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Personality and Individual Differences 168 (2021) 110277

Contents lists available at ScienceDirect

Personality and Individual Differences

journal homepage: www.elsevier.com/locate/paid

Testing the parasite-stress theory of sociality based on the circular model of human values: A multilevel analysis approach

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ARTICLE INFO

Keywords:
Parasite-stress theory
Circular model of human values
Modernization
Multilevel analysis
European Social Survey
World Values Survey

ABSTRACT

Little research has tested the parasite-stress theory of sociality based on a well-framed model of personal values using a multilevel analysis conducted on multinational samples. To robustly examined the validity of this novel theory of cultural evolution, this study used multilevel data of European Social Survey (from 2002 to 2016, 32 countries, N = 374,730) and World Values Survey (from 2005 to 2014, 80 countries, N = 173,540) to investigate the relationships between pathogen prevalence and the conflicting values dimensions (Conservation versus Openness to change; Self-enhancement versus Self-transcendence) of the circular model of human values, accounting for the micro- (age, sex, religious belief, education, and income) and macro-level predictors (modernization and cultural similarity). Results did not support the parasite-stress theory at both the country and individual levels when controlling for a composite index of modernization. Across all analyses, modernization remained a significant predictor of values even when controlling for cultural similarity. No conclusions changed when using an alternative parasite stress estimate. These findings support the modernization theory of value-change but challenge the roles of infectious diseases in cultural evolution.

1. Introduction

The parasite-stress theory of sociality hypothesizes that values are adaptive responses to pathogen threats (Thornhill & Fincher, 2014). Fincher et al. (2008) propose that Collectivistic values function to defend people against infectious diseases, because xenophobia and ethnocentrism inhibit individuals from contacting with outgroup people who could potentially pose unknown risk for the transmission of infectious diseases. Empirical evidence showed that greater Collectivism and lower Individualism were significantly associated with greater historical and contemporary parasite stress (Fincher et al., 2008; Murray & Schaller, 2010). Thornhill et al. (2010) further identified that values were specifically predicted by non-zoonotic pathogen prevalence, because non-zoonotic pathogens cause direct human-to-human transmission. More recently, Fincher and Thornhill (2012) showed a positive relationship between parasite stress and Collectivism across the U.S. states, and Tybur et al. (2016) found that pathogen prevalence influenced Traditionalism value at the individual-level.

Although these findings are inspiring, several issues remained to be addressed. First, past studies largely relied on using aggregate data to test for the parasite-stress theory, but the non-independence of aggregation greatly challenges the validity of this theory. For example, Currie and Mace (2012) found no convincing support for the parasite-stress theory by reclassifying the countries in Fincher et al. (2008) into regions reflecting contemporary regional relationships. Second, there are theoretical and practical problems of the measures of cultural values (e.g., Baskerville, 2003; Gernon & Wallace, 1995; Shenkar, 2001) used in previous research. For example, no evidence that cultural values are largely shared among societal members (Fischer & Schwartz, 2011), thus aggregating individual responses to obtain the country means of values (e.g., Hofstede, 1980) is problematic (Schwartz, 2011). More importantly, since societal members are exposed to culture in their own unique ways (Schwartz, 2011), findings yielded from a cultural-level analysis are less practical at the individual-level (Pollet et al., 2014). Therefore, it would be more theoretically and practically relevant to reexamine the parasite-stress theory at a micro-level. Third, though Tybur et al. (2016) conducted an individual-level analysis, the value dimension investigated (i.e., Traditionalism) was too narrow which was related to political ideology but not universally personal values (Duckitt et al., 2010). Since values are proposed to be universally adaptive responses to infectious diseases (Fincher et al., 2008), using a comprehensively theoretical model of values for testing the parasite-stress theory would yield more convincing evidence to support this novel theory of culturealevolution by showing how pathogen prevalence would influence broader human motivational goals cross-culturally. Unfortunately, little research has attempted to do so. Last, previous

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https://doi.org/10.1016/j.paid.2020.110277
Received 27 May 2020; Received in revised form 15 July 2020; Accepted 16 July 2020
Available online 13 August 2020

research underestimated the importance of correcting for the sampling biases in their multinational samples (e.g., Fincher et al., 2008; Murray & Schaller, 2010; Thornhill et al., 2010; Tybur et al., 2016), resulting in less accurate estimation (European Social Survey, 2014).

