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Quality of Life from an Evolutionary Perspective

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Abstract Quality of Life (QoL) is a multi-dimensional concept that includes: a) the long-term sustainability of the earth; b) good health, education, welfare; and c) the psychological state of wellbeing. This article, which introduces a special issue on QoL from an evolutionary perspective, shows how modern evolutionary science provides a "toolkit" for studying all aspects of QoL.

Keywords Quality of life · Ultimate and proximate causation · Evolutionary mismatch · Multilevel selection

Introduction

The concept of Quality of Life (QoL) became prominent in the 1970s in reaction to economic indicators, such as Gross National Product, that were being used to inform public policy. The argument was that driving up the economic numbers was not increasing the quality of life for the average citizen, calling for a new set of numbers. The concept had great resonance, resulting in the burgeoning use of QoL indicators and research on QoL, as the International Society for Quality of Life Studies and its journal, Applied Research in Quality of Life, attests (Sirgy et al. 2006).

What is QoL? The answer to this question is multidimensional. Over the long term, it is the sustainability of the planet, upon which all life depends. Over the span of a human lifetime, it is health and longevity, access to a good education, and freedom from harm. Then there is a psychological dimension: how well one actually feels on a moment-by-moment basis.

This special issue of Applied Research in Quality of Life examines QoL from an evolutionary perspective. The use of evolutionary theory to inform public policy is both old and new. In its old form, evolution was used to justify social inequality and ruthless competition, which colors the term "Social Darwinism" to this day. In reaction, studying evolution in relation to human affairs became stigmatized for a period of

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decades (Leonard 2009). During this period, evolutionary theory made enormous strides in the life sciences, and the various human-related disciplines made enormous strides of their own, but without explicit reference to evolutionary theory.

The new use of evolutionary theory to inform public policy is based on modern evolutionary science and bears no resemblance to the Social Darwinism of the past. Far from justifying social inequality and ruthless competition, it highlights the importance of prosociality at all scales, from urban neighborhoods to the wealth of nations (Wilson 2011). Prosociality is defined as any attitude, behavior, or institution oriented toward the welfare of others or society as a whole. It is a broader term than altruism and cooperation; for example by including competitive processes that are structured to result in societal benefits.

The premise of the new Social Darwinism is that evolution can serve as a general theoretical framework for understanding and improving the human condition in the same way that it is used to study all aspects of the rest of life. It is important to stress that there is more to evolution than genetic evolution. Humans are undeniably capable of rapid cultural change, but this capacity is both a product of genetic evolution and an evolutionary process in its own right (Jablonka and Lamb 2006). Once evolution is understood as a process requiring variation, selection, and heredity, with genes comprising only one mechanism of heredity, then the fast-paced changes taking place all around us can be understood as evolution operating in warp drive, rather than a mysterious suspension of evolutionary processes.

Another point to stress is that most experts on human-related topics, including academic experts and policy experts, are open-minded about evolution. They acknowledge its explanatory scope for the rest of life and assume that their own ideas are consistent with it. What they frequently don't realize is how a modern evolutionary perspective can add value to the perspectives that they and their colleagues have been taking without explicit reference to evolution (Wilson and Gowdy 2013). This is understandable because in the majority of cases, evolution was not part of their disciplinary training. An enormous task of integration is therefore required to unite the many branches of human-related knowledge with modern evolutionary theory. This integration is a two-way street, with every human-related discipline having much to contribute in addition to much to learn, resulting in a stimulating and mutually respectful dialogue (Wilson and Gowdy 2013; Wilson et al. 2014).

The Evolution Institute (EI; evolution-institute.org) is at the forefront of this movement. Founded in 2007, it has been systematically approaching major policy areas such as child development, education, and economics from a modern evolutionary perspective. QoL became an explicit focus of the EI in a 2011 workshop held in Memphis, TN. A decision to publish a special issue of ARQoL was made during this workshop. Rather than restricting the authors to the workshop participants, we issued an open call for proposals and were gratified by the response. Numerous QoL researchers worldwide had begun to employ a modern evolutionary perspective, independent of our own efforts, and we are pleased to include them in our special issue. Another outcome of this first QoL workshop was the decision to study Norway as a case study of large-scale cultural evolution leading to a high quality of life, a project that is ongoing (Wilson and Hessen 2014).

