Evolution and Human Behavior 40 (2019) 479–491

Contents lists available at ScienceDirect

Evolution and Human Behavior

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

Assortative mating and the evolution of desirability covariation

Daniel Conroy-Beam[a,*], James R. Roney[a], Aaron W. Lukaszewski[b], David M. Buss[c], Kelly Asao[c], Agnieszka Sorokowska[d,e], Piotr Sorokowski[d], Toivo Aavik[f], Grace Akello[g], Mohammad Madallh Alhababha[h], Charlotte Alm[i], Naumana Amjad[j], Afifa Anjum[j], Chiemezie S. Atama[k], Derya Atamtürk Duyar[l], Richard Ayebare[m], Carlota Batres[n], Mons Bendixen[o], Aicha Bensafia[p], Anna Bertoni[q], Boris Bizumic[r], Mahmoud Boussena[s], Marina Butovskaya[t,u], Seda Can[v], Katarzyna Cantarero[w], Antonin Carrier[x], Hakan Cetinkaya[y], Ilona Croy[z], Rosa María Cueto[aa], Marcin Czub[d], Silvia Donato[q], Daria Dronova[t], Seda Dural[v], Izzet Duyar[l], Berna Ertugrul[ab], Agustín Espinosa[aa], Ignacio Estevan[ac], Carla Sofia Esteves[ad], Luxi Fang[ae], Tomasz Frackowiak[d], Jorge Contreras Garduño[af], Karina Ugalde González[ag], Farida Guemaz[ah], Petra Gyuris[ai], Mária Halamová[aj], Iskra Herak[ak], Marina Horvat[al], Ivana Hromatko[am], Chin-Ming Hui[ae], Raffaella Iafrate[q], Jas Laile Jaafar[an], Feng Jiang[ao], Konstantinos Kafetsios[ap], Tina Kavčič[aq], Leif Edward Ottesen Kennair[o], Nicolas Kervyn[ak], Truong Thi Khanh Ha[ar], Imran Ahmed Khilji[as], Nils C. Köbis[at], Hoang Moc Lan[ar], András Láng[ai], Georgina R. Lennard[r], Ernesto León[aa], Torun Lindholm[i], Trinh Thi Linh[ar], Giulia Lopez[q], Nguyen Van Luot[ar], Alvaro Mailhos[ac], Zoi Manesi[au], Rocio Martinez[av], Sarah L. McKerchar[r], Norbert Meskó[ai], Girishwar Misra[aw], Conal Monaghan[r], Emanuel C. Mora[ax], Alba Moya-Garófano[av], Bojan Musil[ay], Jean Carlos Natividade[az], Agnieszka Niemczyk[d], George Nizharadze[ba], Elisabeth Oberzaucher[bb], Anna Oleszkiewicz[d,e], Mohd Sofian Omar-Fauzee[bc], Ike E. Onyishi[bd], Baris Özener[l], Ariela Francesca Pagani[q], Vilmante Pakalniskiene[be], Miriam Parise[q], Farid Pazhoohi[bf], Annette Pisanski[ax], Katarzyna Pisanski[d,bg], Edna Ponciano[bh], Camelia Popa[bi], Pavol Prokop[bj,bk], Muhammad Rizwan[bl], Mario Sainz[bm], Svjetlana Salkičević[bn], Ruta Sargautyte[be], Ivan Sarmány-Schuller[bo], Susanne Schmehl[bp], Shivantika Sharad[bq], Razi Sultan Siddiqui[br], Franco Simonetti[bs], Stanislava Yordanova Stoyanova[bt], Meri Tadinac[bn], Marco Antonio Correa Varella[bu], Christin-Melanie Vauclair[ad], Luis Diego Vega[ag], Dwi Ajeng Widarini[bv], Gyesook Yoo[bw], Marta Zaťková[bx], Maja Zupančič[by]

[a] *Department of Psychological and Brain Sciences, University of California, Santa Barbara, Santa Barbara 93106, United States*
[b] *Department of Psychology, California State University, Fullerton, Fullerton 92831, United States*
[c] *Department of Psychology, University of Texas at Austin, Austin 78712, United States*
[d] *Institute of Psychology, University of Wroclaw, Wroclaw 50-137, Poland*
[e] *Smell & Taste Clinic, Department of Otorhinolaryngology, TU Dresden, Dresden 1069, Germany*
[f] *Institute of Psychology, University of Tartu, Tartu 50090, Estonia*
[g] *Department of Mental Health, Faculty of Medicine, Gulu University, Gulu 0, Uganda*
[h] *English Language Department, Middle East University, Amman 11181, Jordan*
[i] *Department of Psychology, Stockholm University, Stockholm 10691, Sweden*
[j] *Institute of Applied Psychology, University of the Punjab, Lahore 54590, Pakistan*
[k] *Department of Sociology and Anthropology, University of Nigeria, Nsukka 410002, Nigeria*
[l] *Deparment of Anthropology, Istanbul University, Istanbul 34452, Turkey*
[m] *North Star Alliance, NA, Kampala 0, Uganda*
[n] *Department of Psychology, Franklin and Marshall College, Lancaster 17603, USA*
[o] *Department of Psychology, Norwegian University of Technology and Science (NTNU), Trondheim 7491, Norway*

* Corresponding author.
E-mail address: conroy-beam@psych.ucsb.edu (D. Conroy-Beam).

https://doi.org/10.1016/j.evolhumbehav.2019.06.003

[p] EFORT, Department of Sociology, University of Algiers 2, Algiers 16000, Algeria
[q] Department of Psychology, Universita Cattolica del Sacro Cuore, Milan 20123, Italy
[r] Research School of Psychology, Australian National University, Canberra 2601, Australia
[s] EFORT, Department of Psychology and Educational Sciences, University of Algiers 2, Algiers 16000, Algeria
[t] Institute of Ethnology and Anthropology, Russian Academy of Sciences, Moscow 119991, Russia
[u] Russian State University for the Humanities, Moscow 119991, Russia
[v] Department of Psychology, Izmir University of Economics, Izmir 35300, Turkey
[w] Faculty in Sopot, SWPS University of Social Sciences and Humanities, Sopot 03-815, Poland
[x] Psychology Faculty (CECOS), Université Catholique de Louvain, Louvain-la-Neuve 1348, Belgium
[y] Department of Psychology, Ankara University, Ankara 6560, Turkey
[z] Department of Psychotherapy and Psychosomatic Medicine, TU Dresden, Dresden 1069, Germany
[aa] Grupo de Psicología Política y Social (GPPS), Departamento de Psicología, Pontificia Universidad Católica del Perú, Lima 15088, Peru
[ab] Deparment of Anthropology, Cumhuriyet University, Sivas 58140, Turkey
[ac] Facultad de Psicología, Universidad de la República, Motevideo 11200, Uruguay
[ad] Instituto Universitário de Lisboa (ISCTE-IUL), CIS-IUL, Lisboa 1649-026, Portugal
[ae] Department of Psychology, Chinese University of Hong Kong, Hong Kong 0, China
[af] Escuela Nacional de Estudios Superiores, Unidad Morelia UNAM, Morelia 58190, Mexico
[ag] Psychology Department, Universidad Latina de Costa Rica, San José 11501, Costa Rica
[ah] EFORT, Department of Psychology and Educational Sciences, University of Setif 2, Setif 16000, Algeria
[ai] Institute of Psychology, University of Pécs, Pécs 7624, Hungary
[aj] Faculty of Social Sciences and Health Care, Department of Psychological Sciences, Constantine the Philosopher University in Nitra, Nitra 94974, Slovakia
[ak] Louvain Research Institute in Management and Organisations (LOURiM), Université Catholique de Louvain, Louvain-la-Neuve 1348, Belgium
[al] Faculty of Arts, Department of Psychology, University of Maribor, Maribor 2000, Slovenia
[am] Department of Psychology, Faculty for Humanities and Social Sciences, University of Zagreb, Zagreb 10000, Croatia
[an] Dept of Educational Psychology and Counseling, University of Malaya, Kuala Lumpur 50603, Malaysia
[ao] Organization and Human Resource Management, Central University of Finance and Economics, Beijing 102202, China
[ap] Psychology Department, University of Crete, Rethymno 70013, Greece
[aq] Faculty of Education, University of Primorska, Koper 6000, Slovenia
[ar] Department of Psychology, University of Social Sciences and Humanities, Hanoi 100000, Viet Nam
[as] Department of Psychology, F.G. College for Men, F-j/d, Islamabad 44000, Pakistan
[at] Center for Research in Experimental Economics and Political Decision Mating, Department of Economics, University of Amsterdam, Amsterdam 1081, the Netherlands
[au] Department of Experimental & Applied Psychology, Vrije Universiteit Amsterdam, Amsterdam 1081, the Netherlands
[av] Department of Social Psychology, University of Granada, Grenada 18010, Spain
[aw] Department of Psychology, University of Delhi, Delhi 110021, India
[ax] Department of Animal and Human Biology, Faculty of Biology, University of Havana, Havana 0, Cuba
[ay] Faculty of Arts, Department of Psychology, University of Maribor, Maribor 2000, Slovenia
[az] Department of Psychology, Pontifical Catholic University of Rio de Janeiro, Rio de Janeiro 22451-000, Brazil
[ba] Department of Social Sciences, Free Unviersity of Tbilisi, Tbilisi 2, Georgia
[bb] Faculty of Life Sciences, University of Vienna, Vienna 1090, Austria
[bc] School of Education, Universiti Uteara Malaysia, Sintok 6010, Malaysia
[bd] Department of Psychology, University of Nigeria, Nsukka 410002, Nigeria
[be] Institute of Psychology, Vilnius University, Vilnius 1513, Lithuania
[bf] Department of Basic Psychology, School of Psychology, University of Minho, Braga 4710-057, Portugal
[bg] Mammal Vocal Communication & Cognition Research Group, University of Sussex, Brighton BN1 9RH, United Kingdom
[bh] Institute of Psychology, University of the State of Rio de Janeiro, Rio de Janeiro 21941-901, Brazil
[bi] Department of Psychology, Faculty for Humanities and Social Sciences, UNATC-CINETIc, Romanian Academy, Bucharest 30167, Romania
[bj] Department of Environmental Ecology, Comenius University, Bratislava 842 15, Slovakia
[bk] Institute of Zoology, Slovak Academy of Sciences, Bratislava 845 06, Slovakia
[bl] The Delve Pvt Ltd, Islamabad 44000, Pakistan
[bm] Mind, Brain and Behavior Research Center, Department of Social Psychology, University of Granada, Grenada 18010, Spain
[bn] Department of Psychology, Faculty for Humanities and Social Sciences, University of Zagreb, Zagreb 10000, Croatia
[bo] Center for Social and Psychological Sciences, Institute of Experimental Psychology SAS, Bratislava 841 04, Slovakia
[bp] Faculty of Life Sciences, University of Vienna, Vienna 1010, Austria
[bq] Department of Applied Psychology, Vivekananda College, University of Delhi, Delhi 110021, India
[br] Department of Management Sciences, DHA Suffa University, Karachi 75500, Pakistan
[bs] School of Psychology, P. Universidad Catolica de Chile, Santiago 8331150, Chile
[bt] Department of Psychology, South-West University "Neofit Rilski", Blagoevgrad 2700, Bulgaria
[bu] Department of Experimental Psychology, Institute of Psychology, University of São Paulo, São Paulo 03178-200, Brazil
[bv] Department of Communication, University Prof. Dr. Moestopo (Beragama), Jakarta 10270, Indonesia
[bw] Dept. of Child & Family Studies, Kyung Hee University, Seoul 024-47, Republic of Korea
[bx] Faculty of Social Sciences and Health Care, Department of Psychological Sciences, Constantine the Philosopher University in Nitra, Nitra 94974, Slovakia
[by] Department of Psychology, Faculty of Arts, University of Ljubljana, Ljubljana 1000, Slovenia