The circular model of human values is a comprehensive and well-framed model for studying values cross-culturally (Schwartz, 1994a). According to Schwartz (1994a), 10 basic values are organized hierarchically to motivate people to strive for their desired goals. The basic values constitute four higher-order values: Openness to change (OTC, combining the basic values of Self-direction, Stimulation and Hedonism), Conservation (CON, combining the basic values of Security, Conformity and Tradition), Self-transcendence (ST, combining the basic values of Universalism and Benevolence) and Self-enhancement (SE, combining the basic values of Power and Achievement). The two conflicting dimensions: "Conservation versus Openness to change" (CON-OTC) and "Self-enhancement versus Self-transcendence" (SE-ST) underpin the circular structure of human values. This circular structure has been supported in different cultural contexts (e.g., Schwartz et al., 2001; Schwartz et al., 2012; Schwartz et al., 2014), and in experimental studies (e.g., Pakizeh et al., 2007). Moreover, the higher-order values at a cultural-level analysis were strongly related to cultural values of Hofstede (1980) (Beugelsdijk et al., 2020; Schwartz, 1994b). Since personal values are systematically related to psychological and behavioral constructs (Boer & Fischer, 2013), large cross-national surveys (e.g., European Social Survey (ESS) and World Values Survey (WVS)) have included the measurement for the 10 basic values to track how attitudinal and behavioral changes are longitudinally influenced by the universal values.

The ESS is a regional survey project which collects longitudinal data from representative samples to investigate the changes in values, attitudes and behaviors across Europe. The WVS is a global survey project which assesses the changes of values and related outcomes across different countries. The detailed information for the ESS and WVS are available at http://www.europeansocialsurvey.org and http://www.worldvaluessurvey.org, respectively. Studies based on these surveys have reported inspiring findings on values (e.g., Alemán & Woods, 2016; Bilsky et al., 2011) and value-related outcomes (e.g., Beilmann et al., 2018). As respondents are nested within countries, multilevel analysis is applicable to the data, allowing an accurate estimation for the existence of multilevel relationships (Beilmann et al., 2018). Therefore, this study employed a multilevel analysis to test for the associations between parasite stress and universal values to address for the issues identified.

As Conservation and Self-enhancement are self-protection values which motivate people to avoid anxiety by controlling for threats (Schwartz et al., 2012), they were strong predictors of interpersonal prejudice (Wolf et al., 2019) and right-wing authoritarianism and social orientation dominance (Cohrs et al., 2005). Therefore, it was reasonable that Conservation and Self-enhancement values are adaptive responses to high pathogen threats, as these values motivate people to act aggressively against deviants and outgroup people (Cohrs et al., 2005; Wolf et al., 2019). In contrast, Openness to change and Self-transcendence are anxiety-free values which motivate people for self-growth (Schwartz et al., 2012), thus these values were negatively related to interpersonal prejudice and right-wing authoritarianism and social orientation dominance (Cohrs et al., 2005; Feather & McKee, 2008). Thus, it was reasonable that these values were adaptive responses to lower levels of pathogen threats. Taken together, it was reasonable to hypothesized that:

H1. parasite stress would be positively associated with the value-continuum of CON-OTC.

H2. parasite stress would be positively related to the value-continuum of SE-ST.

Since age, sex, education, personal income and religious belief were associated with personal values (Błoński, 2015; Boer & Fischer, 2013; Robinson, 2013; Verkasalo et al., 2009), they were included for the first level of the multilevel analysis. Moreover, modernization was included in the second level to factor out its effect on values, given that modernization predicted value-change cross-culturally (e.g., Hamamura, 2012; Santos et al., 2017). Furthermore, as controlling for cultural similarity is important for cross-cultural research (Scott et al., 2014), the linguistic similarity weighting matrix for contemporary countries (Eff, 2008) was used to partial out the effect of cultural proximity on values, given that culture is transmitted vertically and horizontally by languages (Eff, 2008) and thus linguistic proximity is more likely to reflect cultural cluster than does geographical proximity (Scott et al., 2014). Therefore, if the independent variable survived to significantly predict the dependent variable after cultural similarity was accounted for, the significant relationship was not merely due to cultural proximity (Scott et al., 2014).