In this lead article, I will outline how an explicitly evolutionary perspective can add value to the study of QoL. Evolutionary theory is like a toolkit with multiple tools that

can be employed for the particular problem at hand. I will describe some of the major tools, how they are employed by the other articles in the special issue, and how they can be employed to address additional topics relevant to QoL not covered by these other articles.

Ultimate and Proximate Causation

One of the most important distinctions in evolutionary theory is between ultimate and proximate causation (Mayr 1961). Ultimate causation refers to the forces of selection and drift that cause a given trait to exist in a population, compared to many other traits that could have existed, often on the basis of their fitness-enhancing properties. Proximate causation refers to the mechanisms that cause the trait to exist in a physical sense.

As a straightforward biological example, many animal species living in desert environments have evolved cryptic coloration. The ultimate causal explanation is the same for all of the species: Individuals that were difficult to spot against their background survived and reproduced better than individuals that were easier to spot. The proximate causal explanation differs between taxonomic groups. Insects, snails, reptiles, birds, and mammals all have different physical exteriors – chitin, calcium, scales, feathers, and fur respectively. The coloration of the exteriors is caused by different physiological processes coded by different genes. Insofar as the different physical mechanisms result in heritable variation, they can all converge on the same functional outcome: organisms that are difficult to see against their background. In this fashion, the relationship between proximate and ultimate causation is typically a many-to-one relationship. There are many ways to skin a cat, and there are many proximate mechanisms that can result in a given functional outcome.

A second example that is relevant to human QoL concerns the ability to digest lactose, the primary sugar of milk. All mammals possess this ability during the infant stage of their life cycle but typically lose it in their adult stage, which makes good functional sense because adult mammals don't have access to milk as a resource. This was also true for humans until some cultures started to keep livestock. Genetic mutations enabling adults to digest lactose were favored in these cultures, providing one of the best-documented examples of rapid genetic evolution in humans. In fact, the genetic ability to digest lactose in adults evolved independently in at least two human populations that had culturally evolved to keep livestock, and different genetic mutations were favored in each case (Holden and Mace 2009). This makes sense, since there is no reason to expect the exact same mutation to arise independently in separate populations. Thus, the ability of adult humans to digest lactose has the same ultimate causal explanation (ability to digest an important resource) but different proximate explanations (different genes and metabolic pathways) in the two populations.

How does this example relate to QoL? Basic nutrition is an important component of QoL, and efforts to improve nutrition should be mindful of both genetic and cultural evolution. In the early days of international aid, milk products were shipped around the world without any awareness that they couldn't be digested by a large fraction of the world's population (Friedl 1981). At a finer grain of analysis, the fact that even people

who can digest lactose employ different metabolic pathways coded by different genes could be important for medical applications.

The ultimate/proximate distinction bears centrally upon the use of happiness and subjective wellbeing to measure QoL as elaborated by Grinde (2012a, b) in his contribution to this special issue. From an evolutionary perspective, happiness and all other emotions and moods are proximate mechanisms that motivate human action. Insofar as the proximate mechanisms are adaptive, they motivate actions that enhance our survival and reproduction. But the subjective feeling of happiness (or any other subjective state of wellbeing) is only a small part of a big picture. We did not evolve to be happy and if we formulate policy to drive up happiness numbers, the outcome might be no more beneficial for human welfare than if we drive up economic numbers. This is obvious for examples such as drug use and other hedonistic activities, but it might also be true for other policies that are well meaning but poorly informed about the ultimate/proximate distinction and happiness as part of a complex array of proximate psychological mechanisms that evolved to motivate adaptive behaviors.

The example of lactose tolerance reveals the need to pay equal attention to genetic evolution, cultural evolution, and their interactions (Jablonka and Lamb 2006). There is a widespread tendency to assume the existence of a universal human nature and to search for it by studying what all cultures share in common. Since most research is conducted on WEIRD cultures (White, Educated, Industrial, Rich, and Democratic; Henrich et al. 2010), much that is specific to these cultures is mistaken as universal. Moreover, insofar as a universal human nature does exist, it manifests itself not only in traits that are expressed in nearly all cultures (such as incest avoidance) but in the capacity to adapt to different environments, resulting in cultural differences. Evolutionary biologists spend most of their time studying differences between species – not what they share in common – which wouldn't even include DNA replication. The study of human cultures should similarly focus on the analysis of differences. It is possible, and even likely, that the role of happiness as a proximate psychological mechanism varies among cultures and that no single metric will be applicable across cultures (Grinde 2012a, b; see also Delamonica's contribution to the special issue concerning the challenges of assessing poverty across cultures and time periods).

