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RESEARCH ARTICLE

A Sequential Canonical Cascade Model of Social Biogeography: Plants, Parasites, and People

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Abstract This sequential canonical cascade model of social biogeography is an extension of an integrated model of human cognitive ecology (Cabeza de Baca and Figueredo *Intelligence 47*:63–71, 2014) that predicted state-level life history and cognitive abilities in Mexico. We integrate such population-level factors by utilizing a sample of 66 recognized national polities for which sufficiently complete information was available on all the variables modeled. These national polities were limited to those found in Europe, Asia, and Africa. The Americas and Australia were excluded to avoid sampling parts of the world that had recently undergone massive colonizations by human and nonhuman animals and plants from other zoogeographic zones, which might have disrupted the evolutionarily expected relations between physical, community, and social human ecologies. Data were obtained from national census databases and international organizations, and only national polities with complete data were analyzed, meaning that no missing data were imputed based on values from nearby or otherwise similar polities. This integrated model of social biogeography proposes that abiotic climatic factors in the physical ecology as well as biotic factors in the community ecology produce variations in subsistence and natural resources that then impact biometric markers of life history, triggering changes in social equality, within-group and between-group peace, sexual equality, macroeconomic diversification, and human capital. These effects, in turn, ultimately produce changes in brain volume and aggregate cognitive abilities. The final equation in our cascade model explains 88 % of the variance in aggregate cognitive abilities by supplying more detailed information on socioecological conditions than previous work.

Keywords Parasite burden · Life history theory · Social/sexual equality · Macroeconomic diversification · Human capital · IQ

The Rushton Paradox

Evidence suggests a link between slower life history strategies and cognitive abilities at regional, national, and continental levels of biological and social organization ($r = .88$; Meisenberg and Woodley 2013), as originally predicted by Rushton (1985). However, more recent meta-analytical data indicate that there is no association between life history strategies and cognitive abilities at the individual level of analysis ($\rho = .06$, Figueredo et al. 2014; $\rho = .02$, Woodley 2011). This seeming contradiction has been referred to as the "Rushton paradox" (Meisenberg and Woodley 2013). We propose that, while these results might appear contradictory, they might instead

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highlight the complex interplay between ecological and person-level factors on individual differences (Pollet et al. 2014). The current study attempts to constructively replicate and extend a previously published bioecological model of life history strategies and cognitive abilities (Cabeza de Baca and Figueredo 2014) to a more complete and comprehensive model of social biogeography using population-level indicators from 66 recognized national polities.

Life History Theory

The Individual Differences Level of Analysis

Evolutionary biologists and human behavioral ecologists have noted the existence of ecologically contingent variation in development, behavior, and morphology between and within species (Mace 2000; Stearns 1992). These individual-level models of *life history theory* posit that environmental inputs detected and encoded by an organism alter the allocation of an organism's finite bioenergetic and material resources toward different facets of development that produce a coherent *life history strategy* (Ellis et al. 2009; Stearns 1992). Life history strategies are conceptualized to reside on a slow–fast continuum, emphasizing the point that these strategies are heterogeneous and reflect the varying levels of harshness and unpredictability experienced by the organisms in their immediate environment (Belsky et al. 1991; Ellis et al. 2009). Environments marked by increased levels of unpredictable and uncontrollable injury, illness, or death, independent of age or intrinsic health condition, are stated to produce *fast* life history strategists. Fast life history strategists are generally oriented toward maximizing their development toward the short term, thus investing more time and energy away from parenting and somatic effort and more toward mating (Del Giudice et al. 2015; Ellis et al. 2009). Conversely, predictable and controllable environments are expected to produce *slow* life history strategists, who generally invest their time and energy in the opposite domains: more toward parenting and somatic effort and less toward mating and reproductive effort. Because slow life history strategists generally evolve and develop in relatively stable and controllable environments, they can allocate their time and energy toward long-term viability, increasing their phenotypic quality and longevity as well as the competitiveness of their offspring (Del Giudice et al. 2015; Ellis et al. 2009).

Psychosocial orientations are hypothesized to markedly differ between fast and slow life history strategists on the quantitative levels of cognitive and conative traits possessed by each (Figueredo et al. 2006, 2015). Individuals characterized as fast life history strategists have been shown to possess decreased executive function (Salmon et al. 2009; Wenner et al. 2013), increased sensation seeking (Copping et al. 2013), and increased sexually coercive and hostile behavior (Gladden et al. 2008, 2013), while slow life history strategists display the opposite pattern. Taken together, fast life history strategists pursue opportunistic or antagonistic social strategies characterized by transient social bonds and low-quality relationships, while slow life history strategists pursue prosocial or mutualistic social strategies characterized by enduring social bonds and high-quality, cooperative relationships (Belsky et al. 1991; Figueredo and Jacobs 2010).

The Group Differences Level of Analysis

The examination of human life history strategies between populations, known as *differential K theory* (Rushton 1985), posits that differences in cognition, behavior, and morphology between groups of individuals are the result of varying selection pressures experienced by members of the groups, such as climate. Different incarnations of differential *K* reviewed in Rindermann et al. (2012) all contend that extreme temperatures created distinct characteristics between groups such that individuals in colder, higher altitude climates needed the foresight and intelligence to adapt to their novel environment in order to survive and successfully reproduce (i.e., *slow* life history strategists). This is because seasonal challenges, such as harsh weather and food shortages, in cold and seasonal climates were predictable and hence an *intrinsic* source of mortality, meaning subject to some degree of control by evolvable adaptations on the part of ancestral humans. Conversely, differential *K* theory contends that environments with warmer climates were less difficult to navigate, resulting in the evolution of populations that did not need foresight or intelligence to successfully survive and reproduce in the environment (i.e., *fast* life history strategists). Moreover, the higher prevalence of infectious diseases in the humid tropics were unpredictable and unexplainable for ancestral humans and, hence, an *extrinsic* source of mortality, meaning not subject to any degree of control by evolvable adaptations on the part of ancestral humans and, thus, would not select for either intelligence and foresight.

Limitations of the Differential *K* Theory

While much research examining group-level differences in life history has found evidence supporting this set of theoretical predictions (Rushton 1985), differential *K* theory is limited in a number of important ways. Foremost, it fails to capture and account for within-group heterogeneity that exists across populations. Secondly, the effects of climate have typically been limited to considering only temperature (cold winters theory; Lynn 1991), resulting in a model that, to some extent, ignores the ecological intricacies of the adaptive problems that a group of individuals should encounter in the environment. Lastly, life history theory has more recently experienced many notable and important advances that the original differential *K* theory was lacking. For example, early *r–K* theory, upon which differential *K* theory was originally based, focused on population density-dependent causes for life history evolution (e.g., Pianka 1970), whereas subsequent life history theory focused more on the role of age-dependent schedules of morbidity and mortality, attributable to factors such as environmental harshness and unpredictability (Ellis et al. 2009). In addition to the impact of such natural selective pressures, the impact of social selection pressures is also currently recognized (Figueredo et al. 2015), along with psychosocial *sequelae* such as effects upon time orientation (Chisolm 1993) as well as on the cognitive and strategic differentiation of life history traits between individuals within groups (Woodley 2011; Woodley et al. 2013; Figueredo et al. 2001).

The *cognitive differentiation–integration effort* (CD-IE) hypothesis (Woodley 2011; Woodley et al. 2013) and *strategic differentiation–integration effort* (SD-IE) hypothesis (Figueredo et al. 2001) propose that individuals who evolve and develop in predictable and controllable environments are socially selected to become more cognitively and socio-ecologically *specialized* as a consequence of heightened social competition. Conversely, unpredictable and uncontrollable environments would produce individuals who are socially selected to become more cognitively and socio-ecologically *generalized* to allow contingent switching among unstable sociocultural micro-niches. Whereas sexual selection is produced by the selective pressures acting on traits that lead to mating success, as by either attracting sexual partners or defeating sexual rivals, social selection is produced by the selective pressures acting on traits that lead to social success, as by either attracting social partners or dealing with social competitors. Accordingly, this implies that slow life history individuals and societies comprising mostly slow life history strategists will experience more role differentiation, facilitating cooperation and maximizing resource extraction from the environment, while fast life history individuals and societies with faster life history individuals would experience less role differentiation and suboptimal resource extraction. Slow life history individuals should become more strategically differentiated in behavior to adapt to stable and specific sociocultural micro-niches.

Strategic differentiation permits the long-term allocation of bioenergetic and material resources among components of fitness that have higher fitness "return on investment," where these patterns possess sufficient temporal stability. Different life history "traits" are therefore emphasized over others by conspecific individuals in different micro-niches, and different life history "trade-offs" are made. This strategic differentiation leads to socioecological specialization among individuals (individuation) in personality (conative) dimensions. Such socioecological specialization might manifest itself in anything from the intraspecific trophic specialization of individuals within generalist species of cephalopod (such as *Octopus vulgaris*, *Octopus cyanea*, and *Enteroctopus dofleini*; Mather et al. 2012) to craft specialization in more complex, socially stratified human societies (Costin 2007). Both the absolute and relative distributions of cognitive abilities among individuals and groups are not random and passive "traits," but represent life history allocations in response to ecological conditions: Brain functions are not bioenergetically or developmentally "free." Cognitive abilities are adaptive life history "investments" that must result in fitness benefits to offset the associated fitness costs. Individual "realized niches" will have lesser micro-niche breadth and will be less extensive than the species-typical "fundamental niche" due to their more temporally reliable persistence over evolutionary time.

