



# Of Germs and Culture; Parasite Stress as the Origin of Individualism-Collectivism

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## Abstract

Among four proposed origins of individualism-collectivism, modernization theory, rice versus wheat theory, climato-economic theory, and pathogen stress theory, the latter has gained more attention in cross-cultural and evolutionary psychology. Since the parasite stress theory of values and sociality makes a connection between infectious diseases and cultural orientations, it gained even more popularity during the COVID pandemic. But despite extensive research on parasite stress theory, it is not still clear what kind of infectious disease contributes more to the emergence of cultures, what are the possible mechanisms through which pathogenic threat gives rise to cultural systems, and how parasite stress might affect vertical vs. horizontal dimensions of individualism-collectivism. This review summarizes and integrates major findings of parasite stress theory related to individualism-collectivism and its closely related variables and discusses future directions that researchers can take to answer the remaining questions.

**Keywords** Pathogens · Individualism · Collectivism · Behavioral immune system · Parasite stress theory

“Humans typically labor under the illusion that they control their own destiny. [...], in reality, invisible microbes often control human activities.”

David P. Clark, *Germs, Genes, and Civilization*

Individualistic-collectivist cultural systems define who we are in relation to others (Hofstede, 2001), so it is not surprising that they have been linked to many important variables of interest in psychology, sociology, political sciences, and so on. From long-run economic growth and innovation (Gorodnichenko & Roland, 2011) to the stigmatization of mental disorders (Papadopoulos et al., 2013) to foundations of morality (Yilmaz et al., 2016) and beyond have been tied to individualism-collectivism (IC) dimension of national cultures. Currently, there is a tremendous amount of literature on the correlates and implications of IC, but what factor(s) give rise to IC? Four theories have attempted to answer this question: Modernization theory (Hamamura, 2012), rice vs. wheat theory (Talhelm et al., 2014), climato-economic theory (Van de Vliert et al., 2013), and parasite stress theory (Fincher et al., 2008). Among these theories,

parasite stress theory (PST) has attracted more attention, especially during the COVID-19 pandemic. As the body of literature on PST grows exponentially, a critical examination of its major findings related to IC and clarifications of puzzling questions that have remained unanswered can improve the design of future studies.

This manuscript will first discuss pathogen prevalence as the origin of cross-cultural differences in values and empirical support that PST has received. Then I will review possible mechanisms that explain how pathogens might give rise to different cultures. How PST has guided research during and after some recent pandemics like Swine Flu and COVID-19 will come next, and finally possible new paths that researchers can take to advance this line of work will close this review.

## Parasite Stress Theory

Despite the advancement in medicine, communicable and non-communicable diseases are still the top 10 causes of death worldwide (World Health Organization, 2020). Among the threats to our survival, nothing has been more pressing than communicable diseases during the evolution of our species as infectious and parasitic diseases have probably claimed more lives than non-infectious diseases, violent

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conflicts, and natural disasters combined (Inhorn & Brown, 1990). This selection pressure has equipped humans with physiological, cellular, and tissue-based immune systems. But the activation of these systems is metabolically costly. For example, in children aged 1–16 years, every degree of fever (a physiological mechanism that kills infectious pathogens) requires 16.2% more energy expenditure (Benhariz et al., 1997). So, a set of cognitions and behaviors that prevent pathogenic invaders from entering the body in the first place is highly adaptive.

The set of psychological mechanisms that help people to detect cues of diseases and engage in behaviors that prevent infections, collectively called the behavioral immune system, has explained a myriad of social psychology observations (e.g., prejudice against members of outgroups) as disease-avoidance mechanisms (Ackerman et al., 2018). Wide-ranging implications of the behavioral immune system (Thornhill & Fincher, 2014b), along with Hofstede's findings that geographical latitude was a strong predictor of IC (Hofstede, 2001), helped researchers to speculate about the origin of IC in the context of PST.

