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Pathogens are linked to human moral systems across time and space

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ABSTRACT

Infectious diseases have been an impending threat to the survival of individuals and groups throughout our evolutionary history. As a result, humans have developed psychological pathogen-avoidance mechanisms and groups have developed societal norms that respond to the presence of disease-causing microorganisms in the environment. In this work, we demonstrate that morality plays a central role in the cultural and psychological architectures that help humans avoid pathogens. We present a collection of studies which together provide an integrated understanding of the socio-ecological and psychological impacts of pathogens on human morality. Specifically, in Studies 1 (2,834 U.S. counties) and 2 (67 nations), we show that regional variation in pathogen prevalence is consistently related to aggregate moral Purity. In Study 3, we use computational linguistic methods to show that pathogen-related words co-occur with Purity words across multiple languages. In Studies 4 ($n = 513$) and 5 ($n = 334$), we used surveys and social psychological experimentation to show that pathogen-avoidance attitudes are correlated with Purity. Finally, in Study 6, we found that historical prevalence of pathogens is linked to Care, Loyalty, and Purity. We argue that particular adaptive moral systems are developed and maintained in response to the threat of pathogen occurrence in the environment. We draw on multiple methods to establish connections between pathogens and moral codes in multiple languages, experimentally induced situations, individual differences, U.S. counties, 67 countries, and historical periods over the last century.

Humans currently suffer, and have suffered over their evolutionary history, from infectious diseases. Some of these infectious agents have found their way into human populations relatively recently (e.g., human immunodeficiency virus), but many others are of considerable antiquity, suggesting that disease-causing pathogens have posed debilitating threats to human populations through their evolutionary past (Schaller and Murray, 2011). The presence of strong biological antipathogenic mechanisms in humans, as well as other primate populations, is a testament to the power of pathogens and their role in our evolution. The most well-known mechanism to mitigate pathogenic threats is the body's own immune system, which functions to prevent or limit infections after the disease-causing agents have breached the body.

Although the human immune system is vital, its activation is not without costs. For example, activation of the immune system in response to detection of pathogenic microbes is metabolically taxing, robbing individuals of caloric resources that can otherwise be devoted to other evolutionarily important tasks such as searching for desirable mates, caring for one's kin, and building social ties (Schmid-Hempel, 2003). Thus, it is advantageous for the body to prevent its immune system from being chronically burdened by fighting pathogenic microbes. Immunological defenses in response to pathogens occur only after pathogenic agents have compromised the body's immune surveillance system (i.e., *reactive* defense). Because of the costs associated with generating an adaptive immune response (versus innate), there would have been evolutionarily unique benefits associated with *proactive* defense: the *behavioral* prevention of infection by avoiding infectious diseases (Schaller, 2006; Schaller and Park, 2011).

The behavioral immune system consists of a suite of psychological mechanisms that detect cues of infectious pathogens in the environment, trigger disease-relevant psychological responses, and facilitate behav-

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ioral avoidance of pathogens (Schaller and Park, 2011). If the so-called behavioral immune system evolved to facilitate specific behavioral responses (e.g., avoidance), it may be considered to be a psychologically unique motivational system (Neuberg et al., 2011). Distinct motivational systems are typically associated with distinct affective experiences (Damasio, 2019; Damasio and Carvalho, 2013). The affective experience associated with the behavioral immune system has been found to be *disgust*. There is a substantial body of research implicating the specific role of disgust as a key component of the behavioral immune system (Curtis et al., 2011). The functional relationship between pathogenic agents and disgust manifests in many ways. Specifically, sensory cues that clearly connote proximity to infectious pathogens are especially likely to evoke disgust. Furthermore, behaviors that violate normative expectations in social interactions that are associated with disease transmission (e.g., food preparation, physical proximity, personal hygiene, sexual interaction) can also elicit disgust (Rozin et al., 2008).

Disgust shares some characteristics with other negative affective experiences (e.g., fear, anger, hate), but has a unique influence on information processing systems, which contribute to keeping individuals away from communicable diseases. At the information-processing level, visual attention is engaged for longer periods of time following disgust-eliciting stimuli, compared with neutral or fear-eliciting stimuli (Perone et al., 2021). Disgust can be elicited by objects, such as open wounds, unclean spaces, and dirt, but also by specific forms of social behavior. These behaviors can include unusual sexual acts, eating unusual food, and actions that violate moral codes of conduct (Haidt et al., 1994; Tybur et al., 2013; Wagemans et al., 2018). Consistently, some religions attach moral impurity to particular sexual acts (e.g., extramarital relationships), certain food choices (e.g., eating pork), and touching unclean objects such as urine or feces. Moral psychologists have argued that individuals who are more prone to experiencing pathogen-induced disgust may condemn moral violations more strongly, and may be more likely to value practices associated with moral *purity* such as temperance, chastity, piety, and cleanliness (Haidt and Joseph, 2004). Consistently, Makhanova et al. (2019) and Murray et al. (2019) provide evidence showing that individual differences in pathogen concerns (i.e., germ aversion) are associated with stronger endorsements of moral purity.

The relationship between moral transgressions and disgust may also be apparent in everyday figures of speech such as “you make me sick.” Research has found that people frequently mention moral transgressions as well as physical stimuli such as dirty spaces, body products, and spoiled food when they are asked to list disgusting things (Haidt et al., 1997). In addition, individuals who are presented with moral transgressions rate them as disgusting (Hutcherson and Gross, 2011) and experimentally inducing physical disgust makes moral judgments more severe especially in the domain of moral purity (Eskine et al., 2011; Wheatley and Haidt, 2005). Some researchers have even argued that “although disgust may have originated in defending the body against poison and disease, its role in morality appears to extend far beyond this sphere” (Chapman and Anderson, 2014).

In addition to the mentioned individual-level effects of pathogens on cognitive, emotional, and behavioral tendencies, infectious diseases have been found to shape important society-level outcomes. Pathogen prevalence, as an important ecological factor, can influence cultural and moral systems at the community level (e.g., Bastian et al., 2019; Jackson et al., 2019). For example, cross-cultural research suggests that in geographical regions characterized by historically higher pathogen prevalence, people are less individualistic, exhibit lower levels of openness to new things, and more strongly endorse values that emphasize traditionalism, group loyalty, obedience, and respect for authority (Murray et al., 2013; Tybur et al., 2016; Van Leeuwen et al., 2012). In addition, higher historical pathogen prevalence has been linked to higher society-level conformity pressures (i.e., cultural tightness), higher political conservatism, and linguistic heterogeneity (Schaller and Murray, 2011). There is accumulated evidence suggesting that societies adopt varying rituals and moral values to facilitate coping with chronic prevalence of pathogens (Fincher and Thornhill, 2012), or large-scale temporary increases in the occurrence of a disease such as the 1918 influenza pandemic (Alexander, 2019). Historians of medicine have proposed, using qualitative data, that epidemics are typically followed by changes in social and moral norms, for example increased religiosity, presumably to attenuate the effects of high rates of communicable disease in the environment (Snowden, 2019).

In this work, drawing principally on psychology, anthropology, and behavioral ecology (see Sng et al., 2018), we propose that at the individual level, pathogenic cues are related to moral judgments across individuals and experimental situations. At the society level, we predict that pathogen prevalence is linked to human moral systems across regions, cultures, languages, and historical periods. Specifically, we rely on Moral Foundations Theory (MFT; Graham et al., 2013; Haidt and Joseph, 2004) to operationalize human moral systems from a cultural evolutionary perspective. MFT aims to achieve a parsimonious basis for explaining the links between anthropological and evolutionary accounts of moral intuitions. This framework suggests that moral intuitions derive from innate psychological mechanisms that coevolved with cultural institutions. Care, Fairness, Loyalty, Authority, and Purity — according to MFT (Graham et al., 2013) — are moral systems that possess evolutionarily adaptive underpinnings present in individuals across cultures, with each moral system producing automatic “gut-level” reactions of like or dislike when certain phenomena are perceived in the social world, which in turn guide moral judgments of right and wrong. Moral foundations are *phenotypically plastic*, i.e., although these five foundations have adaptive fitness benefits and are present across human populations, they are environmentally sensitive such that each foundation can be increased or decreased based on the ecologically recurrent problems they can solve. In addition, moral foundations are *context-dependent*, i.e., although each individual values these foundations to some extent, contextual cues can subtly change people’s gut-level judgments in these domains. For example, while conservatives typically value Care and Fairness less than liberals (Graham et al., 2013), their score increases on these foundations when analytic thought is activated using immediate contextual cues (Yilmaz and Saribay, 2017).

Care is rooted in the instinct to protect and nurture offspring and weak individuals in one’s group. Fairness is oriented toward concerns of justice, proportionality, equality, and reciprocity. Care and Fairness are collectively referred to as “individualizing” foundations as they are concerned with the rights of individuals (Graham et al., 2011). Loyalty is geared toward concerns of unity, solidarity, togetherness, family, and tribe. Authority values function to defend authority and social order within a hierarchical structure. Finally, Purity corresponds to physical and spiritual cleanliness, decency, and dignity, valuing sacredness, and suppressing carnal desires. Loyalty, Authority, and Purity are collectively referred to as “binding” foundations as they support and enable group ties while discouraging selfish behavior for the good of the group (Graham et al., 2011). While MFT is a cultural and evolutionarily informed theory of human morality, only recently has research begun to test historical-evolutionary causal mechanisms that account for temporal variations in these moral systems (see Muthukrishna et al., 2021).