We therefore propose an integrated model of social biogeography with the intention of expanding contemporary life history theory to encompass our understanding of these socioecological, cultural, and cognitive *sequelae*.

An Integrated Model of Social Biogeography

An earlier incarnation of an integrated bioecological model of cognitive abilities (Cabeza de Baca and Figueredo 2014) attempted to create a multilayered model of selection pressures that sequentially impacted group-level cognitive abilities. This theoretical model for the social biogeography of human life history and cognitive abilities derives increased levels of cognitive ability through a series of successive causal steps. It begins with the evolution of slower life history strategies based on both the physical ecology, which includes climatological factors, and the community ecology, which includes parasite burden (Stearns 1992).

This model next examines the social ecology of slow life history strategy through tracing the establishment of cooperative and mutualistic social systems whereby enhanced levels of social equality predict peaceful dynamics both within and between social groups and, consequently, increased sexual equality (Chavarria Minera et al. 2015; Figueredo et al. 2015). These social *sequelae*, in turn, lead to the strategic and cognitive differentiation of resource allocation profiles among slower life history strategists: SD-IE and CD-IE effects that foster socioecological niche splitting through intraspecific character displacement and produce mutual competitive release among individuals in saturated, resource-limited environments. Cooperative systems of specialists that each efficiently exploit different social micro-niches, and the mutual exchange of resources so derived, inevitably trigger the action of Ricardo's (1817) *law of comparative advantage*, producing greater aggregate wealth through these emergent social properties than would otherwise be attainable to equal numbers of generalists. Thus, societies with greater role diversification would increase resource extraction and productivity (Baumeister et al. 2016). The triggering of Ricardo's economic principle of comparative advantage had been interpreted from the results of Cabeza de Baca and Figueredo (2014), but remained merely inferential. In the present work, we supply various empirically validated indices of macroeconomic diversification that substantiate this theoretical prediction.

The Current Study

The present study is a replication and extension of the integrated model of human cognitive ecology (Cabeza de Baca and Figueredo 2014) that sought to predict state-level life history and cognitive abilities in Mexico. For the present set of analyses, we continue to integrate such population-level factors by utilizing a sample of 66 recognized national polities for which sufficiently complete information was available on all the variables modeled. These national polities were limited to those found in Europe, Asia, and Africa. The Americas and Australia were excluded to avoid sampling parts of the world that had recently undergone massive invasions ("colonizations") by human and nonhuman animals and plants from other zoogeographic zones, which might have disrupted the evolutionarily expected relations between physical, community, and social human ecologies. Data were obtained from national census databases and international organizations, and only national polities with complete data were analyzed, meaning that no missing data were imputed based on values from nearby or otherwise similar polities.

This integrated model of social biogeography proposes that abiotic climatic factors in the physical ecology as well as biotic factors in the community ecology produce variations in subsistence and natural resources that then impact biometric markers of life history, triggering changes in social equality, within-group and between-group peace, sexual equality, macroeconomic diversification, and human capital. These effects, in turn, ultimately produce changes in brain volume and aggregate cognitive abilities. Because our model proposes a theoretically specified sequence among these factors, we utilized sequential canonical analyses for cascade modeling. The proposed sequence of causal influences among the different bioecological and psychosociological levels of organization can be summarized as follows:

1. *Physical ecology* →
2. *Community ecology* →
3. *Social ecology* →
4. *Cultural ecology* →
5. *Cognitive ecology*

Previous research efforts have examined the effects of physical and community ecological variables upon human behavioral and sociocultural variables at the cross-population level (e.g., Cabeza de Baca and Figueredo 2014; Fincher and Thornhill 2014; van de Fliert 2013). Analogously to cross-species correlational analyses in comparative research, these studies used current ecological data to predict between-population differences in sociocultural phenomena.

Methods

Sample of Recognized National Polities

We selected a sample of 66 recognized national polities for which sufficiently complete information was available on all the variables modeled. All national polities selected for study were located in Asia, Africa, and Europe. The Americas and Australasia were excluded to avoid sampling parts of the world that had recently undergone massive recent invasions ("colonizations") by human and nonhuman animals and plants from other zoogeographic zones, which might have disrupted the evolutionarily expected relations between physical, community, and social human ecologies.

The current genetic structures of Old World populations largely reflect those from several millennia ago in the same regions (Leslie et al. 2015; Martínez-Cruz et al. 2012; Piazza et al. 1988; Qi et al. 2013) or neighboring regions (e.g., Basu et al. 2003; Hanihara 1991). Although telltale patterns of Native American population substructure are recapitulated in the genomes of Mexican *mestizos* (European–Native hybrids) from cosmopolitan populations throughout many regions of the New World, such as Mexico (see Moreno-Estrada et al. 2014), more recent movements from distant geographical regions into the New World have occurred, with many large migration waves occurring in the last 200 years, even though European discovery of these continents predates these subsequent events. As such, the phenotypic characteristics of large portions of modern New World populations remain in mismatch with the ecological conditions to which they were originally adapted. For instance, skin pigmentation in European Americans is extremely low even in desert regions, leading to extremely high melanoma rates when compared to descendants of native groups (Centers for Disease Control and Prevention 2016). Thus, only Old World national polities were considered in the present analyses. No data were imputed based on values from nearby or otherwise similar polities.

Description and Sequencing of Constructs

The measures used in this study are described briefly in the present section, but the detailed sourcing of this information and the presentation of associated psychometric information on the measurement models have been relegated to Appendix 1. All but certain cognitive ecology factors were estimated using indicators dating from AD 2001 to 2015.

For present purposes, the hypothesized factors and their hypothesized causal sequence are as follows:

1. A *brumal factor* was operationalized as the latent common factor indicated by a unit-weighted composite of lower mean annual temperatures, proportion of area of temperate climate, and a composite of latitude above the equator and altitude above sea level for each national polity.
2. A *hydrologic factor* was operationalized as the latent common factor indicated by a unit-weighted composite of the proportion of area of tropical-humid climate and the annual precipitation for each national polity.
3. A *temperate broadleaf deciduous forest* (*TBDF*) *factor* was operationalized as the latent common factor indicated by a unit-weighted composite of three convergent Likert scale estimates, representing a biome (an ecological community of flora and fauna occupying a distinct habitat) characterized by an approximately 6-month annual growing season and subject to temperature-induced drought during the cold winters, at which time trees withdraw chlorophyll from their leaves and often shed them entirely. Stands of aspen, beech, birch, oak, maple, and elm populate a modest realized niche (Svenning and Skov 2004): a latitudinal band constrained not far south 40° North latitude by heat and aridity (Morin et al. 2007) and constrained not far beyond 60° North latitude by permafrost (Alvarez-Uria and Körner 2007) and coniferous competitors.
4. A *population density factor* was operationalized as the natural logarithm of the ratio of total population of each national polity and its total land area.
5. A *parasite burden factor* was operationalized as the natural logarithm of the latent common factor measured by a unit-weighted composite of the disability-adjusted life years and historical infectious disease prevalence for each national polity.
6. *Slow life history* was operationalized as the latent common factor indicated by a unit-weighted composite of lower infant mortality rates, higher life expectancies, lower birth rates, lower teenage pregnancy rates, and higher ratio of reproductive age males to females for each national polity.
7. *Social equality* was operationalized as the latent common factor indicated by a unit-weighted composite of a lower GINI score and higher Index of Power Resources for each national polity.
8. *Within-group peace* was operationalized as the latent common factor indicated by a unit-weighted composite of lower perceived crime rates, lower homicide rates, lower violent crime rates, lower civilian access to weapons, and lower perceived corruption rates for each national polity.
9. *Between-group peace* was operationalized as the higher-order factor measured by a unit-weighted composite of the *infra-national peace* (indicated by lower internal conflict, fewer violent demonstrations, lower political instability, lower political terror, and fewer internal conflict deaths) and the *inter-national peace* (indicated by lower military expenditures, fewer armed personnel, fewer heavy weapons, lower bad relations with neighbors, fewer conflicts fought, fewer external conflict deaths, lower hostility to foreigners, and lower willingness to fight in war) for each national polity.
10. A *sexual equality factor* was operationalized as the latent common factor indicated by a unit-weighted composite of the Gender Gap Index (indicated by economic participation and opportunity, educational attainment, political empowerment, and health and survival) and the Gender Inequality Index (indicated inversely by reproductive health, empowerment, and labor market participation) for each national polity.
11. A *strategic differentiation factor* estimated the degree of diversification of resource allocation profiles among slower life history strategists within each national polity, operationalized as the effects of aggregate life history speed upon the unit-weighted factor loadings of each of the indicators of slow life history factor for each national polity, lower factor loadings indicating more strategic differentiation.
12. A *macroeconomic diversification factor* was operationalized as the latent common factor measured by a unit-weighted composite of the Economic Complexity Index (measuring the internal economic differentiation, and hence the higher inter-individual specialization, within national polities, as assessed by their diversity of their exports to other polities), the reverse-scored GDP Dissimilarity Index (measuring the dissimilarities *between* national polities in their relative distributions of their total GDPs among various macroeconomic sectors, and hence lower diversification of goods and services production *within* each of the national polities), and the reverse-scored Krugman Dissimilarity Index (measuring the dissimilarities *between* national polities in their relative labor force distributions among various macroeconomic sectors, and hence lower inter-individual occupational diversification *within* each of the national polities) for each national polity.
13. A *human capital factor* was operationalized as the latent common factor indicated by a unit-weighted composite of average levels of monetary savings, the average level of educational attainment, and the GDP per capita of individuals within each national polity.
14. A *mean brain volume* was measured by use of mechanical packing of crania with mustard seed, with male and female brain sizes averaged for each national polity.