The pathogenic threat has been considered the ecological factor behind the uniqueness of human social and cognitive capacities (Thornhill & Fincher, 2014a), intelligence (Rózsa, 2008), and worldwide distribution of cognitive abilities (Eppig et al., 2010), and explanatory power of PST to account for geographical variations in traits and behaviors (Murray & Schaller, 2014) has made it a prominent theory for evolutionary studies of cross-cultural psychology. Because pathogen prevalence is higher in some places and lower in others and host immune adaptations are localized, adaptive responses vary from locale to locale. For example, assortative sociality (limited dispersal, ethnocentrism, and xenophobia) in different parts of the world varies as a function of the prevalence of pathogens. Pathogen-dense ecologies are characterized by more restricted dispersal, more ethnocentric views, and stronger xenophobia which are manifestations of collectivism. In ecologies with lower disease stress, on the other hand, these behaviors and cognitions may not be adaptive, and their opposites (devaluing in-group assortative sociality) give rise to individualism (Fincher & Thornhill, 2012).

## Other Theories of the Origins of Individualism-Collectivism

Besides parasite stress theory, there have been other attempts to track the origin of IC, and probably the most important one is modernization theory which attributes individualism to national wealth. Economic growth fosters social changes that liberate people from traditional sources of authority (e.g., family, religion), promotes autonomous

decision-making (Hamamura, 2012), and paves the way for individualism. Economic (and physical) insecurity, on the other hand, can result in greater xenophobia, in-group loyalty, and conformity to traditional norms (Inglehart, 2017). Supporting evidence for modernization theory comes from the studies that show a strong correlation between IC and economic indices (e.g., Minkov et al., 2017), and the rise of individualism in China as a consequence of its economic development has been used to showcase this relationship (Sun & Ryder, 2016).

Besides some limitations of modernization theory like its limitations in explaining the persistence of cultural heritage regardless of economic development (Hamamura, 2012), its most important shortcoming from an evolutionary perspective is that it does not offer any insight into the adaptive functions of cultural systems; it merely explains proximate causes of individualism.

Subsistence style is an ecological factor that has been used to explain cross-cultural differences in psychology. Subsistence strategies affect everyday practices like childrearing (Barry et al., 1959), which is later reflected in the levels of independence and conformity (Berry, 1967). So, different sociocognitive systems originate from different subsistence strategies (Nisbett et al., 2001). Farming, relative to herding, requires more cooperation and interdependence and hence demands collectivist behaviors. A more nuanced and newer version of this idea, rice versus wheat theory, differentiates between farming rice and farming wheat and argues that managing a significant amount of water, building elaborate irrigation systems, and the amount of labor accompanying rice farming make cultures interdependent and collectivist (Talhelm et al., 2014).

Rice versus wheat theory puts IC in a historical context dated back to ancient Greece and China, explains cross-national as well as within-countries differences in holistic and analytical thinking, and has received empirical support (Talhelm, 2020). If future research addresses other forms of subsistence strategies (corn, fish, sugar, etc.) (Talhelm, 2020), this theory might reveal more nuanced cross-cultural differences and their historical drivers. Still, the rice theory has a major limitation. While the advent of agriculture is typically associated with Neolithic Revolution about 12000 years ago (Bocquet-Appel, 2011), collectivist orientations are presumably as old as the genus *Homo*. Simply put, rice theory does not shed light on the evolutionary adaptive functions of IC.

Finally, climato-economic theory goes beyond single-factor explanations and posits the interaction between climate and economy as drivers of IC. Thermal comfort (typically defined as the temperature around 22 °C/72 °F) is conducive to health and nutritional resources. At the same time, the harshness of the climate can be compensated by income resources. So, greater climatic demands

in combination with insufficient resources promote risk aversion and seeking security through collectivism but, in interaction with enough financial resources, encourage seeking better outcomes through individualistic exploration of opportunities (Van de Vliert et al., 2013).

Climato-economic theory has its own supportive evidence (Van de Vliert, 2013a). Indeed, climate change might have been one of the most important factors in shaping modern human civilization as climate stability has been proposed as a necessary condition for settling down and starting the agricultural revolution (Bowles & Choi, 2013), and deviations from thermal comfort account for regional differences in the distribution of personality traits (Wei et al., 2017). But two-factor model proposed by this theory is a double-edge sword; on the one hand, it gives a more sophisticated picture of interactions between two ecological factors; on the other hand, its reliance on money (Van de Vliert, 2013b), a recent cultural invention in our evolutionary history, makes it difficult to generalize its findings to the environment of evolutionary adaptedness. Moreover, geneticists have shown that pathogens are a more important selective pressure for local adaptations than climate and diet regimes (Fumagalli et al., 2011).