Here, our overarching theory is that pathogen threat and prevalence are linked to individual-level and population-level endorsements of moral foundations, particularly Purity. Specifically, we argue that Purity is a particular moral system developed and maintained in response to the threat of chronic and acute pathogen occurrence in the environment. We expect that the connection between pathogens and moral Purity should be manifest in contextual judgments and individual differences at the individual-level. Purity values are related to physical proximity-seeking behavior within groups, less unrestricted sexual activity with outgroup members, and higher cleanliness in interpersonal interactions (see Wagemans et al., 2018). Specifically, Haidt (2012, p. 146) makes the case that “the original adaptive challenge that drove the evolution of the sanctity (i.e., purity) domain [. . .] was the need

to avoid pathogens, parasites, and other threats that spread by physical touch or proximity" and even argues that "if we had no sense of disgust […] we would also have no sense of the sacred" (Haidt, 2012, pp. 173–174). The motivation to avoid any potential threat of physical and mental contamination makes it likely that communities most prone to experience high loads of pathogens would also develop harsher norms around purity-related transgressions (Haidt, 2012; Haidt and Graham, 2007; Horberg et al., 2009; Inbar et al., 2012). Accordingly, we hypothesize higher endorsements of Purity values in societies that have (or have historically had) high levels of pathogen prevalence.

In Studies 1 and 2, we use epidemiological data to examine how pathogen prevalence is linked to moral systems across geographical regions. We hypothesize that regions with higher prevalence of infectious diseases employ community-level moral values, particularly Purity, to cope with (and hopefully reduce) the presence of communicable diseases. For example, an outbreak of an infectious disease in a region can cause residents to lessen social contact, exclude unknown outgroup members (especially those who are perceived to be from the same origin as the disease) through fear of contagion (Kim et al., 2016), care more for immunocompromised persons, and reduce unsafe sexual activity such as short-term sexual encounters. Complementing Studies 1 and 2, in Study 3 we test the hypothesis that if pathogens are accompanied by a particular type of moral system, they should also be linguistically concomitant, that is, they should be likely to be present together in the same context in large language corpora. In Studies 4 and 5, we investigate our individual-level hypotheses. Specifically, we test whether individuals who generally are more avoiding of pathogenic stimuli value particular moral foundations, and whether pathogenic stimuli are able to activate pathogen-neutralizing moral systems related to physical distancing with unknown individuals, unsafe sexual activities, and cleanliness. Lastly, in Study 6, we explore the historical relationship between rates of infectious diseases and moral language as manifested in the 20th century books. In Studies 3–6 (across individuals, languages, situations, and time periods), we did not have any a priori predictions besides for Purity, and our work was exploratory.

Study 1

In this study, we examined the covariation of moral values and pathogen prevalence in geographical regions. The prevalence of infectious diseases is hypothesized to influence moral values. Thus, it is crucial to examine how geographic variation in pathogen prevalence is associated with regional differences in moral values. To test this prediction, in Study 1 we investigated the relationship between pathogen prevalence at the county level in the U.S. and moral values held in those counties. Since political ideology is related to both pathogen avoidance (Tybur et al., 2016) and moral values (Graham et al., 2009; Kivikangas et al., 2021), we controlled for the role of political ideology in our statistical models.

Methods

Pathogen Prevalence. We used county-level pathogen estimates based on infectious diseases data made available by the Centers for Disease Control and Prevention (CDC). The CDC's website (cdc.gov) has information on various infectious (and noninfectious) diseases in the U.S. and provides county-level occurrences of pathogen-related mortality. We used available archival data[1] from 1999 to 2016 and compiled a data set with county-level mortality rate (per 100,000 residents) due to infectious diseases in 2834 unique counties ($M = 23.8$, $SD = 9.0$) across 50 states and the District of Columbia (DC).

Moral Values. We used the estimates of county-level distribution of moral values provided by Hoover et al. (2021). These authors relied on data ($N = 106{,}465$) from www.YourMorals.org, which is an online platform for collecting data on moral values using the Moral Foundations Questionnaire (MFQ; Graham et al., 2011). MFQ is a self-report measure of moral foundations with 30 items measuring the five moral foundations. Although this is a relatively large sample, it cannot be used to directly estimate county-level moral values as it does not use probability sampling at the county level (Hoover and Dehghani, 2020), and many counties have very few respondents. To address these estimation issues, Hoover et al. (2021) used Multilevel Regression and Synthetic Poststratification (MrsP; Leemann and Wasserfallen, 2017), a model-based approach for sub-national estimation that extends Multilevel Regression and Poststratification (MrP; Park et al., 2004). Specifically, county-level estimates were based on the inclusion of a more diverse set of demographic variables. These estimates also account for two levels of regional clustering, the county level and the region level, and include the proportion of Democratic votes as a county-level factor. Finally, the multilevel model also includes a hierarchical auto-regressive prior (Riebler et al., 2016) that, under the presence of spatial auto-correlation, induces local spatial smoothing between proximate counties (Hanretty et al., 2016; Hoover and Dehghani, 2020; Selb and Munzert, 2011). We used estimates of Care, Fairness, Loyalty, Authority, and Purity for each county. County-level moral values estimated by Hoover et al. (2021) can be viewed at mapyourmorals.usc.edu.

Political Ideology. We collected data from presidential elections in the U.S. (MIT Election Data and Science Lab, 2018) and calculated a county-level conservatism index by subtracting the voters for the Democratic party from the Republican party and dividing that by the total voters (including for the Green party) in that county. We then averaged these county-level conservatism estimates for the same periods as with our pathogen data (2000, 2004, 2008, 2012, 2016, and 2020 elections). This method for quantifying county-level conservatism based on voting behavior has been previously used in Reimer et al. (2022).

Analytic Procedure. To test our hypotheses, we ran five linear regression models that estimated each of the five moral foundations as a function of county-level pathogen prevalence and political conservatism. To better compare regression coefficients, we *z*-standardized all outcome and predictor variables. Our models included a spatial autocorrelation component to account for the tendency of neighboring counties to resemble each other and a non-spatial component to capture residual variation across counties (Besag, 1974; Morris et al., 2019). Our models also included a varying (random) intercept to account for differences in policies, resources, and other factors between states (and the District of Columbia) that were not captured by the predictor variables.

To estimate these models, we used the *brms* R package (Bürkner, 2017, 2018) as an interface to fit Bayesian generalized linear multilevel models in Stan (Stan Development Team, 2021). Bayesian inference involves choosing a likelihood function and prior distributions. The likelihood function links the observed data to one or more model parameters (e.g., regression coefficients) by expressing how likely the observed data would have been for different values of said model parameters. Our models used a normal likelihood function. Prior distributions state how plausible different values of said model parameters are before considering the observed data. Our models used weakly informative prior distributions, $\beta \sim$ (Half-)Student-t(3, 0, 2.5), for the fixed intercept, the regression coefficients, as well as the standard deviations of the varying intercept and the spatial and residual county-level variances. Bayesian inference applies Bayes' theorem to update prior distributions in light of the observed data to produce posterior distributions. Posterior distributions state how plausible different values of the model parameters are given the observed data. We report point estimates, based on the median of posterior samples, and 95% uncertainty intervals, based on the quantiles of posterior samples, for relevant model parameters. We also report a Bayesian