ARTICLE INFO

Keywords:
Assortative mating
Trait covariation
Agent-based modeling
Cross-cultural studies

ABSTRACT

Mate choice lies close to differential reproduction, the engine of evolution. Patterns of mate choice consequently have power to direct the course of evolution. Here we provide evidence suggesting one pattern of human mate choice—the tendency for mates to be similar in overall desirability—caused the evolution of a structure of correlations that we call the *d* factor. We use agent-based models to demonstrate that assortative mating causes the evolution of a positive manifold of desirability, *d*, such that an individual who is desirable as a mate along any one dimension tends to be desirable across all other dimensions. Further, we use a large cross-cultural sample with n = 14,478 from 45 countries around the world to show that this *d*-factor emerges in human samples, is a cross-cultural universal, and is patterned in a way consistent with an evolutionary history of assortative mating. Our results suggest that assortative mating can explain the evolution of a broad structure of human trait covariation.

1. Introduction

Mate choice is a pivotal decision on several timescales. Over the lifetime of an individual, a chosen mate represents an important co-operation partner, reproduction partner, and parenting partner. Over deep time, mating dictates the nature of reproduction, lending mate choice the power to generate selection pressures and shape patterns of inheritance across generations. Here we explore one instance in which patterns of human mate choice are predicted to have shaped human evolution. We use agent-based models to show that assortative mating for mate value—a common feature of human mating—predicts the evolution of a signature pattern of trait covariation: a positive manifold of desirability as a mate, such that a person desirable as a mate on any one trait dimension is disproportionately likely to be desirable across other dimensions as well. Further, we analyze a large cross-cultural sample to provide evidence that an analogous positive manifold, which we call *d*, emerges in human samples from around the world. Finally, we compare models of assortative mating to models of rater biases and halo effects and find that these biases cannot exclusively explain the pattern of human trait covariation we observe. This research provides the first evidence of a cross-culturally universal pattern of trait covariation that is itself consistent with an evolutionary history of assortative mate choice.

Humans mate with self-similar partners across a wide array of dimensions. For example, mated partners tend to be improbably similar to one another in terms of education (Mare, 1991), intelligence (Bouchard & McGue, 1981), and physical attractiveness (Feingold, 1988). One critical dimension of assortative mating is that for "mate value," or overall desirability as a mating partner (Sugiyama, 2015). To the extent that all individuals vie for the most consensually desirable partners on the mating market, those highest in mate value tend to have the greatest power of choice and use that power to select high mate value partners (Kalick & Hamilton, 1986). Mated partners consequently tend to have correlated mate values (Shackelford & Buss, 1997).

Such assortative mating for mate value creates "cross-character assortment": correlations between mated partners on otherwise independent traits (Buss & Barnes, 1986). Consider a scenario in which humans mate assortatively for mate value and mate value is determined by just two preferred characteristics: kindness and intelligence. All else equal, a kind person will be higher in mate value and will tend to attract higher mate value partners. These high mate value partners, relative to randomly chosen partners, are disproportionately likely to be intelligent. Assortative mating for mate value will therefore pair kind people with intelligent partners at above-chance rates. Such cross-character assortment does occur in married couples for specific traits; for instance, physically attractive women tend to marry men higher in status and resources (Buss & Schmitt, 2019; Elder, 1969).

When mated partners produce offspring, this pattern of mate choice translates into a pattern of inheritance. Offspring inherit correlated traits from their assortatively mated parents because human individual differences tend to be heritable (Polderman et al., 2015). A kind person mated to an intelligent partner will be relatively likely to produce offspring who are both kind and intelligent. The inheritance of correlated traits, iterated across generations, can cause the evolution of trait covariation: traits that are initially orthogonal in the population gradually become correlated across generations. Consistent with this rationale, human couples do in fact show evidence of assortative mating at both the phenotypic and genetic level (Hugh-Jones, Verweij, St. Pourcain, & Abdellaoui, 2016; Robinson et al., 2017). Further, trait covariances are frequently mediated by genetic factors, including pleiotropic and correlated genes (Keller et al., 2013; Plomin, DeFries, Knopik, & Neiderhiser, 2016). Finally, there exists a robust genetic correlation between height and intelligence, which is consistent with covariance in underlying genes from cross-character assortative mating (Keller et al., 2013).

Beyond height and intelligence, a large prior literature explores, either directly or indirectly, correlations between desirable traits (see Supplementary Table 1 for a non-comprehensive review). Findings from this literature are mixed. Some trait correlations prove robust; others, such as correlations between physical attractiveness and intelligence, find only infrequent support. However, this literature is also marked by relative homogeneity in participant populations and great heterogeneity in sample sizes, measures, and methods. Furthermore, studies in this literature rarely test assortative mating as a potential source of trait covariation. In light of this, in the current research we sought to provide three novel contributions.

First, in conjunction with computational models of assortative mating, we analyze a new sample of real-world data that is both large and includes participants from around the world. Second, unlike the prior literature, we do not focus on covariation in traits themselves but on covariation in desirability—that is, in deviation of trait value from the opposite sex's preferences. This is a subtle but important distinction. To the degree that one sex's ideal preference is not maximal on a trait dimension, mate value will be nonlinear with respect to that trait dimension. For example, people most strongly express a preference for mates in the 90th percentile of intelligence, rather than the 99th (Gignac, Darbyshire, & Ooi, 2018). This preference makes mate value a non-linear function of intelligence: all else equal, high mate value people will be relatively high on intelligence, whereas moderate mate value people could be close to either the 99th or the 75th percentile on intelligence. The trait covariation created by assortative mating for mate value will consequently be nonlinear with respect to these trait dimensions as well. The effects of assortative mating will therefore be clearest when analyzing covariation in terms in desirability, rather than in terms of absolute trait level.

Third and finally, while previous work has explored assortative mating's power to construct covariation between two trait dimensions, assortative mating actually predicts the evolution of a broader covariance structure among preferred traits (Buss & Barnes, 1986). Humans express mate preferences for a wide array of traits (Buss, 1989) and these preferences predict real mate choices (Buss & Schmitt, 2019; Li et al., 2013). When multiple preferences contribute to mate selection, assortative mating for mate value has the potential to produce intercorrelation in desirability across all preferred characteristics. More than just bivariate correlations, what should emerge from assortative mating for mate value across generations is a positive manifold of desirability, which we call *d*, organized around mate value such that a person who is desirable as a mate along any one preferred dimension is disproportionately likely to be desirable across other dimensions as well.

We test this hypothesis using agent-based models and a large cross-cultural sample. We first use a series of evolutionary agent-based models to demonstrate that assortative mating causes the evolution of a general factor of desirability, *d*, within a set of initially uncorrelated traits and to identify a pattern of results diagnostic of this process. Next, we compare data from these simulated populations to a sample of n = 14,487 people from 45 countries around the world. We use this cross-cultural sample to show that this *d*-factor does in fact emerge across human populations and that it is patterned precisely as predicted by our evolutionary agent-based models, suggesting human desirability covariation is partially explained by an evolutionary history of assortative mating.

2. Methods

2.1. Agent-based model

First, we constructed and analyzed an evolutionary agent-based model of a mating market. The primary model generated 200 agents at the start of each model run. Each agent possessed 10 traits; each trait was itself the sum of 100 smaller "gene" values. Gene values were initially drawn from random uniform distributions constrained between values of 0 and 0.08. These start values were chosen so that the average starting trait value would be approximately $M = 4.0$. Agents also had 10 corresponding mate preferences; preferences, like traits, were each the sum of 100 gene values themselves drawn from random uniform distributions. Each agent was additionally assigned an energy value based on the value of their traits. At the start of each model run, the model selected a random value as optimal for each trait dimension. Each agent earned energy proportional to the absolute deviation between their trait value and optimum value for that trait dimension such that agents who were closer to the optimum value across all traits had more energy. These energy values were used to control reproduction and introduce natural selection into the model. Finally, all agents had a sex: half of all agents were randomly assigned to be female and the remaining half were male.

After initialization, agents followed a life cycle in which they computed how attracted they were to one another, selected each other as mates based on these attractions, reproduced with their chosen mates, and then died. This life cycle was repeated for 1000 generations of evolution.

2.1.1. Attraction

In the first phase of the life cycle, agents computed how attracted they were to one another based on their mate preferences. Each agent computed their attraction to all opposite-sex agents. Attraction was calculated as the Euclidean distance between the agent's preference vector and each potential mate's trait vector. These distances were then scaled and transformed such that a value of 10 indicated that the potential mate perfectly matched the agent's preferences, whereas a value of 0 indicated that the potential mate was the worst possible fit to the agent's preferences. This attraction algorithm has shown to be a good model of the algorithm used by human mate choice psychology (Conroy-Beam & Buss, 2017).

2.1.2. Mate selection

The attraction calculation phase produced two matrices: one matrix containing how attractive each male agent found all female agents and another containing how attractive each female agent found all male agents. In the next phase of the life cycle, the model multiplied these attraction matrices together to produce the mutual attraction matrix. Each cell of this matrix represented how mutually attracted all possible agent couples would be. The model next paired the most mutually attracted possible couple and then removed this couple from the mutual attraction matrix. This pairing process iterated until all possible couples were formed.