It is common to assume that genetic evolution is a slow process that has largely been replaced in humans by the fast process of cultural evolution. On the contrary, one of the most important developments in evolutionary biology over the last few decades is that genetic evolution operates on ecological time scales (Carroll et al. 2007) and that this can be true for humans is no less than other species (Cochran and Harpending 2009). Moreover, genetic and cultural traits often co-evolve with each other, with cultural evolution leading the way, as we have seen in the case of lactose tolerance, where a new cultural practice altered selection acting upon genes. There are probably many comparable examples waiting to be discovered, which means that research on QoL and policies designed to increase QoL should be sensitive to the possibility of important genetic differences among populations and individuals within any given population. In one compelling study of single nucleotide polymorphisms (SNPs) on a worldwide scale, Amato et al. (2009) showed that disruptive selection (driving the frequency of a given allele up in some populations and down in others) operates more strongly for psychologically relevant traits than any other category of traits.

In an important elaboration of the ultimate/proximate distinction, Tinbergen (1963) identified four questions that need to be asked for any trait that evolves; they concern function, mechanism, development, and phylogeny. Tinbergen's four-fold distinction adds a temporal dimension to the two-fold ultimate/proximate distinction. It is not enough to study proximate mechanisms in their mature form; we also must know how they develop during the lifetime of the organism. Ultimate causation is a path-dependent historical process that will differ among lineages, even when they are responding to the same selection pressures, as we have seen with the example of adult lactose tolerance in humans.

Hicks and Leonard (2014) highlights the importance of development in studies of QoL by taking a developmental systems approach to racial inequality and health disparities in Memphis, TN. The Evolution Institute's Norway project highlights the importance of historical factors in the current ethos and social organization of a culture that leads to a high quality of life. Recognizing the importance of history is a refreshing contrast to neoclassical economic theory, which ignores history altogether.

To summarize, studying function, mechanism, development, and history as four complementary questions for any particular genetic or culturally evolved trait is one of the most important set of tools in the evolutionary toolkit. It is employed by most of the articles in the special issue and can be employed for many other topics associated with QoL.

Multilevel Selection

All social species are faced with a fundamental problem: The traits that maximize the fitness of individuals, relative to other members of the same group, are typically different than the traits that maximize the fitness of the whole group, relative to other groups. For group-level functional organization to evolve, a process of selection among groups in a multi-group population is required to counterbalance selection among individuals within groups (Wilson 2015). In a multi-tier hierarchy of units, the general rule is "adaptation at any given level requires a process of selection at that level and tends to be undermined by selection at lower levels." Biological examples include: cancer cells, which spread at the expense of other cells within the organism, ultimately to everyone's demise (Pepper et al. 2009); animal societies in which dominant individuals behave more like tyrants than wise leaders, until deposed by the next tyrant (Boehm 1999; Sapolsky 2005); populations that overexploit their resources because exploitative genotypes have a higher relative fitness than "prudent" genotypes (Kerr et al. 2006); and single species that ravage whole ecosystems for no one's benefit but their own (e.g., Timmers 2012).

On rare occasions, mechanisms evolve that largely suppress selection within groups such that between-group selection becomes the primary evolutionary force. When this happens, group members evolve to become so prosocial that the group becomes a higher-level organism in its own right (Maynard Smith and Szathmáry 1995). Nucleated cells did not evolve by small mutational steps from bacterial cells, but as groups of highly cooperative bacteria. Likewise, multi-cellular organisms are groups of highly cooperative cells and the insects of social insect colonies, while physically separate,

coordinate their activities so well that they qualify as super-organisms (Seeley 2010). Life itself might have originated as groups of cooperating molecular reactions.

Only recently have scientists begun to realize that human evolution represents a similar transition. In most primate species, members of groups cooperate to a degree but are also each other's main rivals. Our ancestors evolved to suppress self-serving behaviors that are destructive for the group, at least for the most part, so that the main way to succeed was as a group. Teamwork became the signature adaptation of our species. Extant hunter-gatherer societies still reflect the kind of teamwork that existed among our ancestors for thousands of generations (Boehm 1999; 2011). Individuals cannot achieve high status by throwing their weight around but only by cultivating a good reputation among their peers. Most of human moral psychology – including its other-oriented elements such as solidarity, love, trust, empathy, and sympathy, and its coercive elements such as social norms enforced by punishment – can be understood as products of genetic evolution operating among groups, favoring those that exhibited the greatest teamwork.