[1] http://wonder.cdc.gov/ucd-icd10.html

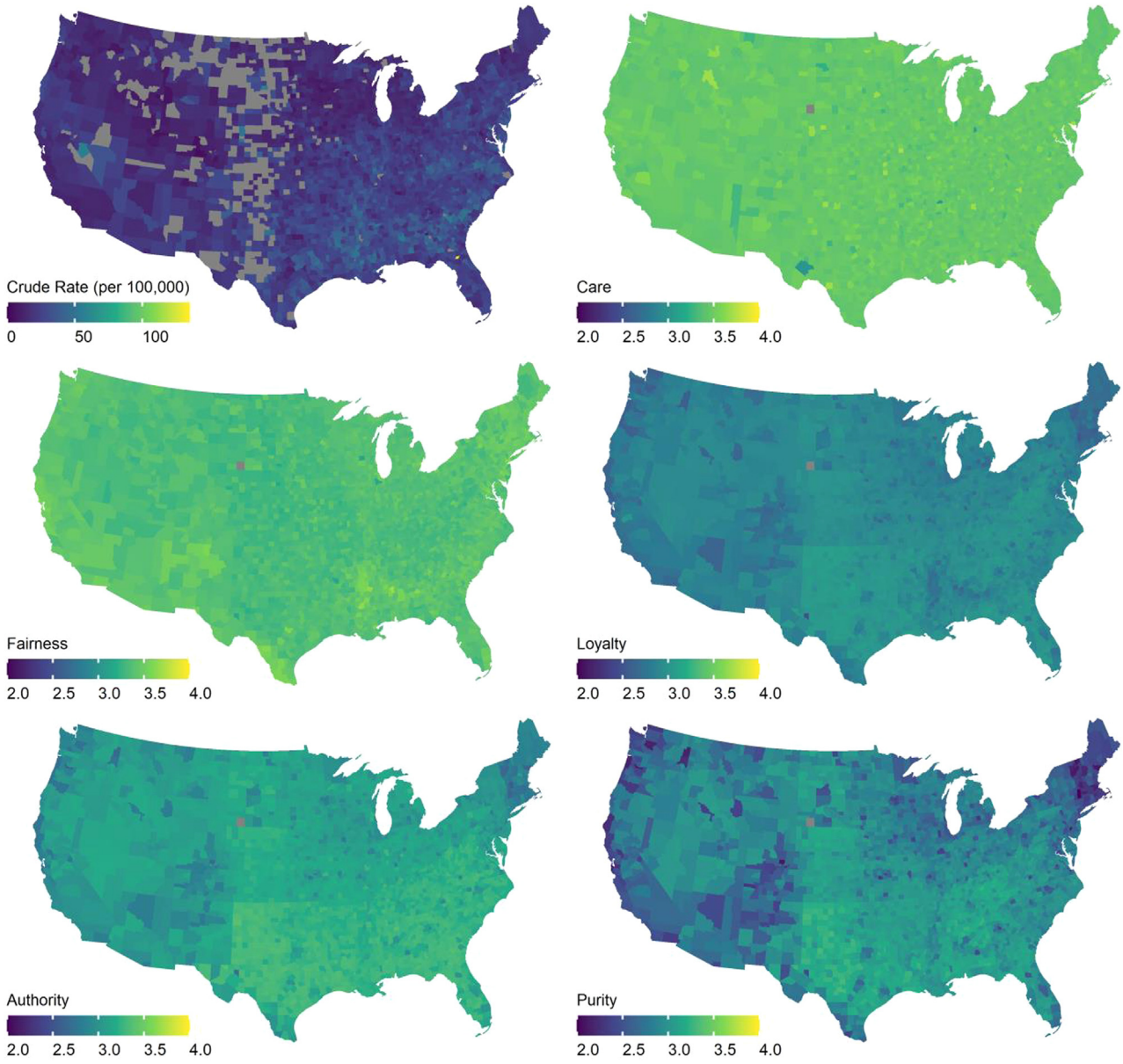


Fig. 1. Maps showing county-level pathogen prevalence and moral values.

analogue of R^2 with its 95% uncertainty interval (Gelman et al., 2019) as a measure of within-sample model fit.[2]

Results

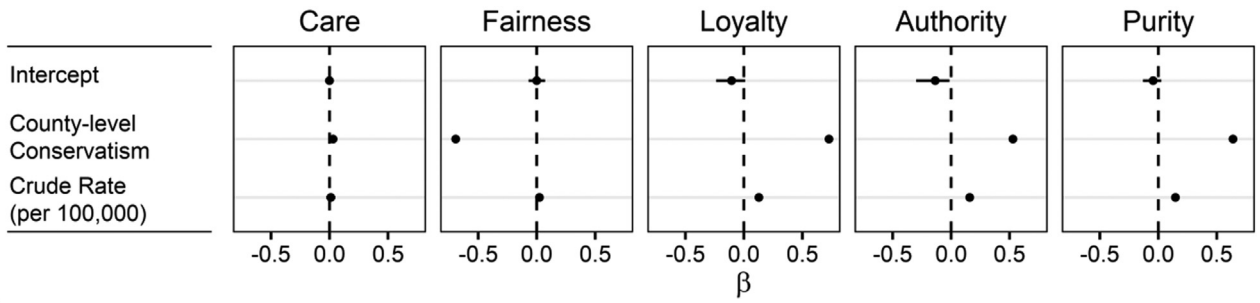
Fig. 1 shows the county-level predictor and outcome variables. Fig. 2 shows the results of our analyses. In line with prior research (Graham et al., 2009; Kivikangas et al., 2021), county-level conservatism was associated with *less* Fairness (β = −0.69, [−0.72, −0.66]) and *greater* Loyalty (β = 0.73 [0.71, 0.75]), Authority (β = 0.53 [0.51, 0.55]), and Purity (β = 0.64 [0.62, 0.66]) but was unrelated to Care (β = 0.03 [−0.01, 0.07]). In line with our hypothesis, county-level pathogen prevalence was associated with *greater* Loyalty values (β = 0.13 [0.11, 0.15]), Authority (β = 0.16 [0.14, 0.18]), and Purity (β = 0.15 [0.13, 0.17]) but was unrelated to Fairness (β = 0.02 [−0.01, 0.05]) and Care (β = 0.01 [−0.03, 0.05]). In summary, Study 1 provided evidence that geographic variation in pathogen prevalence is associated with regional differences in moral values. While Van Leeuwen et al. (2014) previously tested state-level associations between moral values and pathogen prevalence, these authors did not account for geographical auto-correlation. In addition, county-level analysis gives us a more nuanced and fine-grained level of analysis to better understand how local prevalence of pathogens is associated with communities' values. Our current results complement and extend those of Van Leeuwen et al. (2014). In particular, we found that county-level pathogen prevalence in the United States predicted county-level differences in the endorsement of the "binding" foundations, especially Authority and Purity, after controlling for their well-established association with political ideology.

Study 2

Pathogen prevalence can have regional influences on the development and persistence of norms and beliefs (Thornhill and Fincher, 2014; Van Leeuwen et al., 2012). Our estimates of pathogen prevalence in

[2] R^2 values only represent the non-spatial, fixed effects in each model.

A



B

	Care	Fairness	Loyalty	Authority	Purity
R^2	0% [0%, 1%]	50% [48%, 52%]	60% [58%, 61%]	35% [32%, 37%]	51% [49%, 53%]
SD_{State}	0.03 [0.00, 0.09]	0.21 [0.15, 0.29]	0.39 [0.28, 0.55]	0.43 [0.26, 0.63]	0.22 [0.16, 0.32]
$SD_{County - Spatial}$	0.04 [0.00, 0.17]	0.39 [0.31, 0.47]	0.35 [0.29, 0.42]	0.44 [0.37, 0.51]	0.44 [0.38, 0.50]
$SD_{County - Residual}$	1.00 [0.97, 1.02]	0.56 [0.54, 0.58]	0.36 [0.34, 0.38]	0.38 [0.36, 0.40]	0.35 [0.33, 0.37]

Fig. 2. *Results from the geospatial linear regression models estimating each of the five moral foundations as a function of pathogen prevalence and political conservatism. Note.* Point estimates with 95% uncertainty intervals for (**A**) all regression coefficients as well as for (**B**) the within-sample variance explained and the standard deviations for the variance across states and the spatial and non-spatial components of the variance across counties.

Study 1 relied on recent prevalence of infectious diseases in the U.S., making it crucial to replicate that cross-region effect across populations. Previous cross-cultural studies have also shown that moral systems differ across countries (Graham et al., 2011), and that variation in pathogen prevalence is often associated with cultural-psychological outcomes (Murray and Schaller, 2010). We advance this line of research by covering more countries and including more controls in our analysis. Merging these ideas, we postulated that cross-cultural variation in historical pathogen prevalence would be associated with moral systems while controlling for how much those cultures are Western, Educated, Industrialized, Rich, Democratic (WEIRD) (Henrich et al., 2010), homogeneous (Gelfand et al., 2011), or individualistic. Study 2 was designed to evaluate the unique effect of historical ecological pathogen prevalence on contemporary country-level moral values above and beyond cultures' WEIRDness, tightness-looseness, and individualism as potential culture-level confounding variables.

Methods

Pathogen Prevalence. We used the historical pathogen prevalence data compiled by Murray and Schaller (2010), who used epidemiological atlases from the early 20th century to gather prevalence data on nine infectious diseases (leishmanias, schistosomes, trypanosomes, leprosy, malaria, typhus, filariae, dengue, and tuberculosis) in 230 geopolitical regions worldwide. Since we had moral foundations data for 67 countries, we only used the historical pathogen prevalence for the same countries. All 67 countries were contained within Murray and Schaller's (2010) data set.

Moral Values. We used nation-level data based on responses to the MFQ provided by Atari et al. (2020). The data were collected from over 330,000 participants in 67 countries with at least 100 participants per country. We collected estimates of five moral foundations (Care, Fairness, Loyalty, Authority, and Purity). The median sample size in this data set was 439 participants per country.

Cultural Looseness. Cultural tightness (vs. looseness) taps into variance in norms, values, and behavior. Tight cultures typically have many strong norms and a low tolerance of deviant behaviors. Therefore, a tight culture facilitates homogeneity in traditions, norms, and behaviors. Looser cultures score higher on well-being, freedom of choice, tolerance for sexual deviations, and individualism, while being lower on traditionalism, population density, food deprivation, natural disasters, and institutional repression (Gelfand et al., 2011). Cultural looseness has been found to be associated with both moral values (Gelfand et al., 2011) and rate of infectious diseases (Gelfand et al., 2021) across cultures, so we controlled for cultural looseness in our analyses. We collected country-level indices of tightness-looseness from Uz (2015), where smaller indices indicate tighter cultures. Out of 67 countries in our sample, 51 had available data on tightness-looseness.

WEIRD cultural distance. A growing body of research suggests that populations around the globe vary substantially along several important psychological dimensions, and that people from societies characterized as WEIRD are particularly unusual (Henrich et al., 2010). Recently, Muthukrishna et al. (2020) developed and validated country-level cultural distance from the U.S., as a point of comparison. These "WEIRDness scores" are robust indicators of cultural distance, grounded in evolutionary theory. Out of 67 countries in our sample, 46 had data on WEIRD cultural distances.