In short, scholars have outlined several paths to track the origins of IC, and each theory that has been proposed so far has its own strengths and weaknesses and supportive evidence. But the parsimony of PST, the number of empirical studies testing its predictions, and the increasing demand for understating the societal effects of infectious outbreaks have popularized it among evolutionary cross-cultural psychologists and led to the explosion of literature on parasite stress during the COVID pandemic. So, in the next section, I will review empirical support for PST in more detail.

## Empirical Support for PST

In a pioneering study, Fincher et al. (2008) studied historical and contemporary pathogen prevalence and measured IC by four different methods in a sample of 98 regions (mostly countries but also culturally distinct regions within a nation like Hong Kong). They found that both historic and contemporary measures of pathogen prevalence were significantly (and in most cases strongly) correlated with four different measures of IC even after controlling for gross domestic product per capita, Gini index, and population density. The fact that correlations between historic pathogen prevalence and IC were stronger than contemporary measures of prevalence of infectious diseases, the authors argued, supports the causally precedent role of pathogen prevalence.

Subsequent studies during the past decade have supported the link between pathogen prevalence and different components of IC. While Fincher et al. (2008) study examined

modern nations, their findings were replicated in 186 non-industrial, small-scale cultures (e.g., Aztec, Kung) showing that pathogen prevalence is associated with reduced dispersal (philopatry) and socializing children toward collectivist values (obedience rather than self-reliance) (Cashdan & Steele, 2013).

No matter what measure of pathogen prevalence is used, it seems parasite stress findings are relatively robust. For example, Thornhill et al. (2010) used the number of infectious diseases in a region instead of the number of cases (prevalence), whereas Fincher and Thornhill (2012) used disability-adjusted life year (DALY; the loss of the equivalent of 1 year of full health) as a measure of the burden of infectious diseases along with the prevalence of zoonotic and non-zoonotic infectious diseases to compute a combined index of parasite stress. The results of the first study indicated supporting evidence for the predictor role of non-zoonotic parasite prevalence in cross-cultural differences, and the second study found a significant correlation between parasite adversity and the strength of family ties (an indicator of collectivism) and religiosity both in cross-cultural samples of countries and within the states of the USA. The second study also shows that the reliability of findings pertaining to PST does not change with changing the level of analysis.

In short, the parasite stress theory is backed by substantial empirical evidence. Not only IC but also country-level innovation (Murray, 2014), individual-level extraversion and openness to experience (Schaller & Murray, 2008), and even the origins of economic institutions that vary across countries (Nikolaev & Salahodjaev, 2017) have been associated with pathogenic threats. This theory has also survived competitive tests between pathogen prevalence and other ecological threats like natural disasters (Kusano & Kimmelmeier, 2018) as predictors of cross-cultural differences in socio-political freedom.

At the same time, it is not difficult to spot studies that contradict the above-mentioned findings. For example, in the study of the standard cross-cultural sample (Cashdan & Steele, 2013), there was not any association between pathogens and group bias as measured by in-group loyalty and xenophobia. Moreover, competitive tests (e.g., Kusano & Kimmelmeier, 2018) are rare, and those that have compared pathogen prevalence with other ecological and economic factors show pathogens are not always the most important factor in cross-cultural differences. For example, data covering the period 1961 to 2011 regarding individualism practices (e.g., living alone, divorce) shows that while individualism is rising globally, its main driver is socioeconomic development and pathogen prevalence is of less importance (Santos et al., 2017).

In sum, a sizable and continually expanding literature supports the parasite stress hypothesis, but there is an urgent

need for systematic reviews to clarify the degree to which this literature is unified in its support for PST. More importantly, competitive tests and meta-analyses of previous findings need to be conducted to determine the weight of parasitic stress in comparison to other ecological and economic factors in shaping cultural orientations.

