with probability $\frac{1}{2}$ the paternal-origin gene is drawn in the focal individual, in which case their consanguinity is that of two mating partners ϕ .

The consanguinity of a focal juvenile to the paternal-origin gene of another juvenile in the group is:

$$q_{juv|P} = \frac{1}{2} (\beta q_{self} + (1 - \beta)(1 - d_M)^2 q_{juv|I}) + \frac{1}{2} \phi, \quad (2.12)$$

i.e., with probability $\frac{1}{2}$ the paternal-origin gene is drawn from the focal individual, in which case their consanguinity is determined by the probability β that both individuals have the same father, in which case their consanguinity is equal to the consanguinity q_{self} of their father to himself, and the probability $1-\beta$ that they have different fathers as well as the probability $(1-d_M)^2$ that neither of the fathers dispersed, in which case their consanguinity is again that of two juveniles born in the same group $q_{\text{juv } |I}$; and with probability $\frac{1}{2}$ the maternal-origin gene is drawn from the focal individual, in which case their consanguinity is that of two mating partners Φ .

The consanguinity of maternal siblings is given by:

$$q_{\text{sib } |I} = \frac{1}{2} q_{\text{sib } |M} + \frac{1}{2} q_{\text{sib } |P}, \quad (2.13)$$

i.e., the average of the consanguinity $q_{\text{sib } |M}$ of a focal juvenile to the maternal-origin gene of their maternal sibling, and the consanguinity $q_{\text{sib } |P}$ of the focal juvenile to the paternal-origin gene of their maternal sibling.

The consanguinity of a juvenile to the maternal-origin gene of their maternal sibling is given by:

$$q_{\text{sib } |M} = \frac{1}{2} q_{\text{self}} + \frac{1}{2} \phi, \quad (2.14)$$

i.e., with probability $\frac{1}{2}$ the maternal-origin gene is drawn from the focal individual, in which case their consanguinity is q_{self} , and with probability $\frac{1}{2}$ the paternal-origin gene is drawn from the focal individual, in which case the consanguinity is that between mating partners Φ .

The consanguinity of a focal juvenile to the paternal-origin gene of their maternal sibling may differ from the consanguinity to the maternal-origin gene of their maternal sibling such that:

$$q_{\text{sib}|P} = \frac{1}{2}\phi + \frac{1}{2}(\beta q_{\text{self}} + (1 - \beta)(1 - d_M)^2 q_{\text{juv}|I}), \quad (2.15)$$

i.e., with probability $\frac{1}{2}$ the maternal-origin gene is drawn from the focal individual, in which case their consanguinity is that of two mating partners Φ ; and with probability $\frac{1}{2}$ the paternal-origin gene is drawn from the focal individual, in which case their consanguinity is determined by the probability that both individuals have the same father β , in which case consanguinity is equal to the consanguinity to self q_{self} , and the probability $1 - \beta$ that they have different fathers as well as the probability $(1 - d_M)^2$ that neither of their fathers dispersed, in which case their consanguinity is again that of two juveniles born in the same group $q_{\text{juv}|I}$.

The consanguinity between the focal individual and their parents is given by:

$$q_{\text{par}} = \frac{1}{2}q_{\text{mum}} + \frac{1}{2}q_{\text{dad}}, \quad (2.16)$$

i.e., with probability $\frac{1}{2}$ a gene from the mother is drawn, in which case their consanguinity is q_{mum} ; and with probability $\frac{1}{2}$ a gene from the father is drawn, in which case their consanguinity is q_{dad} .

The consanguinity between the focal individual and their mother is given by:

$$q_{\text{mum}} = \frac{1}{2}q_{\text{self}} + \frac{1}{2}\phi, \quad (2.17)$$

i.e., with probability $\frac{1}{2}$ the maternal-origin gene is drawn from the focal individual, in which case the consanguinity is that of the mother to herself, q_{self} ; and with probability

$\frac{1}{2}$ the paternal-origin gene is drawn from the focal individual, in which case the consanguinity is that of the parents to each other, Φ .

The consanguinity between the focal individual and their father is given by:

$$q_{\text{dad}} = \frac{1}{2} \phi + \frac{1}{2} q_{\text{self}}, \quad (2.18)$$

i.e., with probability $\frac{1}{2}$ the maternal-origin gene is drawn from the focal individual, in which case the consanguinity is that of the parents to each other, Φ ; and with probability $\frac{1}{2}$ the paternal-origin gene is drawn from the focal individual, in which case the consanguinity is that of the father to himself, q_{self} .

The consanguinity between the focal individual and their parents' female social partners is given by:

$$q_{F|I} = \frac{1}{2} (\alpha q_{\text{self}} + (1 - \alpha)(1 - d_F)^2 q_{\text{juv}|I}) + \frac{1}{2} (1 - d_F)(1 - d_M) q_{\text{juv}|I}, \quad (2.19)$$

i.e., with probability $\frac{1}{2}$ the maternal-origin gene is drawn from the focal individual, in which case the consanguinity to a random woman in the group is determined by the probability α that this woman is the focal individual's mother, in which case their consanguinity is equal to q_{self} , and the probability $1 - \alpha$ that this woman is not the focal juvenile's mother as well as the probability $(1 - d_F)^2$ that neither this woman nor the focal individual's mother dispersed, in which case their consanguinity is that of two juveniles born in the same group, $q_{\text{juv}|I}$; and with probability $\frac{1}{2}$ the paternal-origin gene is drawn from the focal individual, in which case the consanguinity to a random woman in the group is determined by the probability $(1 - d_F)(1 - d_M)$ that neither this woman nor the focal individual's father dispersed, in which case their consanguinity is equal to $q_{\text{juv}|I}$.

The consanguinity between the focal individual and their parents' male social partners is given by:

$$q_{M|I} = \frac{1}{2} (\beta q_{\text{self}} + (1 - \beta)(1 - d_M)^2 q_{\text{juv}|I}) + \frac{1}{2} (1 - d_F)(1 - d_M) q_{\text{juv}|I}, \quad (2.20)$$

i.e., with probability $\frac{1}{2}$ the paternal-origin gene is drawn from the focal individual, in which case the consanguinity to a random man in the group is determined by the probability β that this man is the focal individual's father, in which case their consanguinity is equal to q_{self} , and the probability $1 - \beta$ that this man is not the focal juvenile's father as well as the probability $(1 - d_M)^2$ that neither that man nor the focal individual's father dispersed, in which case their consanguinity is again that of two juveniles born in the same group, $q_{\text{juv}|I}$; and with probability $\frac{1}{2}$ the maternal-origin gene is drawn from the focal individual, in which case the consanguinity to a random man in the group is determined by the probability $(1 - d_F)(1 - d_M)$ that neither this man nor the focal individual's mother dispersed, in which case their consanguinity is equal to $q_{\text{juv}|I}$.

The consanguinity of the focal individual to the maternal-origin gene of their parents' female social partners is given by:

$$q_{F|M} = \frac{1}{2} (\alpha q_{\text{self}} + (1 - \alpha)(1 - d_F)^2 q_{\text{juv}|M}) + \frac{1}{2} (1 - d_F)(1 - d_M) q_{\text{juv}|M}, \quad (2.21)$$

i.e., with probability $\frac{1}{2}$ the maternal-origin gene is drawn from the focal individual, in which case their consanguinity is determined by the probability α that a woman is the focal individual's mother, in which case their consanguinity is equal to q_{self} , and the probability $1 - \alpha$ that this woman is not the focal juvenile's mother as well as the probability $(1 - d_F)^2$ that neither this woman nor the focal individual's mother dispersed, in which case their consanguinity is that of a juvenile's consanguinity to the maternal-

origin gene of another juvenile born in the same group, $q_{juv|M}$; and with probability $\frac{1}{2}$ the paternal-origin gene is drawn from the focal individual, in which case their consanguinity is determined by the probability $(1-d_F)(1-d_M)$ that neither this woman nor the focal individual's father dispersed, in which case their consanguinity is again equal to $q_{juv|M}$.

The consanguinity of the focal individual to the paternal-origin gene of one of their parents' female social partners is given by:

$$q_{F|P} = \frac{1}{2} (\alpha q_{self} + (1 - \alpha)(1 - d_F)^2 q_{juv|P}) + \frac{1}{2} (1 - d_F)(1 - d_M) q_{juv|P}, \quad (2.22)$$

i.e., with probability $\frac{1}{2}$ the maternal-origin gene is drawn from the focal individual, in which case their consanguinity is again determined by the probability α that a woman is the focal individual's mother, in which case their consanguinity is equal to q_{self} , and the probability $1-\alpha$ that this woman is not the focal juvenile's mother as well as the probability $(1-d_F)^2$ that neither this woman nor the focal individual's mother dispersed, in which case their consanguinity is that of a juvenile to the paternal-origin gene of another juvenile born in the same group, $q_{juv|P}$; and with probability $\frac{1}{2}$ the paternal-origin gene is drawn from the focal individual, in which case their consanguinity is determined by the probability $(1-d_F)(1-d_M)$ that neither this woman nor the focal individual's father dispersed, in which case their consanguinity is equal to $q_{juv|P}$.

The consanguinity of the focal individual to the maternal-origin gene of their parents' male social partners is given by:

$$q_{M|M} = \frac{1}{2} (\beta q_{self} + (1 - \beta)(1 - d_M)^2 q_{juv|M}) + \frac{1}{2} (1 - d_F)(1 - d_M) q_{juv|M}, \quad (2.23)$$

i.e., with probability $\frac{1}{2}$ the paternal-origin gene is drawn from the focal individual, in which case their consanguinity is determined by the probability β that a man is the focal individual's father, in which case their consanguinity is equal to q_{self} , and the probability $1-\beta$ that this man is not the focal juvenile's father as well as the probability $(1-d_M)^2$ that neither this man nor the focal individual's father dispersed, in which case their consanguinity is that of a juvenile's consanguinity to the maternal-origin gene of another juvenile born in the same group, $q_{\text{juv}|\text{M}}$; and with probability $\frac{1}{2}$ the maternal-origin gene is drawn from the focal individual, in which case their consanguinity is determined by the probability $(1-d_F)(1-d_M)$ that neither this man nor the focal individual's mother dispersed, in which case their consanguinity is again equal to $q_{\text{juv}|\text{M}}$.