Individualism. We controlled for individualism as it correlates with both pathogen prevalence in different countries (Fincher et al., 2008) and moral values (Hofstede, 2010). Country-level individualism indices were collected from Hofstede (2010). Individualism, in this framework, is defined as a preference for a loosely-knit social framework in which individuals are expected to take care of only themselves and their immediate families, whereas collectivism represents a preference for a tightly-knit framework in society in which individuals can expect their relatives or members of a particular ingroup to look after them in exchange for unquestioning loyalty (Hofstede, 2010). Except for one country (Afghanistan), we were able to secure individualism indices for all nations in our sample.

Analytic Procedure. Since the number of cultures we had obtained data from was small and countries are naturally geographically clustered, we used hierarchical linear models to examine the predictive effect of country-level pathogen prevalence on country-level moral values, while controlling for WEIRDness, cultural looseness, and individualism. We clustered countries in six geographical regions: Africa, Asia, Europe, North America, Oceania, and South America, yet Oceania was not included in the models as it only contains two countries (Australia and New Zealand) and these countries' looseness indices were missing.

Table 1
Five multilevel models predicting moral values across cultures (Study 2).

	Dependent variable:				
	Care (1)	Fairness (2)	Loyalty (3)	Authority (4)	Purity (5)
Pathogen Prevalence	0.042	−0.011	0.169*	0.288***	0.265**
	(0.055)	(0.060)	(0.069)	(0.086)	(0.088)
Cultural Looseness	−0.002	0.034	0.010	0.006	−0.080
	(0.035)	(0.038)	(0.044)	(0.053)	(0.051)
Individualism	0.001	−0.0003	−0.004	−0.002	−0.004
	(0.002)	(0.002)	(0.002)	(0.002)	(0.002)
WEIRDness Distance	0.084	0.648	1.085	0.518	0.693
	(0.846)	(0.913)	(1.057)	(1.268)	(1.214)
Constant	3.437***	3.610***	2.464***	2.343***	1.914***
	(0.115)	(0.124)	(0.143)	(0.175)	(0.178)
Observations	34	34	34	34	34
Log Likelihood	5.917	3.624	−0.559	−6.106	−5.713
Akaike Inf. Crit.	2.167	6.752	15.119	26.211	25.426
Bayesian Inf. Crit.	12.851	17.436	25.803	36.896	36.111

Note. *$p<.05$
** $p<.01$
*** $p<.001$

Our final sample included 34 countries (Argentina, Bulgaria, Canada, Chile, Egypt, Finland, France, Germany, Hungary, India, Indonesia, Iran, Italy, Japan, Mexico, Netherlands, Nigeria, Peru, Philippines, Poland, Romania, Russia, Serbia, Singapore, Slovenia, South Africa, South Korea, Spain, Sweden, Turkey, Ukraine, United Kingdom, United States, Vietnam) grouped in five regions. Notably, the scatter plots (Fig. 3) represent all countries for which we had data, but some of these countries did not have available data for some of our control variables (e.g., tightness-looseness). Hence, our final analysis including the control variables included 34 countries, mentioned above.

Results

The scatter plots of the relationships between historical pathogen prevalence and moral values across 67 countries with complete data are shown in Fig. 3. After controlling for WEIRDness, cultural looseness, and individualism, multilevel models suggested that historical pathogen prevalence, across 34 countries with complete data on all variables, was not associated with Care ($B = 0.04$, $SE = 0.06$, $p = .451$) or Fairness ($B = -0.01$, $SE = 0.06$, $p = .856$). Loyalty was negligibly positively associated with historical pathogen prevalence ($B = 0.17$, $SE = 0.07$, $p = .021$). However, there was compelling evidence that country-level pathogen prevalence was associated with Authority ($B = 0.29$, $SD = 0.09$, $p = .003$) and Purity ($B = 0.27$, $SD = 0.09$, $p = .005$), over and above WEIRDness, cultural looseness, and individualism.

Endorsement of Purity and historical exposure to pathogens across 67 countries are shown in Fig. 4 (distributions of other moral values are presented in Supplementary Materials). As shown, historical pathogen prevalence (i.e., aggregation of prevalence of infectious diseases in the past century) is associated with contemporary Authority and Purity values across countries (see Fig. 3), above and beyond countries' WEIRDness, looseness, and individualism. Complete models are presented in Table 1.

Taking a historical-evolutionary perspective, strict rules and social hierarchies dominated by designated authorities or prestigious individuals have facilitated group coordination during collective threats such as pathogen outbreaks. Of note, our results show no compelling evidence that Care or Fairness can be predicted by historical pathogen prevalence, especially when clustering is taken into account and potential confounding variables are adjusted for. The effect size of Loyalty was also substantially smaller than that of Authority and Purity. This cross-cultural study replicates the Purity effect found in Study 1 (in U.S. counties), but also highlights the role of historical pathogen prevalence on Authority values (e.g., obedience, respectfulness, hierarchy adherence) across cultures. Purity and Authority values might be two equally important mechanisms to bring order to cultures stressed by high prevalence of infectious diseases, one by strengthening social hierarchies and order-restoring authorities, and the other by reinforcing personal hygiene, inflicting moral/social costs on promiscuity and uncleanliness. We do note here that correlational studies of aggregated country-level data are not optimal for testing hypotheses about psychological processes (e.g., Bromham et al., 2018). Hence, these results should be interpreted in a complementary manner with Study 1, as well as the following studies in which we aim to unpack some of the historical and psychological processes underlying the relationship between historical pathogen prevalence and moral systems.

Study 3

In this study, we examined the semantic association between pathogen-related words and moral foundations using word embeddings — pre-trained models for distributed representation of word meaning induced from patterns of word co-occurrences in a wide-coverage corpus of text. In word-embedding models, each word is represented by a numeric vector such that the geometry of the vectors captures semantic relations between the words. As such, if two concepts are semantically close to one another, they should co-occur in similar linguistic contexts, resulting in their embeddings being closer to one another in the semantic space (Collobert et al., 2011; Garten et al., 2018). Since traces of psychological processes are manifested in language (Jackson et al., 2021), psychologically related concepts should co-occur in similar linguistic contexts (e.g., Garg et al., 2018). Therefore, we expected that pathogen-related concepts should semantically be closer to the specific moral foundations which are psychologically more related to them. Specifically, we used the word-embedding model of semantic representations to examine the semantic similarity between pathogen-related words and words representing moral foundations in English. In order to make sure that these associations are not idiosyncratic features of English, we replicated this analysis in four other languages — Spanish, Farsi, Japanese, and Hebrew — which represent a diverse collection of language families (Romance Indo-European, Indo-Iranian, Japonic, and Northwest Semitic, respectively).

Methods

As discussed above, word embeddings are a popular natural language processing method that represents each word by a vector, such that geometric relatedness — e.g., cosine similarity between vectors — cap-