## Possible Mechanisms

Earliest parasite stress research did not clarify the mechanisms through which regional pathogen exposure can lead to collectivism and individualism, but later this link was attributed to the evolved mechanisms specialized to select cultural values (Thornhill & Fincher, 2014b). But the origin of a social structure as complicated and multifaceted as cultural orientation is highly unlikely to be explained by a single mechanism, and a number of genetic and cognitive processes have been proposed and studied as possible candidates for the link between pathogens and IC.

Building upon the previous research that had shown global variations in the allelic frequency of the serotonin transporter functional polymorphism (5-HTTLRP), researchers (Chiao & Blizinsky, 2010) hypothesized that pathogen prevalence is associated with collectivism as a result of the higher frequency of short allele of 5-HTTLRP. Short (S) allele carriers of 5-HTTLRP comprise 70–80% of samples from East Asia (a region known for its collectivist cultures) while only 40–45% of Europeans are S carriers of the 5-HTT genotype. Across 29 nations included in their data, researchers found a significant and strong correlation between collectivism and the frequency of S carries. More importantly, their mediation analysis revealed that the role of pathogens in IC is mediated by S allelic frequency, suggesting that the 5-HTT gene can be the genetic component through which culture-gene coevolution selects for specific cultural orientations. However, these findings have been challenged by others (Minkov et al., 2015). When 5-HTTLRP dataset was expanded by inclusion of sub-Saharan African countries (countries with low frequencies of S carriers but high levels of collectivism), the association between S-allele frequencies and IC disappeared.

In another similar attempt, oxytocin receptor gene polymorphism (OXTR rs53576) was examined across 12 nations, and the results showed A allelic frequency of OXTR rs53576 is associated with collectivism and mediates the relationship between pathogen prevalence and collectivist values (Luo & Han, 2014). Whether these findings will be replicated in larger samples of countries remain to be clear in the future.

At a more proximate level, cognitive processes might be involved to give rise to collectivist and individualistic thinking. Many components of collectivism like the stricter separation between ingroups and outgroups or inflexibility

regarding social norms imply a rigid thinking style in collectivists. So, researchers (Bartucz & David, 2022) hypothesized that rigid thinking might be the bridge between pathogen prevalence and collectivism. Their investigation of 41 countries supported this hypothesis and the mediation role of rigid thinking between pathogen prevalence and cultural orientations.

Despite these efforts, a lot of pieces are still missing for making the big picture that reveals how pathogens shape cultural practices. A detailed description of how genes and gene expression, probably through interaction with environmental factors like early exposure to diseases, impact the tendency toward a particular cultural system and how such tendency might be reflected in neural networks is still unknown. Considering the role of OXTR rs53576 in relation to parasites and cultures, and the importance of oxytocin in facilitating various aspects of social cognition and interaction (Kavaliere et al., 2022), researchers need to consider the possible role of oxytocin as a neurotransmitter that can chain infectious diseases and cultures. Research on disgust, the emotion that fuels pathogen avoidance, can also shed light on the origin of individualism-collectivism. Previous studies (e.g., Skolnick & Dzokoto, 2013) have documented cross-cultural differences in disgust sensitivity as a result of historical pathogen prevalence. Future studies can look into the possible mediation role of disgust as an affective and motivational state between the presence or severity of disease threat and cultural practices.

## Parasite Stress Theory During Recent Epidemics and Pandemics

The connection between infectious diseases and cultures that PST makes has guided research on IC during some recent epidemics and pandemics.

The Swine Flu pandemic in 2009 was one of the outbreaks that happened after the proposition of PST which provided researchers a chance to test its predictions. In a survey study of 134 East Asian and Western individuals, East Asians had greater concerns about infection. More interestingly, using data from Airports Council International researchers found that immediately following the outbreak, Asia-Pacific airports (located in regions with collectivist cultures) lost more traffic than Europe, North America, and Latin America. Examining the number of passengers of major airlines in Japan, Hong Kong, the USA, and the UK also showed stronger avoidance of international travel among East Asians relative to westerners after the pandemic started (Hamamura & Park, 2010).