The consanguinity of the focal individual to the paternal-origin gene of one of their parents' male social partners is given by:

$$q_{\text{M}|\text{P}} = \frac{1}{2} (\beta q_{\text{self}} + (1 - \beta)(1 - d_M)^2 q_{\text{juv}|\text{P}}) + \frac{1}{2} (1 - d_F)(1 - d_M) q_{\text{juv}|\text{P}}, \quad (2.24)$$

i.e., with probability $\frac{1}{2}$ the maternal-origin gene is drawn from the focal individual, in which case their consanguinity is again determined by the probability β that a man is the focal individual's father, in which case their consanguinity is equal to q_{self} , and the probability $1-\beta$ that this man is not the focal juvenile's father as well as the probability $(1-d_M)^2$ that neither this man nor the focal individual's father dispersed, in which case their consanguinity is that of a juvenile to the paternal-origin gene of another juvenile born in the same group, $q_{\text{juv}|\text{P}}$; and with probability $\frac{1}{2}$ the maternal-origin gene is drawn from the focal individual, in which case their consanguinity is determined by the probability $(1-d_F)(1-d_M)$ that neither this man nor the focal individual's mother dispersed, in which case their consanguinity is equal to $q_{\text{juv}|\text{P}}$.

The consanguinity of a juvenile to the maternal-origin gene of another juvenile born in the same group is given by:

$$q_{\text{juv}|\text{M}} = \frac{1}{2}(\alpha q_{\text{self}} + (1 - \alpha)(1 - d_{\text{F}})^2 q_{\text{juv}|\text{I}}) + \frac{1}{2}\phi, \quad (2.25)$$

i.e., with probability $\frac{1}{2}$ the maternal-origin gene is drawn from the focal individual, in which case their consanguinity is determined by the probability α that both juveniles have the same mother, in which case their consanguinity is equal to q_{self} , and the probability $1-\alpha$ that they do not have the same mother as well as the probability $(1-d_{\text{F}})^2$ that neither the focal individual's mother nor the other juvenile's mother dispersed, in which case their consanguinity is again that of two juveniles born in the same group, $q_{\text{juv}|\text{I}}$; and with probability $\frac{1}{2}$ the paternal-origin gene is drawn from the focal individual, in which case their consanguinity is equal to Φ .

The consanguinity of a juvenile to the paternal-origin gene in another juvenile born in the same group is given by:

$$q_{\text{juv}|\text{P}} = \frac{1}{2}(\beta q_{\text{self}} + (1 - \beta)(1 - d_{\text{M}})^2 q_{\text{juv}|\text{I}}) + \frac{1}{2}\phi, \quad (2.26)$$

i.e., with probability $\frac{1}{2}$ the paternal-origin gene is drawn from the focal individual, in which case the consanguinity to another juvenile in the group is determined by the probability β that both juveniles have the same father, in which case their consanguinity is equal to q_{self} , and the probability $1-\beta$ that they do not share the same father as well as the probability $(1-d_{\text{M}})^2$ that neither the focal individual's father nor the other juvenile's father dispersed, in which case their consanguinity is again that of two juveniles born in the same group, $q_{\text{juv}|\text{I}}$; and with probability $\frac{1}{2}$ the maternal-origin gene is drawn from the other individual, in which case their consanguinity is equal to Φ .

These consanguinity expressions (2.8 – 2.26) define a closed system of simultaneous equations, which we can solve to obtain explicit forms in terms of population parameters. This yields:

$$q_{\text{self}} = \frac{\alpha - d_F^2(1-\alpha) + 2d_F(2-d_M-\alpha) + d_M(4-2\beta-d_M(1-\beta)) + \beta}{\alpha - 2d_F^2(1-\alpha) + d_M(8+\alpha-3\beta-2d_M(1-\beta)) + \beta + d_F(8-3\alpha+\beta-d_M(4+\alpha+\beta))}, \quad (2.27)$$

$$q_{\text{juv | I}} = \frac{\alpha + \beta}{\alpha - 2d_F^2(1-\alpha) + d_M(8+\alpha-3\beta-2d_M(1-\beta)) + \beta + d_F(8-3\alpha+\beta-d_M(4+\alpha+\beta))}, \quad (2.28)$$

$$q_{\text{juv | M}} = \frac{\alpha(2+d_F-d_F d_M+d_M(3-d_M)) + \beta(2-d_F-d_M)(1-d_M\alpha-d_F(1-\alpha))}{2(\alpha - 2d_F^2(1-\alpha) + d_M(8+\alpha-3\beta-2d_M(1-\beta)) + \beta + d_F(8-3\alpha+\beta-d_M(4+\alpha+\beta)))}, \quad (2.29)$$

$$q_{\text{juv | P}} = \frac{\alpha(2-d_F-d_M)(1-d_M-d_F\beta+d_M\beta) + \beta(2+d_M+d_F(3-d_F-d_M))}{2(\alpha - 2d_F^2(1-\alpha) + d_M(8+\alpha-3\beta-2d_M(1-\beta)) + \beta + d_F(8-3\alpha+\beta-d_M(4+\alpha+\beta)))}, \quad (2.30)$$

$$q_{\text{sib | I}} = \frac{2d_F(1-\alpha)(2-d_M+\beta) - d_F^2(1-\alpha)(1+\beta) + 4(\alpha+\beta) + d_M(1-\alpha)(4-d_M-2\beta+d_M\beta)}{4(\alpha - 2d_F^2(1-\alpha) + d_M(8+\alpha-3\beta-2d_M(1-\beta)) + \beta + d_F(8-3\alpha+\beta-d_M(4+\alpha+\beta)))}, \quad (2.31)$$

$$q_{\text{sib | M}} = \frac{d_M(4-d_M-\alpha) - d_F^2(1-\alpha) - d_M\beta(3-d_M) + 2(\alpha+\beta) + d_F(4-3\alpha-\beta-d_M(2-\alpha-\beta))}{2(\alpha - 2d_F^2(1-\alpha) + d_M(8+\alpha-3\beta-2d_M(1-\beta)) + \beta + d_F(8-3\alpha+\beta-d_M(4+\alpha+\beta)))}, \quad (2.32)$$

$$q_{\text{sib | P}} = \frac{\beta(2+d_M+d_F(3-d_F-d_M)) - 2 + d_F + d_M - \alpha(1-d_M-d_F\beta+d_M\beta)}{2(\alpha - 2d_F^2(1-\alpha) + d_M(8+\alpha-3\beta-2d_M(1-\beta)) + \beta + d_F(8-3\alpha+\beta-d_M(4+\alpha+\beta)))}, \quad (2.33)$$

$$q_{\text{par}} = \frac{d_M(4-d_M-\alpha) - d_F^2(1-\alpha) - d_M\beta(3-d_M) + 2(\alpha+\beta) + d_F(4-3\alpha-\beta-d_M(2-\alpha-\beta))}{2(\alpha - 2d_F^2(1-\alpha) + d_M(8+\alpha-3\beta-2d_M(1-\beta)) + \beta + d_F(8-3\alpha+\beta-d_M(4+\alpha+\beta)))}, \quad (2.34)$$

$$q_{\text{mum}} = \frac{d_M(4-d_M-\alpha) - d_F^2(1-\alpha) - d_M\beta(3-d_M) + 2(\alpha+\beta) + d_F(4-3\alpha-\beta-d_M(2-\alpha-\beta))}{2(\alpha - 2d_F^2(1-\alpha) + d_M(8+\alpha-3\beta-2d_M(1-\beta)) + \beta + d_F(8-3\alpha+\beta-d_M(4+\alpha+\beta)))}, \quad (2.35)$$

$$q_{\text{dad}} = \frac{d_M(4-d_M-\alpha) - d_F^2(1-\alpha) - d_M\beta(3-d_M) + 2(\alpha+\beta) + d_F(4-3\alpha-\beta-d_M(2-\alpha-\beta))}{2(\alpha - 2d_F^2(1-\alpha) + d_M(8+\alpha-3\beta-2d_M(1-\beta)) + \beta + d_F(8-3\alpha+\beta-d_M(4+\alpha+\beta)))}, \quad (2.36)$$

$$\phi = \frac{(1-d_F)(1-d_M)(\alpha+\beta)}{\alpha - 2d_F^2(1-\alpha) + d_M(8+\alpha-3\beta-2d_M(1-\beta)) + \beta + d_F(8-3\alpha+\beta-d_M(4+\alpha+\beta))}, \quad (2.37)$$

$$q_{F|I} = \frac{\alpha(2+d_F-d_F d_M+d_M(3-d_M))+\beta(2-d_F-d_M)(1-d_M\alpha-d_F(1-\alpha))}{2(\alpha-2d_F^2(1-\alpha)+d_M(8+\alpha-3\beta-2d_M(1-\beta)))+\beta+d_F(8-3\alpha+\beta-d_M(4+\alpha+\beta))}, \quad (2.38)$$

$$q_{M|I} = \frac{\alpha(2-d_F-d_M)(1-d_M-d_F\beta+d_M\beta)+\beta(2+d_M+d_F(3-d_F-d_M))}{2(\alpha-2d_F^2(1-\alpha)+d_M(8+\alpha-3\beta-2d_M(1-\beta)))+\beta+d_F(8-3\alpha+\beta-d_M(4+\alpha+\beta))}, \quad (2.39)$$

$$\begin{aligned} q_{F|M} = & \left(\left(\alpha \left(4 + d_F^3 (1 - d_M)(1 - \alpha) + d_M(3 - d_M)(4 - d_M - \alpha) - d_F^2 (3 - \right. \right. \right. \\ & d_M(7 - 5\alpha - d_M(2 - \alpha)) - 2\alpha) + d_F(4 - \alpha - d_M(7(2 - \alpha) + d_M(7 - d_M - 2\alpha))) \left. \left. \left. \right) + \right. \right. \\ & \left. \left. 4\beta - 4 + d_M + d_F(3 - d_F - d_M) + \alpha - d_F\alpha(2 - d_F) \right) \left(d_M + d_F(3 - d_F - d_M) + \right. \right. \\ & \left. \left. \alpha(d_M - d_F)(2 - d_F - d_M) \right) \beta \right) / \left(4 \left(\alpha - 2d_F^2(1 - \alpha) + d_M(8 + \alpha - 3\beta - 2d_M(1 - \beta)) + \right. \right. \\ & \left. \left. \beta + d_F(8 - 3\alpha + \beta - d_M(4 + \alpha + \beta)) \right) \right), \quad (2.40) \end{aligned}$$