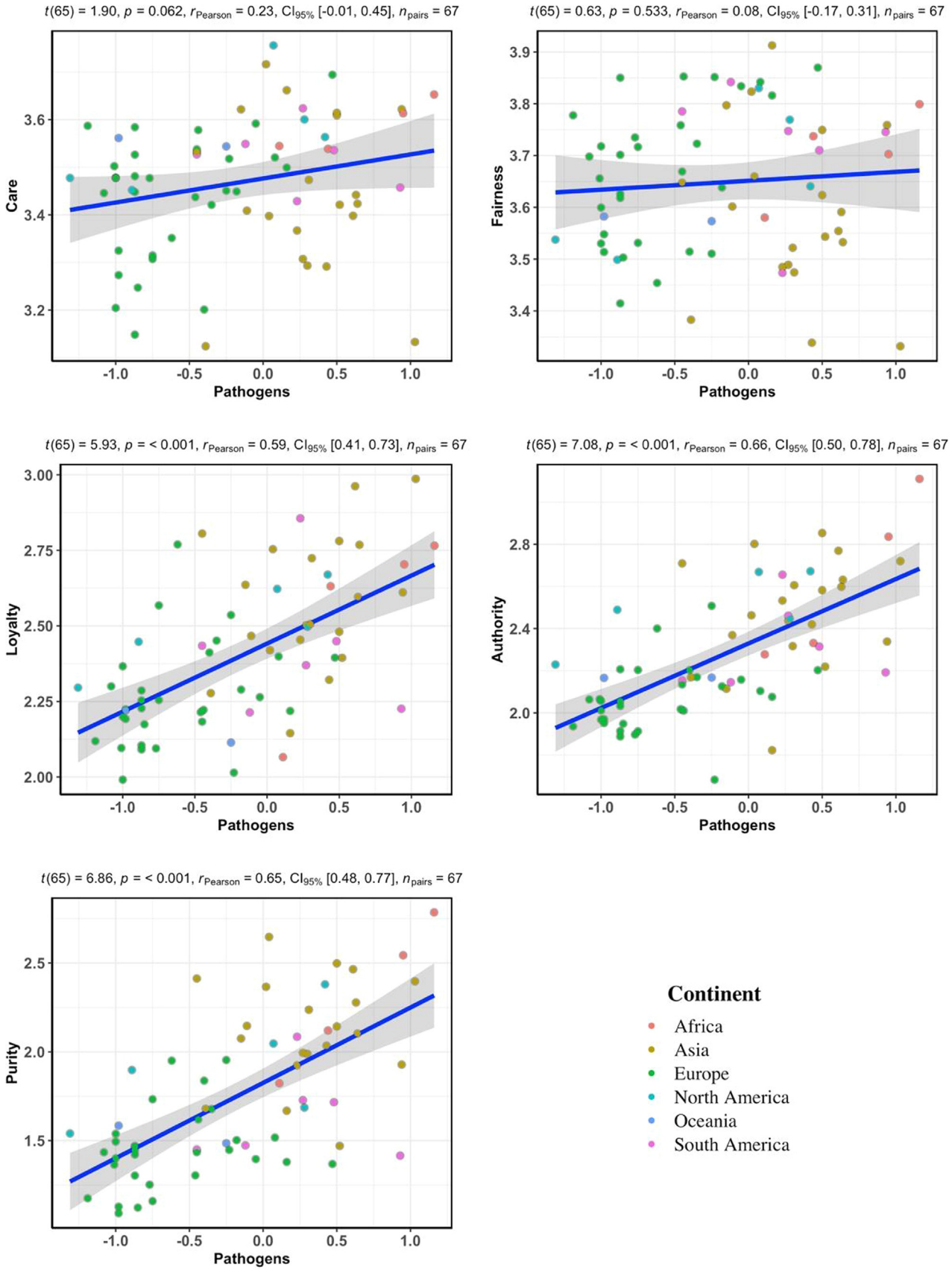


Fig. 3. Cross-country relationships between pathogen prevalence and moral values.

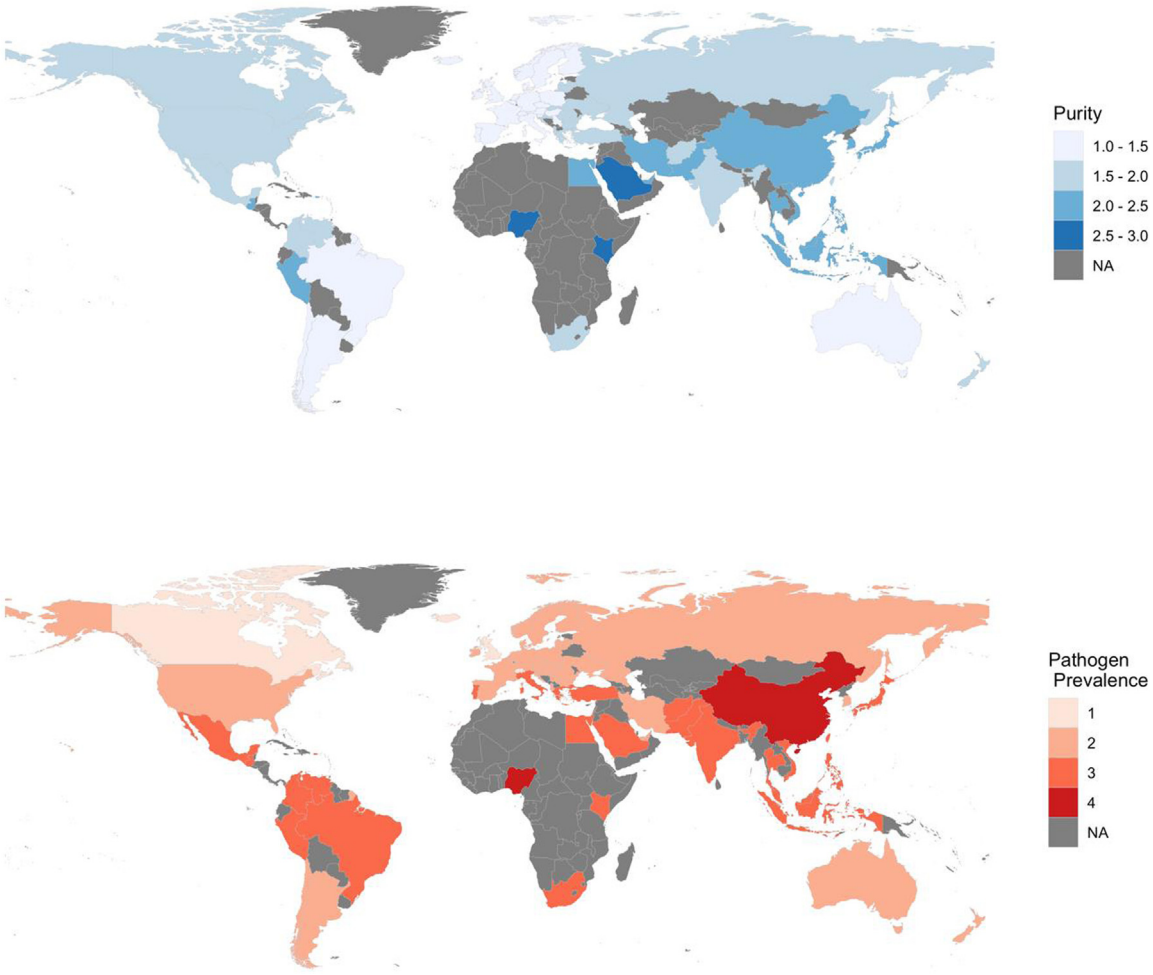


Fig. 4. Historical presence of infectious diseases and contemporary Purity values around the world.

tures clusters of lexical semantic meaning and common usage patterns. These similarities approximate both the intrinsic linguistic relationships among words, such as the relationship among tenses for a given lemma, as well as their usage across large text corpora. The "FastText" algorithm (Bojanowski et al., 2017) generates word vectors using subword information in the same style as the popular "Word2vec" skipgram algorithm (Mikolov et al., 2013), and has been used to generate word embedding sets for a large host of languages (Grave et al., 2018). We used 300-dimension FastText vectors trained on the "Common Crawl" corpora,[3] for each language in our analyses.

We measured the moral loading of pathogen-related words by computing the cosine similarity between each pair of moral- and pathogen-related words. Moral seed words were taken from Garten et al. (2018), and a set of ten pathogen-related words was generated for this work (see Table 2) (translated to Spanish, Farsi, Japanese, and Hebrew by native speakers who were blind to the purpose of the study; see Supplementary Materials). The cosine similarity for all pairs of moral and pathogen-related words are calculated to analyze the semantic similarity between moral foundations and pathogens in natural language (see Garten et al., 2018). To examine the similarities between moral foundations and pathogen-related words, a robust one-way Analysis of Variance (ANOVA) was conducted with *p*-values adjusted for False Discovery Rates (FDR) and pairwise comparisons based on Yuen's trimmed means test. As a measure of effect size, we relied on "explanatory measure of effect size" ξ which does not require equal variances and can be generalized to multiple group settings (Wilcox and Tian, 2011).

Results

Similarity results revealed that Purity and Care words were closest to the pathogen-related words in English (Purity and Care were not different from one another in their similarity to pathogen-related words, $p = .643$). The robust one-way ANOVA showed that differences between the five similarity distributions were significantly different ($F(4, 127.41) = 14.23$, $\xi = 0.45$, 95%CI = [0.34, 0.56], $p < .001$). Post-hoc pairwise tests indicated that Purity was semantically closer to infectious diseases than Authority ($p < .001$), Loyalty ($p < .001$), and Fairness ($p = .011$). Next, Care was shown to be more related to infectious diseases words than were Fairness ($p < .001$), Loyalty ($p < .001$), and Authority ($p < .001$). Similarities of Fairness, Loyalty, and Authority to pathogen words were not different from each other (*p*s > 0.643). In sum, words related to infectious diseases appear substantially more often in similar contexts with Purity and Care words compared with Fairness, Loyalty, and Authority. We also replicated these patterns in Spanish ($F(4, 109.57) = 2.85$, $\xi = 0.24$, 95%CI = [0.09, 0.34], $p = .027$), Farsi ($F(4, 123.22) = 2.58$, $\xi = 0.19$, 95%CI = [0.05, 0.27], $p = .040$), Japanese ($F(4, 112.03) = 6.18$, $\xi = 0.30$, 95%CI = [0.17, 0.38], $p < .001$), and Hebrew ($F(4, 93.37) = 7.63$, $\xi = 0.41$, 95%CI = [0.28, 0.51], $p < .001$), but the effect sizes were smaller in other languages (see Supplementary Ma-

[3] https://commoncrawl.org/

Table 2
Words used in Study 3.

Concept	Words
Pathogens	virus, flu, disease, infection, sickness, germ, contagion, illness
Care	kindness, compassion, nurture, empathy, suffer, cruel, hurt, harm
Fairness	fairness, equality, justice, rights, cheat, fraud, unfair, injustice
Loyalty	loyal, solidarity, patriot, fidelity, betray, treason, disloyal, traitor
Authority	authority, obey, respect, tradition, subversion, disobey, disrespect, chaos
Purity	purity, sanctity, sacred, wholesome, impurity, depravity, degradation, unnatural

terials for details). These findings suggest that across five languages originating from different cultures and language families, pathogen-related words co-occur with Purity and Care more frequently than other moral values, highlighting that Purity and Care values are associated with cognitive processes (e.g., passing moral judgments about suffering or cleanliness) underlying representations of pathogen-related concepts. The co-occurrence of Care-related words and pathogen-related words across languages can be explained by the fact that illness and death are usually used along words such as "compassion," "hurt," and "suffer" which are related to the moral foundation of Care as conceptualized by MFT.