15. A *cognitive abilities factor* was most often measured for each national polity with Raven's progressive matrices, a non-verbal reasoning test, but for some countries, a variety of other tests was instead available.

Statistical Analyses

Our model consisted of a multivariate cascade of factors that were hypothesized to causally influence each other in a theoretically specified order. For this reason, a sequential canonical cascade model was used (Gorsuch 1991; Gorsuch and Figueredo 1991; Figueredo and Gorsuch 2007), which essentially consists of a series of hierarchical regressions in which multiple dependent criterion variables are analyzed sequentially according to a hypothesized causal order. As these dependent criterion variables are expected to causally influence each other, they are entered sequentially as criterion variables into a system of multiple regression equations, with each hierarchically prior criterion variable entered as the first predictor for the next. Thus, each successive dependent variable is predicted from an initial set of ordered predictor variables, each time entering the immediately preceding dependent variable hierarchically as the first predictor, then entering all the ordered predictors from the previous regression equation. Thus, each successive regression enters all of the preceding dependent variables in reverse causal order to statistically control for any indirect effects that might be transmitted through them. Within this analytical scheme, the estimated effect of each predictor (X) is limited to its direct effect on each of the successive dependent variables (Y), controlling statistically for any indirect effects of the predictors through the causally prior dependent variables. The general format for these hierarchical multiple regressions equations can therefore be summarized as follows:

1. $Y3 = \qquad \beta_{31}{*}X1 + \beta_{32}{*}X2 + \beta_{33}{*}X3$
2. $Y4 = \beta_{41}{*}Y3 + \qquad \beta_{42}{*}X1 + \beta_{43}{*}X2 + \beta_{44}{*}X3$
3. $Y5 = \beta_{51}{*}Y4 + \beta_{52}{*}Y3 + \beta_{53}{*}X1 + \beta_{54}{*}X2 + \beta_{55}{*}X3$

An isomorphic graphical equivalent of this system of equations is shown in Fig. 1, which displays a schematic path diagram of a sequential canonical cascade model.

We thus performed a sequential canonical cascade analysis tracking and testing this hypothesized chain of mediating relations. This quantitative multivariate model was designed to explain how a combination of powerful macroeconomic forces (higher economic complexity indices, lower gross domestic product dissimilarity indices, and lower Krugman dissimilarity indices), triggered by the social *sequelae* of slow life history strategy (higher social equality, higher within-group peace, higher within-group peace, and higher sexual equality), inevitably produces massive increases in aggregate wealth by elevating the collective human capital of the entire society, enhancing physical brain volume, and contributing to higher overall levels of human cognitive abilities. This model also seeks to document how this entire cascade of consequences is ultimately set in motion by climatic and other biogeographic factors in the physical and community ecology. The precise specification of the structural model is presented in Appendix 2.

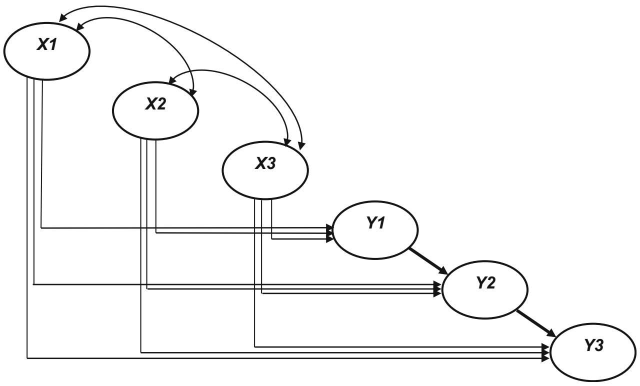

Fig. 1 Schematic path diagram for a sequential canonical cascade model with three predictor ($X1$–$X3$) and three criterion ($Y1$–$Y3$) variables

Results

The multivariate test for the entire sequential canonical analysis (SEQCA) model was statistically significant (Pillai–Bartlett $V = 1.560$, $\eta = .35$, $F_{39,\ 156} = 4.33$, $p < .0001$), providing an omnibus protective test of overall statistical significance. Table 1 displays the results of this analysis.

The *temperate broadleaf deciduous forest* (TBDF) *factor* was significantly increased by both the brumal and hydrological factors, as well as by the interaction between them. This indicates that the TBDF biome generally prevails in cooler and wetter climates, even though the brumal factor (that incorporates markers of temperate climate) and hydrological factors (that includes rainfall) are negatively correlated with one another ($r = -.28$, $p < .05$).

Log(*Parasite Burden*) was significantly decreased by both the temperate broadleaf deciduous forest factor and the brumal factor. This indicates that the TBDF biome and colder climates are not conducive to very high prevalence of parasites. This may be partially attributable to the fact that the TBDF biome does not range up to or below the Tropic of Cancer, which are the points at which parasite burden is known to rapidly augment.

Log(*Population Density*) was significantly increased only by the hydrological factor. Wetter climates are thus conducive to higher population density.

The *slow life history strategy* (*adjusted*) *factor* was significantly decreased only by Log(Parasite Burden). This is

Table 1 Sequential canonical cascade model of social biogeography

Criterion variables	Prior criterion variables	Predictor variables	DF	Semi-partial correlations	$p(H_0)$
Temperate Broadleaf Deciduous Forest		Brumal	1	.36*	.001
		Hydrological	1	.24*	.02
		Brum*Hydr	1	.39	.0004
Log(Parasite Burden)	Temperate Broadleaf Deciduous Forest		1	−.66	<.0001
		Brumal	1	−.45*	<.0001
		Hydrological	1	−.04*	.64
		Brum*Hydr	1	−.01*	.90
Log(Pop. Density)	Log(Parasite Burden)		1	.04	.76
	Temperate Broadleaf Deciduous Forest		1	−.07	.56
		Brumal	1	−.15	.23
		Hydrological	1	.26*	.03
		Brum*Hydr	1	−.11*	.39
LH Strategy (Adjusted)	Log(Pop. Density)		1	.17	.10
	Log(Parasite Burden)		1	−.56*	<.0001
	Temperate Broadleaf Deciduous Forest		1	.01	.90
		Brumal	1	−.03	.75
		Hydrological	1	.04	.68
		Brum*Hydr	1	.16	.13
Social Equality	LH Strategy (Adjusted)		1	.53*	<.0001
	Log(Pop. Density)		1	−.18*	.002
	Log(Parasite Burden)		1	−.64*	<.0001
	Temperate Broadleaf Deciduous Forest		1	.11*	.04
		Brumal	1	−.04	.50
		Hydrological	1	.20*	.0003
		Brum*Hydr	1	.24*	<.0001
Within-Group Peace	Social Equality		1	.81*	<.0001
	LH Strategy (Adjusted)		1	.23*	.0006
	Log(Pop. Density)		1	.04	.48
	Log(Parasite Burden)		1	−.09	.14
	Temperate Broadleaf Deciduous Forest		1	.04	.56
		Brumal	1	−.13*	.04
		Hydrological	1	.14*	.03
		Brum*Hydr	1	.12*	.05
Between-Group Peace	Within-Group Peace		1	.79*	<.0001
	Social Equality		1	.03	.62
	LH Strategy (Adjusted)		1	−.09	.08
	Log(Pop. Density)		1	−.07	.18
	Log(Parasite Burden)		1	.20*	.0003
	Temperate Broadleaf Deciduous Forest		1	.13*	.02
		Brumal	1	−.24*	<.0001
		Hydrological	1	.30*	<.0001
		Brum*Hydr	1	.07	.20
Sexual Equality	Between-Group Peace		1	.76*	<.0001
	Within-Group Peace		1	.36*	<.0001
	Social Equality		1	.22*	<.0001
	LH Strategy (Adjusted)		1	.23*	<.0001
	Log(Pop. Density)		1	−.01*	.87
	Log(Parasite Burden)		1	−.15*	.002

Table 1 (continued)