2.1.3. Reproduction

Agents next reproduced with their chosen partner. Agent couples reproduced in proportion to the sum of their energy values. In this way, agents who had trait values closer to optimum—and mate preferences for these trait values—were more likely to reproduce each generation. Energy values were scaled prior to reproduction such that highest energy couple in each generation had 10% greater reproductive success on average than the lowest energy couple, yielding a moderate selection pressure in favor of optimum traits and preferences. Each offspring inherited each of their preference and trait genes randomly from either parent. A small amount of random normal noise was added to gene values prior to inheritance to simulate mutation; the noise value added to genes was scaled such that the resulting standard deviation added to trait and preference values was equivalent to 0.1% of the total possible trait range. Offspring trait and preference values were then calculated as the sum of their mutated gene values. Half of all offspring were randomly assigned to be female; the other half were randomly assigned to be male. The number of offspring produced each generation was equal to the starting population size.

2.1.4. Death

After reproduction, all agents of the parent generation died. Offspring then began the life cycle anew in the next generation. After 1000 generations of evolution, the model retained the final generation of parent couples. The result for each model run was a final population of $n = 200$ that represented the results of evolution under conditions of assortative mating.

2.2. Cross-cultural data

2.2.1. Participants

Participants in the cross-cultural sample were $n = 14{,}487$ individuals (7961 female) from 45 different countries from all inhabited continents around the world. Supplementary Table 2 shows the sample size from each country. Participants in each study site were recruited from two sources: roughly half of all participants were recruited from university populations and the remaining half were recruited from community samples. Not all study sites kept records of participant sample source; however, among those sites with records ($n = 6637$), 47.14% ($n = 3129$) of participants came from community samples. All participant data was collected in person because online samples tend to be less representative of populations in developing countries (Batres & Perrett, 2014). Participants were $M = 28.79$ years old ($SD = 10.64$) and ages ranged from 18 to 91 ($Mdn = 25$). Most participants ($n = 9236$, 63.75%) reported being in an ongoing, committed, romantic relationship. Of these, 49.26% reported being in a dating relationship, 12.59% were engaged, and 38.14% were married.

We additionally analyzed two smaller, supplementary samples. The first was a sample of newlyweds from Buss (1991). This was $n = 214$ people composing 107 newlywed couples that had each been married for under 1 year at the time of participation. The second was a sample of $n = 382$ people composing 191 romantic dyads. Participants were $M = 49.86$ years old on average ($SD = 14.48$) and were in their relationships for $Mdn = 216.7$ months.

2.2.2. Measures

In the cross-cultural sample, all participants reported their mate preferences in an ideal long-term mate, described as a committed, romantic partner, using a 5-item mate preference instrument. This instrument contained five 7-point bipolar adjective scales on which participants rated their ideal partner's standing on five separate traits: intelligence, kindness, health, physical attractiveness, and financial prospects. Each trait was rated between two extremes, for instance, from 1 representing "very unkind" to 7 representing "very kind." Participants additionally used the same rating scales to describe their own standing on each of these five traits and to rate their actual long-term partner, if they had one. This mate preference instrument was translated into local languages and back-translated by researchers at each study site.

Participants in the newlywed sample reported their ideal long-term mate preferences for 40 personality dimensions using a 40-item Big Five personality questionnaire. For each participant, we also have ratings of each participant's own traits on the same 40 items from four sources: participant self-reports, partner ratings, and the ratings of two independent interviewers.

Participants in the romantic dyad sample reported their ideal preferences in a long-term, committed romantic partner on 20 7-point bipolar adjective scales. These scales included the five dimensions collected in the cross-cultural sample in addition to others, including characteristics such as masculinity/femininity, religiosity, and desire for a family. Participants each additionally rated themselves and their romantic partner on each of these dimensions.

2.3. Data analysis

Data analysis proceeded in several parallel stages for both the agent-based models and the cross-cultural data. First, within each country and each model run, we calculated the average preferences of all males and the average preferences of all females. These preferences were used to compute two values within country and within model run. We first calculated the overall mate value of each agent, each participant, and their partners as the Euclidean distance between that individual's traits and the average preferences of the individual's opposite sex. This mate value estimate is a single summary value that reflects the degree to which each person or agent embodies the preferences of the opposite sex across all dimensions. These distances were scaled such that a value of 10 meant the individual perfectly matched the opposite sex's average preferences and a value of 0 meant the individual provided the worst possible match to the opposite sex's preferences. Prior studies have found that these Euclidean mate values predict both desirability as a mate and power of choice on the mating market (Conroy-Beam, 2017; Conroy-Beam & Buss, 2017). For plotting purposes, agent mate values were standardized to a common scale within model runs before producing figures to control for variation in population mate values across model runs.

Second, we used average preferences to calculate each agent and each participant's "desirability" on each trait dimension. Desirabilities were calculated as the absolute difference between the individual's trait value for each dimension and the opposite sex's average preference value for that dimension; desirability values were re-scaled such that higher values indicated a closer fit to the opposite sex's preferences. Rather than a single summary variable as for mate value, this yields a vector of values for each agent or participant, with each value reflecting the degree to which that agent or participant matches the opposite sex's mate preference on that specific trait dimension. All analyses proceeded analogously for the smaller dyadic samples as well.

Next, we subjected these desirability scores to principal component analysis. Principal component analyses were run separately for each run of the agent-based model and for each country within the cross-cultural sample. Male and female desirability scores were additionally analyzed separately because men and women have different mate preferences (Buss, 1989). Each principal component analysis extracted a single principal component from trait-level desirabilities. From these principal component analyses, we saved the total variance in trait-level desirability explained by this *d*-factor (averaged across males and females), the loadings of each desirability dimension onto this *d*-factor, and each participant or each agent's factor score. If assortative mating has constructed a *d*-factor such that individuals who are desirable on any one trait are likely to be desirable on all other traits, this principal component analysis should yield a principal component that explains above-chance variance in trait-level desirability and that has predictable factor loadings. Conversely, if desirability dimensions *do not* covary under a *d*-factor, this principal component analysis should extract a principal component that explains little total variance or that has unsystematic factor loadings. All data, model script, and analysis script are available on the Open Science Framework (https://osf.io/6g4pq/?view_only=c6031e267223461dad32927f7e70d561).

3. Results

First, we examine the results of the evolutionary agent-based models. Agents within these simulations mate assortatively for overall "mate value;" across model runs, the correlation between partner mate values in the final generation of the model was $r_{\text{mean}} = 0.94$, 95% CI [0.93, 0.94]. This agent-based model therefore allowed us to assess whether an evolutionary history of assortative mating for mate value would construct a *d*-factor from initially random traits such that agents who are more desirable along any given trait dimension tend to be desirable across all others as well.

Fig. 1 shows that the agent populations in the primary agent-based model do in fact evolve a *d*-factor from initially uncorrelated traits. In the first generation of evolution, when agent traits were uncorrelated, the *d*-factor explained just $M = 15.28\%$, 95% CI [15.16%, 15.41%] of the variance in trait-level desirability across model runs. However, after 1000 generations of assortative mating, this *d*-factor increased in size to explain $M = 41.17\%$, 95% CI [39.75%, 42.56%] of the variance in trait-level desirability. Although agent traits were initially distributed randomly, by the final generation of the agent-based model, a *d*-factor evolved such that agents that were desirable as a mate on any given trait dimension were likely to be desirable across all other trait

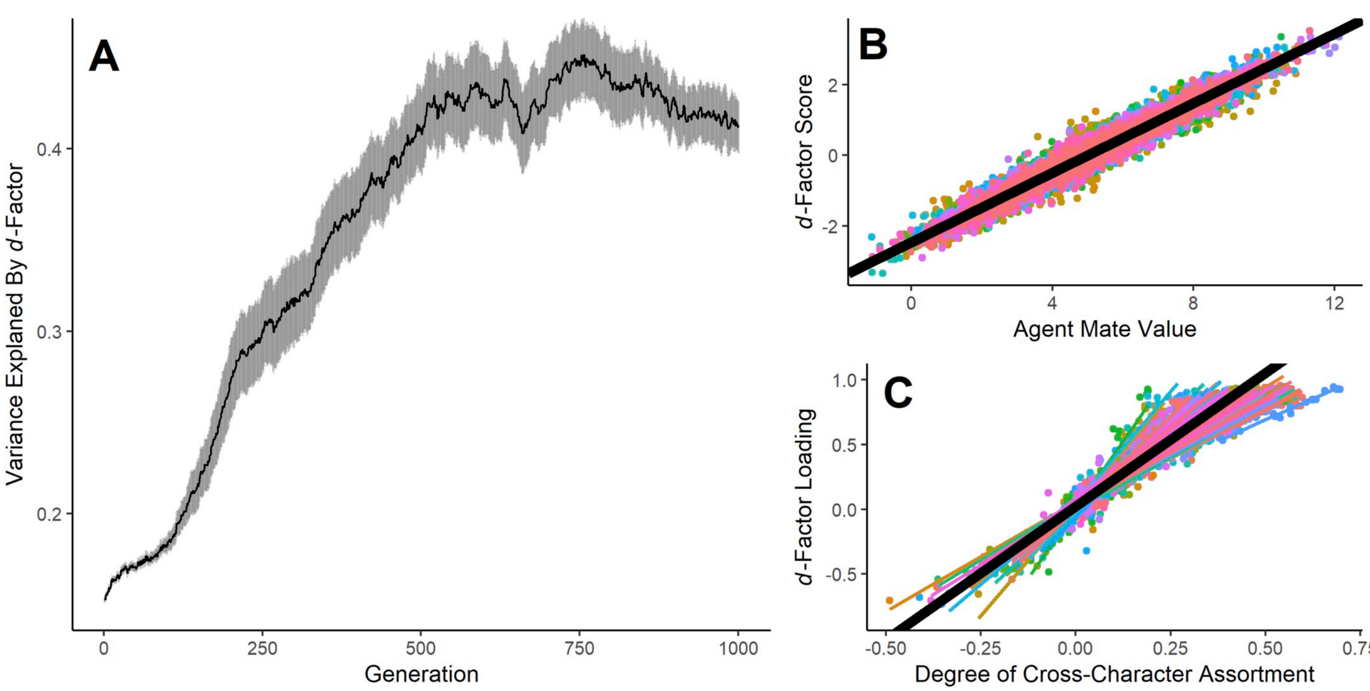

Fig. 1. Results from the primary agent-based model. Agents within this simulation evolve a *d*-factor that explains a moderate portion of trait variation (a). Scores on this *d*-factor strongly predict agent mate value (b). Traits that generate greater cross-character assortment load more strongly onto the *d*-factor (c). Dots represent individual observations; colored lines represent trend lines for individual model runs; black lines represent overall trends across model runs. Different colors correspond to observations from different model runs.

dimensions.