$$\begin{aligned} q_{F|P} = & \left(4\alpha + \alpha(d_F(1 - d_M) + d_M(3 - d_M))(\alpha + d_M + d_F(3 - d_F - d_M) - \right. \\ & d_F\alpha(2 - d_F)) + 4\beta - \beta(\alpha + d_M + d_F(3 - d_F - d_M) - d_F\alpha(2 - d_F))(d_M + \\ & d_F(3 - d_F - d_M) + \alpha(d_M - d_F)(2 - d_F - d_M)) \left. \right) / \left(4 \left(\alpha - 2d_F^2(1 - \alpha) + d_M(8 + \alpha - 3\beta - \right. \right. \\ & \left. \left. 2d_M(1 - \beta)) + \beta + d_F(8 - 3\alpha + \beta - d_M(4 + \alpha + \beta)) \right) \right), \quad (2.41) \end{aligned}$$

$$\begin{aligned} q_{M|M} = & \left(\beta \left(4 + (d_M + d_F(3 - d_F - d_M))(d_F(1 - d_M) + d_M(3 - d_M) + \beta(1 - d_M)^2) \right) + \right. \\ & \alpha \left(4 - (d_F(1 - d_M) + d_M(3 - d_M) + \beta(1 - d_M)^2) \left(d_F + 3d_M - d_F d_M - d_M^2 - \right. \right. \\ & \left. \left. \beta(d_M - d_F)(2 - d_F - d_M) \right) \right) \left. \right) / \left(4 \left(\alpha - 2d_F^2(1 - \alpha) + d_M(8 + \alpha - 3\beta - 2d_M(1 - \beta)) + \right. \right. \\ & \left. \left. \beta + d_F(8 - 3\alpha + \beta - d_M(4 + \alpha + \beta)) \right) \right), \quad (2.42) \end{aligned}$$

and

$$\begin{aligned}
q_{M|P} = & \left(4\beta + \beta(d_M + d_F(3 - d_F - d_M))(4 - 3d_M - d_F(1 - d_M) + d_M^2 - \beta(1 - d_M)^2) + \right. \\
& \alpha \left((1 - d_M)^2 (2 - d_F - d_M)^2 + \beta \left(d_F^2 (3 - d_M)(2 - d_M) - d_F^3 (1 - d_M) - \right. \right. \\
& d_F(7 - d_M - 4d_M^2 + 2d_M^3) + d_M(11 - d_M(17 - 2d_M(5 - d_M))) \left. \left. \right) \right) + \beta^2(1 - d_M)^2 (d_F - \\
& d_M)(2 - d_F - d_M) \left. \right) / \left(4 \left(\alpha - 2d_F^2(1 - \alpha) + d_M(8 + \alpha - 3\beta - 2d_M(1 - \beta)) \right) + \beta + \right. \\
& \left. d_F(8 - 3\alpha + \beta - d_M(4 + \alpha + \beta)) \right). \tag{2.43}
\end{aligned}$$

2.5.2.2 Religiosity optima

Setting the left-hand side of expressions (2.4) and (2.5) to zero and simultaneously solving yields the optimal level of religiosity for female and male juveniles as:

$$z_{FJ}^* = z_{MJ}^* = \frac{1+r_{sib}}{2}, \tag{2.44}$$

if the ε_{FJ} and ε_{MJ} terms are neglected. Consideration of the ε_{FJ} and ε_{MJ} terms reveals that if both sexes adopt this optimal level of religiosity, then any perturbation from this value by either sex will result in selection acting to neutralise this perturbation, such that this optimum is stable. Accordingly, juveniles of both sexes are favoured to exhibit the same level of religiosity, and hereafter we consider that this represents a single, non-sex-specific trait. Consequently, the optimal level of religiosity from the individual's perspective is $z_{i|I}^* = (1+r_{sib|I})/2$, or:

$$\begin{aligned}
z_{ij|I}^* = & \left(2d_M(5 - \alpha)(2 - \beta) - d_M^2(5 - \alpha)(1 - \beta) - d_F^2(1 - \alpha)(5 + \beta) + 8(\alpha + \beta) + \right. \\
& \left. 2d_F(10 - d_M(5 - \alpha) + \beta - \alpha(6 + \beta)) \right) / \left(8(\alpha - d_F^2(1 - \alpha) + 2d_F(2 - d_M - \alpha) + \right. \\
& \left. 2d_M(2 - \beta) - d_M^2(1 - \beta) + \beta) \right). \tag{2.45}
\end{aligned}$$

From the maternal-origin gene's perspective the optimum is $z_{ij|M}^* = (1+r_{\text{sib}|M})/2$, or:

$$\begin{aligned}
z_{ij|M}^* = & \left(-3d_F^2(1 - \alpha) - 3d_M^2(1 - \beta) + 4(\alpha + \beta) + d_M(12 - \alpha - 7\beta) + d_F(12 - 7\alpha - \beta - \right. \\
& \left. d_M(6 - \alpha - \beta)) \right) / \left(4(\alpha - d_F^2(1 - \alpha) + 2d_F(2 - d_M - \alpha) + 2d_M(2 - \beta) - d_M^2(1 - \beta) + \beta) \right). \tag{2.46}
\end{aligned}$$

From the paternal-origin gene's perspective the optimum is $z_{ij|P}^* = (1+r_{\text{sib}|P})/2$, or:

$$\begin{aligned}
z_{ij|P}^* = & \left(-d_M^2(2 - \alpha)(1 - \beta) - d_F^2(1 - \alpha)(2 + \beta) + 4(\alpha + \beta) + d_F(8 - 5\alpha - \right. \\
& \left. d_M(4 - \alpha + \beta) + 3\beta - 2\alpha\beta) + d_M(8 - 3\alpha - 3\beta + 2\alpha\beta) \right) / \left(4(\alpha - d_F^2(1 - \alpha) + \right. \\
& \left. 2d_F(2 - d_M - \alpha) + 2d_M(2 - \beta) - d_M^2(1 - \beta) + \beta) \right). \tag{2.47}
\end{aligned}$$

Setting the left-hand side of expressions (2.6) and (2.7) to zero and simultaneously solving yields the optimal level of religiosity for women as:

$$z_{FA}^* = \frac{2r_F + \sqrt{4(2+r_F)z_{MA} + (1-2z_{MA}+r_F(2+z_{MA}))^2}}{2(2+r_F)}, \tag{2.48}$$

and for men as:

$$z_{MA}^* = \frac{2r_M + \sqrt{4(2+r_M)z_{FA} + (1-2z_{FA}+r_M(2+z_{FA}))^2}}{2(2+r_M)}. \tag{2.49}$$

Here again, the optimal levels of religiosity for adults of both sexes depend on the relatedness to one's parents' social partners, expressed relative to the relatedness to one's parents, as well as the level of religiosity exhibited by adults of the opposite sex.

As above, we can calculate the optima from the individual's perspective ($z_{iA|I}^*$), the maternal-origin gene's perspective ($z_{iA|M}^*$) and the paternal-origin gene's perspective ($z_{iA|P}^*$) in adults by inserting the respective consanguinities. The levels of religiosity exhibited when both sexes are behaving optimally may be found by evaluating equation (2.48) at $z_{MA} = z_{MA}^*$ and evaluating equation (2.49) at $z_{FA} = z_{FA}^*$ and simultaneously solving for z_{FA}^* and z_{MA}^* ; A numerical illustration of these optima is provided in **Figures 2.1 and 2.2.**

3 Kin selection favours religious traditions: Ancestor worship as a cultural descendant-leaving strategy

Abstract

Recent years have seen renewed interest in the role of religious systems as drivers of the evolution of cooperation in human societies. One suggestion is that a cultural tradition of ancestor worship might have evolved as a “descendant-leaving strategy” of ancestors by encouraging increased altruism particularly between distant kin. Specifically, Coe and others have suggested a mechanism of cultural transmission exploiting social learning biases, whereby ancestors have been able to establish parental manipulation of kin recognition and perceived relatedness as a traditional behaviour, leading to increased altruism among co-descendants and thereby maximising the ancestor’s long-term inclusive fitness. Here, we develop a demographically explicit model in order to quantify the resulting increase in altruism and concomitant “ancestor-descendant conflict”, and to determine the evolutionary feasibility of religiously motivated cultural norms that promote altruism among co-descendants. Our analysis reveals that such norms could indeed drive an overall increase in altruism with potential for ancestor-descendant conflict, particularly in low-dispersal settings. Moreover, we find that natural selection can favour traditions encouraging increased altruism towards co-descendants under a range of conditions, with the inclusive-fitness costs of enacting an inappropriately high level of altruism being offset by inclusive-fitness benefits derived from the cultural tradition facilitating kin recognition.

3.1 Introduction

Humans regularly cooperate with distant or non-relatives, including unfamiliar individuals, on a scale that is exceptional within the animal kingdom (Melis and Semmann, 2010). This poses an evolutionary puzzle and researchers have attempted to solve this by drawing on a range of explanatory mechanisms such as direct, indirect or generalised reciprocity (e.g., Barta *et al.*, 2011; Panchanathan and Boyd, 2004; Pfeiffer *et al.*, 2005), the development and policing of social norms (e.g., Chudek and Henrich, 2011; Fehr and Gaechter, 2002; Fehr and Schurtenberger, 2018), and cultural group selection (e.g., Chudek and Henrich, 2011; Henrich, 2004; Richerson *et al.*, 2016). In this context, it has been repeatedly suggested that religion might have functioned as a catalyst in the promotion of large-scale cooperation in humans (e.g., Atran and Henrich, 2010; Bulbulia, 2008; Bulbulia and Freaan, 2010; Crespi, 2016; Crespi and Summers, 2014; Kiper and Sosis, 2014; Norenzayan *et al.*, 2016; Powell and Clarke, 2012; Szocik, 2017; Wilson, 2002).