Accordingly, the micro- and macro-level predictors were combined in one multilevel model where Y_{ij} represents for CON-OTC or SE-ST for individuals (i) within countries (j), thus the two levels of the multilevel analysis were described as follow:

$$\text{Level 1: } Y_{ij} = \beta_{0j} + \beta_{1j}(\text{AGE}) + \beta_{2j}(\text{SEX}) + \beta_{3j}(\text{RELIGIOUS BELIEF}) + \beta_{4j}(\text{EDUCATION}) + \beta_{5j}(\text{INCOME}) + \varepsilon_{ij}$$

$$\text{Level 2: } \beta_{0j} = \gamma_{00} + \gamma_{01}(\text{PARASITE STRESS}) + \gamma_{02}(\text{MODERNIZATION}) + \gamma_{03}(\text{CULTURAL PROXIMITY LAGGED VARIABLE}) + \upsilon_{0j}.$$

2. Methods

2.1. Participants and procedure

Participants were respondents of the ESS (from 2002 to 2016, 32 countries, N = 374,730) and WVS (from 2005 to 2014, 80 countries, N = 173,540). Descriptive statistics are presented in Tables S1 and S2. Since some variables, such as personal values and linguistic proximity, were not available for some countries, not all countries in the original ESS and WVS datasets were included for analyses.

2.2. Measures

2.2.1. Micro-level measures

2.2.1.1. Demographic variables. Both surveys assessed age based on the year of birth, and a dichotomous question was used for sex (1 = *men* and 2 = *women*). For religious belief, the ESS used a dichotomous question (1 = *yes* and 2 = *no*), while WVS used a 3-point Likert scale (1 = *a religious person* to 3 = *a convinced atheist*). For education attainment, the ESS used a 5-point scale (1 = *less than lower secondary education* to 5 = *tertiary education completed*), while The WVS used an 8-level grading educational system (1 = *inadequately completed elementary education* to 8 = *university with degree/Higher education - upper-level tertiary*). For household income, the first three ESS rounds asked respondents to indicate their answers on a scale of 12 ranges expressed by euros (1($J < 150$ *Euro*) to 12($N \geq 10{,}000$ *Euro*)). Starting from Round 4, the ESS measured actual household income by categorizing respondents' answers into 10 levels based on deciles which were of the actual household income distribution in a given country (1(J = *1st decile*) to 10 (H = *10th decile*)). Thus, the standardized scores of all rounds were computed and then averaged, and greater scores would indicate higher income. The WVS assessed household income by asking respondents to specify their "income decile" in their own country with a scale ranging from 1 = *lower step* to 11 = *highest step*, and greater number on this scale would indicate higher income.

2.2.1.2. Personal values. The ESS and WVS assessed respondents' values with a 21-item and 10-item Portrait Values Questionnaire (PVQ,

Schwartz et al., 2001), respectively. The scales measured respondents' 10 basic values by providing respondents several statements describing how a person feels about her/himself and others, and then respondents were asked to indicate how much the person is or is not like the respondents themselves. For example, the ESS assessed Security value by a statement "It is important to him(her) to live secure", and a similar statement in the WVS was "Living in secure surroundings is important to this person". Respondents provided their answers on a 6-point Likert scale (1 = *very much like me* to 6 = *not at all like me*). Respondents' answers were reversed coded so that higher scores would indicate greater values. This study showed high Cronbach alphas for the PVQ (ESS: 0.82; WVS: 0.74). The ipsatized scores of the 10 basic values were calculated for the four higher-order values (Schwartz et al., 2001), and then the value-continuum of CON-OTC was calculated by subtracting OTC from CON, and the value-continuum of SE-ST was calculated by subtracting ST from SE. Therefore, higher scores on CON-OTC and SE-ST would indicate greater Conservation and Self-enhancement, respectively.

2.2.2. Macro-level measures

2.2.2.1. Cultural values. According to Fincher et al. (2008), four measures of cultural Individualism (Hofstede, 1980; Suh et al., 1998) and Collectivism (Gelfand et al., 2004; Kashima & Kashima, 1998) were employed. These measures were developed from cross-cultural values surveys and were used in different studies (e.g., Fincher et al., 2008).

2.2.2.2. Parasite stress. Since the historical parasite stress index (Murray & Schaller, 2010) was optimal for cross-national research (Tybur et al., 2016), it was used in this study. According to Murray and Schaller (2010), the historical infectious disease prevalence of each region/country was estimated based on several epidemiological atlases, and a 4-point scale (0 = *completely absent or never reported* to 3 = *present at severe levels or epidemic levels at least once*) was employed to assess the severity of the disease prevalence. The ratings were standardized to compute a total score for historical parasite stress. Additionally, as non-zoonotic parasite stress was uniquely associated with values (Thornhill et al., 2010), this study also employed this parasite stress estimate for alternative analyses. Fincher and Thornhill (2012) developed this measure by using the classification of infectious disease types in Smith et al. (2007) to identify the regional prevalence of non-zoonotic pathogens based on the GIDEON database (Global Infectious Disease & Epidemiology Network; www.gideononline.com). Higher scores on both indexes all represent higher parasite stress.