Criterion variables	Prior criterion variables	Predictor variables	DF	Semi-partial correlations	$p(H_0)$
	Temperate Broadleaf Deciduous Forest		1	.06	.24
		Brumal	1	.04	.43
		Hydrological	1	.22*	<.0001
		Brum*Hydr	1	.06	.22
Strategic Differentiation	Sexual Equality		1	.44*	<.0001
	Between-Group Peace		1	−.30*	.0009
	Within-Group Peace		1	.21*	.02
	Social Equality		1	−.04	.66
	LH Strategy (Adjusted)		1	.26*	.004
	Log(Pop. Density)		1	−.02	.80
	Log(Parasite Burden)		1	−.44*	<.0001
	Temperate Broadleaf Deciduous Forest		1	−.06	.50
		Brumal	1	−.09	.30
		Hydrological	1	−.01	.94
		Brum*Hydr	1	.01	.88
Macroeconomic Diversification	Strategic Differentiation		1	.66*	<.0001
	Sexual Equality		1	.33*	<.0001
	Between-Group Peace		1	.04	.61
	Within-Group Peace		1	.11	.10
	Social Equality		1	.06	.39
	LH Strategy (Adjusted)		1	.08	.23
	Log(Pop. Density)		1	−.21*	.003
	Log(Parasite Burden)		1	−.13	.06
	Temperate Broadleaf Deciduous Forest		1	.07	.31
		Brumal	1	.12	.09
		Hydrological	1	.33*	<.0001
		Brum*Hydr	1	−.08	.24
Human Capital	Macroeconomic Diversification		1	.48*	<.0001
	Strategic Differentiation		1	.04	.48
	Sexual Equality		1	.64*	<.0001
	Between-Group Peace		1	.06	.37
	Within-Group Peace		1	.22*	.0008
	Social Equality		1	.01	.88
	LH Strategy (Adjusted)		1	.15*	.02
	Log(Pop. Density)		1	.13*	.05
	Log(Parasite Burden)		1	−.12	.07
	Temperate Broadleaf Deciduous Forest		1	.08	.21
		Brumal	1	.12	.07
		Hydrological	1	.13*	.05
		Brum*Hydr	1	−.12	.07
Mean Brain Volume	Human Capital		1	.59*	<.0001
	Macroeconomic Diversification		1	.13*	.04
	Strategic Differentiation		1	.09	.17
	Sexual Equality		1	.07	.28
	Between-Group Peace		1	−.13	.06
	Within-Group Peace		1	.16*	.01
	Social Equality		1	.15*	.03
	LH Strategy (Adjusted)		1	−.04	.51

Table 1 (continued)

Criterion variables	Prior criterion variables	Predictor variables	DF	Semi-partial correlations	$p(H_0)$
	Log(Pop. Density)		1	.19*	.005
	Log(Parasite Burden)		1	−.12	.06
	Temperate Broadleaf Deciduous Forest		1	.02	.78
		Brumal	1	.51*	<.0001
		Hydrological	1	−.16*	.012
		Brum*Hydr	1	−.09	.18
Cognitive Abilities	Mean Brain Volume		1	.73*	<.0001
	Human Capital		1	.41*	<.0001
	Macroeconomic Diversification		1	.25*	<.0001
	Strategic Differentiation		1	.08	.06
	Sexual Equality		1	.15*	.0003
	Between-Group Peace		1	−.10*	.02
	Within-Group Peace		1	.10*	.01
	Social Equality		1	−.03	.43
	LH Strategy (Adjusted)		1	.09*	.03
	Log(Pop. Density)		1	.09*	.02
	Log(Parasite Burden)		1	−.16	.0001
	Temperate Broadleaf Deciduous Forest		1	.05	.23
		Brumal	1	.08	.06
		Hydrological	1	.20*	<.0001
		Brum*Hydr	1	−.12*	.004

*$p < .05$

consistent with modern theories of life history evolution that link the evolution of faster life histories to higher levels of extrinsic morbidity and mortality, such as those that can be generated by high prevalence of parasites. The lack of any significant effect of Log(Population Density) upon slow life history strategy, even though it was entered hierarchically prior to Log(Parasite Burden) in the cascade model, also fails to support the older density-dependent theories of life history selection. Similarly, although the temperate broadleaf deciduous forest factor had a statistically significant and positive bivariate correlation with slow life history strategy ($r = .36$, $p < .05$), this effect appears to have been fully mediated in the cascade model by Log(Parasite Burden).

Social equality was significantly increased by the slow life history strategy (adjusted) factor, but was significantly decreased by both Log(Population Density) and Log(Parasite Burden). This indicates that the predominance of slow life history strategy within a population tends to generate egalitarian societies, except where interfered with by either higher population densities or parasite prevalence. Social equality was also significantly increased by the temperate broadleaf deciduous forest factor, the hydrological factor, and the interaction between the brumal and the hydrological factors. This indicates that the TBDF biome and cooler, moister climates also tend to favor the evolution of egalitarian societies.

Within-group peace was significantly increased by the social equality factor, the slow life history strategy (adjusted) factor, the hydrological factor, and the interaction between the brumal and the hydrological factors, but was significantly decreased by the brumal factor. This indicates that an egalitarian society where slow life history strategy predominates is less subject to internal conflicts and that this harmonious scenario is favored within cooler, moister climates that are not excessively cold.

Between-group peace was significantly increased by the within-group peace, the temperate broadleaf deciduous forest, and the hydrological factors, but was again significantly decreased by the brumal factor. Paradoxically, between-group peace was also increased by Log(Parasite Burden), which is contrary to the expected increase in ethnocentrism predicted by assortative sociality theory (Fincher and Thornhill 2008a, b).

Sexual equality was significantly increased by the between-group peace, within-group peace, social equality, slow life history strategy (adjusted), and hydrological factors, but was significantly decreased by Log(Parasite Burden). As with social equality, this indicates that a socially egalitarian society where slow life history strategy predominates is also more likely to be a sexually egalitarian society and that this harmonious scenario is once again favored within moister climates, but that sexual equality generally requires greatly diminished levels of both internal and external conflict.

Strategic differentiation among life history traits was significantly increased by the sexual equality, within-group peace, and slow life history strategy (adjusted) factors, but was significantly decreased by both between-group peace and Log(Parasite Burden). This is generally consistent with SD-IE theory (Figueredo et al. 2001), with the exception that part of the previously reported effect of slow life history strategy is now shown to be mediated through some of its social *sequelae*, sexual equality and within-group peace, and that SD-IE is directly interfered with by higher prevalence of parasites. The antagonistic role of between-group peace might appear to be paradoxical, but might nonetheless be explicable if the SD-IE effect is subject to some degree of group selection, and thus favored by higher levels of intergroup competition, under a multilevel selection model (see Woodley and Figueredo 2013).

Macroeconomic diversification was significantly increased by the strategic differentiation, sexual equality, and hydrological factors, but was significantly decreased by Log(Population Density). The very large and positive effect of strategic differentiation upon macroeconomic diversification was one of the major novel predictions of the present model and was therefore amply supported.

Human capital was significantly increased by the macroeconomic diversification, sexual equality, within-group peace, and slow life history strategy (adjusted), Log(Population Density), and hydrological factors. The very large and positive effect of macroeconomic diversification upon human capital was hardly a novel prediction of this model with respect to conventional economic theory. It nonetheless helps to establish the plausibility of the causal mechanism by which strategic differentiation was previously supposed to foster the development of human capital, as this relation is now shown to be fully mediated by macroeconomic diversification (Cabeza de Baca and Figueredo 2014).

Mean brain volume was significantly increased by the human capital, macroeconomic diversification, within-group peace, social equality, Log(Population Density), brumal, and hydrological factors. These positive relations all make theoretical sense as they indicate favorable socioecological circumstances that might be interpreted as conducive to the allocation of higher levels of somatic effort toward enhancing the phenotypic quality of individuals, including physiological investment in greater brain mass.

Cognitive abilities were significantly increased by the mean brain volume, human capital, macroeconomic diversification, sexual equality, within-group peace, slow life history strategy (adjusted), Log(Population Density), and hydrological factors, but mean aggregate IQ was significantly decreased by both between-group peace and Log(Parasite Burden) as well as by the interaction between the brumal and hydrological factors. Once again, these positive relations all make theoretical sense as they indicate favorable socioecological circumstances that might be interpreted as conducive to the allocation of higher levels of somatic effort toward increasing the robustness and long-term viability of individuals, including physiological investment in enhanced cognitive abilities. Once again, the otherwise paradoxical antagonistic role of between-group peace might be explicable under the presumption that higher levels of cognitive ability are favored by exacerbated levels of intergroup competition, consistent with the directly relevant multilevel selection model proposed by Woodley and Figueredo (2013).

Discussion

The purpose of the present study was to construct and test an integrated model of human social biogeography to predict national-level mean life history strategies and aggregate phenotypic intelligence quotients in 66 recognized national polities within the Eastern Hemisphere. We believe that the current analyses produced compelling evidence that both ecological and social forces appear to impact national-level life history strategies and phenotypic levels of aggregate cognitive abilities in the manners expected by theory. While these results do not present a definitive explanation for life history and cognitive ability variations present between these national-level polities, the protective multivariate omnibus null hypothesis tests revealed that a substantial proportion of the pooled multivariate variance ($\eta = .35$) was explained by the integrated model of human social biogeography. Our evolutionary interpretations of these findings simultaneously presume that: (1) specific environments shape adaptive phenotypes via selective pressures on both genetic and cultural traits and (2) specific phenotypes (and their associated genotypes, if such phenotypes are heritable) actively seek environments within which they fit optimally.