Some researchers (e.g., Clark and Coe, 2021; Coe *et al.*, 2010; Coe and Palmer, 2008; Coe and Palmer, 2013; Palmer *et al.*, 2008; Palmer *et al.*, 2013; Palmer and Steadman, 1997; Steadman and Palmer, 2008) have taken a similar approach in their investigation of cultural traditions that specifically emphasize altruism among kin, both on a conceptual level and in their study of the ethnographic record. They propose that the introduction of traditions that are often found in religious systems, such as ancestor worship, has led to a significant increase in cooperative behaviour among close and distant kin, and potentially among non-kin in the long run. For instance, Coe *et al.* (2010) suggest that individuals might have been manipulated to increase their altruism towards identifiable co-descendants of a common ancestor via the transmission of

cultural norms promoting the cooperation among kin specifically, together with being given the means of recognising said kin. By influencing their children such that they recognise and cooperate with distant kin as if they were close kin, and pass these teachings on to their own children, some ancestors might have encouraged cooperative behaviour among their descendants to an extent beyond what would otherwise be predicted by kin selection, reciprocity, or cultural group selection. Under this view, religious traditions such as ancestor worship have thus ultimately served as a “descendant-leaving strategy” (Palmer and Steadman, 1997), i.e., to maximise the respective ancestor’s long-term inclusive fitness, with their genes having spread more successfully as a result.

Such norms might encourage behaviour opposing an individual’s own inclusive fitness interests and hence give rise to what has been termed “ancestor-descendant conflict” (Coe *et al.*, 2010), i.e., the extension of parent-offspring conflict (Trivers, 1974) to more distant ancestor-descendant relationships. Coe *et al.* (2010) present a model illustrating the proposed conflict and its resolution by calculating an expected amount of altruism within particular pairs of individuals of varying kinship from three quantities: the number of generations descended from a common ancestor, the degree of genetic relatedness between the respective co-descendants, and the success rate of parental manipulation. Importantly, the success rate of parental manipulation represents the strength of the ancestor’s influence on the degree of altruism expected between co-descendants in subsequent generations such that the resulting altruism might be greater than that corresponding to the individual’s assumed basic inclusive fitness interests, i.e., that which is expected from their genetic relatedness. Accordingly, the authors conclude that by considering the impact of parental manipulation as a traditional behaviour, the

increased altruism among distant kin in so-called traditional societies found in the ethnographic record can be explained.

This is an intriguing idea. However, Coe *et al.*'s (2010) model does not allow for the evaluation of the overall amount of altruism occurring in a population and hence the extent of ancestor-descendant conflict. In order to do that, one would need to know how frequently relatives of different degrees encounter each other. That is, in order to determine the amount of altruism expected from culturally taught norms and/ or genetic relatedness, one would need to assess the probability of encounters between co-descendants in a group, which would be expected to vary with demographic circumstances, and which in turn would shape the extent and potential resolution of the proposed ancestor-descendant conflict. Moreover, it is difficult to see why a mechanism such as ancestor worship would not be counteracted by natural selection, e.g., by acting on the cognitive foundations which influence an individual's susceptibility to supernatural concepts. In light of the proposed ancestor-descendant conflict, it is therefore reasonable to ask whether and when a cultural system such as ancestor worship could evolve.

We develop a demographically explicit model to quantify the overall amount of altruism in a population with a religious system of ancestor worship and the potentially ensuing ancestor-descendant conflict, exploring the discrepancy between the culturally intended altruism, i.e., the amount of altruism between co-descendants in a group expected from cultural norms, on the one hand, and the amount of altruism in a group expected from individuals acting according to their genetic relatedness, on the other, under a range of demographic settings. To assess the evolutionary feasibility of the suggested mechanism, we examine the inclusive fitness consequences for an actor who

adopts a cultural norm – that promotes the identification of co-descendants and increased altruism towards them – either fully, partially, or not at all, under a range of success rates of parental manipulation and cultural norms. This enables us to derive comparative predictions about the conditions under which a cultural system such as ancestor worship could have evolved as well as some of its properties, that is, how the proposed ancestor-descendant conflict might have been resolved.

3.2 Model

We closely follow Coe *et al.*'s (2010) model, which considers the uniparental transmission of a culturally taught trait promoting altruism in a lineage of female descendants. The authors' calculations of genetic relatedness – with, for example, maternal sisters being related by one half – imply standard diploid autosomal inheritance, female monogamy, and outbreeding. The formula they use to calculate the expected amount of altruism further implies a proportional relationship between altruism and the relatedness valuation that individuals place upon their respective social partner. Coe *et al.* (2010) assume that this relatedness valuation is given by the individuals' actual genetic relatedness plus a potential increase in the relatedness valuation due to the ancestral influence, with this increase being modulated by the success rate of parental manipulation. The level of altruism an individual exhibits if following the cultural rule is therefore proportional to the relatedness valuation encouraged by the cultural norm, which the authors assume to be unity, i.e., individuals are expected to value their co-descendants as they would value themselves. Importantly, the culturally transmitted trait as described by the authors includes both the means for the identification of co-descendants as well as the prescribed relatedness valuation

determining the expression of altruism towards these.

We assume a large population divided into social groups, with each group containing n pairs of women and men raising children, and we focus on social interactions between these women. Mothers pass the cultural instructions on how to recognise co-descendants and a prescribed relatedness valuation R for these, i.e., the ‘cultural coefficient of relatedness’, on to their daughters. Upon reaching maturity, daughters either disperse with probability d or else remain in their natal groups with probability $1-d$, and sons always disperse, with dispersers travelling sufficiently far to ensure that they do not encounter relatives in their new groups, which ensures outbreeding as assumed by Coe *et al.* (2010). Further, we assume non-overlapping generations, group fissioning, and density-dependent regulation which maintains a constant number of groups of constant size across generations (cf. Stucky and Gardner, 2022). In line with Coe *et al.*’s (2010) suggested success rate of parental manipulation, daughters can accept, reject (or, equivalently, be ignorant of) or partially accept the cultural norm, and accordingly vary in their choice of social partners and their expression of altruism towards these during adulthood.

3.3 Results

3.3.1 *Altruism expected from cultural norms*

If individuals fully adopt a cultural norm which causes them to recognise and value co-descendants according to a cultural relatedness coefficient R , then we expect an overall amount of altruism $A_{\text{culture}} = \gamma \times R$, where γ is the probability that two randomly chosen adult female group members are co-descendants. The probability that two adult females in generation $t+1$ are co-descendants is given by:

$$\gamma_{t+1} = (1-d)^2 \left(\frac{1}{n} + \left(1 - \frac{1}{n}\right) \gamma_t \right). \quad (3.1)$$

That is, neither of them has dispersed which occurs with probability $(1-d)^2$ and: either they share the same mother with probability $1/n$, in which case they are co-descendants; or they have different mothers with probability $1-(1/n)$, in which case they are co-descendants if their mothers (of generation t) were co-descendants which occurs with probability γ_t . So, at equilibrium ($\gamma_{t+1} = \gamma_t = \gamma$) we obtain:

$$\gamma = \frac{(1-d)^2}{n-(n-1)(1-d)^2}. \quad (3.2)$$

Thus, the overall amount of altruism A_{culture} arising from full adoption of the cultural norm is:

$$A_{\text{culture}} = \frac{(1-d)^2}{n-(n-1)(1-d)^2} R, \quad (3.3)$$

which is an increasing function of the cultural relatedness coefficient R and a decreasing function of both dispersal rate d and group size n (**Fig. 3.1a**). This means that a higher culturally prescribed relatedness valuation leads to a higher average amount of altruism A_{culture} . More importantly, average altruism would be lower in populations containing larger groups with a higher dispersal rate than in more viscous populations containing smaller groups, since the likelihood of meeting a co-descendant is decreasing with increasing dispersal rate and group size.

3.3.2 Altruism expected from genetic relatedness

If individuals behave according to their genetic relatedness, there are two scenarios to consider. On the one hand, if individuals cannot recognise their co-descendants in the

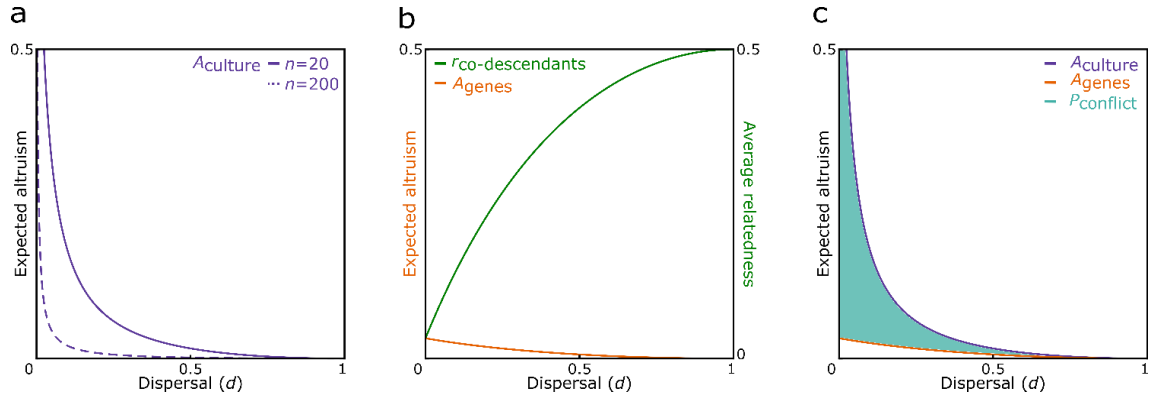


Fig. 3.1 Ancestor worship can lead to ancestor-descendant conflict. **a)** In smaller groups ($n = 20$) ancestor worship can increase the overall level of altruism among co-descendants A_{culture} to a greater extent than in larger groups ($n = 200$) since average relatedness of co-descendants decreases with group size, **b)** the amount of altruism expected from genetic relatedness A_{genes} decreases with increasing dispersal whereas average relatedness between co-descendants $r_{\text{co-descendants}}$ increases since it becomes more likely to encounter closely related as opposed to distantly related co-descendants (here, $n = 20$), and **c)** the potential for ancestor-descendant conflict P_{conflict} is greatest in more viscous populations since the probability of meeting a co-descendant – which determines the culturally encouraged amount of altruism A_{culture} – would be high, but the average degree of genetic relatedness between co-descendants $r_{\text{co-descendants}}$ – which modulates the genetically expected amount of altruism A_{genes} – would be low (here, $n = 20$).

absence of or due to fully rejecting a cultural norm promoting increased kin altruism, they will be expected to behave altruistically towards all group members according to the average genetic relatedness of group members in the population. On the other hand, if individuals partially accept the cultural norm such that they can use this information to enable them to recognise their co-descendants, but they reject the instructions to increase their altruism towards them, they will be expected to behave altruistically only towards their co-descendants and according to the average relatedness among them.