Evidence that assortative mating produced this *d*-factor comes from two additional effects (Fig. 1). First, if the *d*-factor represents a general dimension of desirability as a mate, agent *d*-factor scores should strongly correlate with their overall mate value. Indeed, a multilevel model with agents nested within model runs shows that, in the final generation, agent mate values strongly predict their factor scores on the *d*-factor across model runs, $\beta = 0.98$, $SE = 0.001$, $p < .001$.

Second, if the *d*-factor evolves because of assortative mating's tendency to create cross-character assortment, traits that generate stronger cross-character assortment should tend to load more strongly onto the *d*-factor. To test this prediction, we calculated the cross-character assortment generated by each trait dimension as the average correlation between desirability on that dimension and partner desirability across each of the other nine trait dimensions. We then used each trait's cross-character assortment estimate to predict its factor loading onto the *d*-factor. Indeed, in the final generation of the agent-based model, traits that generated stronger cross-character assortment tended to load more strongly onto the *d*-factor across model runs, $\beta = 1.10$, $SE = 0.03$, $p < .001$. That is, more than merely correlating with one another, trait-level desirabilities correlate in a systematic way: each trait dimension's loading onto the *d*-factor is proportional to its actual involvement in cross-character assortative mating.

Fig. 2 shows that the pattern of effects found in the primary agent-based model do not appear in a model in which mate choice is random with respect to mate preferences and agents therefore do not mate assortatively for overall mate value. In this model, rather than pairing based on mutual attraction, agents are placed into random couples in each generation. Here the *d*-factor explains only a small proportion of the variance in trait-level desirability in both the first generation, $M = 15.39\%$, 95% CI [15.27%, 15.51%] and the final generation, $M = 16.32$, 95% CI [16.16%, 16.48]. Agent mate values do predict their *d*-factor scores, but relatively weakly, $\beta = 0.26$, $SE = 0.02$, $p < .001$. Finally and critically, a trait's ability to generate cross-character assortment does not predict its loading on to the *d*-factor when mate choice is not assortative for mate value, $\beta = -0.03$, $SE = 0.03$, $p = .28$. These results indicate mate choice that is not assortative for mate value will not, on its own, cause the evolution of a *d*-factor as observed in the primary agent-based model.

3.1. Alternative selection assumptions

The results of these primary agent-based models suggest that assortative mating will cause the evolution of a *d*-factor. However, it is possible that these results are artifacts of the particular selection model we assumed. In particular, these models were parameterized such that agent trait and preference values began with distributions centered near $M = 4.0$. But the optimal values for each trait dimension were chosen randomly between values of 1 and 7. This means that some traits by default will tend to be subject to more stabilizing selection whereas others will be subject to directional selection. This is a simplification of selection and it is important to ensure that the results we observe are not artifacts of this simplification.

The results of two variations of the primary agent-based model suggest that these results are robust to assumptions about the nature of selection. In the first of these variations, we altered the start conditions of the model such that the optimal value for all traits was 4.0. This means that all traits in this model begin and remain under stabilizing selection throughout the duration of each model run. This model produces the same pattern of results as the primary agent-based model. A *d*-factor still evolves such that agents desirable as a mate on one dimension tend to be desirable across others as well, ultimately explaining $M = 32.83\%$ of the variance in trait-level desirability, 95% CI [31.08%, 34.58%]. Agent mate value still strongly predicted *d*-factor scores in this model, $\beta = 0.90$, $SE = 0.02$, $p < .001$. Finally, *d*-factor loading was still correlated with traits' involvement in cross-character assortment, $\beta = 1.17$, $SE = 0.04$, $p < .001$.

Furthermore, because the *d*-factor is a byproduct of assortative mating, this pattern of results remains even if selection is removed from the models entirely. In the second variation of the primary model, agents mated assortatively based on their preferences but reproduced randomly with respect to their traits, meaning there was no selection on

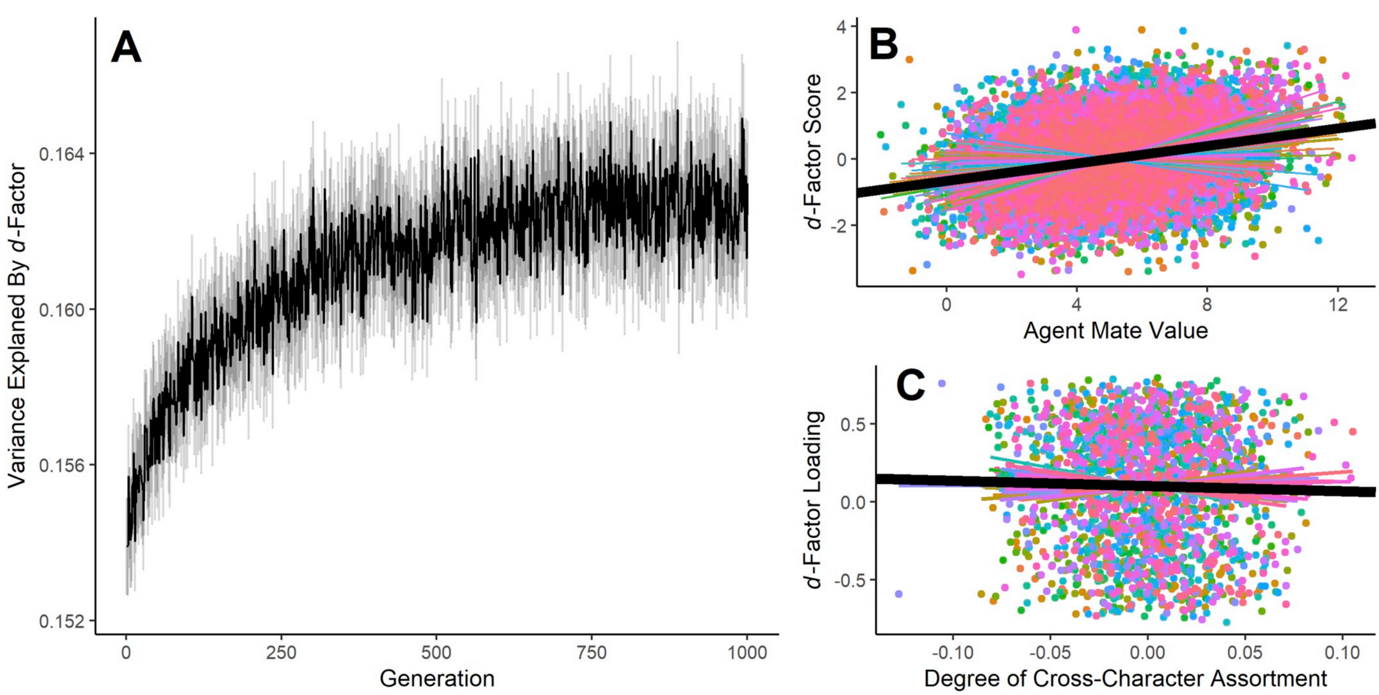

Fig. 2. Results from the agent-based model in which agents do not mate assortatively for mate value. The *d*-factor explains only a small proportion of the variance in trait-level desirability (a). Agent mate value only weakly predicts agent scores on the *d*-factor (b). Finally, traits that generated more cross-character assortment do not load more strongly onto the *d*-factor (c). Colored lines represent individual model runs; black lines represent average trends across model runs; dots represent individual observations.

either preferences or traits. Even in this model, a *d*-factor still evolves that explains a greater proportion of the variance in trait-level desirability by the final generation ($M = 45.67\%$, 95% CI [43.64%, 47.69%]) relative to the first generation ($M = 15.23\%$, 95% CI [15.10%, 15.37%]). Just as in the primary model, agent mate value still strongly predicted *d*-factor scores, $\beta = 0.97$, $SE = 0.004$, $p < .001$, and trait dimensions that generated stronger cross-character assortative mating still loaded more strongly onto the *d*-factor $\beta = 1.21$, $SE = 0.04$, $p < .001$. Overall, the *d*-factor observed in the primary, assortative agent-based model—but not in the random agent-based model—does not appear to be an artifact of the selection model assumed in the primary model.

3.2. The d-factor across cultures

We next compared the results of these agent-based models to the human cross-cultural sample to determine whether the assortative or random choice model best approximates real-world data. Consistent with prior research (e.g. Gignac et al., 2018), participants on average expressed high but not maximal preferences on each of the five dimensions; the average preference value across traits and across participants was $M = 5.85$ ($SD = 1.12$) out of a maximum of 7. Accordingly, trait-level desirabilities were strongly but imperfectly correlated with absolute trait values; Supplementary Table 3 presents the correlations between absolute trait values and desirabilities for both males and females across countries.

When these desirabilities are subjected to principal components analysis, precisely the same pattern observed in the assortative agent-based model emerges in all 45 countries of the human cross-cultural sample (Fig. 3). We estimated the *d*-factor separately for each country by extracting the first principal component from participant trait-level desirabilities in that country. Across all countries, this *d*-factor explained $r^2_{\text{mean}} = 42.33\%$, 95% CI [40.15%, 44.51%] of the variance in trait-level desirability. As in the primary agent-based model, participants who were more desirable as a mate along any one preference dimension were more likely to be desirable across all preference dimensions.

A multilevel model predicting participant factor score from overall mate value, with participants nested within country, showed that, as in the primary agent-based model, participant mate value strongly predicted *d*-factor scores, $\beta = 0.99$, $SE = 0.02$, $p < .001$. Finally, a multilevel model predicting *d*-factor loading from cross-character assortment found a significant relationship, $\beta = 0.35$, $SE = 0.05$, $p < .001$, such that, across countries, traits that generated more cross-character assortment also loaded more strongly onto *d*. This means that desirability dimensions are not only correlated, but that they show a systematic pattern of covariance: in human data, just as in agent-based models of evolution under assortative mating, preferred trait dimensions load onto the *d*-factor to the degree that they are actually involved in cross-character assortative mating.

3.3. The d-factor, rater biases, and halo effects

The results of the primary agent-based model as well as the primary analysis of the cross-cultural sample document a *d*-factor that appears patterned as though it evolved through a history of assortative mating. However, participant rating biases could provide an alternative explanation for this *d*-factor. Participant trait ratings are not pure measures of the underlying trait values and almost certainly reflect participant perceptual and rating biases to some degree. These biases, rather than assortative mating, could in principle explain the emergence of the *d*-factor in human data and likely do contribute to the rating covariation we observe. Nonetheless, several alternative agent-based models and analyses suggest that it is unlikely that rating and perceptual biases exclusively explain the existence of the *d*-factor observed in the cross-cultural sample.