We now permit ourselves to use some frankly causal language to weave our interpretations of these results into a coherent narrative, with the understanding that our data are merely correlational in nature and do not empirically support any definitive inferences of causation. The brumal and hydrological factors representing colder and wetter winters give rise to the growth of temperate broadleaf deciduous forest. The presence of this forest biome plus colder weather jointly reduces the prevalence of human parasites in the environment. Climates that are more humid foster increased human population density, except where inhibited by colder weather. A decreased parasite burden on human populations permits the evolution and development of slower life history strategies. Human populations dominated by slower life history strategists achieve higher levels of social equality, although higher population densities and parasite burdens serve to decrease social equality. In addition, the presence of temperate broadleaf deciduous forests and colder and wetter winters also serve to foster higher levels of social equality. Social equality and slower life history strategies, in turn, promote within-group peace. Colder winters appear to disrupt within-group peace, except in more humid climates. Within-group peace leads to between-group peace, paradoxically aided in doing so by a higher parasite burden, more temperate broadleaf deciduous forests, and more humid climates. Otherwise, between-group peace is only reduced by cold winters. Between-group peace, within-group peace, slower life history strategies, and more humid climates serve to foster sexual equality, whereas higher parasite burdens serve to decrease it. Sexual equality, within-group peace, and slower life history strategies jointly create the requisite conditions fostering the strategic differentiation of life history traits. Strategic differentiation, sexual equality, and more humid climates then lead to the macroeconomic diversification of human societies, only inhibited by higher population densities and higher parasite burdens. Macroeconomic diversification, sexual equality, within-group peace, slower life history strategies, higher population densities, and more humid climates then jointly produce gains in embodied human capital. Higher levels of human capital and macroeconomic diversification, along with within-group peace, social equality, higher population densities, and colder winters, produce higher mean brain volumes in these populations, only decreased by warmer humid climates. Finally, higher mean brain volumes, higher levels of human capital, macroeconomic diversification, sexual equality, within-group peace, slower life history strategies, higher population densities, and warmer humid climates all contribute to increasing human cognitive abilities, only inhibited by the prevalence of between-group peace (cf. Woodley et al. 2013).

The Mediating Role of Temperate Broadleaf Deciduous Forest

The presence of temperate broadleaf deciduous forest heuristically demarcates a salubrious zone, most consonant with human biological needs. Rich soils and generous rainfall allow select sections of Eurasia, when cleared and intelligently cultivated, to yield sustenance, creating export surplus, capital, wealth, and leisure upon which complex culture depends. Representing the Earth's "Goldilocks" zone, temperate broadleaf deciduous forest distribution is sufficiently southerly to provide one or more growing seasons while sufficiently northerly to presumably take advantage of parasite-inhibiting seasonal cold. Substantial bivariate correlation coefficients were found for temperate broadleaf deciduous forest with most of our major dependent criterion variables, including slow life history strategy ($r = .36$, $p < .05$), social equality ($r = .64$, $p < .05$), within-group peace ($r = .57$, $p < .05$), between-group peace ($r = .52$, $p < .05$), sexual equality ($r = .63$, $p < .05$), human capital ($r = .58$, $p < .05$), brain size ($r = .44$, $p < .05$), and cognitive ability ($r = .59$, $p < .05$).

We found temperate broadleaf deciduous forest to mediate most of the effects of climate on parasite burden, and then parasite burden to mediate the effects of temperate broadleaf deciduous forest on all subsequent dependent criterion variables save for social equality and between-group peace—for both of which it contributed some additional explanatory power. We therefore considered two different interpretations of the direct and indirect effects of temperate broadleaf deciduous forest on human parasite burden: (1) merely serving as an indicator of "cold winters" (Lynn 1991), as temperate forests only grow where these occur; and (2) instead exerting a direct causal influence on parasite burden by generally suppressing parasite abundances in the environment. These two explanations are not mutually exclusive, as they might both be partially correct.

The expression "cold winters" implies seasonal variation in temperature, where it is warm in the summer and cold in the winter (Lynn 1991). Based on the distribution of human parasite prevalence (Wertheim et al. 2012), the seasonal frosts occurring as low as between 25° and 35° North latitude may be sufficient to thwart most ectoparasites and their vectors. As Darwin (1859) stated, the effects of abiotic threat from without exceed those of biotic threat from within. The increased need for food and shelter produced by "cold winters" might be sufficient to augment *resource-dependent monogamy* (Sun 2003; Low 2003; Miller 1994a, b), which reliably compels cooperation (at least at the family level) by: (1) reducing the viability of short-term mating; (2) increasing the benefits of parental investment; and (3) reorienting female choice toward male constancy and conscientiousness—with resultant changes in male psychology and physiology.

Nevertheless, endoparasites can persist into temperate climates because they shelter in thermoregulated bodies (Davidson et al. 2014). Thus, the reduced prevalence of endoparasites in northern latitudes requires further explanation. For example, helminth worms are an important class of endoparasite that complete their life cycle in human and animal viscera, but they are often transmitted through contact with the soil, in which their eggs might easily be able to overwinter (Bethony et al. 2006). Temperate broadleaf deciduous forest latitudes are most dense between 40° and 60° North latitude, however, and are active climatic agents in that they moderate temperature flux (Swift and Messer 1971) and alter evapotranspiration cycles (Wilson et al. 2001). Additionally, TBDF leaf litter itself seems to have some causal role in soil accretion, forming rich brown alfisols (Woodward 2016) and young inceptisols (Khan 2013) receptive to generations of preindustrial cultivation (Marsh and Kaufman 2013). More importantly, helminth worms are impeded in their growth and transmission by tannins and related allopathic chemicals that color temperate broadleaf deciduous forest autumn leaves

(Dawson 2016), from which they are not reabsorbed in spite of being costly to produce (Coley 1986).

Thus, temperate broadleaf deciduous forest leaf litter may causally reduce residual parasite load in both plants and animals. Light protection, antioxidant healing, cold protection, water retention, and vigor signaling are among the candidate explanations of tannin production (Dawson 2016), with other flora being affected as much as fauna (Ruehle 1973). Nevertheless, the ability to incapacitate root-attacking helminth worms may be a major driving force in the evolution of the tannins produced by temperate broadleaf deciduous forest trees. Whatever selective pressures evoked costly tannin production, co-opted allopathic compounds (Fürstenberg-Hägg et al. 2013) demonstrably reduce helminth transmission and infestation in humans and their coevolved domesticates (Min and Hart 2003; Hoste et al. 2006; Villalba et al. 2009, 2010). It is therefore likely that the presence of temperate broadleaf deciduous forest acts directly to suppress human parasite burden, although this may be a non-adaptive side effect of the evolution of tannin production in the trees themselves.

We propose that the primary adaptive function of this annual "carpet bombing" of the forest floor by parasite-suppressing agents, soaking the soil with a "deadly tea" of toxic tannins when rained upon in Mediterranean-like climates having winter rains (cf. Diamond 1997), is to kill helminths that might otherwise be able to overwinter underground and, more specifically, in the *rhizosphere*. The rhizospheric ecosystem of plants encompasses all biotic interactions within the volume of soil that surrounds and adheres to their roots. It includes both floral (metaphytal, mycorrhizal, and bacterial) and faunal (metazoan) components comprising the entire ecological spectrum of interactions (symbiotic, commensalistic, parasitic, and amensalistic; Cardon and Whitbeck 2007). Nematodes are a fixture of plant rhizospheric fauna, and many rhizospheric nematodes engage in parasitic interactions with plants, representing a major source of root diseases in certain tropical and subtropical ecological contexts (Luc et al. 2005). Further, soil-transmitted helminths have been characterized as "the most common infectious agents of humans in developing countries and produce a global burden of disease that exceeds better-known conditions, including malaria and tuberculosis" (Hotez et al. 2008, p. 1311). Thus, an evolutionary side effect of indiscriminately killing helminths in the soil is inadvertently reducing one of the major components of the parasite burden on humans.

The Mediating Role of Parasite Burden

The results we have presented are generally consilient with previously documented effects of parasite burden upon human cognitive ability (Fincher and Thornhill 2014); however, our data indicate that these effects are generally *indirect* rather than *direct*. The most important of these is the major effect that parasite burden has on accelerating life history (LH) speed; faster LH speeds, in turn, through various meditational steps described in our cascade model, inhibit the evolution and development of higher levels of cognitive ability.

Fincher and Thornhill (2008a, b, 2012, 2014) have proposed that the effect of parasite burden on cognitive ability is attributable to the influence of parasite burden in disrupting the evolution and development of higher levels of social complexity in human populations as a result of cultural fractionation by highly localized assortative sociality mechanisms that are exquisitely adapted for avoiding contagion from outgroups (Eppig et al. 2011; Fincher and Thornhill 2014; Thornhill et al. 2009). These decreased levels of social complexity would have resulted in lower levels of cognitive ability (Eppig et al. 2010). Our results indicate that, once again through various multiply mediated pathways involving effects upon LH speed, parasite burden is indeed generally *inhibitory* of certain forms of social complexity, such as strategic differentiation and macroeconomic diversification, and that this has various deleterious indirect effects upon human intelligence.

Interestingly, although no direct effect of parasite burden on brain volume was detected, a direct effect was found on cognitive ability, possibly as a result of LH resource allocations (cf. Davis 2014) toward immunological parasite resistance and away from investments influencing cognitive performance (e.g., neuroanatomical features such as the degree of myelination, gyrification, and hemispheric specialization). Importantly, however, major indirect effects can be observed through various meditational steps. The presence of indirect meditational pathways indicates the complementary action of other causal antecedents in the evolution of cognitive ability, including those that act through increasing encephalization.