Teamwork in our ancestors included physical activities such as childcare, hunting and gathering, and offense and defense against other groups. Human teamwork also acquired a mental dimension, including an ability to transmit learned information across generations that surpasses any other species. This enabled our ancestors to adapt to their environments much more quickly than by the slow process of genetic evolution. They spread over the globe, occupying all climatic zones and hundreds of ecological niches. The diversity of human cultures is the cultural equivalent of the major genetic adaptive radiations in dinosaurs, birds, and mammals (Pagel and Mace 2004; Pagel 2012). The invention of agriculture initiated a positive feedback process between population size and the ability to produce food, leading to the mega-societies of today.

Cultural evolution differs from genetic evolution in important respects but not in the fundamental problem that exists at every level of a nested hierarchy of social units (Turchin 2005). Just like genetic traits, cultural traits can spread by benefitting lower-level units at the expense of the higher-level good or by contributing to the higher-level good. There can be cultural cancers, no less than genetic cancers. And for teamwork to exist at any given level of a hierarchy, there must be mechanisms that suppress lower-level selfishness. A nation or the global village is no different in this respect than a human village, a hunter-gatherer group, an ant colony, a multi-cellular organism, or a nucleated cell.

Modern nations differ greatly in how well they function at the national scale (Acemoglu and Robinson 2012; Pickett and Wilkinson 2009; Turchin 2005). Some manage their affairs efficiently for the benefit of all their citizens. They qualify as at least crude superorganisms. Other nations are as dysfunctional as a cancer-ridden patient or an ecosystem ravaged by a single species. Whatever teamwork exists is at a smaller scale, such as a group of elites exploiting the nation for its own benefit. The nations that work have safeguards that prevent exploitation from within, like scaled-up villages. The nations that don't work will probably never work unless similar safeguards are implemented. Accomplishing teamwork at the level of a nation is hard enough, but it isn't good enough because there is one more level of the nested hierarchy. A nation can be as good as gold to its own citizens and still be a selfish member of the global village.

This very brief summary of multilevel selection in relation to human affairs has myriad implications for QoL studies. It provides an alternative paradigm to neoclassical economic theory, which pretends that lower-level self-interest robustly benefits the common good (Gowdy et al. 2013). It identifies small groups with a high degree of control over each other as a fundamental unit of human social organization that should probably be retained in large-scale society. And it suggests ways that large-society can emulate the social control mechanisms that take place spontaneously in small groups.

Weaver (2014) employs multilevel selection theory in his article for the special issue. He treats physical disorder in cities as an example of lower-level selection prevailing over higher-level selection, using analytic techniques borrowed from theoretical biology and a dataset from the city of Seattle. The Evolution Institute's Norway project employs multilevel selection theory at a larger scale as an example of a nation that functions well because it retains a balance of power among its constituents and an ethos of equality. These are in danger of being destabilized, however, and Norway sometimes selfishly feathers its own nest at the expense of the rest of the world (Wilson and Hessen 2014).

Evolutionary Mismatch

Evolutionary mismatch is a state of disequilibrium between an organism and its environment. It occurs when a trait evolves in one environment and then the environment changes, with the result that the trait has a detrimental effect in the latter environment that it did not have in the earlier one.

Mismatch is an integral part of evolution in changing environments and resolves itself with subsequent evolution – but that is often not fast enough from the standpoint of human and environmental welfare. As an example, when baby sea turtles hatch and emerge onto the surface of a beach, it is critical for their survival to make their way to the sea as quickly as possible. The cue that they have evolved to use is light reflected from the sea surface, but this cue is subverted by lights from beach houses, which cause the baby turtles to head inland (Schlaepfer et al. 2002). This mismatch is so catastrophic that the sea turtle population on an island is likely to go extinct before genetic evolution can resolve the problem, calling for an environmental intervention such as crews of volunteers to gather the turtles or a lights out policy during hatching season.