3.3.1. Rater bias

For instance, one possible alternative explanation for the *d*-factor is that participants simply differ in rating style such that participants who rate themselves more positively on any one dimension are biased to rate themselves and their partner desirably across all other dimensions. This

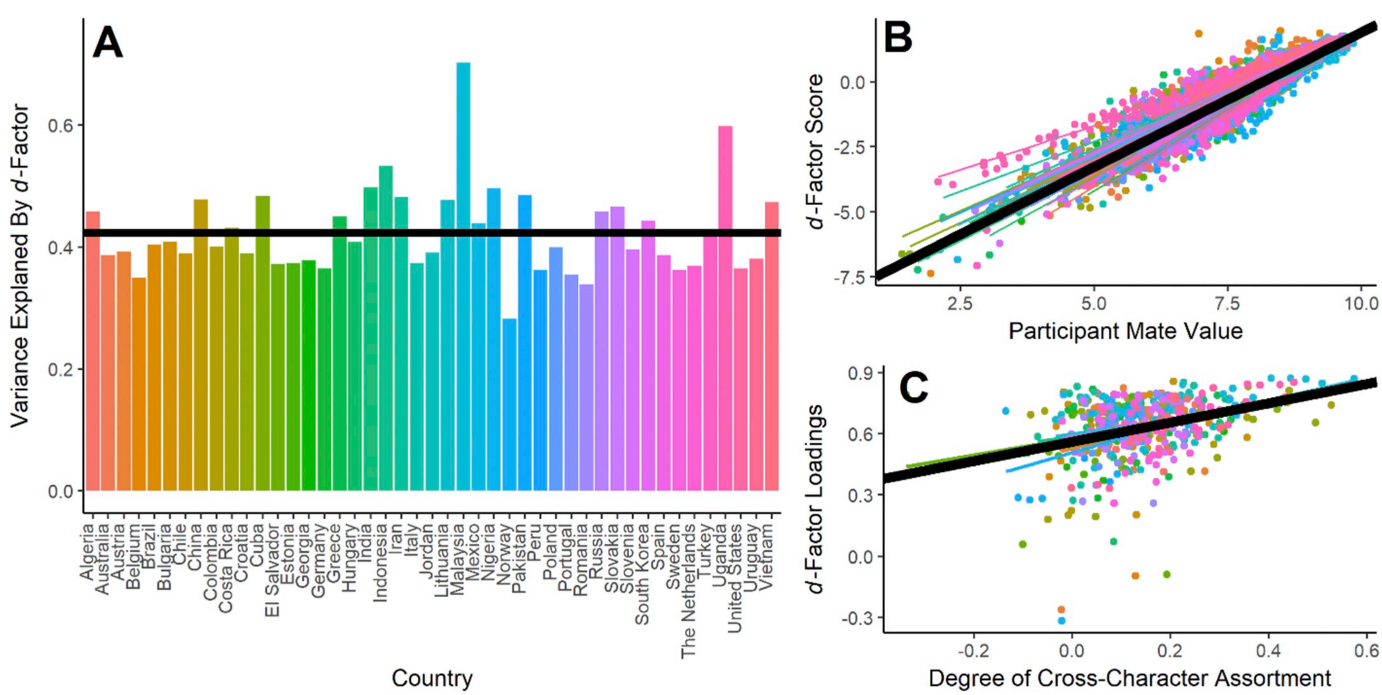

Fig. 3. Results from the human cross-cultural sample. Across countries, the *d*-factor explains a moderate amount of variance in trait-level desirability (a). Scores on the *d*-factor are strongly correlated with participant mate value across countries (b). Desirability dimensions that are more involved in cross-character assortment load more strongly onto the *d*-factor across countries (c). Dots represent individual observations; colored lines represent trends from individual countries; black lines represent average trends across countries. Different colors correspond to observations from different countries.

participant rating bias, rather than assortative mating, could potentially explain the cross-cultural pattern of covariation in desirability across trait dimensions.

Consistent with this possibility, an agent-based model of rater bias can produce a similar pattern of results as the primary, assortative agent-based model. Unlike the primary model, agents in the rater bias model did not evolve a set of true trait values based on their mating behavior. Instead, each agent was assigned a "bias" score drawn randomly from a normal distribution centered on $M = 4$ with $SD = 2$. Agents then "reported" perceptions of their traits and their partner's traits using their bias scores. The model generated each agent's biased self-reports by adding random normal noise to the agents' bias scores; the amount of noise added was set such that bias would explain approximately as much variance in trait ratings as the *d*-factor does in the cross-cultural sample. Agent preferences were furthermore preset to a value of 7 for all dimensions; this simplification ensured that bias directly manipulated desirability across all trait dimensions. This model therefore represents the consequences of trait ratings emerging exclusively from biased perceptions, and not from assortative mating for mate value, which allows us to identify and test the predictions made by a rater bias hypothesis for the emergence of the *d*-factor.

This rater bias model is capable of producing a similar pattern of results as the primary agent-based model and cross-cultural sample. The *d*-factor in this data does in fact explain a substantial proportion of variance, $M = 43.67\%$, 95% CI [43.19%, 44.16%]; *d*-factor scores strongly predict agent mate value, $\beta = 0.99$, $SE = 0.001$, $p < .001$; and trait dimensions load onto the *d*-factor more strongly when they are more involved in cross-character assortment, $\beta = 0.74$, $SE = 0.02$, $p < .001$. From these results, it would appear rater bias on its own could account for the pattern of trait covariation observed across cultures.

However, the similarity between the rater bias model and human data disappears when agent trait ratings are supplied by multiple, distinct raters—as in the newlywed and romantic dyad samples. Because agent trait ratings are based on bias and not on reality, agents are not guaranteed to agree with their partners on how desirable they are on any given trait dimension. To illustrate this, we re-analyzed the rater bias model using exclusively "other-reports" for all agents; that is, each agent's trait ratings came from their mate's rating rather than their own. The key difference emerges in the relationship of *d*-factor loadings to cross-character assortment. Because each agent in a couple is rated by a different rater (in this case, the agent's mate), and because raters do not necessarily share the same rating biases, the degree of cross-character assortment implied by agent trait ratings no longer tracks trait loading onto the *d*-factor in this re-analysis, $\beta = 0.01$, $SE = 0.02$, $p = .68$.

Does the same occur in human data when participant trait ratings are supplied by different raters? To determine this, we conducted the same analyses on the newlywed and romantic dyad samples. We first analyzed the newlywed sample using composite trait ratings based only on the third-party interviewer ratings. This removes participant rating biases from the data entirely. These analyses produced the same results as in the cross-cultural sample and the primary agent-based model. The *d*-factor explained $r^2 = 25.52\%$ of the variance in trait-level desirability when trait ratings are based only on interviewer reports. Scores on this *d*-factor were still strongly related to participant mate value, $\beta = 0.95$, $SE = 0.02$, $p < .001$. Finally, traits loaded on to the *d*-factor in this sample to the extent that they generated cross-character assortment, $\beta = 0.62$, $SE = 0.09$, $p < .001$.

Furthermore, we conducted all analyses again using different trait rating sources for each participant and their partner, analogous to the final set of analyses for the rating bias model. Here we used Interviewer 1's ratings for all female participants and Interviewer 2's ratings for all male participants (results do not change if this choice is reversed). If the *d*-factor emerges in the newlywed sample exclusively because of rater biases, we should see the correlation between trait *d*-factor loading and cross-character assortment disappear in this sample as it did in the rating bias model because interviewers do not necessarily share rating biases. However, it does not. Even when participants and their partners are rated by different raters, traits load onto the *d*-factor more strongly when they generate stronger cross-character assortment, $\beta = 0.35$, $SE = 0.10$, $p = .002$.

We conducted the same analyses on the romantic dyad sample. For the first analyses, we used self- and partner-report composites for trait measures. Again, the same pattern of effects observed in the primary

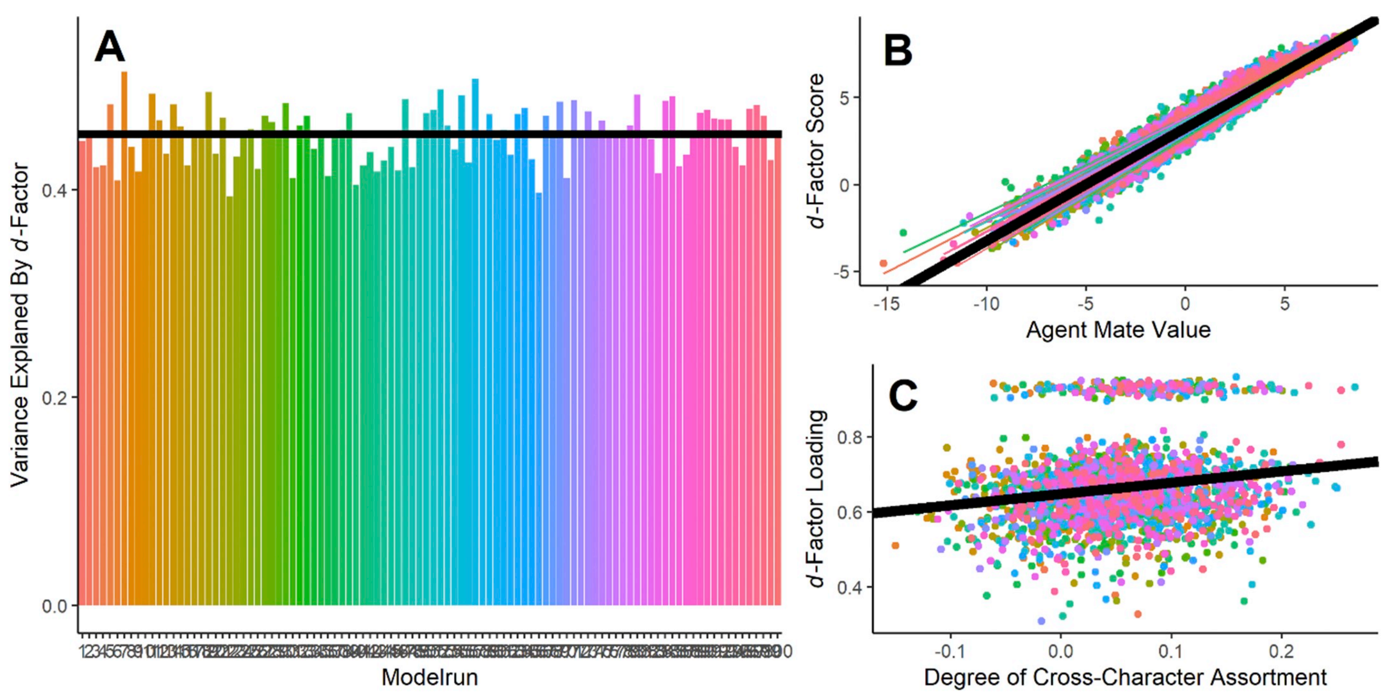

Fig. 4. Results from an agent-based model of the halo effect in which trait ratings are biased on the basis of one trait for which agents do mate assortatively. This does produce a *d*-factor that explains a large proportion of variance in trait-level desirability (a); scores on this *d*-factor are correlated with agent mate value (b); and traits load onto the *d*-factor more strongly when they more strongly generate cross-character assortment (c). However, *d*-factor loadings are strongly bimodal (c).

agent-based models and the cross-cultural sample emerged in this sample even when trait ratings were not based exclusively on self-report. The d-factor explained $r^2 = 25.52\%$ of the variance in trait-level desirability. Scores on the d-factor strongly predicted participant mate value, $\beta = 0.95$, $SE = 0.02$, $p < .001$. Finally, traits loaded on to the d-factor in this sample to the extent that they generated cross-character assortment, $\beta = 0.62$, $SE = 0.09$, $p < .001$. Finally, and inconsistent with the rater bias agent-based model, the same pattern of results remains even when analyses are based exclusively on partner-reports, meaning female partners were rated by a different rater (their mate) than male partners. The d-factor still explains $r^2 = 25.52\%$ of the variance in trait-level desirability; d-factor scores strongly predict participant mate value ($\beta = 0.95$, $SE = 0.02$, $p < .001$); and, crucially, traits that generate more cross-character assortment loaded more strongly onto the d-factor ($\beta = 0.55$, $SE = 0.14$, $p < .001$).