Ebola virus disease has been around since 1976, but its largest outbreak in 2014 made it a worldwide concern (Centers for Disease Control & Prevention, 2021). Although the USA had

only a total of 11 cases of Ebola (Centers for Disease Control & Prevention, 2019), at least two studies have been conducted to examine the psychological effects of this disease on the US population. Surveying a representative sample of 1000 Americans showed that more perceived vulnerability to Ebola can lead to greater xenophobic responses which are moderated by IC (Kim et al., 2016). Further analysis of the same data in a different study (Chuang et al., 2021) replicated its supportive findings of PST. These studies raise the possibility that in the modern world not only the pathogens but also their potential threat perceived through media might be enough to shift individualist cultures toward collectivism.

Finally, the COVID-19 pandemic provided an unprecedented opportunity for scientists to test all aspects of PST. For example, a study of the prevalence, morbidity, and fatality of COVID-19 in more than 54 countries using different measures of IC found associations between cultural orientation and mortality rate (death per unit of population) of COVID-19 although correlations were not significant for COVID-19 prevalence (Rajkumar, 2021). Although most studies of PST of IC are correlational in nature, it is still possible to find patterns that imply causal relationships. For instance, an examination of posts of 126,165 users of Weibo in China and their use of personal, group-related, and relationship-related words before and during the pandemic demonstrated an upward trend in the usage of collectivist words after the pandemic started (Han et al., 2021). The same pattern was observed in South Korea. More than 7000 participants valued collectivism more strongly after the announcement of the first confirmed cases in South Korea than before the announcement (Na et al., 2021). Patterns of relative successes and failures of countries in combating the COVID pandemic show collectivism might be indeed an antipathogen system. Examining the data of the first 60 days of the outbreak in different countries showed COVID-19 spread faster in individualist societies than in collectivist cultures (Jiang et al., 2021). Although the relative failure of Western developed countries is partly due to the proportion of the elderly in these countries who are more vulnerable to COVID infection, collectivist societies, despite their lower levels of human development and health care systems, excelled at containing the infection, in some cases by orders of magnitudes (Liu, 2021). The most plausible explanation for this pattern is that people in collectivist regions are more likely to wear a mask (Lu et al., 2021), accept vaccination (Holt et al., 2022; Mo et al., 2021), and show support for and practice social distancing (Im & Chen, 2020; Wang, 2021).

## Future Directions

Among two important threats to human survival, predation and parasite, the selection pressure of the former has been reduced by the innovation of weaponry and technologies a

long time ago (Thornhill & Fincher, 2014a), but our species has not had a respite from the latter. Parasite stress theory of sociality and values has provided scientists with a framework to generate falsifiable hypotheses about this selection pressure and how it might be one of the most important factors in shaping cultural systems. Although PST has been under investigation for more than a decade, the COVID pandemic has sparked a lot of interest in this topic. Currently, there are several gaps in the PST literature that future scientists can fill in, and there are several possible directions they can take to advance the field.

How the prevalence of the infectious disease is measured in this line of work needs reconsideration. Some studies of parasite stress theory have used the historical prevalence of nine infectious diseases (leishmaniasis, schistosomes, trypanosomes, leprosy, malaria, typhus, filariae, dengue, and tuberculosis), a method that was first introduced to evolutionary psychology by Low (1990), then popularized by Gangestad and Buss (1993) study of mate preferences, and later extended by Murray and Schaller (2010). These diseases were chosen because of the accessibility to their worldwide records and their damage to human reproductive fitness. But an analysis of infectious diseases (split into STD and non-STD infections) and outcomes predicted by PST showed that the effects of pathogenic stress across the states of the USA can be almost exclusively explained by STDs (Hackman & Hruschka, 2013). It has been already found that human-to-human and multi-host transmissible infections (non-zoonotic diseases) account for PST findings and not zoonotic diseases that are only transmitted from animals to humans (O'Shea et al., 2022; Thornhill et al., 2010; Zmigrod et al., 2021). But what type of non-zoonotic infectious disease (e.g., bacterial, viral) and what exact disease (e.g., HIV, tuberculosis) contribute more to the cross-population differences can be explored more thoroughly in future studies.

