TOWARDS UNIFICATION OF THE SOCIO-ECOLOGICAL SCIENCES: THE VALUE OF COUPLED MODELS

by
Timothy M. Waring and Peter J. Richerson

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ABSTRACT. The major environmental problems of the twenty-first century, including climate change, water scarcity, pollution and resource exhaustion, represent a new category of crisis and highlight the desperate need for an integrated science of socio-ecological phenomena. To help establish the foundations of such a science, we explore three traditions of mathematical theory: the Lotka–Volterra interactions of ecological theory, niche construction models of population genetics, and theory from the gene–culture coevolution tradition. We review the theoretical tools of each of these traditions in explaining cultural articulation with the environment. Although the theoretical core of the science we propose does not exist, cultural evolutionary theory supplies useful tools to analyse endogenous culture, cultural dynamics, and deeply rooted behavioural links to the environment. We also present a coupled model for demonstration, and suggest that coupled socio-ecological models can provide a formal theory to help address the emergent socio-ecological problems of the future.

Keywords: coevolution, coupled models, cultural evolution, socio-ecological, mathematical theory

Introduction

Human domination of the biosphere is such a recent and profound ecological alteration that the processes of evolution itself have changed fundamentally (Maynard Smith and Szathmáry 1995). To understand the interactions between human populations, cultures and their environments, it is useful to keep historical trajectories in focus. For at least ten millennia, human populations have fundamentally altered the ecosystems they have occupied (Diamond 1997; Redman 1999). Innumerable human-induced ecological alterations include hydrological alteration (Rosenberg *et al*. 2000), soil loss, nutrient addition (Vitousek *et al*. 1997a), introduction of non-native species (Vitousek *et al*. 1997b; Mooney and Cleland 2001), anthropogenic fire regimes (Horton 1982; Stewart 2002), both intentional and unwitting "artificial" selection of native species (Law and Salick 2005), massive loss of biodiversity, and even ecosystem collapse (Miller *et al*. 2005). The existence and activities of human populations constitutes a significant imposition on ecosystem function. Together, human ecological modifications have been summarized as ecological 'simplification' (Western 2001) – a crude restructuring of material and energetic flows to suit the short-term needs of the human population, while reducing non-human ecological complexity.

Western (2001) is surely correct that human-dominated ecosystems are less biodiverse, but it is not immediately clear that human dominated ecosystems are on the whole less complex, and they are certainly not easier to study. But ecological systems under human influence *must* be understood. The human population appropriates approximately one-quarter of global net primary productivity (Vitousek *et al*. 1986; Haberl *et al*. 2007), constituting a massive re-plumbing of ecological energy pathways. Some estimate that humanity currently consumes more resources than the earth is capable of regenerating (Wackernagel *et al*. 2002), endangering the long-term sustainability of civilizations. Further, the major environmental problems of the twenty-first century are deeply socio-ecological in nature because they are exceptionally intertwined with social dynamics, justice, and political and cultural matters. Many modern environmental problems are anthropogenic, and the course that they take depends in every step on both environmental and social processes.

Designing effective responses to these socio-environmental challenges depends on a strong understanding of the human–environmental interactions themselves. Currently, however, these phenomena are studied on the margins of natural and social sciences alike. Furthermore, developments in ecological economics (Costanza *et al*. 1997), human ecology (Hawley 1986), environmental sociology (Hannigan 1995), studies of population–environment interactions (Entwistle and Stern 2005), and integrated assessments of specific environmental problems (Morgan and Dowlatabadi 1996) show that the study of the relationships between human populations, cultures, and systems with natural systems is feasible, and even fruitful. But a unified science is needed soon, and we have not even a common framework to unite these approaches.

Norgaard (1984a, 1984b) suggested that researchers consider human–environment interactions as a coevolution between “sociosystems” and ecosystems. Norgaard’s generalized Darwinian conceptual model is sufficiently broad to serve as the basis for such a unified framework, but remains insufficiently elaborated to qualify as a theory of socio-ecological coevolution (Winder 2005; Kallis 2007). Hodgson and Knudsen (2006) argue that for any such unified theory a generalized Darwinism is necessary, but never sufficient. That is, although the components of the evolutionary algorithm (variation, heredity and selection) are necessary for any fully formed science of behavioural change, to move beyond vague verbal models, more precision is required. We argue that by specifying the three components of the Darwinian algorithm *and* clarifying the details of the constraints and forces involved that the coevolutionary framework could become the theory we need. Below we aim to improve socio-ecological coevolutionary theory by exploring and summarizing the mathematical tools from various theoretical traditions best for building coupled models of environmental change and human behaviour.