2.2.2.3. Modernization index. To measure the multifaceted structure of modernization (Stockemer & Sundström, 2016), data for a sets of indicators of modernization (Table S3 presents the ten indicators) (Ayalon, 2013; Melkote & Steeves, 2015; Stockemer & Sundström, 2016) were obtained from World Development Indicators of the World Bank (worldbank.org/data-catalog/world-development-indicators) for 217 countries/regions across 1960 to 2018. The indicators were standardized and entered into a principle axis factoring analysis using a direct oblimin rotation, and missing data were estimated using the EM method. Table S3 shows that a two-factor solution was most appropriate (Cronbach alpha = 0.90). While female labor force might reflect the "women empowerment" dimension, the rest of the indicators captured the societal development dimension of modernization. According to Table S4, the two dimensions had a weak relationship ($r = -0.06$, $p > .35$), but societal development was robustly associated with various modernization related outcomes (Grossmann & Varnum, 2015; Hamamura, 2012; York & Gossard, 2004). Thus, the societal development index was used for modernization (Table S5 presents the index for each country). A higher score on this index would indicate greater modernization.

2.3. Statistical approach

Fist, country-level analyses were conducted according to Fincher et al. (2008). Specifically, the two parasite stress estimates were separately entered into several multiple regression models to predict the 6 dependent variables (two value-continuums and four cultural values indexes) when controlling for modernization. Therefore, the *p*-value was adjusted using the Bonferroni correction ($p = .05/12 = .004$). Second, WLS analyses adjusting for sampling biases were conducted. The weighting score for the WLS was the product of post-stratification and population weights (Schnittker, 2019). The population weight in WVS was calculated according to the formula provided by ESS researchers (European Social Survey, 2014). Third, multilevel analyses were conducted according to previous research (e.g., Beilmann et al., 2018). An unconditional model testing the country random effect was specified, and the Intraclass Correlation Score (ICC) was computed to describe the effect size (Lorah, 2018). The ICC values of 0.05, 0.10 and 0.15 indicate small, medium and large effect sizes, respectively (Hox, 2002). Next, a Level-1 model was specified to test for the associations between values and micro-level predictors. Then, a Level-2 model was specified by including the macro-level predictors in the preceding model. The effect size of each fixed effect was measured by f^2 (Lorah, 2018). The f^2 values of 0.02, 0.15, and 0.35 represent for small, medium, and large effect sizes (Lorah, 2018), respectively. Last, According to Scott et al. (2014), culturally lagged variables were created to control for cultural similarity effects across all analyses.

All analyses were conducted using SPSS 26.0.

3. Results

3.1. Multiple regression analysis

Simple country-level analyses were conducted according to Fincher et al. (2008). Table S6 shows that the associations between the variables were significant ($0.21 \leq |rs| \leq 0.90$, all $ps < .05$), albeit SE-ST had a marginally significant ($r = 0.24$, $p = .06$) relationship with Collectivism of Kashima and Kashima (1998). Nearly all of the multiple regressions (11 out of 12) in Table S7 revealed that parasite stress lost its significance in predicting values when accounting for modernization, whereas modernization remained a strong predictor of personal and cultural values across all analyses ($0.52 \leq |\beta s| \leq 0.93$, all $ps < .001$), albeit modernization was non-significantly related to the Collectivism dimension of Kashima and Kashima (1998) ($\beta = -0.26$, $p = .13$).

3.2. Weighted least square analysis

The WLS was conducted to correct for the sampling biases in ESS and WVS data. The WLS found that most of (11 out of 16) the signs of regression coefficients of parasite stress estimates changed from positive to negative when modernization was accounted for (Tables S9 and S10). For example, parasite stress was positively associated with SE-ST in Models 2 ($0.01 \leq \beta s \leq 0.23$, all $ps < .01$), but the signs of the coefficients changed to negative in Models 3 and 4 ($-0.18 \leq \beta s \leq -0.05$, all $ps < .001$). Moreover, Models 4 showed that modernization remained a robustly negative predictor of values when controlling for cultural similarity ($-0.34 \leq \beta s \leq -0.02$, all $ps < .01$) across all analyses. Models 4 also indicated that values were clustered within proximate groups ($0.01 \leq |\beta s| \leq 0.12$, all $ps < .05$).