It would be difficult to overestimate the importance of mismatch for human QoL. Our diets, exercise regimes, and social lives are radically different from what our ancestors experienced during most of our genetic evolutionary history. Many of the diseases that afflict people in industrialized societies are rare or absent in societies that approximate a pre-agricultural lifestyle (Lindeberg 2010). Some of the best documented examples of health-related mismatches would be difficult to understand except from an evolutionary perspective. As an example, for most of the history of medicine since the discovery of germs, it was assumed that good hygiene consisted of eliminating germs and other organisms inhabiting our bodies. The idea that the vertebrate immune system evolved in the presence of these organisms over a period of 400 million years, and that removing them might cause the immune system to "misfire" in a variety of ways, did not dawn upon medical researchers until the late 20th century (Strachan 2000). The term microbiome was not coined until the turn of the 21st century, reflecting

the dawning awareness that we serve as a habitat for a diverse ecosystem of species whose cells number on the order of 10 times the number of our own cells. Not all species in our microbiomes are friendly, but all things considered, we need our microbiomes as much as we need our own genes (Dethlefsen et al. 2007).

Our ability to culturally adapt to our environments can provide solutions to genetic mismatches. When our ancestors spread out of Africa and started to inhabit colder regions of the world, they adapted by making clothes, not by genetically evolving fur. But cultural evolution can also create its own mismatches. The first agricultural societies were well-adapted in the sense of displacing hunter-gatherer societies, but the shift in diet was negative in some respects for individual human health, a problem that only genetic evolution or subsequent cultural evolution can solve. Furthermore, even though cultural evolution is typically fast compared to genetic evolution, it can still require decades and centuries. Improving QoL over shorter time scales requires examining our past culturally evolved traits, in addition to our genetically evolved traits, in relation to current environments.

It is possible that the process of cultural evolution can itself misfire in modern environments in the same way as the vertebrate immune system. Consider a cultural practice such as bottle feeding infants, which is manifestly bad for their survival and health compared to breastfeeding (e.g., Kramer et al., 2008). Why did this practice become widespread, and why is it difficult to eliminate – despite its harmful effects? The answer is due in part to the inappropriate triggering of a prestige bias, which causes low-status individuals to copy the behaviors of high-status individuals. This bias makes sense in the context of small-scale society, where high-status individuals earn their reputations on the basis of behaviors that are worth emulating, but it tragically misfires when women from developing countries (perceived as low status) emulate practices that have become common in industrial societies (perceived as high status), especially as portrayed by commercial interests. In this fashion, practices that increase QoL can fail to spread and practices that decrease QoL can spread like wildfire. To solve these problems, we need to gain a sophisticated understanding of our capacity for cultural change as a set of adaptations that evolved in the context of a set of ancestral environments, which are now being expressed in a set of modern environments.

Mismatch is such an important topic for human and environmental welfare that the Evolution Institute has made it a major focus in collaboration with the National Science Foundation's National Evolutionary Synthesis Center (NESCent), which will result in an edited volume titled "Evolutionary Mismatch and What to Do About It." The lead article for the volume is available on the EI website (Lloyd et al. 2014) and deserves to be a core reading for QoL researchers. One article in the special issue that touches upon mismatch is Minguez et al. (2014).

Measuring QoL

The original focus of QoL was to develop indices to guide public policy, similar to economic indices such as GNP. Indices such as the UN Human Development Index (HDI) include measures of major elements of QoL such as life expectancy, education, income, and inequality. These national-level indices play an important role, but they need to be complemented by a very different approach to measuring QoL. Other

measurement issues are considered by Delamónica (2014) for poverty, Grinde (2012a, b) for happiness, and Minguez et al. (2014) for family policy indicators in this special issue.

Consider some of the specific factors impacting QoL discussed in this article and other articles in the special issue: a) the adult ability to digest lactose, b) how genes and environments interact during human development in inner city neighborhoods, c) how the history of any given culture such as Norway enables and constrains its ability to function at a large scale, d) how the pursuit of high QoL at small social scales can undermine QoL at larger social scales, and e) how a panoply of problems impacting QoL can be based on a mismatch between traits adapted to past environments misfiring in current environments.