A socio-ecological problem

The invasive species problem is a quintessential example of human ecological alteration. Biological invasions highlight the difficulty of solving inter-linked environmental–social problems because both social forces and ecological forces are constantly at play in determining the outcomes. Although often unappreciated, invasive species are reckoned to be one of the most severe anthropogenic ecological disturbances (Diamond 2005). Despite many attempts at a predictive theory of biological invasions, ecologists have had to resort to practical, brute force methods (Kolar and Lodge 2001). Biological invasions are particularly demanding because, rather than being a purely energetic or material re-arrangement, anthropogenic biological invasions are a re-assortment of species, and of biological information. The effects are, therefore, as much evolutionary (Mooney and Cleland 2001) as they are ecological. Making the evolutionary aspect of invasions even more salient is the new prospect of biological invasions on the level of the gene. Genetically modified organisms, especially crop plants, are currently being exposed to natural conditions and wild populations around the world, and in some cases, these exposures can result in the introgression of tailored genes into wild populations (Quist and Chapela 2001). But, while the evolutionary genetics are relatively well understood we have no basis to model or predict such phenomena when they depend on human systems.

Biological invasions are often modelled as the result of a series of sequential ecological filtering processes. Typical ecological explanations of the establishment of a species highlight the similarity of the donor and recipient climates and ecosystems, and stress that for a species to establish in the recipient system it must have characteristics that enable it to be transported, survive the transport, grow in local conditions, and out-compete local species for niche space. Such filter models are useful (e.g., Simberloff and Stiling 1996), but they neglect the fact that human actions and decisions play a duet with the ecological processes at every stage. As Kowarik (2003) points out, the unexplored driver of biological invasions is human agency. Understanding and predicting human behaviour is a tenacious problem of its own, apart from the challenges of integrating social and ecological theory in the quest for a useful socio-ecological science. Thankfully, foundational theory linking human behaviour with environmental phenomena enhances the possibilities for such a science to emerge.

Some beginnings

To develop a mature science, theories must be precise enough to support hypotheses that are both precise and predictive. To that end we focus on finding mathematical models that can help unite social and ecological dynamics, noting that models, of course, imply a parallel programme of empirical work. Formal quantitative theory extends from mathematical models on one extreme to computational simulations on the other, and itself lies entirely at one end of the spectrum of all theory stretching from quantitative to conceptual. Each type of research and theory has its place. Qualitative research allows researchers to probe further and faster than those who are slowed by statistical requirements. Formal methods and quantitative analyses must follow slowly in the path of qualitative research, never covering as much ground, but strengthening and clarifying the results of interpretive research. Simulations provide a useful middle ground, acting as a type of virtual laboratory allowing the exploration of scenarios of extremely complex systems not feasible in reality.

Mathematical theory must come behind all of these theoretical approaches, because its function is to congeal understanding into mechanics that can produce clear and realistic predictions. For our purposes here, two benefits of simple mathematical models deserve highlighting. First, we should note that evolving socio-ecological systems will always be vastly more complex than both the data we collect, and any model or theory we use to represent them. The natural limits to our representations and records of this complexity ensure that the intricacy of our theories must always be traded off against our ability to test them (Burnham and Anderson 1998). We propose that general, simple and testable theory is now very sorely needed. Second, mathematical models provide a precise method of scientific communication between researchers, and a necessary pre-requisite of consensus. Simple models offer a kind of scientific currency that can be easily shared, tested, rejected, accepted, amended and retested. Simple models aid education too, as they are more easily communicated to students and colleagues in other disciplines. Given that major environmental problems require interdisciplinary approaches, and that synthetic work particularly stands to benefit from simple, well-chosen models we feel that simple mathematical models are of certain value.

Scattered amidst the divergent fields of ecological theory, cultural evolution, niche-construction, and gene–culture coevolution, we find formal tools that may help to lay a foundation for a theory of nature and culture. We examine each tradition as it might aid a unified theory of socio-ecological coevolution.

Gene–culture coevolution

The tradition of gene–culture coevolution gains a mathematical foothold on the phenomenon of culture as an evolutionary system by modelling culture with formal techniques derived from evolutionary biology. First proposed by Cavalli-Sforza and Feldman (1973), gene–culture theory shares concepts with, but is distinct from sociobiological attempts (Wilson 1975) to integrate cultural change and genetic evolution. The version of gene–culture coevolution developed by Lumsden and Wilson (1981) imagines that the "complete coevolutionary circuit" includes genetic constraints on cultural evolution but not vice versa. Since that time, gene–culture coevolutionary theory has come to make room for the selective influence of culturally constructed environments acting on genes (Laland and Brown 2002), and recognizes both cultural and genetic evolutionary forces as ultimate causes of human behaviour.

Gene–culture research has led to models explaining the coevolution of sign language with deafness, incest taboos, and the evolution of handedness among other phenomena (Boyd and Richerson 1985; Aoki and Feldman 1991, 1997; Kumm *et al.* 1994; Laland *et al.* 1995; McElreath and Henrich 2008). The gene–culture approach has significant and powerful applications, especially as new evidence on the nature of current human genetic evolution suggests the increasing importance of cultural factors (Balter 2005). (See Appendix A for mathematical discussion.)