Consequently, if individuals cannot recognise their co-descendants and behave altruistically towards all group members according to their average genetic relatedness, we expect an overall amount of altruism $A_{\text{genes}} = r_{\text{group}}$, where r_{group} is the average genetic relatedness between group members, and is given by:

$$r_{\text{group}} = \gamma \times r_{\text{co-descendants}} + (1 - \gamma) \times 0, \quad (3.4)$$

i.e., a proportion γ of group members are co-descendants and are related on average by $r_{\text{co-descendants}}$ and a proportion $1-\gamma$ are not co-descendants and are related by 0. The relatedness of co-descendants can be expressed as:

$$r_{\text{co-descendants}} = \sum_{k=0}^{\infty} \delta_k r_k, \quad (3.5)$$

where δ_k is the probability that a co-descendant is a k th cousin, i.e., they are k generations descended from a common ancestor, and r_k denotes the relatedness between k th cousins. Note that $\delta_k = (1-\delta_0)^k \delta_0$, where δ_0 denotes the probability of a co-descendant being a sister and is given by $\delta_0 = ((1-d)^2/n)/\gamma$, and that $r_k = (1/4)^k 1/2$.

Making these substitutions obtains:

$$r_{\text{co-descendants}} = \frac{2(n-(n-1)(1-d)^2)}{4n-(n-1)(1-d)^2}. \quad (3.6)$$

Substituting eq. (3.6) into eq. (3.4) obtains:

$$r_{\text{group}} = \frac{2(1-d)^2}{4n-(n-1)(1-d)^2}. \quad (3.7)$$

Therefore, the overall amount of altruism A_{genes} is:

$$A_{\text{genes}} = \frac{2(1-d)^2}{4n-(n-1)(1-d)^2}. \quad (3.8)$$

If individuals are able to recognise their co-descendants and behave altruistically towards them according to their genetic relatedness, we expect an overall amount of altruism of $A_{\text{genes}} = \gamma \times r_{\text{co-descendants}}$ – and this level of altruism is exactly the same as that which arises when individuals are not able to recognise their kin, as derived above. That is, although kin recognition leads to co-descendants individually receiving more altruism, this increase is exactly offset by the reduction in the level of altruism received

by non-co-descendants. This owes to Coe *et al.*'s (2010) assumption that expressed altruism is a linear function of relatedness valuation (cf. Faria and Gardner, 2020).

In either case, then, the level of altruism A_{genes} is a decreasing function of both dispersal rate d and group size n (**Fig. 3.1b**). Therefore, the average amount of altruism expected from genetic relatedness A_{genes} in a group would also be lower in populations with a higher dispersal rate and containing larger groups than in more viscous populations containing smaller groups, since the likelihood of meeting a co-descendant γ is reduced. This is despite the fact that average relatedness between co-descendants $r_{\text{co-descendants}}$ would be higher in populations with a higher dispersal rate, since it becomes more likely to meet a close – as opposed to a distantly related – co-descendant with increasing dispersal d , when meeting a co-descendant.

3.3.3 Ancestor-descendant conflict

We find that the culturally encouraged and the genetically expected levels of altruism in a group can differ in the degree of overall amount of expressed altruism, i.e., there is potential for an ancestor-descendant conflict as anticipated by Coe *et al.* (2010), which is given by:

$$P_{\text{conflict}} = A_{\text{culture}} - A_{\text{genes}} = (1 - d)^2 \left(\frac{R}{1+(n-1)(1-(1-d)^2)} - \frac{2}{3n+1+(n-1)(1-(1-d)^2)} \right), \quad (3.9)$$

and which, as expected, is also a decreasing function of both dispersal rate and group size (**Fig. 3.1c**). Ancestors introducing a cultural tradition to increase altruism among their co-descendants would be expected to prescribe a cultural relatedness coefficient R equal to 1, so as to maximise their own inclusive fitness. Considering this, we find that the ancestor-descendant conflict would be greatest in populations containing larger

groups with a low dispersal rate, since the probability of meeting a co-descendant – which determines the culturally encouraged amount of altruism A_{culture} – would be high, but the average degree of genetic relatedness between co-descendants – which modulates the genetically expected amount of altruism A_{genes} – would be low, whereas the conflict would be smallest in populations containing larger groups with a high dispersal rate, since both the probability of meeting a co-descendant and the average degree of genetic relatedness between co-descendants would be low.

3.3.4 The evolutionary potential of ancestor worship as a descendant-leaving strategy

In order to assess the evolutionary feasibility of a cultural system such as ancestor worship, we investigate the inclusive fitness consequences for individuals in varying ecological scenarios and according to (i) whether they fully accept the cultural norm conveyed through ancestor worship, thus recognising their co-descendants and treating them according to the cultural relatedness coefficient; or (ii) whether they fully reject the cultural norm (or, equivalently, are ignorant of it and of their kin relations altogether), thus treating everyone in the group according to the average genetic relatedness of group mates; or (iii) whether they only partially accept the cultural norm, thus recognising their co-descendants and treating them according to a modulated cultural relatedness coefficient, i.e., exploring the effects of varying success rates of parental manipulation.

To do this, we need to specify an explicit inclusive fitness function. A simple functional form that complies with Coe *et al.*'s (2010) assumption that the amount of

expressed altruism is proportional to the relatedness valuation the individual places upon her social partners is:

$$W_i = \varepsilon - s \frac{1}{2} x^2 + s x \rho, \quad (3.10)$$

where: ε is an individual's baseline fitness; s is her expected number of social partners; x is the amount of altruism she exhibits; and ρ is her genetic relatedness to her social partners. That is, the optimal level of altruism (i.e., satisfying $dW_i/dx|_{x=x^*}=0$) is $x^* = \rho$.

If (i) an individual fully accepts the cultural norm, i.e., she recognises her co-descendants and directs her culturally encouraged altruism towards them, then $s = \gamma \times (n-1)$, $x = R$, and $\rho = r_{\text{co-descendants}}$. This means that a proportion γ of the $n-1$ other women in the group are identifiable co-descendants, who the focal individual treats as being valued by R according to the cultural relatedness coefficient, but who are genetically related to the focal individual by $r_{\text{co-descendants}}$. For a cultural norm that encourages individuals to value their co-descendants as they would value themselves (i.e., $R = 1$), inclusive fitness is an increasing function of dispersal rate and a decreasing function of group size. Fully following this norm would, however, decrease an individual's inclusive fitness relative to her baseline fitness in all ecological scenarios (i.e., for all $0 < d < 1$ and $n > 1$), since she would be committed to express a level of altruism always exceeding that which would be expected from genetic relatedness. This effect becomes smaller with increasing dispersal, though, since the likelihood of encountering co-descendants decreases whereas the average relatedness of co-descendants increases. Allowing for variation in the cultural relatedness coefficient (i.e., for $R < 1$), however, leads to a range of scenarios in which an individual's inclusive fitness could be increased relative to her baseline fitness (see below and **Fig. 3.2a**).

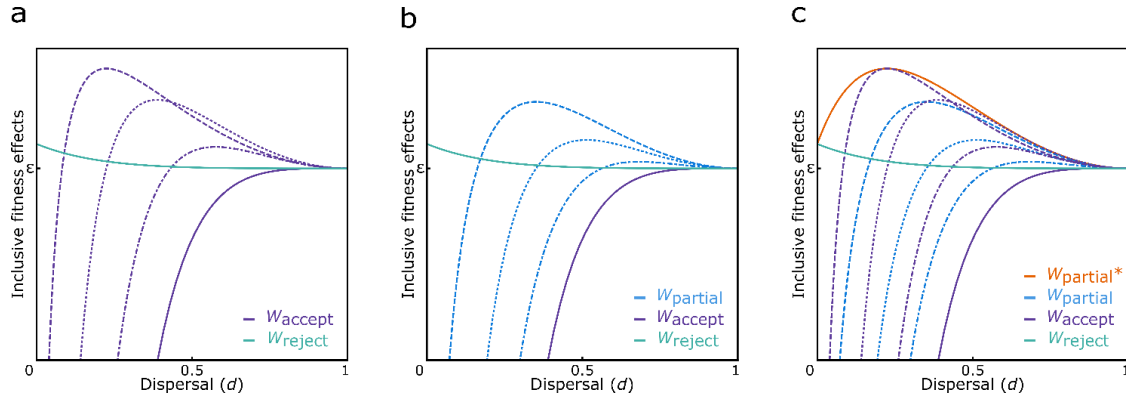


Fig. 3.2 Inclusive fitness effects of ancestor worship. **a)** Fully accepting a cultural norm such as ancestor worship promoting increased altruism among co-descendants according to a cultural relatedness coefficient R (here, from left to right: $R = 1/4, 1/2, 3/4$, and 1) can increase an individual's inclusive fitness (W_{accept}) above that of an individual rejecting/being ignorant of such cultural norms (W_{reject}) in a range of dispersal conditions (unless $R = 1$ or $d = 1$); **b)** accepting the cultural norm partially (here, from left to right: $\chi = 1/4, 1/2, 3/4$) can increase an individual's inclusive fitness (W_{partial}) above that of an individual fully accepting the norm (W_{accept} , for $R = 1$) and that of an individual rejecting/being ignorant of the cultural norm (W_{reject}) in a range of dispersal conditions; and **c)** partially accepting the cultural norm such that an individual can recognise their co-descendants but treats them according to their genetic relatedness (for $\chi = 0$) can increase the individual's inclusive fitness (W_{partial}^*) above that of any of the other strategies in all conditions, unless everyone disperses. In all panels we assume $n = 20$.