Study 4

The previous studies were community-level analyses, investigating the relationship between ecological pathogen prevalence and region-level moral values, in addition to linguistic association of pathogen and morality-related words. Indeed, macro-level analyses of communities cannot be generalized to individual-level processes as that risks committing the ecological fallacy. Given that group and individual levels of analysis often do not yield isomorphic results (Oyserman et al., 2002), deeper insights can be gained by simultaneously analyzing the independent effect of group-level and individual-level processes. In Study 4, we aimed to examine how individual differences in moral values are related to pathogen avoidance intentions. This study further clarified individual-level moral psychological processes in avoiding infectious diseases. Specifically, we examined the relationship between moral foundations and pathogen avoidance intentions while controlling for political orientation and religiosity in a cross-sectional design using a stratified sample from the United States.

Methods

Participants. We aimed to recruit a sample of 500 participants to detect small correlational effects (ρ = 0.15) with high power (95%). We recruited a stratified national U.S. sample from Qualtrics Panels, balanced with respect to age, sex, and political affiliation. Participants (N = 513) were almost half (51.3%) female and predominantly (63%) White American. In terms of age, 11.1% were in the 18–24 range, 18.1% were in the 25–34 range, 16.8% were in the 35–44 range, 18.9% were in the 45–54 range, 17.0% were in the 55–64 range, and 18.1% were 65 years old or older. In terms of political affiliation, 263 participants (51.3%) identified as a Democrat while the rest identified as a Republican.

Design and Materials. Our Institutional Review Board (IRB) approved this study (UP-19–00395). We collected data in this study in March 2019. To measure the constructs of interest, participants completed a set of measures including the short Moral Foundations Questionnaire (MFQ-20; Graham et al., 2011) (Cronbach's αs = 0.62 - 0.73) and a 2-scenario measure of pathogen avoidance intentions (Cronbach's α = 0.59, 95%CI = [.52, 0.66]) along with their demographic details. These two hypothetical scenarios, designed for this study, were "Imagine that a few months ago you booked a flight to a beautiful country abroad for a vacation. One or two days before your flight you find that there has been an outbreak of a dangerous infectious disease in that country, but the local authorities have controlled the situation. How likely is it for you to go on this vacation?" and "Some infectious diseases cannot be transmitted through skin contact unless one's skin has small bloody cuts. How likely is it for you to sit next to a person with such a disease on the bus?". Both questions were rated on a 7-point Likert-type scale ranging from 1 (*Extremely unlikely*) to 7 (*Extremely likely*). In this cross-sectional observational study, all items and measures were counterbalanced. We used linear regression models to account for sex, and political ideology, along with moral foundations to predict pathogen avoidance intentions.

Results

In a linear model controlling for sex and political ideology, Purity was significantly positively associated with pathogen avoidance intentions (β = 0.25, SE = 0.09, p = .006). Fairness was also shown to have a negative association with pathogen avoidance (β = −0.34, SE = 0.13, p = .010). Other moral values, political ideology, and sex had non-significant effects (ps > 0.07). These results highlight the individual-level processes between pathogen avoidance intentions and moral Purity. These patterns are consistent with our cross-cultural and linguistic analyses (Studies 2 and 3), implicating Purity values in relation to intentions of avoiding infectious diseases at the individual level. The relationship between Fairness values and pathogen-avoidance intentions in this study is also interesting. While this relationship should be replicated in future research using different stimuli and different samples, we believe this negative relationship might be due to the wording of our stimuli. For example, someone who scores high on Fairness might deem it unfair to avoid sitting next to another person, or they might think that they deserve to go on their vacation if the authorities have controlled the situation.

Study 5

When people feel more in immediate danger of infectious diseases they report lower levels of sociability (i.e., decreased interest in frequent contact with others) and produce more avoidant motor responses (Mortensen et al., 2010). Research also suggests that moral vigilance is increased when people are experimentally exposed to salience of infectious disease threats (Murray et al., 2019). In order to complement our previous analyses using an MFT framework, in the current study we used an experimental design and expose participants to visual cues of pathogens and assess their moral judgments compared with a control group exposed to neutral stimuli.

Methods

Participants. Based on prior work and a power analysis to detect a small-to-moderate effect size (r = 0.20) at p = .05 and 90% power, we aimed to collect 320 participants. We recruited 334 participants from Amazon Mechanical Turk. After removing the participants who failed an attention check, a total of 316 participants remained in the sample (130 male, 182 female, 4 other). Most participants were White Americans (n = 247), followed by Black Americans (n = 41). The mean age was 32.6 years (SD = 11.3 years).

Design and Materials. Our Institutional Review Board (IRB) approved this experimental study (UP-18–00712). We collected data in

this study in April 2019. Culpepper et al. (2018) identified main domains of pathogen-related disgust and generated a novel visual stimulus set of 20 images depicting scenes of highly salient pathogen risk, along with a paired control set (20 images) that are visually comparable but lack the pathogen cues. Participants were randomly assigned to the experimental (vs. control) group, receiving experimental (vs. control) stimuli. Participants in the experimental (vs. control) group were given three pathogen images (vs. non-pathogen counterparts), randomly chosen from the set of 20 images. Participants were asked to look at them for a few seconds and then answer questions about these images. As a manipulation check, we asked participants to rate how "pleasant" each scene was (1 = *"Not at all pleasant"*, 5 = *"Extremely pleasant"*). Right after being exposed to pathogen (vs. non-pathogen) cues, participants completed the 30-item MFQ (Graham et al., 2011) (Cronbach's α = 0.62 - 0.78) along with their demographic details. Participants also completed the Short-Form of the Positive and Negative Affect Schedule (PANAS; Thompson, 2007) after completing the MFQ to measure their momentary negative affect (Cronbach's $\alpha = 0.81$) after being exposed to experimental (vs. control) stimuli. We controlled for negative affect to account for the role of negative affect that might be evoked by pathogen stimuli in moral judgments. We also controlled for participants' political affiliation (1 = "*Very Democrat*"; 7 = "*Very Republican*") and religiosity (0 = "*Not religious at all*"; 10 = "*Very religious*").

Results

The zero-order correlation between dummy-coded experimental condition and Purity was smaller than the effect size on which we based our power analysis ($r = 0.10$, $p = .073$). We ran regression analyses to predict scores on moral foundations by condition (experimental [$n = 162$] vs. control [$n = 154$]), while statistically controlling for sex, age, negative affect, political ideology, and religiosity. Results suggested that being exposed to pathogen cues does not predict Care ($B = 0.18$, $SE = 0.49$, $p = .723$), Fairness ($B = -0.30$, $SE = 0.48$, $p = .527$), Loyalty ($B = 0.25$, $SE = 0.65$, $p = .705$), or Authority ($B = 0.50$, $SE = 0.60$, $p = .404$). However, participants in the experimental (vs. control) condition scored an average of 1.54 ($SE = 0.74$, $p = .038$) points higher on the Purity questionnaire items than participants in the control condition. We also compared the "pleasantness" ratings to make sure that our experimental manipulation worked. The experimental group ($M = 0.18$, $SD = 0.41$) rated the images significantly less pleasing compared to the control group ($M = 1.09$, $SD = 0.65$), $t = 14.63$, Welch-corrected $df = 256.45$, $p < .001$, Cohen's $d = 1.65$, $r = 0.67$.

Notably, as a robustness check, we examined the role of the manipulation on Purity, excluding two MFQ items that explicitly mention "disgust" (i.e., "Whether or not someone did something disgusting" and "People should not do things that are disgusting, even if no one is harmed") (four items, Cronbach's $\alpha = 0.77$). The effect of our pathogen manipulation did not change meaningfully, zero-order $r = 0.10$, $p = .078$. After accounting for sex, age, negative affect, political affiliation, and religiosity, the effect of our experimental manipulation was significant ($B = 0.91$, $SE = 0.43$, $p = .035$).

Therefore, in experimental settings, visual cues to pathogens can influence Purity judgments, but not moral judgments in other domains. This effect is independent of how much negative affect people experience when exposed to pathogenic visual stimuli. Domain-specific effects of pathogen cues highlight the adaptive benefits of Purity in immediate pathogen-rich environments. In other words, Purity is a context-sensitive, environmentally-plastic, pathogen-neutralizing suite of moral psychological mechanisms that function to avoid pathogen contact.

Study 6

Our community-level analyses were observational, hence no strong claims can be made with regard to the historical direction of the effect in the relationship between Purity and pathogen prevalence. Also, our data were contemporary, masking historical precedence of these variables over one another. For example, it is not clear whether particularly low levels of Purity (and other moral values) precede higher levels of pathogen prevalence or, alternatively, high levels of pathogen prevalence cause moral values to change in subsequent years. Here, we explore this question by combining historical data on infectious diseases in the U.S. as well as historical language data on moral values. Indeed, cultural and societal changes can be captured using linguistic analysis of large historical corpora of books and texts produced in recent history (Atari and Dehghani, 2021; Greenfield, 2013). Specifically, we rely on moral language used in published books in the 20th century (Michel et al., 2011), and historical prevalence of infectious diseases in the U.S. to examine the temporal link between infectious diseases and severity of moral language, while controlling for fluctuations in strength of social norms (cultural looseness) as a potential confounder.