As the studies above show, the gene–culture coevolutionary framework is usually employed to account for the long time scale of human genetic evolution, for example in the investigation of the emergence of culture itself. The focus has been on human genetics and culture rather than on the ways in which genetics of other species coevolve with human cultural traits (Durham 1991). In building a theory of cultural–environmental articulation, however, we are also interested in the short time scales of rapid ecological processes in which shifts of opinion and practice take place. Gene–culture studies that integrate the genetics of non-human species and human cultural processes would need to focus on these shorter timescales. This is a natural focus since one hypothesis for the origin of human culture is that it was an adaptation to the highly variable climates of the last ice age (Richerson *et al.* 2005). Cultural evolutionary theory has also been applied to the study of rapid evolution, for instance in understanding the on-going human transition to low fertility in the last two centuries (Newson *et al.* 2007). Human cultures also exert selective effects on other species, especially domesticates, weeds and diseases (e.g., Law and Salick 2005). For example, a potential application of dual inheritance models in the environmental realm is in the area of crop diversification and evolution (Brush 1992; Perales *et al.* 2005). Clearly crop breeding, wild diversification and cultural evolution are all dynamically linked. A gene–culture coevolutionary model might couple breeding and human selection with natural selection on plant genes. In turn, human populations depend upon the productivity of crops and domestic animals to sustain productive economies. Gene–culture coevolutionary concepts and models are thus applicable to the human evolutionary interaction with other species as well.

Niche construction

Odling-Smee *et al.* (2003) develop the idea that durable environmental changes created by organisms are not just the products of natural selection themselves, but also feedback into evolution effecting the selection of genes (and in humans, culture) in the future environment. Odling-Smee *et al.* (2003) treat these durable environmental effects as a third system of inheritance, after genes and culture, and describe the resulting environmentally mediated coevolution as ‘niche construction’ (Odling-Smee *et al.* 2003). Like gene–culture studies, niche construction uses the mathematical language of population genetics. It is worth noting that these two traditions are better suited to modelling changes in trait frequencies in a population rather than numeric changes in the population itself. Niche construction models go one step further by incorporating heritable behavioural variation (held in genes, culture, or both) and the environment, which is also heritable. Niche construction effectively ties genes, culture, and the dynamically coupled aspects of the environment into a common analytical framework. Niche construction models are, therefore, well suited to our needs as they dynamically link the changing environment to evolving behaviour (see Appendix B for mathematical discussion).

Although most niche construction models have utilized the longer-term vertical transmission of behaviour between generations (either genetic or vertically inherited cultural behaviour) as opposed to horizontal transmission within generations, this is not fundamental. It is possible, for instance to build a niche-construction model that tracks a culturally inherited behaviour (such as sheep farming) and the state of the environment (such as the amount of forest). In this case the cultural trait of sheep farming will be inherited between and within generations, and trees will be cut and grow on essentially the same time scale. Niche construction models could form an important foundation in mathematical theory of the ecological–cultural interface.

Ecological theory

Many authors recount examples of how humans and other species interact in common ecological communities. For instance, Crosby (1986) demonstrates the importance of cultural forces in the biological expansion of European landscapes in colonized areas. Europeans expanded dramatically, and with little cultural and genetic admixture, into areas like temperate North America, New Zealand, and Australia. In these areas native human populations were not adapted to European diseases and the climate happened to favour European domesticates. Wells and McShane (2004) explore the factors that determine the success of development projects that attempt to integrate local cultural systems with ecological processes to achieve sustainable results. And, on a more theoretical level, Diamond suggests that areas with higher natural primary productivity might be less likely to suffer social collapse as a result of a bounty of natural resources (Diamond 2005). Diamond’s suggestion strikes at the types of theoretical questions that formal environmental–cultural models could address. Do productive environments give rise to more durable societies in the face of human exploitation and population growth? If they do, the theoretical improvements we have been describing will aid in determining why and how.

Ecological models have been used for related questions about the ecological ramifications of human societies (Richerson and Boyd 1998; Erickson and Gowdy 2000; Richerson *et al.* 2001; Turchin 2003; Efferson 2008), and can be used to address Diamond’s hypothesis. The most time-tested ecological model is the *logistic equation*, in which a population[1] interacts with an environment of a given carrying capacity (see Equation 1). Theoretical ecologists derive models of interspecies interactions by expanding the logistic equation to include effects of other species on the carrying capacity of the environment for the focal species (see Hastings 1997 for a basic treatment). The resulting coupled differential equations are called Lotka–Volterra systems after pioneering ecological theorists. Used carefully, this mathematical core of ecological theory can effectively describe interactions in human communities and in mixed communities of humans, and other species.

Consider a human population of size N that grows in an environment with a carrying capacity (K). Using the logistic equation, we can incorporate social considerations (Richerson and Boyd 1998). First, although the carry capacity (K) is in the simplest case a constant, we can make it a function of anything we want in principle:

$$\frac{dN}{dt} = rN\left(\frac{K(T) - N}{K(T)}\right) \tag{1}$$

Here, K is not a constant, but a function, K(T), and can be made dependent upon, for example, culturally evolving technology (T) or the depletion of a non-renewable resource. By specifying the mechanism of technological change, for example, one generates novel population dynamics as well. The point here is not any particular linkage between technological growth and population, but rather that such questions can be handled in simple formal models to provide a healthy medium of communication between disciplines.