It is an essential feature of the Fincher and Thornhill (2008a, b, 2012, 2014) model that the transmission of dangerous infectious diseases can be potentially reduced by assortative sociality, biased toward local conspecifics, and limited dispersal in humans and other organisms as this reduces contact with contagions harbored by outgroup conspecifics. Genetic and cultural divergence among populations may follow from assortative sociality. Consistent with those theoretical predictions, high regional parasite prevalence has been found to be positively associated with higher regional cultural diversity (Fincher and Thornhill 2008a, b) and genetic diversity (Woodley and Fernandes 2014; see Martin and McKay 2004 for an empirical demonstration at the comparative level). Pathogen prevalence is also positively associated with measures of collectivism (Fincher et al. 2008), ethnocentrism, xenophobia Letendre et al. (2012)), and religiosity (Fincher and Thornhill 2012), traits which are likely to lead to group cohesion and intergroup differentiation. Nevertheless, the present results do not support the predictions of this theory for between-group conflict as a direct effect of pathogen prevalence, but only as mediated through the psychosocial *sequelae* of slower LH strategies.

The rationale for modeling parasite burden as causally influencing LH speed by selecting for faster LH strategies was our considering parasite burden to represent a source of *extrinsic* morbidity–mortality, and our model specification would thus superficially appear to contradict all the theory and evidence supporting assortative sociality theory. Nevertheless, although it is common in evolutionary ecology to speak of morbidity–mortality as extrinsic or intrinsic as if these conditions constituted a dichotomy (Ellis et al. 2009), it would be more correct to characterize those terms as representing the opposing poles of a continuous dimension. This graded continuum would characterize *how much control* can be exerted by evolvable adaptations to the threats rather than simplistically describing whether it can be exerted either completely or not at all. Parasite burden is a good example of an intermediate case, where countermeasures such as the evolved *behavioral immune system* (Fincher and Thornhill 2008a, b, 2012, 2014) can ameliorate the extent of the morbidity–mortality, but cannot completely eliminate these hazards from the human ecology.

The Mediating Role of Sexual Equality

Our sequential cascade modeled the sexual equality factor, unlike the social equality factor, as positively causally influenced by both within-group and between-group peace rather than vice versa. Even though previous research has found that sexual inequality predicts social conflict, including civil, wars, civil unrest, and international conflicts (Caprioli 2003, 2005; Hudson and den Boer 2012), few studies had examined the impact of within-group and between-group conflict upon sexual equality. According to predictions made for humans based on the primatological literature, coalitions established by males and coalitional intra-group and intergroup conflict are a risk factor of sexual coercion (Smuts 1992, 1995). Sexual equality presents a protective context for females: Societies with high levels of sexual equality are predicted to have lower rates of sexual coercion.

Similarly, social inequality has also been hypothesized to be associated with sexual coercion. According to Smuts (1992), men capable of monopolizing resources in non-egalitarian societies, and influencing the sanctioning of adulterous individuals, are more efficient in guarding their mates and obtaining access to females of other males. According to Smuts, not only are high-status males predicted to control the behavior of females, but low-status males endorse these practices to avoid the costs of male–male conflict.

It is worth noting that this perspective does not assume females to be non-violent. Nevertheless, the rates, types, and outcomes of violence between the sexes differ. With respect to intrasexual conflict, for example, males have been found to display higher levels of belligerence and aggression both within cultures as well as across cultures (e.g., the rates of homicides perpetrated and suffered by males: Daly and Wilson 1988; males as combatants and casualties both in intra-group and intergroup conflict: LeBlanc and Register 2004; Keeley 1997; Gat 2010; Wrangham et al. 2006; males incurring more physically aggressive competition; Buss and Duntley 2011; rates of male physical aggression against females: Novak and Hatch 2009)). Furthermore, with respect to male–female physical violence, males rather than females use more severe acts of violence (Archer 2009; Campbell and Cross 2012).

The Mediating Role of Macroeconomic Diversification

Cabeza de Baca and Figueredo (2014) proposed a model tracing how the social *sequelae* of slower life history strategies (e.g., cooperative and mutualistic social systems, social equality, peaceful dynamics both within and between social groups, and sexual equality) foster the strategic and cognitive differentiation of resource allocation profiles among life history traits. They then interpreted these SD-IE and CD-IE effects as leading to higher levels of embodied human capital specifically by triggering the action of Ricardo's (1817) law of comparative advantage to produce greater aggregate wealth, although they presented no additional data to support that mediational hypothesis empirically. In the present analyses, however, we were now able to model explicitly the effects of strategic differentiation as mediated largely by macroeconomic diversification, as measured by three independent macroeconomic indices of diversity in employment, production, and export profiles.

The Rushton Paradox Revisited: an Emergent Social Property

With this work, we believe that we have solved the riddle of the so-called Rushton paradox (Meisenberg and Woodley 2013). We do not claim that this is the *only possible* solution, but merely that we have proposed a very plausible one when others appear to be lacking in the literature and shown it to be at least consistent with existing data.

We can briefly reconstruct the relevant part of our story as follows. Slower life history strategies promote higher levels of parental, nepotistic, and somatic effort, directly generating higher levels of human capital. Indirectly, slower life history strategies also promote higher levels of cognitive and strategic differentiation, facilitating social specialization and economic division of labor, thus triggering the consequences of Ricardo's (1817) law of comparative advantage and so generating *emergent* higher group-level economic productivity and development that are not evident at the individual level of analysis. These emergent, socially generated material benefits would favor expanded brain development and enhanced aggregate cognitive abilities. Such effects would be analogous to those underlying the observed secular increases on IQ test scores with economic development, labeled the *Flynn effect*. Furthermore, slower life history strategies should also promote highly differentiated and specialized societies and so select for specialized mental abilities, thus preferentially favoring heterogeneous increases in the various *specific* intelligences over *general* cognitive abilities.

Limitations of the Present Study

As with the majority of studies done both in evolutionary psychology and in the evolutionary sciences in general, we are using current data to make inferences about past evolution. All but certain cognitive ecology factors were estimated using indicators dating from AD 2001 to 2015. We reported the exact years for which the different data were collected (see Appendix 1) only in the service of full disclosure and scientific integrity. However, we make no claims attributing any importance to these different dates within that limited span of time. They were simply the dates for which the most information was available on any relevant dimension in the broad category of recent biodemography. The data were then treated as essentially cross-sectional, describing the approximately "current" (twenty-first century) state of affairs in each of these national polities. Using those data, we tested causal theories that hypothesized a sequencing of effects based on evolutionary ecological principles. There was no *causal inference*, as such, in terms of deriving this sequence of effects from the data; instead, there was *theory testing* against the available data, in a Popperian (1962) sense, to determine whether our predictions were or were not consistent with the empirical observations. In general, we believe that they were and that our cascade model offers a reasonably good account of this welter of otherwise poorly understood associations.

Nevertheless, a potential limitation of this work concerns the use of proximal-level indicators of constructs (such as temperature and precipitation) that may distally have been quite different due to historical changes in the physical ecology. This is important as historically different levels of these indicators (such as colder or more variable temperatures, or lower precipitation) may have shaped the population means of many of the psychosocial indicators considered here in such a way that might compromise the present pattern of hypothesized causal influence. For example, historically colder climates may have created selective pressures favoring both slower life history (*K*) and higher general intelligence (*g*) independently (Meisenberg and Woodley 2013). This suggests an alternative pattern of mediation to the one examined in the present analysis.

Testing the robustness of the present pattern of causal inference to possible proximal–distal confounding of levels will eventually require elaborating the model to incorporate historical measures of the relevant physical–ecological variables. These historical measures can then be used to determine the effects of alternative distal-level models (such as the cold winters theory; Lynn 2006) on the present pattern of proximal-level causal inference. Phylogenetic reconstruction methods (for a review, see Nunn 2011) of the biodemographic traits would also permit estimating ancestral states of variables for which historical data are not available, which could then be used to examine the longitudinal, rather than cross-sectional, associations among the variables studied.

In addition, there is always the possibility of feedback loops in what otherwise might appear to be a unidirectional causal sequence. There are some statistical models, called *non-recursive* models, which can deal with those kinds of effects. Unfortunately, non-recursive models cannot be estimated by normal least squares methods, but require more specialized algorithms such as two-stage least squares (2SLS) estimation, and these algorithms demand more restrictive conditions of the data for the model to be properly identified (e.g., see Berry 1984). The problem is that those restrictive conditions are simply not satisfied by the present data, so the best that we can do is acknowledge the possibilities of some reciprocal causation within the causal sequence specified.

Conclusions

We nonetheless conclude these findings to be consilient with a recently proposed model of multilevel selection (Figueredo et al. 2015) that describes a hierarchical cascade of consequences wherein: (1) *natural* selective pressures generate both *individual* and *social sequelae*; producing (2) *social* selective pressures that generate *sexual sequelae*; in turn producing (3) *sexual* selective pressures that generate further *sexual sequelae*. These generative natural selective pressures *constrain* (but do not *determine*) the social selective pressures, which then constrain the sexual selective pressures that drive both evolution and development. This integrated model of human social biogeography also assimilates pertinent concepts of the social privilege theory (Gottfredson 2006), which emphasizes sociocultural forces, and the differential *K* theory (Rushton 1985), which emphasizes bioecological forces, to generate hypotheses consilient with both theoretical frameworks. The current integrative model presents the social privilege and differential *K* theories as *complementary*: The final equation in our cascade model of social biogeography explains 88 % of the variance in aggregate cognitive abilities by supplying more detailed information on socioecological conditions than previous attempts at explanation.