If instead (ii) an individual rejects the cultural norm altogether or if there is no such norm in place, i.e., she does not recognise her co-descendants and treats everyone in her group according to the group's average genetic relatedness, then $s = n-1$, $x = r_{\text{group}}$, and $\rho = r_{\text{group}}$. This behaviour would also increase an individual's inclusive fitness relative to her baseline fitness. This effect, however, is a decreasing function of increasing dispersal and group size (for all $0 < d < 1$ and $n > 2$; **Fig. 3.2a**). Alternatively, if (iii), in line with Coe *et al.*'s (2010) suggested success rate of parental manipulation, individuals only partially accept the culturally encouraged relatedness valuation, then $s = \gamma \times (n-1)$, $x = \theta$, and $\rho = r_{\text{co-descendants}}$, where $\theta = \chi \times 1 + (1-\chi) \times r_{\text{co-descendants}}$ is the relatedness valuation resulting from parental manipulation by an extent χ . That is, the relatedness valuation is a weighted average of the culturally encouraged value of 1 and

the actual genetic relatedness $r_{\text{co-descendants}}$, with χ providing the relative weight placed on the cultural value. Following the cultural norm only partially (i.e., for all $\chi < 1$) would also increase an individual's inclusive fitness relative to her baseline fitness in a range of scenarios (**Fig. 3.2b**). This effect, however, is a decreasing function of the success rate of parental manipulation, since the individual would increase her relatedness valuation of co-descendants beyond what would be appropriate from her gene's perspective (i.e., for all $\chi > 0$). This becomes clear in the specific case of an individual who partially accepts the norm such that she recognises her co-descendants and directs her altruism towards these but rejects the culturally prescribed relatedness valuation (i.e., for $\chi = 0$). Here, inclusive fitness is an increasing function of dispersal rate and group size at lower dispersal rates and a decreasing function of dispersal rate and group size at higher dispersal rates, eventually approaching zero when approaching full dispersal. Importantly, the inclusive fitness effects of this strategy are exceeding the effects of any other behaviour in any of the conditions – all else being equal – since the individual would be able to recognise and direct her altruism towards her co-descendants in a way that is optimal from her gene's perspective (**Fig. 3.2c**).

Comparing the inclusive fitness effects for individuals performing the aforementioned strategies, we find that the inclusive fitness of individuals following a cultural norm that encourages them to recognise and direct increased altruism towards co-descendants according to a cultural coefficient of relatedness fully or partially (for $\chi > 0$) would always be lower than the inclusive fitness of individuals only partially accepting the norm such that they recognise co-descendants but treat them according to their genetic relatedness (i.e., for $\chi = 0$, unless $R = r_{\text{co-descendants}}$), all else being equal. A cultural system solely involving kin recognition would therefore be more beneficial than

a system involving kin recognition and increased kin altruism. Consequently, we find that natural selection would not favour a system such as ancestor worship as a cultural promoter of increased kin altruism to evolve in a population if kin recognition was uncoupled from the norm encouraging the increase in altruism, under the assumptions of our model. However, if the identification of co-descendants was promoted via cultural traditions related to ancestor worship as proposed by Coe *et al.* (2010), such that individuals brought up in a system without or rejecting these traditions could not recognise their co-descendants, we find that natural selection could favour cultural traditions which promote altruism between co-descendants exceeding that which is expected from genetic relatedness in a range of conditions, i.e., when the inclusive fitness of an individual following the cultural norm exceeded that of an individual ignorant of the traditions and thus their kin relations.

3.3.5 When does natural selection favour ancestor worship?

In order to determine when ancestor worship would be favoured by natural selection we determine the conditions under which adoption of ancestor worship improves the individual's inclusive fitness relative to what it would be if the individual fully rejected or was fully ignorant of the cultural tradition. This is where the benefits that come from being able to identify co-descendants outweigh the costs of enacting an inordinate amount of altruism towards them. Specifically, we identify the value of R which represents the maximum cultural relatedness coefficient and likewise, the value of χ which represents the maximum success rate of parental manipulation such that the individual breaks even in terms of these benefits and costs balancing out. We expect that ancestors would want to drive the accepted cultural relatedness coefficient as high

as possible in order to maximise their inclusive fitness. Accordingly, the maximum cultural relatedness coefficient (i.e., satisfying $\gamma \times (n-1) (-\frac{1}{2} R^2 + R r_{\text{co-descendants}}) = (n-1) (-\frac{1}{2} r_{\text{group}}^2 + r_{\text{group}}^2)$) is:

$$R_{\max} = \frac{2(1+(n-1)(1-(1-d)^2)) + \sqrt{n(1+(n-1)(1-(1-d)^2))(1-(1-d)^2)}}{3n+1+(n-1)(1-(1-d)^2)}, \quad (3.11)$$

and the maximum success rate of parental manipulation (i.e., satisfying $\gamma \times (n-1) (-\frac{1}{2} (\chi \times 1 + (1-\chi) \times r_{\text{co-descendants}})^2 + (\chi \times 1 + (1-\chi) \times r_{\text{co-descendants}}) r_{\text{co-descendants}}) = (n-1) (-\frac{1}{2} r_{\text{group}}^2 + r_{\text{group}}^2)$ for $\chi > 0$) is:

$$\chi_{\max} = \frac{2\sqrt{n(1+(n-1)(1-(1-d)^2))(1-(1-d)^2)}}{3n-n(1-(1-d)^2)-(1-d)^2}. \quad (3.12)$$

Replacing χ with χ_{\max} in the expression for θ , we recover the expression for R_{\max} ; i.e., effectively the potential maximum amount of expressed altruism among co-descendants due to ancestral influence on their perceived relatedness, which is evolutionarily feasible from the perspective of the manipulated individual's inclusive fitness.

Reasonable approximations for these quantities are obtained by expressing them in the limit of infinite group size, with $R_{\max} = \theta_{\max} = \frac{4(1-(1-d)^2)}{4-(1-d)^2}$ and $\chi_{\max} = \frac{2(1-(1-d)^2)}{3-(1-(1-d)^2)}$. These provide good approximations for even relatively small values of n (i.e., for R_{\max} and θ_{\max} : within 5% of error for $n > 56$, for all $d \geq 0.1$; and for χ_{\max} : within 5% of error for $n > 46$ for all d). These approximations of R_{\max} , θ_{\max} and χ_{\max} are all increasing functions of dispersal rate. Numerical investigation suggests that this is also the case even for smaller values of n , where the approximations do not hold as closely. Following from this, we find that in populations with a higher dispersal rate it is more likely for cultural traditions promoting altruism towards co-descendants to evolve and/or be sustained at a

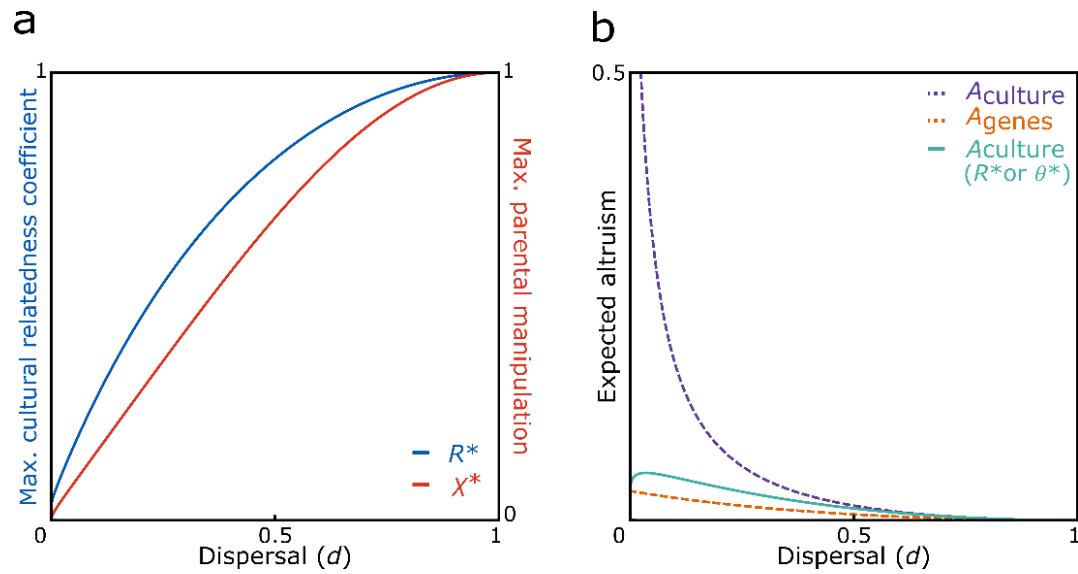


Fig. 3.3 Potential ancestor-descendant conflict resolution. **a)** The introduction of norms leading to an intermediate degree of altruism between co-descendants via an ecologically variable cultural relatedness coefficient R^* or success rate of parental manipulation χ^* , respectively, allows for the evolution of ancestor worship in a range of conditions, and **b)** can lead to a reduction of the discrepancy between the culturally promoted amount of altruism A_{culture} and the amount of altruism expected from genetic relatedness A_{genes} , indicating a resolution to the proposed ancestor-descendant conflict. In both panels we assume $n = 20$.

comparatively higher degree in large groups (**Fig. 3.3a**). More importantly, the introduction of a cultural coefficient of relatedness R_{max} and a success rate of parental manipulation χ_{max} as functions of dispersal rate and group size leads to a range of potential cultural traditions resulting in an intermediate degree of altruism between co-descendants and a significant reduction of the discrepancy between the amount of altruism intended by ancestors and the amount of altruism expected from genetic relatedness, providing a resolution to the proposed ancestor-descendant conflict (**Fig. 3.3b**).

3.4 Discussion

It has been repeatedly suggested that religious beliefs and behaviours have played an important role in facilitating the unusual extent of cooperation found in human societies.

For instance, it has been proposed that the introduction of cultural traditions such as ancestor worship as a descendant-leaving strategy has led to increased altruism specifically between distant kin. More precisely, Coe *et al.* (2010) have presented a mechanism of cultural transmission exploiting social learning biases, by which ancestors might have been able to establish parental manipulation of kin recognition and perceived relatedness as a traditional behaviour, eventually leading to increased altruism among co-descendants and thereby maximising the respective ancestor's inclusive fitness. Here, we developed a demographically explicit model to quantify the proposed increase in altruism, assess the associated potential for ancestor-descendant conflict, and investigate the evolutionary feasibility of religiously motivated cultural norms promoting increased altruism among co-descendants. Our analysis reveals that such norms could indeed generate an overall increase in altruism with potential for ancestor-descendant conflict as Coe *et al.* (2010) had anticipated. Moreover, we find that kin selection could favour cultural traditions promoting increased altruism among co-descendants under a range of conditions.