3.3. Weighted multilevel analysis

3.3.1. The analysis on CON-OTC

Table 1 shows that 8.6% to 8.7% of the variability associated with CON-OTC was due to cross-country differences, thus it was meaningful to further examine the country-level scores presented in Tables S1 and

Table 1
The multilevel analysis for the value-continuum of CON-OTC.

Variables	Model 1: Unconditional model		Level 1 (Model 2): Micro-level model				Leve 2 (Model 3): Full model			
	ESS	WVS	ESS		WVS		ESS		WVS	
	ICC = 0.086	ICC = 0.087	ICC = 0.080		ICC = 0.100		ICC = 0.037		ICC = 0.026	
							(ICC = 0.037)[a]		(ICC = 0.023)[a]	
			Fixed effect estimate	Effect size[b] f^2	Fixed effect estimate	Effect size[b] f^2	Fixed effect estimate	Effect size[b] f^2	Fixed effect estimate	Effect size[b] f^2
Intercept			−0.24***		0.44***		−0.10 $^{p=.61}$		0.34** $^{p=.004}$	
							(−0.06 $^{p=.70}$)[a]		(0.47***)[a]	
Sex (2 = *Female*)			0.18***	0.007	0.23***	0.007	0.18***	0.006	0.21***	0.008
Religious belief			−0.38***	0.046	−0.30***	0.037	−0.36***	0.029	−0.27***	0.011
Education			−0.10***	0.010	−0.03***	0.014	−0.09***	0.009	−0.02***	0.064
Age			0.02***	0.131	0.02***	0.041	0.02***	0.143	0.02***	0.046
Income			−0.07***	0.026	−0.05***	0.012	−0.08***	0.000[c]	−0.05***	0.029
Historical parasite stress							0.05 $^{p=.64}$	0.000[c]	−0.07 $^{p=.55}$	0.000[c]
							(−0.04 $^{p=.67}$)[a]	(0.000)[a]	(−0.10** $^{p=.007}$)[a]	(0.002)[a]
(Non-zoonotic parasite stress)										
Modernization							−0.42* $^{p=.02}$	0.007	−0.33** $^{p=.003}$	0.003
							(−0.53** $^{p=.006}$)[a]	(0.011)[a]	(−0.48***)[a]	(0.008)[a]
Cultural proximity							1.86$^{\Psi}$ $^{p=.06}$	0.004	0.46 $^{p=.15}$	0.000[c]
							(1.49$^{\Psi}$ $^{p=.09}$)[a]	(0.003)[a]	(0.08 $^{p=.86}$)[a]	(0.000)[a]

Note.
ESS = European Social Survey.
WVS = World Values Survey.
The superscript "p" denotes the exact p-value.
[a] Results of multilevel analyses based on non-zoonotic parasite stress.
[b] The effect size f^2 was calculated as $R^2/(1-R^2)$, where R^2 is the variance explained for a given multilevel model, the calculation procedure for the R^2 is provided in Lorah (2018).
[c] Negative values were fixed to 0.
$^{\Psi}$ $p < .1$.
* $p < .05$.
** $p < .01$.
*** $p < .001$.

S2. Table S1 shows that across European countries, Poland scored the highest on Conservation values while Iceland highly prioritized Openness to change values. Globally, the highest Conservation score was found in Georgia while Switzerland was found to be the highest on Openness the change (Table S2).

The Level-1 model investigated how personal predictors would be associated with values. Table 1 shows that all predictors were significantly related to CON-OTC ($0.007 \leq f^2$s ≤ 0.131, all ps $< .001$). Specifically, being a female, had religious belief, low education attainment, older age and an unfavorable economic condition were all significant predictors of Conservation values. Particularly, age was the strongest micro-level predictor, as it explained 4.1% to 13.1% of the variance in CON-OTC. Therefore, people attached greater importance to security, conformity and tradition when getting older.