These represent just the tip of an iceberg of factors impacting QoL in any real-world population. Each one calls for a separate research program with its own set of measurements. Thinking of a society as like an organism provides a useful guide to the measurement approach that is needed. Hundreds of physiological processes are required to keep us alive, each with their own regulatory mechanism that is integrated with the other mechanisms. When we go for a checkup, an entire battery of measurements is taken to monitor these processes and check for the many diseases that might afflict us. If a human society is like an organism, then it also will need a battery approach to measuring and improving QoL.

Two examples will illustrate how specific factors associated with QoL can be improved with monitoring and regulatory mechanisms. These examples also illustrate how different tools of the evolutionary toolkit can be employed to improve QoL. The first example involves the problem of selling tobacco products to minors, which is against the law but still needs to be monitored and enforced. The federal government does this by employing teams of minors who attempt to buy tobacco products in convenience stores. When their success rate exceeds a certain value in a given state, the state is put on notice that it will lose millions of dollars in block grants unless the problem is fixed. But how can a state fix the problem?

An important insight is that these problems tend to fix themselves at a smaller scale. In a small group, norms are easily established by consensus and enforced by rewards and punishments. Therefore, the challenge is to implement something similar at a statewide scale. Embry et al. (2010; discussed in Wilson et al. 2014) were able to accomplish this for the states of Wyoming and Wisconsin by implementing a monitoring and regulation procedure that included the following elements: a) establishing the rule of not selling tobacco products to minors as an important norm (the mere fact that it is against the law was not sufficient), b) richly rewarding convenience store clerks who complied with the law, and c) mildly punishing clerks who did not comply with the law and enforcing stronger sanctions against those that did not respond to mild punishment. With this monitoring and regulatory machinery in place, the states of Wyoming and Wisconsin were able to bring the problem under control within 60 days. Additional research showed that minors actually used less tobacco as a result; they were not able to fully compensate by finding other ways of obtaining tobacco. Thus, the program was successful at improving physical health, one of the most important components of QoL. The key to the success of the program was to implement at a state-wide scale a monitoring and regulatory process that takes place spontaneously at the scale of small groups.

The second example involves how parents raise their children (see also the 2014 contribution of Minguez et al. to the special issue). Nearly all parents want the best for their children but parent-offspring interactions sometimes result in negative outcomes for everyone involved. Environmental stressors such as poverty, single-family households, and the presence of adults who do not have the best interests of the children in mind do not fully account for the negative outcomes. A key insight is that family interactions that lead to negative long-term outcomes can nevertheless be psychologically reinforcing over the short term. Children are rewarded when they overcome parental opposition to get their way, and parents are rewarded when they temporarily impose their will upon their children – leading to a tragic co-evolutionary race to the bottom and the acquisition of social skills in children that predispose them to failure as adults.

Other families reward each other over the short term in ways that lead to positive long-term outcomes, and these skills can be taught. A program called Triple P (for Positive Parenting Program; http://www.triplep.net/glo-en/home/) has been developed to teach the skills to individual families as well as on a population-wide scale. In one study, social service providers were given Triple P training in nine South Carolina counties chosen randomly from 18 counties in a randomized control design. The effectiveness of the program was monitored through social service and public health statistics, including foster care placements and emergency room visits by children. These statistics improved over a two-year period in the counties that received Triple P training, compared to the matched sample of counties. The cost of the program was estimated at $15/child and was greatly offset by the monetary and societal benefits (Prinz et al. 2009). Triple P is currently being implemented in 25 nations worldwide and deserves to become even more widespread.

Conclusions

These two examples of monitoring and improving QoL in real-world populations are both encouraging and daunting. Their success is encouraging, but it is daunting to think that they are only two of hundreds of specific factors that contribute to QoL in real-world populations. Does this mean that something similar needs to be accomplished for all the other factors? I believe that this is the correct inference. Aggregate measures of QoL at the national scale, such as the UNHDI, are like the mouths of rivers that reflect contributions from hundreds of tributaries. Unless QoL is monitored, studied, and improved at the tributary level, it cannot be improved at the river level.

Fortunately, it is not necessary to start from scratch. Every scale of government (broadly defined) is already in the business of gathering and processing information and using the resources at hand to improve QoL to the best of its ability. There is tremendous room for improvement – once we have a clear idea of what needs to be done. Until now, a comprehensive vision has been limited by the lack of a general theoretical framework that can be applied to every problem at the tributary level in addition to the river level. This article and special issue of ARQoL provide an introduction to how evolution can provide such a theoretical framework for QoL.

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