Whether individualism and collectivism are the opposites of a continuum or they are two different constructs has been debated (Taras et al., 2014), and some studies have even supported a more nuanced four-dimension classification of cultures as horizontal and vertical individualism and collectivism (Fatehi et al., 2020). While many studies of PST have utilized measures that consider IC as a single continuum, those that have used two- or four-dimension measures have had stimulating findings. By adopting 16 items from Triandis and Gelfand (1998), eight items that assess collectivism and the other eight measuring individualism, researchers found an increase in collectivism in South Korean participants after the COVID pandemic, while individualism scores remained the same (Na et al., 2021). More interestingly, while vertical individualism is negatively associated with intentions to engage in social distancing (Biddlestone et al., 2020), horizontal individualism has positive effects on

mask-wearing (Chung et al., 2021). So, while using one- or two-dimension measures of IC has been more common, how pathogens affect vertical and horizontal dimensions of cultures is a question worth exploring.

Possible mechanisms through which pathogen prevalence causes cross-cultural differences in IC are not well studied. Genetic studies are especially promising as genetic adaptations to historical pathogen prevalence are now documented and show acid phosphatase locus 1 (ACPI), interleukin-6 (IL6), interleukin-10 (IL10), and human leukocyte antigen (HLA) polymorphisms are possible candidates that researchers can look into their roles in mediating the relationship between pathogens and cultures (Fedderke et al., 2017).

Finally, the non-independence of countries as the units of analysis, a statistical issue called Galton's problem, has been used to criticize PST research. Proponents of non-independence argue that considering proximity and shared ancestry, nations cannot be viewed as independent, but independence of observations is a major assumption of most hypothesis significance testing procedures. To deal with this problem, researchers have used different methods. For example, in their study of religiosity and family ties, Fincher and Thornhill (2012) divided the countries into six world regions according to the method introduced by Murdock (1949), and their results were similar to what they found when they analyzed countries individually. But this method has been criticized on the ground that it relies on traditional societies, not contemporary populations (Currie & Mace, 2012). Their reanalysis of Fincher and Thornhill's data regarding religiosity showed that when grouping is based on more recent historical relations, correlations between pathogens and religion are not consistent across regions. But a more sophisticated approach to dealing with the problem of non-independence is the use of hierarchical modeling, and whenever researchers have taken the hierarchical structure of the data (e.g., Horita & Takezawa, 2018; Mullett et al., 2020), the robustness of PST findings is limited. Actually, when relatedness, proximity, and covariation are controlled for, PST might not have a better explanatory power in explaining cross-national findings over other socio-ecological factors like biodiversity or climate (Bromham et al., 2018). But these studies typically question the causal inference from correlational studies and not necessarily the merits of PST. As scientists have recently noted, lack of any control for non-independence is a general problem that applies to most cross-cultural studies, not specific to PST (Claessens & Atkinson, 2022).

On the other side of Galton's problem controversy, some argue that "phylogenetic correction" (i.e., treating nations as non-independent) is not a method that should be applied to all comparative studies (Westoby et al., 1995). Phylogenetic correction is necessary when the question under investigation is phylogenetic creation of a cultural trait, but it is

irrelevant for comparative analysis of persistence of cultural items (Thornhill & Fincher, 2013).

It is unlikely that the controversy around Galton's problem in comparative research comes to an end anytime soon, but considering the advantages and disadvantages of worldwide cross-cultural comparisons (Ember & Ember, 2000), future research should continue to take advantage of comparative method. Furthermore, using newer methods of inferring causation from observational (Yao et al., 2021) or longitudinal data (VanderWeele et al., 2016) can shed new light on the causal link between parasite stress and IC.

## Conclusion

It has been more than a decade since PST brought its evolutionary perspective to cross-cultural investigations of the origins of IC. Although modernization, rice versus wheat, and climato-economic theories have supportive evidence as well, PST has its own advantage in directing research during epidemics and pandemics. Some refinements of measurements of pathogen prevalence and IC along with attempts to find mediation mechanisms that affect the link between pathogenic threats and cultural orientations can further improve PST literature, and appropriate handling of non-independence data can reveal the reliability of PST findings.

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## Declarations

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