Methods

Pathogen Prevalence. Data were adapted from Grossmann and Varnum (2015), who reported 9 of the most frequent infectious diseases reported by the historical records of the CDC. This data set included tuberculosis, syphilis, gonorrhea, malaria, typhoid and paratyphoid fever, diphtheria, pertussis, measles, and poliomyelitis. The data included prevalence rates from 1912 through 2012.

Moral Language Usage. In order to collect yearly usage of moral language, we relied on Google Ngram data, which is the largest available time-stamped corpus through 2008 (Michel et al., 2011). The current data ranged from 1900 to 2008 from books published in the U.S. The corpus consists of words and phrases (i.e., n-grams) and their usage frequency over time. We relied on the Moral Foundations Dictionary (MFD; Graham et al., 2009) and collected the frequency for each word in the dictionary from 1900 to 2008. Notably, the MFD has a "general moral language" category (e.g., "right", "transgress", "goodness") that was controlled for in our analyses.

Cultural Looseness. Cultural looseness was controlled for, as it correlates with both moral values and existence of pathogenic threats (Gelfand et al., 2011; Jackson et al., 2020). We used Jackson et al. (2019) estimates of cultural looseness in recent history. These authors used Google Ngram data, published between the years 1800 and 2000 and reported standardized frequency of loose (e.g., "Allow", "Freedom", "Autonomy") and tight (e.g., "Restrain", "Prevent", "Adhere") words.

Analytic Procedure. Prior to our analyses, we de-trended our time-series vectors by regressing out monotonic effect of time, general moral language, and cultural looseness. Then we subjected each time-series vector to augmented Dickey-Fuller root tests, to evaluate whether a time-series vector has an underlying trend that renders it non-stationary. We next used standardized vectors to examine the correlation between moral language and pathogen prevalence, and used cross-correlations to test whether moral norms *preceded* decrease in the prevalence of infectious diseases. Finally, we conducted additional tests of Granger causality to assess the relationship between moral norms and pathogen prevalence (as well as the reverse relationships) in the 20th century. Granger tests of causality are more conservative than cross-correlations as they evaluate whether one time-series variable is predicting changes to another time-series variable above and beyond values of the outcome.

Results

Cross-correlations (the correlations between two variables at different time lags) are visualized in Fig. 5: negative lags (left side of the dashed red line) indicate that pathogen prevalence precedes changes in moral language usage, while positive lags (right side of the dashed red line) indicate that moral language usage precedes pathogens. As can be seen, pathogen prevalence predicted immediate slight increases

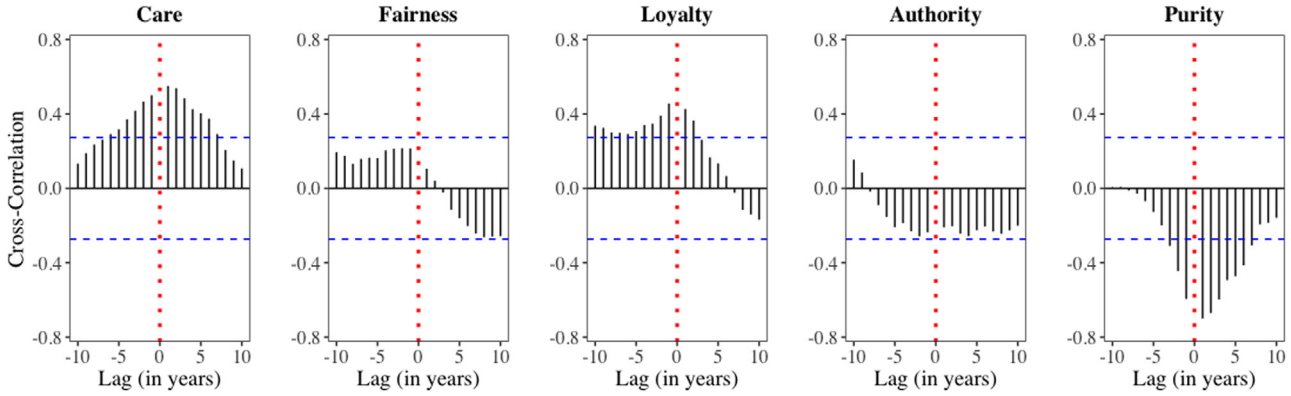


Fig. 5. Cross-correlations between pathogen prevalence and indicators of moral language. Correlations outside the dashed blue horizontal lines are significant at $\alpha = 0.01$. Negative lags (left side of the dashed red vertical line) indicate that shifts in pathogen prevalence led to shifts in moral language, whereas positive lags (right side of the dashed red vertical line) indicate that shifts in pathogen prevalence followed shifts in moral language.

Table 3
Granger Causality Test Results with 1-year-lagged and 5-year-lagged Models.

Granger Causality Model	1-year lag		5-year lag	
Pathogen → Care	F(1,86)	= 0.14	F(5,78)	= 4.06**
Pathogen → Fairness	F(1,86)	= 1.71	F(5,78)	= 0.91
Pathogen → Loyalty	F(1,86)	= 0.31	F(5,78)	= 2.84
Pathogen → Authority	F(1,86)	= 0.96	F(5,78)	= 2.97
Pathogen → Purity	F(1,86)	= 2.36	F(5,78)	= 0.49
Care → Pathogen	F(1,86)	= 8.91**	F(5,78)	= 1.86
Fairness → Pathogen	F(1,86)	= 0.04	F(5,78)	= 1.71
Loyalty → Pathogen	F(1,86)	= 2.47	F(5,78)	= 1.67
Authority → Pathogen	F(1,86)	= 0.79	F(5,78)	= 1.11
Purity → Pathogen	F(1,86)	= 20.11***	F(5,78)	= 3.44**

Note. $^{**}p < .01$ $^{***}p < .001$

in Care and Loyalty. However, the largest effect was observed for Purity. Cross-correlations between Purity language and pathogen prevalence suggested that not only do they significantly co-occur in the same years, but pathogen prevalence seems to drop immediately in subsequent years of high Purity norms in the United States (see Fig. 5), supporting the prediction that Purity functions to reduce communicable diseases. We further investigated the direction of these relationships in Granger causality tests (Table 3). We found strong evidence, consistent with cross-correlations, that Purity immediately "Granger caused" pathogens to drop (1-year lag), and the effect held for the 5-year lag too. Of note, high Care values seem to also precede higher rates of infectious diseases, but the effect did not hold for the 5-year lag. In the reverse models in Table 3 (pathogens "Granger causing" moral foundations), we did not find evidence suggesting that pathogen prevalence can have immediate 1- or 5-year effects on moral foundations except for a small effect on Care values with a 5-year lag.

In this study, the results indicate that historical prevalence of pathogens highly co-occurs with moral values associated with group cohesion, specifically Purity values (indexed by more frequent usage of Purity words), after controlling for other types of moral language and historical estimates of cultural looseness. Cross-correlations and Granger causality tests revealed a pattern where higher levels of Purity values co-occur with, and immediately causes, lowered levels of pathogen prevalence in the United States in the 20th century. Therefore, it seems that psychological mechanisms associated with Purity can act as a unique pathogen-neutralizing mechanism (possibly through social and physical distancing; Dehghani et al., 2016), lowering subsequent levels of infectious diseases. The finding that lower Purity values are historically related to more infectious diseases can be explained by the fact that low Purity values bring about higher unprotected sexual encounters, higher physical proximity-seeking, and lesser aversion toward disgusting things, which in turn can exacerbate the contagion of infectious diseases such as sexually transmitted infections. Notably, in Study 5, we found evidence that exposure to pathogens increases Purity values. In our exploratory historical analysis (Study 6), however, we found that moral purity preceded lower pathogen levels. It is possible that the relationship between Purity and pathogens is bidirectional and includes feedback loops. Future research should use stronger tests of causality across less WEIRD cultures and non-English languages to further examine this complex relationship.

General discussion

A single pandemic caused by an infectious disease can kill tens of millions of people worldwide and make hundreds of millions ill (see Ackerman et al., 2021). In addition to biological systems to fight off pathogens, humans have developed behavioral systems to avoid pathogenic agents before bodily contact, or to stay away from highly contagious environments. Here, in a series of studies, we demonstrate that across hyperlocal geographical regions (Study 1), nations (Study 2), linguistic contexts (Study 3), individuals (Study 4), and experimental conditions (Study 5), presence of pathogens is consistently linked to moral Purity systems. Indeed, Purity values may function to neutralize infectious diseases, possibly through lowered sexual contact, hygienic practices, avoidance of unfamiliar foods and/or persons who may be perceived to be associated with the origin of the disease. Finally, our historical analysis in Study 6 demonstrated that high moral Purity norms in the 20th century in the U.S. is followed by a decrease in infectious diseases.