Erickson and Gowdy (2000) combined logistic equations for human population and resource growth in a Lotka–Volterra approach to investigate the different success of the Polynesian cultures of Tikopia and Easter Islands. The Erickson and Gowdy models help to explain why the human population of Easter Island suffered a severe crash, while that of Tikopia remained roughly stable. The authors argue that a difference in cultural practices generated the different fate of the two island societies (Erickson and Gowdy 2000) in part addressing Diamond's (2005) hypothesis.

Most studies of this sort use the logistic formalism to model human populations in their interactions with other resources or species, but we can also use the same tools to model social processes *within* human societies. From an ecological point of view, human sub-populations might well be modelled as several interacting species: peasants and lords, miners and farmers, producers of wool and producers of wine, and so on (Richerson and Boyd 1998; Turchin 2003).[2] Richerson and Boyd (1998) suggest using Lotka–Volterra predator–prey dynamics to investigate the relationship between social classes that can be said to compete or exploit one another. For instance, the "upper" classes might "parasitize" the productivity of the working classes. Peter Turchin (2003) developed similar models using Lotka–Volterra systems to show how endogenous demographic and economic factors might account for historical collapses of societies (see Appendix C for mathematical discussion).

We now have three formal traditions from which to borrow, gene–culture coevolution, niche construction, and the Lotka–Volterra ecological theory. Although the first two are best suited to model cultural change, they do not in themselves supply the cultural complexity that underpins the critical but elusive human agency. In the next section we explore the culture–environmental connection sprouting from the gene–culture tradition, and evaluate cultural evolution as the final cornerstone in our foundation for a formal science of the environmental–cultural interface.

Can a science be built?

In order to manage ecological and social diversity simultaneously, we need a theory that imputes cultures with their own intricate dynamics. Cultural evolutionary theory, an offshoot of gene–culture research, currently supplies the richest mathematical treatment of cultural dynamics. The formal study of the evolution of culture springs from the dual inheritance models of gene–culture research (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985), but describes the evolutionary dynamics of culture on shorter time scales without regard to genetic processes (Aunger 2000; Laland and Brown 2002). A major goal of the field is to employ knowledge about our evolved social psychology to build predictions about the distribution and dynamics of human behaviour. Cultural evolutionists argue that culture springs from the deep human ability to learn socially. Because individuals are selective in their use of imitation, social learning acts to both transmit and select behavioural variation between individuals. The field of cultural evolution therefore seeks to discover and test different types of social learning mechanisms useful for different social and environmental scenarios. Cultural evolutionary theorists have developed a suite of theoretical social learning mechanisms such as conformity, and prestige-biased and success-biased imitation (Boyd and Richerson 1985; McElreath *et al.* 2005; Richerson *et al.* 2005). Although these models of social learning deliver the precise predictions of cultural phenomena that are so critical in our endeavour, they still require more empirical testing (Laland and Brown 2002). Despite this weakness, a few key characteristics of the cultural evolutionary tradition make it a critical component of any science of culture and the environment.

Environmental influences on cultural evolution

Cultural evolutionary theory helps to illuminate one powerful example of environmental effects on culture that comes from the archaeological history of Tasmania. Around 8,000 years ago, Tasmanian technology, which had until that point included complex and sophisticated items such as boats, bows, and fishing nets, began to regress, until by the point of European contact none of these items were in production or use. Archaeological evidence shows that this technological regression coincided with a rise in sea-level which cut Tasmania off from the Australian mainland, but does not explain why Tasmanians did not continue to use and build the survival tools that were still of great value. Henrich (2004) employed a cultural evolutionary model with imperfect cultural transmission to explain this phenomenon. Henrich's (2004) model shows that if imitation processes are imperfect (a safe assumption), then population size limits the maximum level of technological complexity attainable by a given society. When Tasmania became geographically isolated, Tasmanians were unable to observe or learn from Australian technology. This limited the effective population size of the island with regards to maintaining complex traditions such boat craft. Diamond (1997) argues that this sort of process works up to the continental scale, explaining why the largest continent, Eurasia, was the most technically advanced at the point of the effective globalization of culture following the European voyages of discovery. While this theory awaits more empirical testing, it highlights a potential fundamental connection between environmental and geographic factors and cultural change – a connection which has only been modelled with cultural evolutionary tools.

Deriving intuitions from gene–culture models, studies of cultural evolution demonstrate that while natural selection should have created a social learning capacity that *attempts* to act in a fitness-maximizing manner, the informational content of culture may sometimes be neutral or maladaptive (Boyd and Richerson 1985). Furthermore since innate psychological mechanisms cannot always judge the quality of the content of social information, evolved social learning mechanisms must instead use contextual cues in determining how to employ social learning at any given time. These contextual cues can be drawn from characteristics of either the social group or the environment. Social cues are salient bits of information about peers, such as their relationships, age, sex, ethnic identity, or social status. Environmental cues are also theorized to cue social learning mechanisms in powerful ways.