3.3.2. The halo effect

A second alternative hypothesis for the d-factor is the halo effect. Rather than the d-factor emerging due to assortative mating or rating style, it is possible that traits appear to covary simply because people falsely generalize desirability on one trait dimension to other trait dimensions. Such a halo effect could potentially account for the d-factor as well as produce a d-factor that persists across different raters' perspectives as long as (1) people mate assortatively for some trait (e.g. physical attractiveness) (2) this trait can be accurately perceived, but (3) perceptions of this trait inspire biased ratings for *other* traits such that, for instance, physically attractive people are spuriously rated as possessing other desirable characteristics.

We created an agent-based model of this process to assess the possibility that such a halo effect could by itself account for the d-factor. In each run of this model, we generated 100 agent couples. Mated agents were assigned random but correlated physical attractiveness values, generated such that the correlation between partner physical attractiveness was approximately $r = 0.30$. These agents then "rated" themselves and their partners. Agents were able to perceive and report their and their partners' physical attractiveness with reasonable accuracy, such that true attractiveness predicted approximately $r^2 = 60\%$ of the variance in attractiveness perceptions. These physical attractiveness perceptions were then used to produce the "biased" perceptions of the agents' other 9 traits by adding random normal noise to the physical attractiveness perceptions, again scaled such that bias would explain approximately 45% of the variance in trait ratings.

Such a model of rating bias with partial assortative mating can indeed produce a d-factor similar to that observed in the primary agent-based model and cross-cultural sample even when trait ratings come from different raters (Fig. 4). However, this model makes a separate prediction which is not supported by any of the human samples. Specifically, as can be seen in Panel C of Fig. 4, this rating bias model predicts that desirability factor loading onto the d-factor will be sharply bimodal. Across model runs, the trait upon which rating biases are based loads heavily onto the d-factor whereas the biased ratings all load relatively weakly. This bimodality can be seen clearly in a histogram of factor loadings across model runs in this rating bias model (Fig. 5A). This bimodality of factor loadings is not found across countries in the cross-cultural sample (Fig. 5B); here, loadings are unimodal and, if anything, distributed oppositely with a left skew rather than right skew. In fact, the distribution of factor loadings in the cross-cultural sample is far more consistent with that observed across models in the primary, assortative agent-based model (Fig. 5C).

Finally, a second model of the halo effect could account for coordination of bias among raters and produce a more realistic distribution of d-factor loadings. The bimodal distribution of factor loadings produced in the halo effect model could emerge because we assumed that all traits are equally subject to the halo effect. However, if the halo effect more strongly influences some trait ratings, then trait d-factor loadings might distribute more continuously, as in the human data and primary agent-based model. We constructed a second model of the halo effect that assumes this variable degree of bias. Here, agents mate assortatively for physical attractiveness just as in the first halo effect model and other trait ratings are generated by adding random normal noise to agents' accurately perceived physical attractiveness values. However, the standard deviation of this noise varies such that the noise added to some traits has a low deviation (and these traits are therefore strongly affected by the halo effect) whereas the noise added to others has a relatively large standard deviation (and these traits are therefore weakly affected by the halo effect).

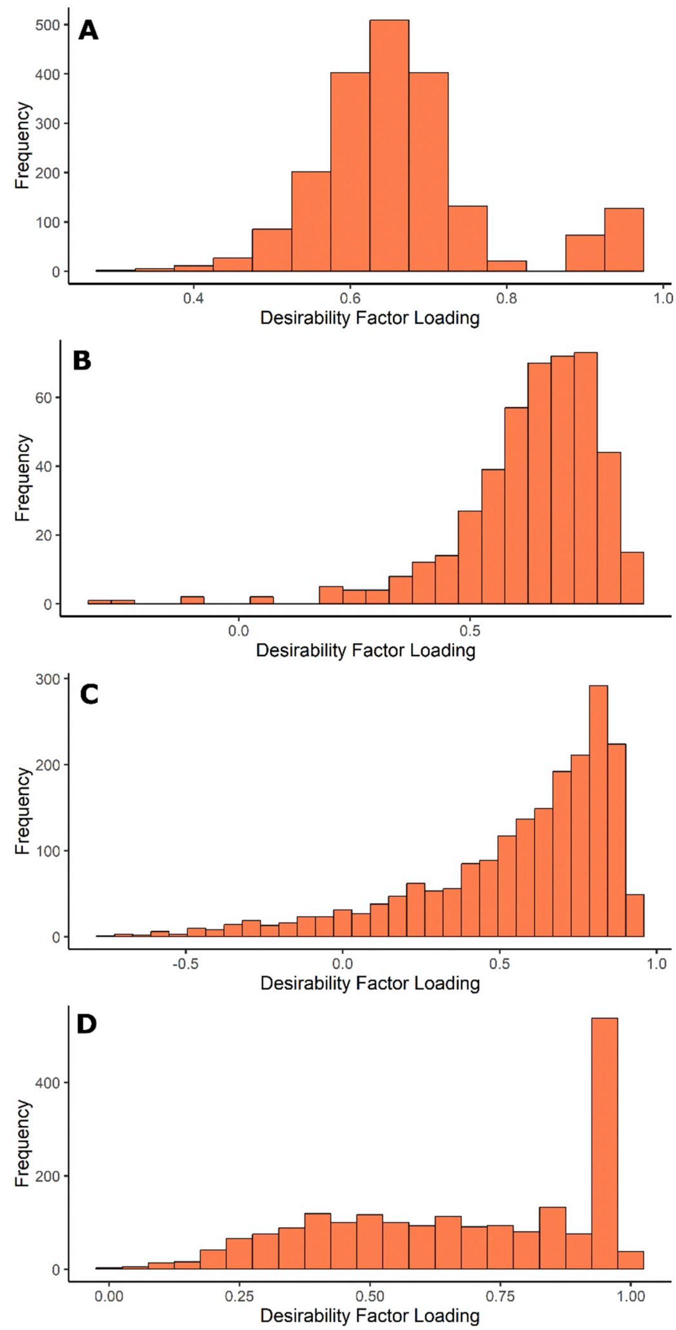

Fig. 5. Histograms of trait d-factor loadings across model runs and across countries from (a) an initial agent-based model of the halo effect, (b) the human cross-cultural sample, (c) the primary, assortative agent-based model, and (d) the revised halo effect model. The assortative agent-based model best reproduces the left-skewed distribution of factor loadings observed in the cross-cultural sample, however the revised halo effect model produces a more realistic distribution than the initial halo effect model.

Fig. 6 shows that this model of the halo effect can reproduce the pattern of effects from the cross-cultural sample even when different raters provide trait ratings of each agent and their partner. Furthermore, as can be seen in Panel D of Fig. 5, the distribution of factor loadings is considerably less bimodal than in the initial halo effect model and therefore is more realistic—although, still with an overabundance of high factor loadings. However, this revised halo effect model makes a new prediction that is not strongly supported by our human samples. In this model, the degree of halo effect a trait is subject to affects both its loading onto the *d*-factor (stronger halo effect yields larger correlation with other biased ratings) and the degree of coordination between raters (weaker halo effect yields weaker coordination between raters). For this reason, loading on the *d*-factor has a strong, linear relationship with inter-rater agreement. That is, there is a stronger correlation between different raters' perceptions of the same trait value for traits that load more strongly onto the *d*-factor, $\beta = 0.89$, $SE = 0.01$, $p < .001$ (Fig. 7A).

This novel prediction is not strongly supported in either of the human samples for which we can calculate inter-rater agreement. In the newlywed sample, we calculated the inter-rater agreement for each trait by calculating the correlation between the two interviewers' trait ratings for each participant. Among the two dyadic samples, this newlywed sample is more consistent with the revised halo effect model: there is a significant positive relationship between inter-rater agreement and *d*-factor loading, $b = 0.17$, $SE = 0.07$, $p = .02$. However, inspection of the plot (Fig. 7B) suggests that the relationship in this sample is more likely non-linear, where inter-rater agreement is highest for traits that load either strongly or weakly onto the *d*-factor, but not for intermediate loadings; indeed, a quadratic model (AIC $= -108.39$) fits this data better than a linear model (AIC $= -99.00$). This does not resemble the corresponding relationship within the halo effect model. The romantic dyad sample provides even less evidence for this prediction: in this sample, there is no correlation between *d*-factor loading and inter-rater agreement, $b = -0.11$, $SE = 0.19$, $p = .58$, and the relationship is, if anything, going in the opposite direction as the halo effect model predicts (Fig. 7C). Overall, while it is likely that rater biases and halo effects contribute to the *d*-factors observed in human samples to some degree, these analyses indicate it is unlikely that these biases exclusively explain the observation of the *d*-factor.

3.4. Additional alternative explanations for the d-factor

Several further analyses establish that the *d*-factor observed in the primary agent-based models and the cross-cultural human sample is robust and diagnostic of an evolutionary history of assortative mating (see supplementary material). First, the pattern of results observed in the primary agent-based model is robust to higher mutation rates and to lower levels of assumed trait heritability. Second, trait covariation could alternatively emerge because different traits are manifestations of a common underlying condition variable (Tomkins, Radwan, Kotiaho, & Tregenza, 2004; Wolf & Weissing, 2010). However, the pattern of results observed in the primary agent-based model and across countries does not emerge in a simulation in which agent traits are manifestations of an underlying condition factor and mate choice is not assortative for mate value.