The Level-2 model investigated how the micro- and macro-level variables would be associated with individual-level values. Because modernization was found to be a confounder in previous country-level analyses, alternative Level-2 models only including the micro-level variables and historical parasite stress (i.e., excluding modernization and cultural proximity from the models) were specified. The results showed that historical parasite stress was positively associated with CON-OTC, albeit the relationship was only significant among WVS (fixed effect estimate = 0.19, $p = .006$) but not ESS (fixed effect estimate = 0.18, $p = .15$) countries. This finding partially supported *H1* that greater parasite stress would be related to greater Conservation. However, when modernization was included in the Level-2 models, the effects of parasite stress became non-significant (ESS: fixed effect estimate = 0.05, $p = .64$; WVS: fixed effect estimate = −0.07, $p = .55$). Modernization was robustly associated with CON-OTC (ESS: fixed effect estimate = −0.42, $p = .02$; WVS: fixed effect estimate = −0.33, $p = .003$), controlling for cultural proximity, albeit the effect size was relatively small (0.3% to 0.7%).

Finally, the ICC values of the Level-2 models were only between 2.6% to 3.7%, suggesting that once the contextual variables were accounted for, the national differences in the individual-level CON-OTC became significantly small. Since modernization was the only significant macro-level predictor of personal values, it was speculated that the significantly decreased ICC values were due to modernization. To test this assumption, additional Level-2 models only including the micro-level predictors and modernization were conducted. The results showed that the ICC values of the Level-2 models were between 2.5% and 4.0%. Thus, modernization largely explained the cross-country differences in CON-OTC.

Alternative analyses based on the non-zoonotic parasite stress estimate did not change the conclusion that modernization confounded the relationships between pathogen prevalence and CON-OTC at the

Table 2
The multilevel analysis for the value-continuum of SE-ST.

Variables	Model 1: Unconditional model		Level 1 (Model 2): Micro-level model				Leve 2 (Model 3): Full model			
	ESS	WVS	ESS		WVS		ESS		WVS	
	ICC = 0.133	ICC = 0.162	ICC = 0.140		ICC = 0.146		ICC = 0.086 (ICC = 0.086)[a]		ICC = 0.031 (ICC = 0.031)[a]	
			Fixed effect estimate	Effect size[b] f^2	Fixed effect estimate	Effect size[b] f^2	Fixed effect estimate	Effect size[b] f^2	Fixed effect estimate	Effect size[b] f^2
Intercept			0.07 $^{p=.34}$		−0.40***		0.76***		−0.58***	
							(0.72** $^{p=.001}$)[a]		(−0.50***)[a]	
Sex (2 = *Female*)			−0.33***	0.019	−0.20***	0.008	−0.33***	0.020	−0.17***	0.005
Religious belief			−0.03***	0.003	0.12***	0.000[c]	−0.03***	0.000[c]	0.10***	0.000[c]
Education			−0.02***	0.000[c]	−0.02***	0.009	−0.02***	0.001	−0.01***	0.054
Age			−0.01***	0.063	−0.02***	0.062	−0.01***	0.049	−0.01***	0.023
Income			0.06***	0.011	0.05***	0.011	0.06***	0.000[c]	0.03***	0.020
Historical parasite stress							0.06 $^{p=.69}$	0.000[c]	0.04 $^{p=.79}$	0.000[c]
							(−0.07 $^{p=.60}$)[a]	(0.000[c])[a]	(−0.08$^{\Psi}$ $^{p=.05}$)[a]	(0.001)[a]
(Non-zoonotic parasite stress)										
Modernization							−0.75***	0.047	−0.50***	0.007
							(−0.87***)[a]	(0.046)[a]	(−0.57***)[a]	(0.014)[a]
Cultural proximity							0.16 $^{p=.57}$	0.000[c]	−0.45 $^{p=.14}$	0.000[c]
							(0.22 $^{p=.41}$)[a]	(0.000[c])[a]	(−0.32 $^{p=.29}$)[a]	(0.000[c])[a]

Note.
ESS = European Social Survey.
WVS = World Values Survey.
The superscript "*p*" denotes the exact *p*-value.
[a] Results of multilevel analyses based on non-zoonotic parasite stress.
[b] The effect size f^2 was calculated as $R^2/(1-R^2)$, where R^2 is the variance explained for a given multilevel model, the calculation procedure for the R^2 is provided in Lorah (2018).
[c] Negative values were fixed to 0.
$^{\Psi}$ $p < .1$.
** $p < .01$.
*** $p < .001$.

individual-level (Table 1, the superscript "a" denotes for the relevant results). Accordingly, it was modernization but not pathogen prevalence that significantly influenced CON-OTC at the individual-level, and the significant effect of modernization was not due to cultural proximity. Thus, *H1* was not supported after accounting for modernization.