Boyd and Richerson (1985) theorized that social learning may be fundamentally influenced by both the stability and complexity of the surrounding ecological environment. Some models of culture (Rogers 1988; Henrich and Boyd 1998) demonstrate that as an ecological task becomes increasingly difficult or complex, ever more instruction, observation and social learning is required for success. Some tasks are just too difficult to solve alone. McElreath *et al.* (2005) demonstrate that as environmental stability decreases, the benefit of imitated information declines, and thus so should imitative social learning of all types. Thus, both complexity and stability of the environment may affect how individuals regulate their imitation strategies, and therefore guide the very way in which culture is transmitted.

These hypotheses alone should spur interest in socio-ecological coevolution, but empirical tests have confirmed them as well. McElreath *et al.* (2005) found that individuals requested more social information when the environment was difficult to master and less when the environment became increasingly unstable. McElreath *et al.*'s results match theoretical models of the adaptive value of social learning, and reveal a deep connection between ecological environment and mode of cultural evolution.

Field research

One difficulty with research on social learning parameters in the laboratory (McElreath *et al.* 2005) is achieving clarity in contextual interpretation: are individuals conformist because all humans are conformist or because university students in America are? Cross-cultural comparisons have consequently become an important component of cultural evolutionary research (Paciotti and Hadley 2003; Henrich *et al.* 2004; McElreath 2004; Efferson *et al.* 2007).

New cross-cultural research has shown that environmental factors exert a strong influence on norms of sharing, reciprocity, and fairness (Henrich *et al.* 2004). This research uses the experimental economic methods such as the ultimatum game[3] to test social norms. In this research, socio-ecological factors play prominent roles. For the Lamalera whale hunters of Indonesia, sharing large material gains is a common practice, and thus the Lamalera topped the charts for the most equitable play in the ultimatum game. On the other extreme are such societies as the Hadza foragers of Tanzania, who avoid and dislike the sharing of hard-won food resources, and whose ultimatum game offers were consistently small, and always accepted. This cross-cultural data strongly suggest that the ecological niche of human populations, and the nature and timing of resource availability, have significant influences on fundamental social norms such as sharing (Henrich *et al.* 2004). In the previous section we saw how environmental stability and complexity may influence the mode of cultural evolution. Henrich *et al.*'s (2004) research suggests that environmental factors like resource availability may *also* select cultural variants, influencing the content of culture as well. Taken together, these two types of research reveal a fundamental socio-ecological link, which if further validated, provides an excellent model of a unified coevolutionary science.

The endogeneity of culture

Cross-cultural studies not only show the importance of environmental forces and strategic considerations, but also point to the significance of purely endogenous cultural phenomena. Practices such as female infanticide (Sudha and Irudaya Rajan 1999), beliefs in the health benefits of eating rare or endangered species (Mainka and Mills 1995), and socially transmitted preferences for oversized automobiles (Miller 2001) can only be understood with respect to the culture in which they arise. In our search for formal theory to help explain these culturally controlled patterns of behaviour, cultural evolutionary models have an advantage because they include many endogenous cultural mechanisms. For instance Boyd and Richerson's (1985) "similarity bias" in cultural transmission suggests that individuals will choose whom to imitate based on similarity to self. This mechanism alone can account for cultural differentiation between groups that can persist *even after* any adaptive rationale disappears. Such cultural inertia and other internal cultural forces can generate behaviours that would be unpredictable with economic models or other non-evolutionary theory.

Internal cultural dynamics drove McElreath *et al.* (2003) to use a combination of micro-evolutionary cultural forces to model the dynamics of ethnic identity. In their model, arbitrary and superficial socially learned traits could serve as distinguishing characteristics upon which individuals differentiate themselves. Such "ethnic markers" can affect how individuals make imitation decisions, and over time delineate boundaries between ethnicities. Their model demonstrates how simple mechanisms of social learning can generate self-reinforcing culture. Where factors like ethnicity and conformity are important (perhaps everywhere) human interactions with the environment will seem random without a model of these internal cultural forces.

Ethnic marker models illustrate the sort of synthesis that formal theory makes possible. Anthropologists speak of the importance of culture and highlight the value of cultural diversity, but conservation biologists, whose science relies on delineating explicit mechanisms, often disregard their assertions. Models like those summarized above offer a common vocabulary by which anthropologists and ecologists can represent the nexus between cultural values and evolving ecological systems.

Creating coupled socio-ecological models

We recommend that scholars of socio-ecological coevolution construct simple models consisting of two or more equations sharing a few key variables. With one equation representing a cultural, economic or demographic process and another for an ecological process, such models can dynamically couple any two realms including culture, environment, human populations, human genes, and the populations of other species. For modelling human populations and subpopulations or the interaction of humans and other species, the Lotka–Volterra equations from ecology are a flexible, well-studied set of tools. When describing cultural or genetic changes evolutionary biology provides the best formal theory. Economic models are of obvious use. To integrate cultural changes with human genetics, gene–culture coevolution models are best, and niche construction models are well suited to integrating the evolution of gene, culture, the environment, or even all three.