Appendix 1: Measurement Model Specification

SAS 9.3 was utilized to construct the unit-weighted factors and estimate all bivariate Pearson's product–moment correlation coefficients. All common factor scores were estimated using SAS PROC STANDARD and DATA by simple unit weighting (Gorsuch 1983): (1) All subscale scores were estimated as the means of the standardized scores for all non-missing items on each subscale and (2) all scale scores were estimated as the means of the standardized scores for all non-missing subscales on each scale (Figueredo et al. 2000; McKnight et al. 2007).

For efficiency of presentation, the description of the indicators used in these analyses is supplemented with the factor structure tables showing the unit-weighted loadings (see Appendix Table 2) of each set of indicators from its latent common factor, operationalized as part–whole correlations, each serving as convergent validity coefficients among the indicators (Gorsuch 1983). All but certain cognitive ecology factors were estimated using indicators dating from AD 2001 to 2015.

Measures of Physical Ecology

Mean national latitudes and elevations were obtained from Wikipedia (2015a, b). The primary data source for annual mean national humidities and temperatures was Climate Charts (2015), with some missing data imputed for mean annual temperatures from Weatherbase (2015). Based on these basic parameters:

1. A *brumal factor* was operationalized as the latent common factor indicated by a unit-weighted composite of lower mean annual temperatures, proportion of area of temperate climate, and a composite of latitude above the equator and altitude above sea level for each national polity, where this "Boreal Index" was calculated by the following formula from quantitative physical ecology:

Boreal *Index* = (Absolute Latitude/333, 000 m) + Altitude above Sea Level)/482, 803 m)

2. A *hydrological factor* was operationalized as the latent common factor indicated by a unit-weighted composite of the proportion of area of tropical-humid climate and the annual precipitation for each national polity.

Measures of Community Ecology

Temperate Broadleaf Deciduous Forest Biome (TBDF) Three global biome maps with national boundaries were visually analyzed: (1) *biome map* (Wikipedia 2016); (2) *map of biomes around the world* (World Wildlife Federation—Discover Boreal and Temperate Forests 2016); and *map of temperate forests* (Marietta College 2016). Borders were matched against variously available regional and world maps for the biome maps with superimposed national boundaries wherein no nations were labeled. A Likert scale numerical coding scheme was adopted to facilitate quantitative analysis: assigning a 0, 1, 2, or 3, denoting *no*, *some*, *most*, or *all* TBDF coverage, respectively. These three maps had sufficient resolution to allow definite classification in all but 11 of 198 (66 countries × 3 maps) instances. Poor resolution or intersecting coordinate grids introduced uncertainty for Bulgaria, Japan, India, Turkey, and Croatia, but coding uncertainties recurred across maps only in the cases of Slovenia, Switzerland, and Austria. Nevertheless, at least one map proved definitive even in these three cases. A unit-weighted factor was constructed from these three convergent estimates, in which the three maps thus functioned as checks on one another, both within countries and for subtle globally mapped TBDF range variation.

Parasite Burden The per capita disability-adjusted life years (DALY) for each national polity was obtained from the World Health Organization Site (2015). Historical infectious disease prevalences for each national polity were obtained from Murray and Schaller (2010). The logarithm of the unit-weighted composite of these two indicators was used for the analyses, consistent with the predictions of population biology.

Measures of Social Ecology

Population density was estimated for each national polity by dividing the total population of each country by its total land area, as obtained from the CIA World Factbook (2006). The logarithm of the calculated population density was used for the analyses, consistent with the predictions of population biology.

Slow life history strategy (*adjusted*) was operationalized as the latent common factor indicated by a unit-weighted composite of the following five sociodemographic indicators:

1. *Infant mortality* (CIA World Factbook 2006), statistically adjusted for the specific effects of *parasite burden*, functions as an indicator of age-specific social and environmental harshness, which has been argued to represent a central force in the evolution of life history strategies (see Ellis et al. 2009).
2. *Life expectancy* (or longevity; CIA World Factbook 2006), statistically adjusted for the specific effects of *parasite burden*, has been argued to represent an intrinsic component of life history as it is related to morbidity–mortality and also reflects investments in somatic effort

(e.g., Charnov 1991; van Schaik and Isler 2012; Williams 1957), being thus related to covitality (Figueredo et al. 2004, 2007).

3. *Birth rate* (CIA World Factbook 2006) functions as a measure of fertility, and thus mating effort. As such, it represents an important indicator of the well-known life history trade-off between mating and parental effort (MacArthur and Wilson 1967).
4. *Teenage birth rate* (or *adolescent fertility rate*; World Bank 2014) is the number of births per 1000 women aged 15–19 years. In addition to measuring fertility, teenage birth rate represents early investments in mating effort, and it is well known that this is intrinsically related to the overall life history speed (van Schaik and Isler 2012; Stearns 1992).
5. *Operational sex ratio* (tertiary OSR or adult sex ratio; United Nations, Department of Economic and Social Affairs, Population Division 2015a, b) is the number of males per 100 females in the population of reproductive age.

Social equality was operationalized as the latent common factor indicated by a unit-weighted composite of the following two socioeconomic indicators:

1. The *GINI coefficient* (Gini 1912; World Bank 2014) is intended to represent the income distribution of a nation's residents and is the most commonly used measure of inequality. A low *GINI* represents a nation with a more equal income distribution.
2. The Power Resources Index (Vanhanen 2009; Finnish Social Science Data Archive 2015) is calculated by multiplying the Index of Occupational Diversification, the Index of Knowledge Distribution, and the Index of the Distribution of Economic Power Resources and then dividing the product by 10,000.

Within-group peace, indicating lower rates of conflict among *individuals*, was measured by a unit-weighted composite of the *perceived crime rate*, the *homicide rate*, the *violent crime rate*, the *civilian access to weapons*, and the *perceived corruption rate* (The Institute for Economics and Peace 2015).

Between-group peace was operationalized as the higher-order factor measured by a unit-weighted composite of the *infra-national peace* and the *inter-national peace* factors:

1. *Infra-national peace*, indicating lower rates of conflict among *subnational polities*, was measured by a unit-weighted composite of *internal conflict*, *violent demonstrations*, *political instability*, *political terror*, and *internal conflict deaths rate* (The Institute for Economics and Peace 2015).
2. *Inter-national peace*, indicating lower rates of conflict among *national polities*, was measured by a unit-weighted composite of *military expenditures*, *armed personnel*, *heavy weapons*, *bad relations with neighbors*, *conflicts fought*, *external conflict deaths*, *hostility to foreigners*, and *willingness to fight in war* (The Institute for Economics and Peace 2015).

Sexual equality was operationalized as the latent common factor indicated by a unit-weighted composite of the Gender Gap Index and the Gender Inequality Index for each national polity:

1. The Gender Gap Index (World Economic Forum 2009a, b) assesses how resources and opportunities are divided between male and female individuals within each national polity, as indicated by the four areas of *economic participation and opportunity*, *educational attainment*, *political empowerment*, and *health and survival.*
2. The Gender Inequality Index (United Nations Development Programme 2010, *Human Development Report*) is a composite measure estimating the loss of collective achievement within each national polity due to gender inequality, as indicated by the three dimensions of *reproductive health*, *empowerment*, and *labor market participation*.

Strategic differentiation (Figueredo et al. 2001) estimates the degree of diversification of resource allocation profiles among slower life history strategists within each national polity, operationalized as the effects of aggregate life history speed upon the CPEM-derived (see Gorsuch 2005) unit-weighted factor loadings of *low birth rate*, *low teen pregnancy*, *low infant mortality*, *higher operational sex ratios*, and *higher life expectancies*.

Measures of Cultural Ecology

Macroeconomic diversification was operationalized as the latent common factor measured by a unit-weighted composite of the Economic Complexity Index, the reverse-scored GDP Dissimilarity Index, and the reverse-scored Krugman Dissimilarity Index for each national polity. Operational definitions for each of these three macroeconomic indices were obtained from the Glossary of *The Atlas of Economic Complexity 2010* (The Observatory of Economic Complexity 2015a, b) and from Goschin et al. (2009):

1. Economic Complexity Index (ECI; Hidalgo and Hausmann 2009; The Observatory of Economic Complexity 2015a, b) measures the internal economic differentiation, and hence the higher inter-individual

specialization, *within* national polities, as assessed by the diversity of their exports to other polities.

2. GDP Dissimilarity Index (GDP-DI, based on the KDI; Krugman 1991, 1998) measures the dissimilarities *between* national polities in their relative distributions of their total GDPs among various macroeconomic sectors, and hence lower diversification of goods and services production *within* each of the national polities. GDP data were obtained for each national polity from the CIA World Factbook (2013), the World Bank (2014), and the Countries of the World (2015).
3. Krugman Dissimilarity Index (KDI; Krugman 1991, 1998) measures the dissimilarities *between* national polities in their relative labor force distributions among various macroeconomic sectors, and hence lower interindividual occupational diversification *within* each of the national polities. KDI data were obtained for each national polity from the CIA World Factbook (2013) and the World Bank (2014).