Two further results suggest this pattern of effects is specifically explained by assortative mating and is not a mathematical inevitability or a byproduct of background trait covariation. First, it is possible that the *d*-factor and mate value relate simply because they are both calculated based on deviations between an individual's traits and the opposite sex's preferences. However, whereas mate value is directly the deviation between a person's traits and the opposite sex's preferences, the *d*-factor is a structure of covariances between deviations across dimensions. Any relationship between mate value and the *d*-factor thus depends on the existence of such a pattern of covariances. Indeed, the pattern of effects observed across countries does not emerge when mate value and the *d*-factor are calculated based on scrambled participant traits that do not share the raw data's correlational structure. This shows that a *d*-factor is not inevitable, but rather depends on the particular covariance structure produced by assortative mating. Second, the *d*-factor could be a byproduct of some other source of covariation with no intrinsic connection to mate value. However, the pattern of results observed in the cross-cultural sample and primary agent based model do not emerge when mate value and *d* are computed based on

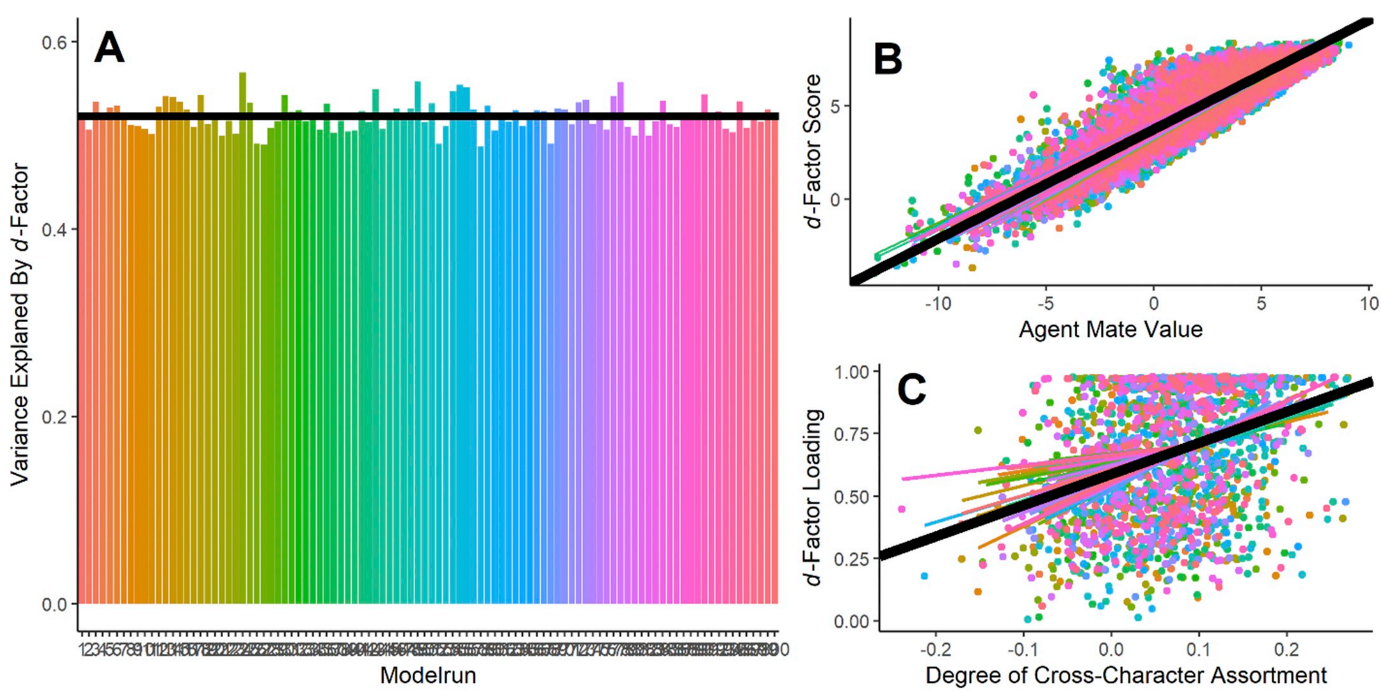

Fig. 6. Results from an agent-based model of the halo effect in which trait ratings are biased on the basis of one trait for which agents do mate assortatively and in which degree of bias varies across traits. This does produce a *d*-factor that explains a large proportion of variance in trait-level desirability (a); scores on this *d*-factor are correlated with agent mate value (b); and traits load onto the *d*-factor more strongly when they more strongly generate cross-character assortment (c).

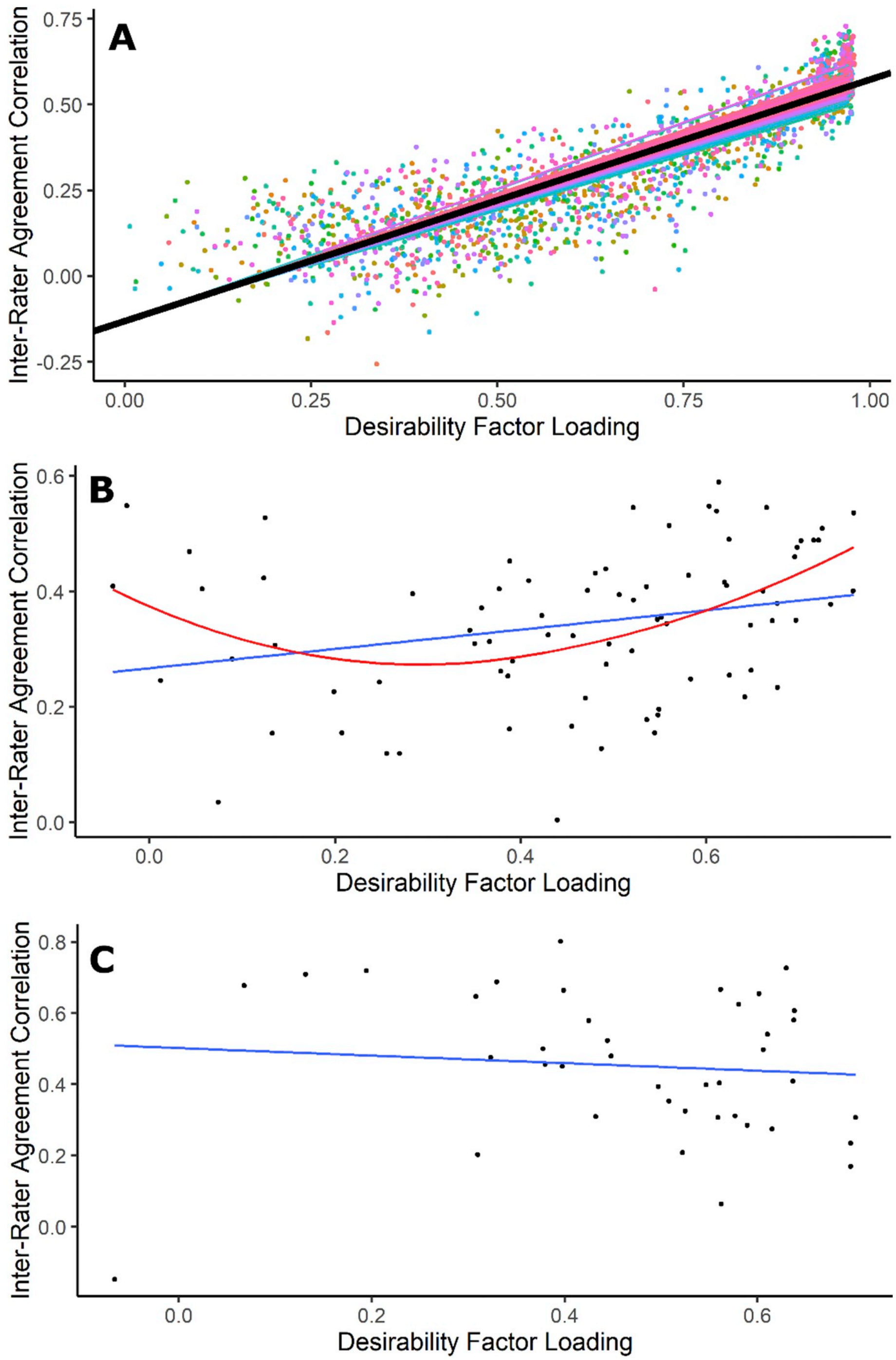

Fig. 7. Relationship between inter-rater agreement and *d*-factor loading for (a) the revised halo effect model, (b) the newlywed sample, and (c) the romantic dyad sample. Colored lines in panel (a) represent the relationship in individual model runs whereas the black line indicates the overall trend line. The blue line in panel (b) represents the linear fit of this relationship whereas the red line represents the output of a LOESS smoother. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

deviations from random values rather than from the opposite sex's mate preferences. This demonstrates that the *d*-factor is specifically organized around the opposite sex's mate preferences and is not simply a byproduct of independent trait covariation.

4. Discussion

These results document a pattern of desirability covariation, *d*, that emerges across 45 countries such that a person who is desirable as a mate on any one trait dimension is more likely to be desirable as a mate across all other trait dimensions. Importantly, scores on the *d*-factor are strongly correlated with individual mate value. Finally, more than merely correlating with one another, desirability dimensions load onto this *d*-factor to the degree that they actually generate cross-character assortment. This pattern of results is precisely the same pattern that emerges in agent-based models of evolution under assortative mating but that does not emerge in models without assortative mating. Overall, this suggests that an evolutionary history of assortative mating has produced a specific pattern of desirability covariation in humans.

The potential for mate choice to shape evolutionary processes has long motivated research on human mating. However, empirical demonstrations of this power are difficult to provide and are consequently relatively rare within the literature. This research provides one such demonstration. Starting with the well-documented assumptions of assortative mating for mate value and heritable individual differences, we used evolutionary simulations to predict and provide the first evidence for a cross-culturally universal *d*-factor. This lends critical support to the widely held assumption that human mating provides a window into human evolution. Further, it highlights the value of agent-based modeling for studies of human mating. We cannot turn back the clock on evolutionary time and directly observe the effects of human mating on human evolution as they occurred generation after generation. But with agent-based models, we can create simulated populations and observe the consequences of evolution under different, experimentally manipulated mating systems. These consequences provide predictions to test against human data, as we did here, allowing inferences about the evolutionary effects of mate choice.