To make the process more concrete, we create and discuss a simple coupled model below as a tutorial. We develop a simple model of a single biological species that is affected by a habitat modification practice in an evenly distributed human population. Such a model could cover any number of common scenarios, such as the coevolution of ornamental plants with an aesthetic preference, or an invasive species and a practice of eradication. Table 1 categorizes such socio-ecological interactions by the relationship between the human behaviour and the species.

A single coupled cultural–ecological model can account for the entire range of interactions exhibited in Table 1. First we will set the uncoupled dynamics of the species and the behaviour. The species exhibits typical density dependent growth according to the logistic Lotka–Volterra equation. We will model the behaviour as spread through the human community in a conformist fashion, where

		Effect of Practice on Species (α)		
		Helpful (+)	Neutral (0)	Harmful (-)
Effect of Species on Practice (β)	Helpful (+)	(+,+) Charismatic species generate an affection, enhancing growth	(0,+) Species spreads awareness, without effect on itself	(-,+) Noxious species, generates a dislike, damaging growth
	Neutral (0)	(+,0) Species benefited by habitat modification	(0,0) No effects, cultural and ecological dynamics operate in isolation	(-,0) Species damaged by habitat modification
	Harmful (-)	(+,-) A poorly yielding crop is slowly removed from active planting	(0,-) Social catalyst species, changes management, without effect on itself	(-,-) Beautiful invasive plant which reduces intentions for eradication

Table 1. The interactions between a human practice and a biological species can be categorized by their effects on one another. Where $\beta < 0$, the individuals of the species exert a negative force on the spread of the practice. Conversely, where $\alpha > 0$, the instances of the practice impart a positive influence on the growth of the species. Setting α or β to zero will remove the interaction term, signifying no effect of one process on the other.

individuals adopt the behaviour of the majority of their peers, creating a tipping-point behaviour for the human population as a whole (Henrich and Boyd 1998). Thus, before specifying any type of interaction, the human practice (P) and the non-human population (N) change according to their own internal dynamics:

$$\tfrac{dN}{dt} = rN(1 - N/K) \qquad (2)$$

$$\tfrac{dP}{dt} = DP(1 - P)(TP - 1) \qquad (3)$$

where D is the strength of conformity, varying from 0 to 1. The practice model is analogous to a genetic frequency equation, and is entirely proportional rather than numeric.[4] The term T is the tipping point, below which the number of people adopting the behaviour will diminish to zero, and above which conformist imitation will drive everyone to eventually adopt it. Although the logistic equation is designed to handle numerical growth, for simplicity we will set K, the carrying capacity, to 1, forcing population growth to be a proportional phenomenon. In a true application of such a model to a real scenario one would not make such a choice.

To link the two dynamic systems we will now include α and β from Table 1. The influence of the practice on the species, α, should adjust the growth rate of the species. We therefore substitute r in Equation (1) for the growth term $(r + \alpha P)$ in Equation (3), which sums the intrinsic growth rate of the species, r, and the habitat modification effect, αP, which is proportional to the frequency of the practice. This description of population growth, dN/dt, is identical to a low-density mutualism model (Addicott 1981; Wolin and Lawlor 1984), in which the benefit of the mutualist partner (in our example, the practice) on the population is largest at low densities. Next, among many possible alternatives, we can imagine that the effect of the population on the frequency of the practice, β, should alter the strength of conformity, D. To conceptualize this think of a community of gardeners who imitate each other. The more salient a plant is in either positive or negative terms, the more any given gardener will want to treat it appropriately, and to do that they imitate what the majority of their neighbours do. We can model the influence of the imitation effect of the species as a proportional effect of the size of the species population on the strength of conformity, $(D + \beta N)$ in parallel with the changes to the population recursion.[5]

$$\tfrac{dN}{dt} = N(r + \alpha P)(1 - N/K) \tag{4}$$

$$\tfrac{dP}{dt} = P(D + \beta N)(1 - P)(TP - 1) \tag{5}$$

The two interaction parameters, α and β are bounded between -1 and 1, and their signs determine the related case in Table 1. The system of (3) and (4) yields simple dynamics. As one might expect, unless the interaction parameters α and β are sufficiently strong the long run outcomes for the species and the practice are effectively independent. For instance, because of the tipping point nature of the conformist behaviour, under most circumstances the behaviour will either entirely die off, or come to dominate. Similarly, under most circumstances, the population of the species in question will either be die off or grow to meet its natural carrying capacity, K. However, in a few situations there are more interesting dynamics. If the influence of the practice on the species is negative (say in the case of an extermination practice or exploitation via harvest) and the effect of the species on the practice is not extremely negative (an unlikely situation in the case of an extermination practice), then the conformist tipping point can make the difference between the survival and eradication of the species as long as the extermination practice, α, is larger than the species natural growth rate, r. Under such conditions the success or failure of the practice uniquely determines the success or failure of the species. This makes sense, of course, and anyone who has spent time attempting to keep weeds at bay will attest to how fast those natural rates of growth are. Still, even in this case, ultimately the species will either be extinguished, or will flourish, and the behaviour will dominate if it is pushed above the tipping point, or will vanish if it falls below.