Human capital factor was operationalized as the latent common factor indicated by a unit-weighted composite of three macroeconomic indicators within each national polity. Operational definitions for the construct of human capital were obtained from Bourdieu (1986):

1. *Gross domestic savings rates* (1975–2005 average; World Bank 2014) were calculated for each national polity as gross national income less total consumption, plus net transfers. Missing data were imputed from LABORSTA (2015).
2. *Educational levels* (1950–2010 average) for each national polity were obtained from Barro and Lee (2013). Missing data were imputed from the World Bank (2014).
3. *Gross domestic products* (1985–2005 average) or the GDPs for each national polity were obtained from Heston et al. (2011).

Measures of Cognitive Ecology

Mean brain volumes for each national polity were obtained from Beals et al. (1984). Measurements were conducted by use of mechanical packing with mustard seeds. Male and female brain sizes were averaged for each national polity.

Cognitive abilities data were obtained from Lynn and Vanhanen (2006), which is an updated and expanded edition of Lynn and Vanhanen (2002). National mean aggregate IQs were most often measured with Raven's progressive matrices, a non-verbal reasoning test, and for some countries, a variety of other tests were employed. None of the missing values imputed by Lynn and Vanhanen for national IQs were employed in the present analysis.

Table 2 Measurement models: indicators of latent common factors

Brumal indicators	Brumal factor loadings	
Mean temperature (reversed)	.59*	
Boreal index	.75*	
Monthly temperature range	.90*	
Hydrological indicators	Hydrological factor loadings	
Humidity	.86*	
Rainfall	.86*	
TBDF Likert estimates	TBDF factor loadings	
Biome map	.96*	
Map of biomes around the world	.95*	
Map of temperate forests	.96*	
Log(Parasite Burden) indicators	Log(Parasite Burden) factor loadings	
Infectious DALY/100K	.86*	
Historical infectious disease prevalence	.91*	
LH indicators	LH strategy factor loadings	
	(Unadjusted for LPB)	(Adjusted for LPB)
Birth rate	−.90*	−.79*
Teen pregnancy	−.93*	−.81*
Infant mortality	−.94*	−.68*
Operational sex ratio	.52*	.50*
Life expectancy	.93*	.65*
Social equality indicators	Social equality factor loadings	
Income equality (GINI)	−.90*	
Index of power resources (IPR)	.90*	
Within-group peace indicators	Within-group peace factor loadings	
Perceived crime rate	−.83*	
Homicide rate	−.86*	
Violent crime rate	−.85*	
Access to weapons	−.86*	
Perceived corruption rate	−.59*	
Infra-national peace indicators	Infra-national peace factor loadings	
Internal conflict	−.91*	
Violent demonstrations	−.85*	
Political instability	−.88*	
Political terror	−.91*	
Internal conflict deaths	−.77*	
Inter-national peace indicators	Inter-national peace factor loadings	
Military expenditure	−.53*	
Armed personnel	−.56*	

Table 2 (continued)

Heavy weapons	−.50*
Bad relations with neighbors	−.75*
Conflicts fought	−.50*
External conflict deaths	−.43*
Hostile to foreigners	−.65*
Willing to fight in war	−.51*
Between-group peace subscales	Between-group peace factor loadings
Infra-national peace	.91*
Inter-national peace	.91*
Sexual equality indicators	Sexual equality factor loadings
Gender gap index	.94*
Gender inequality index	−.94*
LH loadings	Strategic differentiation factor loadings
Low birth rate	−.92*
Low teen pregnancy	−.90*
Low infant mortality	−.60*
Operational sex ratio	−.62*
Life expectancy	−.73*
Macroeconomic diversification indicators	Macroeconomic diversification factor loadings
ECI	.70*
GDPDI	−.74*
KDI	−.61*
Human capital indicators	Human capital factor loadings
National savings rate	.73*
National education level	.84*
National GDP	.85*

LH life history, *LPB* Log(Parasite Burden), *ECI* Economic Complexity Index, *GDPDI* GDP Dissimilarity Index, *KDI* Krugman Dissimilarity Index

$*p < .05$

Appendix 2: Structural Model Specification

We utilized SEQCA to model a theoretically specified *cascade model* of effects using Unimult 2 statistical software (UM2; Gorsuch 2016). The sequence of criterion variables for the present study was theoretically specified as follows:

1. Temperate Broadleaf Deciduous Forest = β_{31}*Brumal + β_{32}*Hydrological + β_{33}*Brumal*Hydrological
2. Log(Parasite Burden) = β_{41}*Temperate Broadleaf Deciduous Forest + β_{42}*Brumal + β_{43}*Hydrological + β_{44}*Brumal*Hydrological
3. Log(Population Density) = β_{51}*Log(Parasite Burden) + β_{52}*Temperate Broadleaf Deciduous Forest + β_{53}*Brumal + β_{54}*Hydrological + β_{55}*Brumal*Hydrological
4. Slow Life History Strategy = β_{61}*Log(Population Density) + β_{62}*Log(Parasite Burden) + β_{63}*Temperate Broadleaf Deciduous Forest + β_{64}*Brumal + β_{65}*Hydrological + β_{66}*Brumal*Hydrological
5. Social Equality = β_{71}*Slow Life History Strategy + β_{72}*Log(Population Density) + β_{73}*Log(Parasite Burden) + β_{74}*Temperate Broadleaf Deciduous Forest + β_{75}*Brumal + β_{76}*Hydrological + β_{77}*Brumal*Hydrological
6. Within-Group Peace = β_{81}*Social Equality + β_{82}*Slow Life History Strategy + β_{83}*Log(Population Density) + β_{84}*Log(Parasite Burden) + β_{85}*Temperate Broadleaf Deciduous Forest + β_{86}*Brumal + β_{87}*Hydrological + β_{88}*Brumal*Hydrological
7. Between-Group Peace = β_{91}*Within-Group Peace + β_{92}*Social Equality + β_{93}*Slow Life History Strategy + β_{94}*Log(Population Density) + β_{95}*Log (Parasite Burden) + β_{96}*Temperate Broadleaf Deciduous Forest + β_{97}*Brumal + β_{98}*Hydrological + β_{99}*Brumal*Hydrological
8. Sexual Equality = β_{101}*Between-Group Peace + β_{102}*Within-Group Peace + β_{103}*Social Equality + β_{104}*Slow Life History Strategy + β_{105}*Log(Population Density) + β_{106}*Log(Parasite Burden) + β_{107}*Temperate Broadleaf Deciduous Forest + β_{108}*Brumal + β_{109}*Hydrological + β_{1010}*Brumal*Hydrological
9. Strategic Differentiation = β_{111}*Sexual Equality + β_{122}*Between-Group Peace + β_{113}*Within-Group Peace + β_{114}*Social Equality + β_{115}*Slow Life History Strategy + β_{116}*Log(Population Density) + β_{117}*Log(Parasite Burden) + β_{118}*Temperate Broadleaf Deciduous Forest + β_{119}*Brumal + β_{1110}*Hydrological + β_{1111}*Brumal*Hydrological
10. Macroeconomic Diversification = β_{121}*Strategic Differentiation + β_{122}*Sexual Equality + β_{123}*Between-Group Peace + β_{124}*Within-Group Peace + β_{125}*Social Equality + β_{126}*Slow Life History Strategy + β_{127}*Log(Population Density) + β_{128}*Log(Parasite Burden) + β_{129}*Temperate Broadleaf Deciduous Forest + β_{1210}*Brumal + β_{1211}*Hydrological + β_{1212}*Brumal*Hydrological
11. Human Capital = β_{121}*Macroeconomic Diversification + β_{132}*Strategic Differentiation + β_{133}*Sexual Equality + β_{134}*Between-Group Peace + β_{135}*Within-Group Peace + β_{136}*Social Equality + β_{137}*Slow Life History Strategy + β_{138}*Log(Population Density) + β_{139}*Log(Parasite Burden) + β_{1310}*Temperate Broadleaf Deciduous Forest + β_{1311}*Brumal + β_{1312}*Hydrological + β_{1313}*Brumal*Hydrological

12. Mean Brain Volume = β_{141}*Human Capital + β_{142}*Macroeconomic Diversification + β_{143}*Strategic Differentiation + β_{144}*Sexual Equality + β_{145}*Between-Group Peace + β_{146}*Within-Group Peace + β_{147}*Social Equality + β_{148}*Slow Life History Strategy + β_{149}*Log(Population Density) + β_{1410}*Log(Parasite Burden) + β_{1411}*Temperate Broadleaf Deciduous Forest + β_{1412}*Brumal + β_{1413}*Hydrological + β_{1414}*Brumal*Hydrological
13. Mean Aggregate IQ = β_{151}*Mean Brain Volume + β_{152}*Human Capital + β_{153}*Macroeconomic Diversification + β_{154}*Strategic Differentiation + β_{155}*Sexual Equality + β_{156}*Between-Group Peace + β_{157}*Within-Group Peace + β_{158}*Social Equality + β_{159}*Slow Life History Strategy + β_{1510}*Log(Population Density) + β_{1511}*Log(Parasite Burden) + β_{1512}*Temperate Broadleaf Deciduous Forest + β_{1513}*Brumal + β_{1514}*Hydrological + β_{1515}*Brumal*Hydrological

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