While promising, this research does have limitations and leaves open some important future directions. First, although we do find evidence of a *d*-factor consistent with an evolutionary history of cross-character assortative mating, assortative mating is also clearly not explaining all of the trait covariation in our data. This can be seen, for instance, in the fact that the correlation between *d*-factor loading and cross-character assortment is weaker in the cross-cultural sample than it is in the agent-based models, indicating other factors are influencing the degree of trait covariation in our data. These other factors likely include measurement variance, rater biases, condition-dependence processes, facultative calibration, and even direct effects between traits—for instance, intelligence may directly affect financial prospects by influencing occupational success. Teasing apart the relative contributions of assortative mating and these other sources of observed covariation is a clear next step for future research.

The issue of rater bias and halo effects is particularly important. Although our analyses suggest these biases cannot exclusively explain the *d*-factor, they likely do contribute to a substantial degree. Parsing out the proportion of desirability covariation that comes from true variance rather than rater bias will be a critical but vital challenge for future research. Furthermore, the *d*-factor and bias can provide mutually compatible explanations for observed trait covariation because the existence of the *d*-factor provides a coherent evolutionary functional explanation for the existence of halo effects to begin with. Well-designed person perception adaptations should take advantage of evolutionarily recurrent statistical regularities that aid in making useful inferences about others. As the primary agent-based model and cross-cultural sample suggest, if assortative mating does actually construct desirability covariation, then any halo effects in trait ratings do not necessarily represent unrealistic bias; rather, they could represent rational inference in the face of incomplete information. In a world in which desirability does covary due to assortative mating, person perception adaptations should generate inferences about the desirability of unknown characteristics on the basis of the desirability of known characteristics and the structure of real-world desirability covariation. If this were the case, one might expect that halo effect "biases" track the structure of assortative mating, such that people are more likely to generalize desirability among traits that more strongly generate cross-character assortment than among traits less involved in assortative mating. Our data do not allow tests of this prediction, but future research could explore this possibility.

A second important future direction is resolving the mixed findings in this broader research area. For instance, although in our samples physical attractiveness, intelligence, and health load onto the *d*-factor in theoretically consistent ways, some studies have failed to find correlations between these traits (e.g. Feingold, 1992; Mitchem et al., 2015). These inconsistencies must be explained. One obvious candidate explanation is difference in measurement. For example, prior studies finding null correlations between physical attractiveness and intelligence have often used standardized intelligence tests whereas our samples exclusively used rated intelligence. It is possible that these measures produce different results because they tap different constructs. For instance, rated intelligence measures might be more likely to show covariance patterns consistent with assortative mating because they more closely tap the folk concept of intelligence that actually drives mate choice. After all, people select their mates on the basis of their lay perceptions, and not on the basis of standardized intelligence examinations. However, this does open a clear question for future research: if the folk concept of intelligence does not tightly map onto *g*, what precisely does it track?

We should also stress that the *d*-factor hypothesis does not make strong predictions about the nature of bivariate relationships between traits. The *d*-factor represents covariation in desirability across dimensions, where desirability is absolute deviation from the opposite sex's preferences. This covariation is agnostic with respect to the direction of these deviations. The existence of a *d*-factor is equally consistent with positive trait correlations (e.g. physically attractive people being more intelligent) as it is with negative trait correlations (e.g. physically attractive people being less intelligent) or non-linear relationships. It is even possible—albeit unlikely—for there to be no correlation in trait values but still correlation in desirability if, for instance, trait variability increases with deviation from ideals. Moreover, the *d*-factor concerns covariation in desirability across all dimensions that contribute to mate value—not bivariate relationships between specific traits. For these reasons, the clearest tests of the existence and nature of the *d*-factor will come from looking at desirability covariation across multiple dimensions and not at bivariate relationships among traits.

Overall, the universality and patterning of the *d*-factor in our cross-cultural samples resemble a fingerprint of assortative mating on the evolution of human trait distributions. Previous work has provided evidence for the organizing effects of mate choice between specific preferred trait dimensions (Keller et al., 2013). Our results show that these patterns of desirability covariation emerge not merely between specific traits but rather across all preferred trait dimensions and that these patterns of trait covariation emerge across cultures from around the world. Assortative mating appears to have shaped patterns of inheritance throughout human evolution such that mate value is not distributed randomly across individuals; rather, desired traits covary around an underlying dimension of mate value. This conclusion, if valid, contributes to explaining the existence of human trait covariation across domains and highlights the importance of mate choice in broadly understanding human evolution.

Acknowledgments

We thank everyone who participated in this study as well as the research assistants who assisted in translating forms, recruiting participants, and inputting data. The work of Truong Thi Khanh Ha was supported by grants 501.01-2016.02 from the Vietnam National Foundation for Science and Technology Development (NAFOSTED). Anna Oleszkiewicz was supported by the Foundation for Polish Science (START scholarship). This study was conducted in line with project NIR № 01201370995 "Cross-cultural and interdisciplinary researches. Biosocial and cross-cultural analysis of models of tolerance and basic values of culture in modern society" (Marina Butovskaya and Daria Dronova). PS and AS were supported by National Science Center—Poland (2014/13/B/HS6/02644).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2019.06.003.

References

Batres, C., & Perrett, D. I. (2014). The influence of the digital divide on face preferences in el salvador: People without internet access prefer more feminine men, more masculine women, and women with higher adiposity. *PLoS One, 9*(7), e100966. https://doi.org/10.1371/journal.pone.0100966.

Bouchard, T. J., & McGue, M. (1981). Familial studies of intelligence: A review. *Science, 212*(4498), 1055–1059. https://doi.org/10.1126/science.7195071.

Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences, 12*(01), 1–14. https://doi.org/10.1017/S0140525X00023992.

Buss, D. M. (1991). Conflict in married couples: Personality predictors of anger and upset. *Journal of Personality, 59*(4), 663–703.

Buss, D. M., & Barnes, M. (1986). Preferences in human mate selection. *Journal of Personality and Social Psychology: Personality Processes and Individual Differences, 50*(3), 559–570. https://doi.org/10.1037/0022-3514.50.3.559.

Buss, D. M., & Schmitt, D. P. (2019). Mate preferences and their behavioral manifestations. *Annual Review of Psychology, 70*, 77–110.

Conroy-Beam, D. (2017). Euclidean mate value and power of choice on the mating market. *Personality and Social Psychology Bulletin*0146167217739262. https://doi.org/10.1177/0146167217739262.

Conroy-Beam, D., & Buss, D. M. (2017). Euclidean distances discriminatively predict short-term and long-term attraction to potential mates. *Evolution and Human Behavior, 0*(0), https://doi.org/10.1016/j.evolhumbehav.2017.04.004.

Elder, G. H. (1969). Appearance and education in marriage mobility. *American Sociological Review, 34*(4), 519–533. https://doi.org/10.2307/2091961.

Feingold, A. (1988). Matching for attractiveness in romantic partners and same-sex friends: A meta-analysis and theoretical critique. *Psychological Bulletin, 104*(2), 226–235. https://doi.org/10.1037/0033-2909.104.2.226.

Feingold, A. (1992). Good-looking people are not what we think. *Psychological Bulletin, 111*(2), 304.

Gignac, G. E., Darbyshire, J., & Ooi, M. (2018). Some people are attracted sexually to intelligence: A psychometric evaluation of sapiosexuality. *Intelligence, 66*, 98–111. https://doi.org/10.1016/j.intell.2017.11.009.

Hugh-Jones, D., Verweij, K. J. H., St. Pourcain, B., & Abdellaoui, A. (2016). Assortative mating on educational attainment leads to genetic spousal resemblance for polygenic scores. *Intelligence, 59*, 103–108. https://doi.org/10.1016/j.intell.2016.08.005.

Kalick, S. M., & Hamilton, T. E. (1986). The matching hypothesis reexamined. *Journal of Personality and Social Psychology, 51*(4), 673–682. https://doi.org/10.1037/0022-3514.51.4.673.

Keller, M. C., Garver-Apgar, C. E., Wright, M. J., Martin, N. G., Corley, R. P., Stallings, M. C., ... Zietsch, B. P. (2013). The genetic correlation between height and iq: Shared genes or assortative mating? *PLoS Genetics, 9*(4), e1003451. https://doi.org/10.1371/journal.pgen.1003451.

Li, N. P., Yong, J. C., Tov, W., Sng, O., Fletcher, G. J., Valentine, K. A., ... Balliet, D. (2013). Mate preferences do predict attraction and choices in the early stages of mate selection. *Journal of Personality and Social Psychology, 105*(5), 757.

Mare, R. D. (1991). Five decades of educational assortative mating. *American Sociological Review, 56*(1), 15–32. https://doi.org/10.2307/2095670.

Mitchem, D. G., Zietsch, B. P., Wright, M. J., Martin, N. G., Hewitt, J. K., & Keller, M. C. (2015). No relationship between intelligence and facial attractiveness in a large, genetically informative sample. *Evolution and Human Behavior, 36*(3), 240–247. https://doi.org/10.1016/j.evolhumbehav.2014.11.009.

Plomin, R., DeFries, J. C., Knopik, V. S., & Neiderhiser, J. M. (2016). Top 10 replicated findings from behavioral genetics. *Perspectives on Psychological Science, 11*(1), 3–23. https://doi.org/10.1177/1745691615617439.

Polderman, T. J. C., Benyamin, B., de Leeuw, C. A., Sullivan, P. F., van Bochoven, A., Visscher, P. M., & Posthuma, D. (2015). Meta-analysis of the heritability of human traits based on fifty years of twin studies. *Nature Genetics, 47*(7), 702–709. https://doi.org/10.1038/ng.3285.

Robinson, M. R., Kleinman, A., Graff, M., Vinkhuyzen, A. A. E., Couper, D., Miller, M. B., ... Visscher, P. M. (2017). Genetic evidence of assortative mating in humans. *Nature Human Behaviour, 1*, 0016. https://doi.org/10.1038/s41562-016-0016.

Shackelford, T. K., & Buss, D. M. (1997). Marital satisfaction in evolutionary psychological perspective. *Satisfaction in Close Relationships*, 7–25.

Sugiyama, L. S. (2015). Physical attractiveness: An adaptationist perspective. *The handbook of evolutionary psychology*John Wiley & Sons, Inc.https://doi.org/10.1002/9781119125563.evpsych112.

Tomkins, J. L., Radwan, J., Kotiaho, J. S., & Tregenza, T. (2004). Genic capture and resolving the lek paradox. *Trends in Ecology & Evolution, 19*(6), 323–328. https://doi.org/10.1016/j.tree.2004.03.029.

Wolf, M., & Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1560), 3959–3968. https://doi.org/10.1098/rstb.2010.0215.