More specifically, our demographically explicit model allows us to take Coe *et al.*'s (2010) ideas of cultural norms encouraging increased altruism among kin and investigate their consequences in terms of overall levels of altruism in the population. Given that individuals accept these norms, we find that they could lead to a strong increase in overall altruism, specifically in more viscous populations made up of smaller groups as compared with populations characterised by a higher dispersal rate and larger groups, since it becomes less likely to meet a co-descendant with increasing dispersal and group size. Accordingly, we find potential for ancestor-descendant conflict as anticipated by the authors, and in addition, our analysis reveals that the extent of this

conflict would be greatest in large groups in more viscous populations. More importantly, we find that natural selection could favour traditions encouraging increased altruism towards co-descendants in a range of conditions, given a demographically variable rate of ancestral manipulation and given that information about kin relations is strongly tied to the respective norms promoting increased altruism among kin. This would allow individuals to direct their altruistic behaviour towards co-descendants as opposed to non-kin, thereby offsetting some of the inclusive fitness costs incurred by the increase in expressed altruism. The inclusive fitness benefits due to kin recognition will vary, however, depending on the specific demography and hence relatedness structure of a population. For instance, in more viscous populations it would be less costly for individuals to behave indiscriminately altruistic, since they would be more likely to be surrounded by relatives, and kin recognition would therefore have less of an impact. Accordingly, ancestors might be expected to attain a higher rate of manipulation of their descendants' perceived relatedness in populations of large groups and a high rate of dispersal as opposed to more viscous populations. In these cases, we might expect increased altruism towards distant kin to occur, since here both ancestors and descendants would be able to maximise their inclusive fitness, providing a resolution to the proposed ancestor-descendant conflict.

Previously, it has been suggested that religious cognition and behaviour might have originated as a product of kin selection, and more specifically as a means to suppress intra-family conflict (Crespi, 2016; Crespi and Summers, 2014). Indeed, kin selection could favour religiosity (Stucky and Gardner, 2022; **Chapter 2**), i.e., the susceptibility to supernatural concepts, such that individuals may be manipulated into cooperative behaviour towards related social partners by using culturally evolved

narratives about supernatural entities. A culturally transmitted trait containing such narratives and exploiting this susceptibility as well as social learning biases could indeed be represented by the religious practice of ancestor worship, i.e., “the communicated acceptance of the claim that dead ancestors influence and/or are influenced by their living descendants” (Clark and Coe, 2021: p. 281). The veneration of specific deceased kin – genealogical, cultural, or mythical – has been suggested to be a widespread and diverse phenomenon in past and present societies and is regarded to play an important role for social cohesion and organisation (e.g., see Couderc and Sillander, 2012, for a summary of the ethnographic literature and conceptions of ancestor worship/ ‘ancestralship’ in general and an in-depth overview of ancestor worship in Borneo societies; see Steadman *et al.*, 1996, for a view on the universality of ancestor worship; and see Peoples *et al.*, 2016, for an opposing view on the distribution and phylogenetic history of ancestor worship).

For example, evidence from colonial accounts and the archaeological record points to elaborate, long-lived, and widespread practices of ancestor cult in prehistoric Andean societies (Hastorf, 2003; Lau, 2021; Mantha, 2009). Local kin groups (*ayllu*) regularly interacted with their respective founding ancestors (*mallqui*) in rituals involving the ancestors’ mummified bodies and other cult objects representing the venerated deceased, such as stone effigies. These devotional practices for individuals, who were perceived as valued family members, and the collective effort put into the production of their effigies are suggested to have promoted the descendants’ group identity (Lau, 2021). By the time of the arrival of the Spanish colonialists, some of these groups had developed into complex, more inclusive, social units consisting of several kin collectives. These collectives were organised hierarchically according to the relative

genealogical distance of their respective ancestors to the founding progenitor of the larger community, with the associated above-ground mortuary structures representing the territorial and social boundaries of different groups (Mantha, 2009). Moreover, archaeological evidence from the Titicaca Basin indicates that, following the decline of the Chiripa culture (around 250 BC), the focus of ancestor veneration shifted from the female to the male in this region (Hastorf, 2003).

Among present-day Bentian communities in southeast Borneo, ancestors are often invoked in rituals and public discourse as sources of potency, authority, and morality. They can take various forms and be addressed individually or as an anonymous collectivity and take on different, context-dependent roles. Importantly, in their collective role of ‘elders who came before’ (*ulun tuha one*) they represent the moral ideals of customary law (*adat*), thereby promoting “socio-centric values which encourage integration and relation-affirming behavior” (Sillander, 2012: p. 94). Individually invoked ancestors as genealogical forebears of status and/ or resources can function to integrate as well as differentiate groups, however. Furthermore, some revered ancestors have attained their status due to their importance to the community, with no actual genealogical links to their devotees (Sillander, 2012), reflecting the rather flexible and inclusive bilateral kinship system of Bentian groups (Sillander, 2016). In contemporary China, ancestor veneration remains to be an important cultural tradition in many provinces, too, despite major political and demographic shifts of the last 100 years. Next to regular visits to the gravesites of ancestors, families are obliged to maintain a family genealogy which familiarises members with the structure of the kinship system, their position therein, as well as their responsibilities. One central responsibility of the descendants concerns the continuation of the male family line. And

indeed, a recent study investigating the demographic implications of ancestor worship in China found positive correlations of involvement in ancestor worship practices with lower age at marriage, more offspring, a higher probability of having at least one son, and more sons in general (Hu and Tian, 2018).

Here, we have investigated how ancestor worship might have evolved as a descendant-leaving strategy as proposed by Coe *et al.* (2010), and consequently influenced the extent and direction of cooperative behaviour in human societies. To do this, we have adopted the authors' assumptions of proportionality of expressed altruism and relatedness, uniparental transmission of the cultural trait in a lineage of female descendants, female monogamy, and outbreeding, in the design of our model. However, this constrains our analysis such that it ignores the possibility of altruism being a non-linear function of relatedness as well as more realistic scenarios allowing for variation in general demography and individual costs and benefits. For instance, owing to the assumption of proportionality of expressed altruism and relatedness, the increase in overall altruism predicted by our analysis is entirely based on the increased relatedness valuation promoted by ancestor worship. Yet, if we assume that altruism is a convex function of relatedness, the promotion of kin recognition could lead to an additional increase in the overall amount of altruism, whereas assuming that altruism is a concave function of relatedness, the promotion of kin recognition could lead to a decrease in overall amount of altruism (cf. Faria and Gardner, 2020). In either case, we would expect this to alter the extent of the potential for ancestor-descendant conflict.

Furthermore, our model investigates a sex-specific cultural trait assuming a strongly sex-biased demography in favour of the respective sex. Allowing for a less sex-biased demography or a demography biased towards the other sex would possibly alter

the relatedness structure of a population and the associated trade-offs for individuals and might therefore result in different conditions under which ancestor worship could evolve. For instance, mating systems causing reproductive skew or sex differences in dispersal rate can potentially lead to sex differences in levels of religiosity owing to the resulting sex differences in relatedness between group members (Stucky and Gardner, 2022; see **Chapter 2**). It could be expected that such individual variation in the susceptibility to supernatural concepts have had an impact on the cultural transmission of a trait exploiting this susceptibility, aside from potential sex differences in individual costs and benefits that could arise from sexual selection (e.g., see Andersson, 1994). In addition, we have assumed group fissioning such that there are no kin competition effects under limited dispersal (Gardner and West, 2006). Allowing for other dispersal scenarios could lead to the increase of local resource competition among kin and might therefore affect our results relating to the maximum rate of ancestral manipulation. In the future, it could therefore be interesting to explore how variation in demographic factors and individual costs and benefits might influence the conditions for a cultural trait such as ancestor worship to evolve, and ultimately to align our model's assumptions with more complex real-world examples as described above in order to test our predictions.

Nevertheless, from our analysis we can see how a cultural system exploiting cognitive biases to promote increased altruism among kin could generally arise, given the counterbalancing inclusive fitness effects of kin recognition. Ancestors who introduced cultural traditions such as ancestor worship might therefore have been more successful in leaving descendants as has been proposed, potentially resulting in the spread of such cultural traditions. And since groups with these traditions might have

been more altruistic overall than groups lacking these, it would be useful to investigate the effects of such traditions at the between-group level, specifically including scenarios where the cultural manipulation of perceived relatedness might have been extended to non-kin, i.e., in networks of ‘fictive kinship’ (Calhoun, 2002). In conclusion, cultural traditions such as ancestor worship might have been favoured by kin selection with potential implications for the cultural evolution of religious systems.

5 Discussion

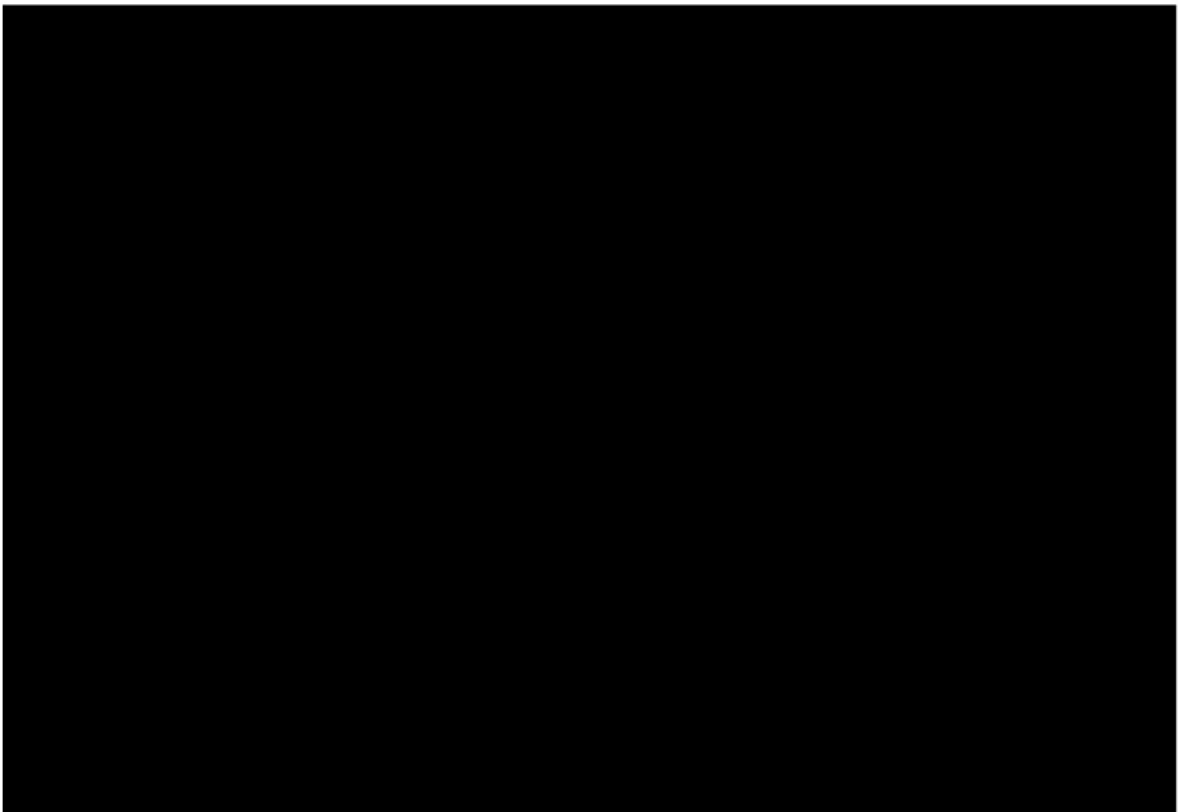
Religion has been put forward as a promising example of a cultural phenomenon with considerable impact on the gene-culture coevolution of humans, explaining the unusual degree of cooperation found in human societies (e.g., Boyd and Richerson, 2008; Ferretti and Adornetti, 2014; Fieder and Huber, 2021; Henrich, 2004; Lo and Sasaki, 2017). More specifically, religion – defined here as “a shared system of beliefs and actions concerning superhuman agency” (Barrett, 2000: p. 29) – has been suggested to lead to the suppression of intra-group competition and the promotion of cooperation in human groups such that it might have contributed to one of the “major evolutionary transitions” (Szathmáry and Maynard Smith, 1995), i.e., the transition in individuality to large-scale human societies (termed “human ultrasociality”, Turchin, 2013).