3.3.2. The analysis on SE-ST

According to Table 2, about 13.3% to 16.2% of the variance in SE-ST was due to cross-country differences. An examination on the national scores of SE-ST showed that across the European countries, Lithuania and Iceland was the highest on Self-enhancement and Self-transcendence values, respectively (Table S1). Globally, Haiti and Brazil scored the highest on Self-enhancement and Self-transcendence values, respectively (Table S2).

Table 2 shows that all variables in the Level-1 model were significantly associated with SE-ST ($0.000 \leq f^2$s ≤ 0.063, all *p*s $< .001$). Specifically, being a male, had low education attainment, younger age and a favorable economic condition were all significantly associated with greater Self-enhancement values. Although the association between religious belief and SE-ST was different among the ESS countries (fixed effect estimate $= -0.03$, $p < .001$) and WVS countries (fixed effect estimate $= 0.12$, $p < .001$), the extremely small effect size ($0.000 \leq f^2$s ≤ 0.003) suggested that this association was trivial to be interpreted. Age had the largest effect size, as it explained 6.2% to 6.3% of the variance in SE-ST. Therefore, younger people valued power and achievement, whereas older people prioritized benevolence and universalism values.

Additional Level-2 models only including the micro-level variables and historical parasite stress were specified. The results showed that when modernization was not included in the models, historical parasite stress was significantly and positively associated with SE-ST (ESS: fixed effect estimate $= 0.38$, $p = .02$; WVS: fixed effect estimate $= 0.36$, $p < .001$). This supported *H2* that greater parasite stress would be related to greater Self-enhancement. However, once modernization was included in the Level-2 models, the effect of parasite stress became non-significant (ESS: fixed effect estimate $= 0.06$, $p = .69$; WVS: fixed effect estimate $= 0.04$, $p = .79$). Modernization remained a significantly negative predictor of the individual-level SE-ST ($-0.75 \leq$ fixed effect estimates ≤ -0.50, $0.007 \leq f^{2s} \leq 0.047$, all *p*s $< .001$), controlling for cultural proximity.

Last, Table 2 shows that the contextual variables largely explained the between-country differences in SE-ST as indicated by the small ICC values of the Level-2 models ($0.031 \leq$ ICCs ≤ 0.086). Since modernization was the only significant macro-level predictor of SE-ST, an additional Level-2 model only including the micro-level variables and modernization was conducted, showing that the unexplained variance in the random effect was between 3.3% and 8.3%. Therefore, modernization substantially explained the between-country differences in SE-ST.

Alternative analyses based on non-zoonotic parasite stress supported the aforementioned findings, showing that pathogen prevalence

was non-significantly associated with SE-ST across countries when accounting for modernization (Table 2, the superscript "a" denotes for the relevant results). Modernization significantly explained 1.4% to 4.6% of the variance in SE-ST, controlling for cultural proximity. Thus, it was modernization but not pathogen prevalence that significantly influenced SE-ST at the individual-level, and the effect was not due to cultural similarity. Accordingly, *H2* was not supported after modernization was controlled.

4. Discussion

Contradicting previous findings (e.g., Fincher et al., 2008; Tybur et al., 2016), parasite stress was not a significant predictor of cultural and personal values once modernization was accounted for. These results challenge the parasite-stress theory of sociality (Fincher et al., 2008). Several reasons could account for the current findings.

First, past research only factored out the effect of modernization by using single modernization indicators (e.g., Fincher et al., 2008), but the current study controlled for the effect of modernization by using a composite index which substantially captures the multifaceted concept of modernization (Stockemer & Sundström, 2016). Second, the adjustment for the biases in multinational samples was underestimated in previous studies, thus the adjustment for the sampling biases in this research tends to yield more accurate statistical estimation. Third, previous findings only suggested that pathogen prevalence was a significant predictor of cultural values (Fincher et al., 2008; Thornhill et al., 2010) or politically-related value-constructs (Tybur et al., 2016), but the current findings indeed emphasize that pathogen prevalence tends to be less robust in explaining broader personal motivational goals when a comprehensive and updated model of values was employed (Schwartz & Bardi, 2001), particularly when a multifaceted modernization construct was accounted for (Stockemer & Sundström, 2016). Accordingly, the current contradictory findings highlight that pathogen prevalence was not a compelling predictor of values cross-culturally, which thus challenge the validity of parasite-stress theory as a novel theory of cultural evolution.