The unique relationship between pathogen salience and Purity highlights the evolutionarily crucial role of moral Purity in survival of individuals and flourishing of groups across historical periods and geographic regions in the face of recurring increase in the occurrence of infectious diseases. At the county and national levels, Purity values might be more successfully transmitted and sustained within pathogen-rich ecologies if such norms lead to reduced contact with pathogenic agents (see Murray and Schaller, 2016). Prior psychological work indicates that pathogens can result in the cultural evolution of prophylactic norms and rituals (Tanaka et al., 2002; Tybur et al., 2016) embedded in Purity value systems, possibly through lowering the likelihood of unsafe sex, avoidance of unhygienic food, and shunning pathogen-rich places. In addition, Purity has been shown to have a particularly unique effect in promoting within-coalition alliances, an effect referred to as "purity homophily" (Dehghani et al., 2016), which in turn can provide ingroup coalitions in times of disease outbreaks especially in pathogen-dense ecologies (Navarrete and Fessler, 2006). Indeed, in ancestral environments, interaction with ingroup members may have posed less risk of

disease transmission than interaction with an outgroup member, since individuals possessed antibodies to many of the pathogens present in their own community, in contrast to those circulating among people coming from other regions (this argument has been questioned by some scholars; see De Barra and Curtis, 2012).

In this work, we provided a collection of methodologies, drawing upon multiple disciplines, to further establish the link between pathogen salience and morality across different levels and contexts. Indeed, some of our studies (e.g., Study 5) may be considered a conceptual replication (and extension) of prior experiments examining the relationship between infectious-disease salience and moral judgment (e.g., Makhanova et al., 2019; Murray et al., 2019; Van Leeuwen et al., 2012, 2014). Importantly, we did not test a singular hypothesis across these studies, rather, we tested inter-related hypotheses about how pathogens are linked to moral systems across time and space. Studies 1 and 2 focused on aggregate population-level dynamics and their results should be interpreted as such. Study 3 focuses on language usage in large natural language corpora. Studies 4 and 5 were designed to replicate previous work at the individual level. Finally, Study 6 was a historical psychological exploration of temporal dynamics between Purity norms and the prevalence of infectious diseases in the United States.

In Studies 1, 2, and 6, Loyalty was found to be related to pathogen prevalence suggesting that in aggregate levels across time and history, Loyalty values may have been associated with pathogen loads in the environment. Interestingly, Hruschka et al. (2014) collected data from eight societies using an experimental protocol that pits following an impartial rule of allocation against giving to one's community, and found that cross-cultural variation in following an impartial rule of giving is more consistent with a general response to material security and institutional quality than a specialized response to the risk of exposure to pathogens. Hence, future work is recommended to examine the relationship between pathogen prevalence and Loyalty (and Authority) using a collection of self-report and behavioral measures along with variables such as government effectiveness, economic development, and material security to get a more accurate picture of their inter-relations.

At the individual level, people in high avoidance of infectious diseases might find Purity rituals (e.g., refraining oneself from sexual intercourse with an unknown individual) appealing for a number of reasons. First, "pure" sexual practices often expose individuals to substantially fewer sexually transmitted infections (Bauch and McElreath, 2016). Second, Purity practices facilitate safer and more traditional food preparation techniques which often include ingredients with antimicrobial properties (Billing and Sherman, 1998). Third, hygiene-related Purity rituals (e.g., burial rituals) can coordinate behaviors to limit pathogen transmission. We argue that each of these lower-order mechanisms have intrapersonal (e.g., refraining oneself from contact with pathogens) and interpersonal (e.g., penalizing others' contact with pathogens) components.

Care values, as implicated in our linguistic, temporal, and county-level analyses, might be specific to the suffering and mortality accompanied by severe infectious disease (see Studies 1, 2, and 3). Particularly, it could be the case that pathogen outbreaks may lead to temporary, subsequent increases in the tendency to care for afflicted individuals. In addition, individuals typically talk about harms, sufferings, and deaths when speaking about infectious disease, which explains our linguistic findings in Study 3. Authority values were also linked to country-level pathogen prevalence in our cross-cultural analysis, almost as strongly as Purity values (Van Leeuwen et al., 2012). This finding can be understood within cultural evolution frameworks which combine familial transmission with selective learning from locally prestigious individuals. In high-pathogen ecologies, individuals may be safer as long as they are under the protection of intensive kinship networks and abide by powerful prestigious authorities (who potentially have more social power and/or more knowledge), whereas such an effect may not hold for historically low-pathogen, WEIRD cultures such as the U.S. or Canada. These results, along with little to no evidence regarding the relationship between pathogen prevalence and ingroup loyalty, are wholly consistent with previous findings in the cultural evolution literature (Hruschka and Henrich, 2013). Lack of strong and consistent links between pathogen prevalence, Fairness, and Loyalty across time and space may also suggest that Fairness and Loyalty are less pathogen-plastic, i.e., less dependent upon the ecological factor of pathogen prevalence across time and place. Purity, on the other hand, appears to be highly *functionally flexible* with respect to pathogens in the environment, i.e., sensitive to costs and benefits of pathogen avoidance in the environment. The results of these studies broadly support the theory that purity-based moral systems have their functional roots in the survival and reproduction of individuals, and that Purity norms are culturally learned to counter the collective threat of pathogen prevalence (see Boyd et al., 2011).

While we highlight the specialized role of Purity in response to pathogenic threats, we also warn against its exclusive nature in contemporary intergroup dynamics. That is, Purity may function as a double-edged sword in fending off pathogenic threats such as COVID-19: on the advantageous side, Purity values encourage social distancing through perceived severity of the threat; and on the socially destructive side, they can lead to antipathic sentiment toward outgroup members (e.g., Hoover et al., 2021), especially those who are perceived to be somehow associated with the origin of the outbreak (i.e., the Chinese in the case of COVID-19) (Faulkner et al., 2004; see Misra et al., 2020). Purity values can predispose people to negatively evaluate outgroup members who are perceived to be potential carriers of pathogens, subsequently justifying prejudicial or exclusive behaviors (e.g., hate crimes against outgroup members) or policies (e.g., imposing travel bans or deportations). For example, Moran et al. (2021) showed that when the threat of COVID-19 was made salient, people more strongly supported bans on incoming travel from countries associated with the emerging outbreak.

The effects of pathogen salience on xenophobic attitudes have been found to be explained by Purity and Authority (Bianco et al., 2021). While it might be tempting to assume that these effects reflect the belief that "outsiders" are carriers of exotic diseases, recent work (e.g., Karinen et al., 2019) supports a different explanation: Outgroup members (e.g., immigrants) may be perceived to behave in ways that deviate from local norms, which tacitly connotes a disease threat (perhaps because so local norms themselves have historically emerged to counter pathogen transmission (Fabrega, 1997; Schaller et al., 2021).

In addition, recent research suggests that regional variation in Purity across U.S. counties is reliably associated with lower vaccination rates (Reimer et al., 2022), which can be thought of as an ironic effect since Purity values may have culturally evolved to guard people against diseases, but the same values in contemporary settings seem to discourage vaccination, one of the most effective ways to combat communicable diseases at individual and population levels (Amin et al., 2017). This ironic effect may be attributable to the contemporary pandemic mismatch: while historically infectious diseases have been easily detectable (e.g., open sores), the cues to COVID-19 are limited due to asymptomatic and presymptomatic transmission of the disease (Ackerman et al., 2021), coupled with some politicians' rhetoric downplaying the threat of the disease (Calvillo et al., 2020).

This research is not without limitations. First, our individual-level studies showed small effect sizes and should be replicated with larger samples beyond WEIRD populations. It could be the case that in chronically high-pathogen environments, such manipulations to make diseases more salient might fail to engender any behavioral change. Second, while we focus on Purity as having consistent links with pathogens across methodologies and levels of analysis, we do not reject the idea that pathogen loads can induce variations in other moral foundations such as Loyalty and Authority. We simply posit that unlike other moral foundations, Purity has a consistent and replicable relationship with pathogen salience across studies. Third, MFT theorists have recently revised the theory, arguing that the Fairness foundation should be split into Equality (intuitions about equal treatment and equal outcome for individuals) and Proportionality (intuitions about individuals getting

rewarded in proportion to their merit or contribution) (Atari et al., 2022). These authors have also developed an improved Moral Foundations Questionnaire (i.e., MFQ-2). With the present data, we cannot speak to the potential role of pathogen prevalence in equality and proportionality. In addition, most of our studies have relied on MFQ (Graham et al., 2011) which has psychometric limitations (see Atari et al., 2022). Fourth, future county-level analyses in the United States should use more proxies for county-level conservatism (e.g., based on self-report surveys) as well as other relevant controls such as tightness and religiosity.

By integrating insights from psychology, anthropology, and behavioral ecology paired with methodologies from multiple disciplines, this research illuminates a unified way to better understand and explain historical and contemporary variation in moral Purity (as well as other moral foundations) in response to infectious diseases. These basic moral systems may in turn predict cultural outcomes, such as religious, economic, political institutions, hence linking ecological factors to psychological outcomes, and eventually large-scale institutions that regulate and oversee social behaviors. This set of studies suggests that Purity consistently functions as a mechanism to allay pathogenic threats across time and space at different levels of analysis, further shedding light on historical-evolutionary architecture and socio-ecological plasticity of human moral systems.

Author contributions

MA and MD conceptualized the study. MA, JG, JH, AMD, and MD collected the data. MA, NKR, BK, AMD, and JH conducted the statistical analyses. MA wrote the manuscript. FK and SB provided feedback. All authors edited and approved the final version of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.cresp.2022.100060.

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