With this model we can illustrate both the advantages and complications of coupling ecological and cognitive equations. To avoid misleading results, one needs to make sure that the modified equations do not violate the disciplinary principles from which the equations were derived. For instance, under certain circumstances, the system of equations (3) and (4) can create oscillations analogous to predator–prey oscillations found in Lotka–Volterra systems. This is a red herring, however. That oscillatory behaviour occurs when the negative effect of the practice on the species overwhelms the natural conformity rate, D, and reverses the sign of the conformity equation (5). This causes the practice to become more common even below the tipping point – a violation of the derivation of the conformist dynamic, and therefore a mathematical mistake.[6] Thus the correct formulation of Equation (5) should be:

$$\tfrac{dP}{dt} = P \cdot \max(0, D + \beta N)(1 - P)(TP - 1) \tag{6}$$

ensuring that the cognitive principles of the original equation are not violated. Despite such caveats, and the importance of careful integration, this coupled model is useful. This model suggests that if conformity is the dominant mode of cultural evolution in a given ecological management scenario of a density dependent species that socio-ecological interactions can only select between equilibria, but not establish new ones. Precisely, the model suggests that behaviour and species alike will each either die off or grow to dominance. This is an empirical prediction that bears testing. Moreover, the model states that extermination–growth oscillations do not occur in such situations. This is another significant prediction, and one that could be tested. But extermination–growth oscillations do seem to occur in reality (they occur in gardens). Thus perhaps conformity alone does not sufficiently characterize behavioural dynamics in ecological management.

This model presents a simple example of how a population of a wild, invasive, native or cultivated species might interact with human socially learned preferences and practices. In developing this model we made choices that may well be flawed. Does conformity alone best capture human social learning dynamics in this case, or would a different mechanism such as status-seeking, ethnically guided behaviour, or some combination of social forces be more appropriate? Are the ways we coupled practice to population α, and population to practice, β, realistic? The objective of model building is to ask such questions in pursuit of a model that describes the problem at hand to a useful degree. The point of the model is not full accuracy; models cannot achieve and should never strive for full accuracy. Instead, we have built a simple coupled model of socio-ecological phenomenon, and in so doing provided a very precise framework for the next researcher to exploit, imitate or critique.

Conclusions

We need a science of socio-ecological coevolution, but science needs theory, and theory needs a means for building and testing hypotheses. We submit the simple coupled model as a key tool in the socio-ecological enterprise. We have found three theoretical traditions that help in constructing such models; niche construction, gene–culture coevolution, and ecological theory. While both niche construction and gene–culture models are under-tested empirically, rapid progress is being made by the application of the Lotka–Volterra formalism to human social groups. But, our endowment of ecological knowledge stands in stark contrast to our functional understanding of social systems. It is the quantitative dynamics of culture that need the most scrutiny, and which will produce the greatest rewards. For this, theoretical work on the evolution of culture provides a theoretical cornerstone. Cultural evolutionists theorize deep connections between the environment and cultural change, and have identified unique internal cultural forces such as ethnic identity. Despite a developing tradition of scientific anthropology that seeks to test cultural evolutionary models, the greatest need for this body of theory is further empirical tests.

We are also in need of a way of integrating the far-flung disciplinary approaches to studying links between culture and environment. This need for cross-disciplinary integration is old (Snow 1959) but even more pressing today (Wilson 1998) as new problems of hideous complexity seem to arise almost yearly. As we have seen, the foundations for a ground up, simple, and integrative formal theory of socio-ecological processes exist, although it lacks a central theoretical core. We are in need of a new synthesis. We implore scholars to adopt a common theoretical and scientific language to aid in the pursuit of a fully formed science of socio-ecological coevolution. To that end, simple, portable mathematical models serve us well, providing precision, communicability and empirical tractability, while enabling incremental improvement.

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Notes

1. In symmetry with the strengths of the evolutionary formal techniques or gene–culture coevolution and niche construction which are best for modelling *cultural change*, ecological models based on the logistic equation are well suited to model *demographic and economic change*.
2. Note that this application of the logistic equation matches its original purpose of modelling numerical phenomena by avoiding the complex issue of change of behaviour within groups of individuals over time.
3. Experimental economics is an increasingly popular and productive tool in economic and ecological anthropology. The methods consist of asking participants to play structured games with other players that allow choices involving real payoffs, monetary or otherwise. For example, in the ultimatum game, one player is allowed to decide how to split a donation from the experimenter between herself and a second player. The second player is allowed to either accept or reject the offer, in which case neither player receives any payment. Because both players are informed of all of these rules, the game is effectively a measure of an unspoken norm of fairness.
4. As in genetic frequency equations, the $P(1 - P)$ term is the binomial variance of the behaviour in the population, and the $(TP- 1)$ term is the effect of conformity. Note that if $T = 1$, this term switches sign as P goes from < 0.5 to > 0.5. Thus below the tipping point conformity reduces P but above it, P increases.
5. Note that these changes assume that N varies between 0 and 1.
6. Other formulations of this simple interaction avoid this problem, but we highlight it here intentionally.