The findings that modernization was a robust predictor of values are consistent with recent research examining the global changes in Individualism (Santos et al., 2017), thus the current finding contributes to our understanding on the modernization theory of value-change (Hamamura, 2012; Inglehart & Baker, 2000). On one hand, the present findings at the country-level are comparable to Santos et al. (2017) showing that it was modernization (i.e., socioeconomic development) but not pathogen prevalence that strongly predicted individualist practices and values cross-culturally. Therefore, the robust role of modernization in predicting the changes of values is observed across different studies, which substantially challenges the argument in Fincher et al. (2008) that parasite stress would inhibit economic development and thus result in value-change. Indeed, greater modernization will allow societies to allocate more resources to infectious diseases prevention (e.g., health education) and control (e.g., invention of vaccines) to decrease pathogen-related morbidity and mortality (Dick et al., 2015). The advancement of technology will also allow practitioners to monitor infectious diseases more effectively so as to reduce the influences of pathogens on human societies (Milinovich et al., 2014). Therefore, it is likely that the evolutionary role of infectious diseases in shaping human values is substantially influenced by the progress of modernization.

On the other hand, the individual-level findings further highlight that the significant associations between modernization and values were not merely due to cultural similarity, thus modernization has unique effects on personal values. Indeed, the significantly decreased ICC values of the Level-2 models substantially support the important role of modernization in explaining the between-country differences in personal values. These findings support the modernization theory of value-change that the increasing wealth and growing number of opportunities allow individuals for greater freedom to prioritize and pursue their own goals (Inglehart & Baker, 2000), and the changes in social institutions (e.g., modern workplace) foster individual autonomy (Hamamura, 2012). The current multilevel findings that modernization was positively related to Openness to change are consistent with findings in Hamamura (2012) that the rise of Individualism observed in societal (e.g., smaller average household sizes) and psychological (e.g., individuals were less willing to follow traditional norms) changes was related to greater modernization. Although Hamamura (2012) reported that people's desire for achievement increased but trust of others decreased with the increase of modernization, the current findings showed that greater modernization was associated with an increase in the concerns for the welfare of others and a decline of pursuing for self-interests. This partially supports the findings in Boer and Fischer (2013) that the increase in societal Individualism opens up the psychological space for people to act more consistently according to their Self-transcendence values.

Although modernization had a large effect on values at the country-level, the relatively smaller effect observed at the individual-level is not surprising, given that no strong evidence supports that cultural values are substantially shared by individuals within societies (Fischer & Schwartz, 2011), since societal members are exposed to culture in their own unique ways (Schwartz, 2011). In other words, as a contextual predictor, modernization is reasonable to explain a relatively larger proportion of variance in cultural values because aggregation greatly decrease the individual differences in value-priorities, whereas modernization would explain a relatively smaller proportion of variance in values at the individual-level due to the influences of unique personal experiences on value-priorities (Schwartz, 2011). The current multilevel findings that age had the largest effect on values support the aforementioned explanation and the life-stage theory of value-change (Egri et al., 2012; Robinson, 2013) which suggests that life stage influences personal values orientations, because people in different developmental stages need to trade-off between different gains and losses which contribute to their own unique experiences (Robinson, 2013), and thus result in individual differences in value-priorities (Schwartz, 2011). As Robinson (2013) suggested that a multilevel analysis would yield a straightforward estimation for the effect of age on values, the current multilevel findings on age substantially strengthen the validity of the life-stage theory of value-change (Egri et al., 2012; Robinson, 2013).

This study offers directions for future research to elaborate on. First, since the advancement of technology would reduce the threats of pathogens, it is reasonable that the relationships between parasite stress and values would be different in high versus low modernized countries. However, the current research did not explicitly test this possibility. Thus, future research could examine how modernization would moderate the association between pathogen prevalence on values at the country and individual levels. Second, because the current study used cross-sectional data, future research is suggested to conduct longitudinal and experimental studies to establish causality for the variables. For example, tracking how personal values would change during and after the COVID-19 pandemic would be one option. Moreover, researchers could prime participants to perceive themselves facing the threat of pathogen prevalence, or by using a contextual priming paradigm to induce participants' perceived modernity to experimentally examine the causal relationships between the variables of interest.

CRediT authorship contribution statement

Mac Zewei Ma:Conceptualization, Investigation, Formal analysis, Writing - original draft.

Acknowledgement

The author received no financial support for this research.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.paid.2020.110277.

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