Given that religious beliefs are often associated with what appears to be maladaptive, counterintuitive contents and costly practices, the challenge remains for scholars of the evolutionary sciences to explain their existence and associated cooperative effects, though (Powell and Clarke, 2012; Sosis, 2009). It has therefore been proposed that religion might have originated as the aggregate “by-product” (Barrett, 2000) of human social cognition, with proximate mechanisms such as a “hyperactive agent-detection device” (Barrett, 2000), “theory of mind” (Premack and Woodruff, 1978), and teleological tendencies (e.g., Kelemen and DiYanni, 2005) contributing to the susceptibility to supernatural concepts, and in combination with content- and context-dependent transmission biases leading to the spread of those concepts (e.g., Barrett, 2000; Gervais *et al.*, 2011; Henrich, 2009; Sperber and

Hirschfeld, 2004). The cross-culturally recurrent integration of the single elements in religious systems indicates, however, that these cognitive mechanisms have subsequently been selected for in the course of the evolution of religion, and potentially due to fitness effects resulting from the promotion of cooperation (Crespi and Summers, 2014; Powell and Clarke, 2012; Sosis, 2009). How these effects have come about remains debated, with “adaptationist” hypotheses emphasising different aspects of religious systems, involved mechanisms, and levels of selection (see **Tables 2.1 & 4.1**).

In this thesis, I have investigated the diverse selection pressures that might have produced and shaped the evolution of religious beliefs and behaviours, by formalising some of these hypotheses. First, I explored how patterns of genetic relatedness may have modulated the evolution of religion via a kin-selection model, based on an idea by Crespi and Summers (2014) who argue that religion may have evolved to suppress intra-family and, in extension, intra-group conflict (**Chapter 2**; Stucky and Gardner, 2022). My analysis has revealed that religiosity – the susceptibility to supernatural concepts – could have been favoured by natural selection in small-scale, ancestral human groups due to indirect fitness benefits offsetting some of the costs of altruistic behaviours promoted through religious manipulation. Furthermore, I developed predictions how variation in the demography of a population, e.g., in sex-specific reproductive skew and dispersal patterns, can give rise to variation in intra-family and intra-group relatedness and therefore variation in individual age- and sex-specific religiosity; and potentially generate parent-of-origin specific patterns of gene expression with concomitant clinical disorders related to the genetic basis for cognitive mechanisms underlying religiosity.

Second, considering that social learning biases in humans can be exploited to manipulate kin recognition, I investigated whether religiously motivated, culturally transmitted social norms such as ancestor worship could have evolved to generate increased altruism among distant kin, an idea put forward by Coe and colleagues (2010; **Chapter 3**; Stucky and Gardner, 2023). Indeed, natural selection could favour traditions encouraging increased altruism towards distant kin in a range of conditions, despite the potential for ancestor-descendant conflict. Culturally transmitted information on kin relations – albeit modulated regarding the degree of relatedness – allows individuals to direct their altruistic behaviour towards co-descendants as opposed to non-kin, leading to indirect fitness benefits offsetting some of the costs incurred by the increase in altruism.



Following from this, it is plausible to propose that religion has evolved as a cultural adaptation to group-living, with inclusive fitness benefits driving the selection

of its underlying cognitive traits and therewith the genetic basis for these. By exploiting pre-existent, socio-cognitive features unique to humans, culturally transmitted norms and behaviours involving supernatural concepts and promoting cooperation could arise and spread. Via indirect fitness benefits (i.e., kin-selection) in small-scale, ancestral groups, and direct fitness benefits – resulting from individual (e.g., via signalling) as well as group-level interactions (i.e., cultural group selection) – in larger groups of unrelated individuals, religion might have indeed contributed to the rise of complex, large-scale, cooperative human societies. The jury is still out on whether these can be regarded as “superorganisms” (Wilson, 2002) and evidence for an evolutionary transition in individuality, however (e.g., Aunger and Greenland, 2023; Carmel, 2022; Kesebir, 2012; McShea, 2023; Powers *et al.*, 2016; Stearns, 2007; Turchin, 2013; Waring and Wood, 2021; and see below).

More generally, my findings reaffirm that cultural institutions such as religion can 1) generate adaptive – i.e., inclusive-fitness beneficial – cooperative behaviours presumably more rapidly than via genetic selection; 2) effectively and flexibly provide fitness relevant information via extrasomatically stored information – e.g., about kin relations – thereby generating inclusive fitness benefits counteracting costs, and consequently promoting an increase in cooperative behaviour not expected via genetic selection; and 3) lead to homogenising effects in cooperative behaviours – i.e., creating stable equilibria – and thereby selection on a higher hierarchical level, thus producing additional selection pressures for the evolution of cooperation and the cognitive mechanisms involved, e.g., those underlying the susceptibility to supernatural concepts.

Considering the flexibility of cultural institutions, however, it can be expected that a cognition susceptible to supernatural ideas might serve various functions. Indeed,

the evolution of religion as a cultural promoter of cooperation might just be one side of the coin. The benefits that arise from the suppression of intra-group conflict, increased cooperation, and potentially the subsequent success in inter-group competition might not be equally distributed within communities, nor the costs for that matter. For instance, Soler and colleagues (2014) have suggested that at least with the emergence of doctrinal religions involving moralising, punitive deities, religious norms and practices have been utilised for the profit of specific groups within larger communities. By exploiting cognitive features underlying religious beliefs and behaviour, authorities and elites in stratified societies might have used religious concepts and rituals for their own purposes, i.e., disproportionately extracting resources from lower-ranking groups (Soler, 2016; Soler *et al.*, 2014; Soler and Lenfesty, 2016). In this context, supernatural concepts can serve as a means of social control by legitimising hierarchical structures and creating (Soler, 2016) or maintaining (Solt *et al.*, 2011) social inequality, with the status quo being internalised via rituals encouraging deference to authority and respect for property (Whitehouse, 2021). An extreme example of such a co-optation of religious practices for the purpose of stabilising power inequalities can be found in the cross-cultural, predominantly past, occurrence of ritual human sacrifice (Dunbar, 2022; Shaver *et al.*, 2016). Albeit short-lived in human history, ritual killings may have played an important role in the development of large-scale stratified societies via effects of collective coordination (Bulbulia, 2018; Bulbulia *et al.*, 2017; Watts *et al.*, 2016).

Furthermore, religious systems may be viewed in the light of sexual conflict, with various elements benefiting males at the expense of females' reproductive success (Soler, 2016; Soler and Lenfesty, 2016). Religious texts and norms often involve the regulation and restriction of female sexuality, and at times even sanctify and encourage

violence predominantly directed at women when discussing such matters as promiscuity (Sela *et al.*, 2016). Such norms supposedly reflect psychological mechanisms of their male authors and served to increase paternity certainty (Sela *et al.*, 2016; Soler and Lenfesty, 2016). Systems based on religiously sanctioned inequality have recurrently disintegrated or transformed eventually, however. Often, the exploited group(s) developed a defensive response, as demonstrated by historical examples of counter movements, schisms, and revolutions such as the Protestant Reformation, millenarian sects, and atheism (Soler, 2016; Soler and Lenfesty, 2016).

More generally, religion might exacerbate violent behaviour in various kinds of conflict in “evolutionarily relevant contexts” such as “threats to one’s status, reproductive success, or fitness in general” (Sela and Barbaro, 2016: p. 294). For example, religious practices creating ‘identification’ or ‘fusion’ have been suggested to lead to a disproportionate increase in outgroup derogation and inter-group violence with detrimental consequences for individuals (Whitehouse, 2021). More specifically, religious systems have apparently been co-opted for the purpose of terroristic acts as an effective means to solve collective action and coordination problems and promote group acceptance of extreme behaviours (Kiper and Sosis, 2016). Such dynamics of conflict associated with religion could represent evolutionary disequilibria, i.e., speaking against the hypothesis of religious systems as “superorganisms”, or maladaptive effects of a religious cognition, after all.

My work has underlined the value of formalising ideas in the literature on the evolution of religion more specifically and concerning human social behaviour more generally, allowing me to explore the selection pressures that could have shaped the origin and maintenance of religious beliefs and behaviours in the context of

cooperation. Verbal models in the behavioural sciences, specifically concerning the study of religion, are often ambiguous in their description of conditions, mechanisms, and selection pressures. By making the assumptions of verbal models and mathematical sketches explicit and examining their consequences, I was able to produce qualitative predictions about 1) the conditions – i.e., specific demographic scenarios (**Chapters 2 & 3**), the potential impact and properties of the culturally transmitted mechanisms involved (**Chapters 3 & 4**), and individual costs and benefits of specific practices (**Chapter 4**) – in which religious beliefs and behaviours could have been favoured by natural selection, and 2) how variation in these conditions would be expected to translate into variation in the expression of religion; and 3) to devise potential ways for empirical testing of these predictions. Mathematical models based on ideas relating to the role of religion in the generation of social inequality and violence, as presented above, therefore provide an exciting avenue for the future exploration of the ongoing evolution of religious beliefs and behaviours in the context of cooperation and conflict in human societies.

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