Timothy M. Waring
Sustainability Solutions Initiative, and
School of Economics
University of Maine
Orono, ME, 04469
USA
E-mail: timothy.waring@maine.edu

Peter J. Richerson
Department of Environmental Science and Policy, and
Graduate Group in Ecology
University of California – Davis
Davis, CA, 95616
USA
Email: pjricherson@ucdavis.edu

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Appendix A

Models of gene–culture coevolution

The basic structure of cultural evolutionary models is exactly the same as for evolutionary models of genes. Typical models are difference equations with a time step of one generation

$$P_{t+1} = P_t + forces \tag{A.1}$$

where P represents some state variable of the population, typically the frequency of people possessing one cultural variant as opposed to another. As in the genetic case, the forces acting in an evolving cultural system, such as random error, are partly endogenous to the cultural system. One such force is Boyd and Richerson's (1985) indirectly biased imitation, or "indirect bias". An example is imitating people for a given trait because they carry markers of prestige, a separate trait. Indirect bias can generate a runaway cultural process similar to genetic sexual selection, which can be disconnected from the direct influence of environmental or socioeconomic factors. However, many evolutionary forces connect the evolution of cultural variation to the environment.

Consider, for example, the way individual learning might couple cultural evolution to the environment. Information about the world that an individual learns by her own effort will typically be controlled by reinforcement that comes from the environment. But what individuals learn, others can acquire from them by social learning or cultural transmission. This gives cultural evolution a component of the inheritance of acquired variation that Boyd and Richerson (1985) called 'guided variation'. The Boyd and Richerson model of guided variation is:

$$X_{t+1} = aX_t + (1-a)H \tag{A.2}$$

Where X measures the mean value of a quantitative character in a population, such as mean number of cows families try to keep. The term a varies between zero and one, and measures the relative importance of culture, while 1 – a measures the strength of individual learning and H measures an aspect of the environment, such as the optimal size herd for a family to maintain. In Africa, many Bantu-speaking peoples live in moist environments where cattle diseases make cattle keeping impractical (H = 0). If a population of such people moves to a savannah environment where keeping cattle is very rewarding (H >> 0), some individuals will experiment with cattle and discover these rewards. If these people are highly tradition-minded, a >> (1-a), and on a generation-to-generation time scale the impact of experimentation may be quite modest. Nonetheless, so long as (1-a) > 0, the equilibrium for this system is X = H; in the long run the average number of cows in a family herd will be the optimal number. Guided variation acts like non-random mutation and pushes the population towards an optimal subsistence system.

This model illustrates the adaptive advantage of culture. Natural selection will also be operating on X to drive it towards H. Cultural variation is another kind of heritable variation so it is just as subject to natural section as genetic variation (the details of variation and selection notwithstanding). But in the case of culture, we have two evolutionary forces that both interact to push X towards H, selection and guided variation, whereas a genetic system has only selection. An important result of these dual forces of optimization is that human cultural systems can track changing environments much faster can genetic systems, consequently, humans generally adapt much more swiftly to new habitats than other species. Cultural evolution has underwritten the great adaptive radiation of human subsistence systems from caribou hunting to coral reef fishing, from tropical forest gardening to pastoral nomadism.

Appendix B

Niche construction

Odling-Smee *et al.* (2003) develop the idea that the evolution of organisms and their environments are dynamically linked. Most of the evolutionary models of both genes and culture assume that the environment is exogenous to the evolving system, and does not carry information forward through time. Sometimes this assumption is more or less correct, but often parameters of the environment are modified by organisms in ways that feed back on the evolution of the organisms. Odling-Smee *et al.* call this evolutionary environmental feedback *niche construction*, and humans are the master niche constructors. Consider, for example, how the construction of modern human infrastructure transforms the economic system and personal lives. Odling-Smee *et al.* argue that evolutionary theory needs to represent this coupling, and to do so use coupled equations of the form:

$$\frac{dG}{dt} = f\left(G,C,E\right) \tag{B.1}$$

$$\frac{dC}{dt} = g\left(G,C,E\right) \tag{B.2}$$

$$\frac{dE}{dt} = h\left(G,C,E\right) \tag{B.3}$$

where *dG*/*dt*, *dC*/*dt* and *dE*/*dt* represent changes in genetic, cultural and environmental features, respectively. An organism might have a genetically controlled trait, G, such as reflex speed, and a learned or "cultural" trait, C, such as certain foraging habits. Finally the results of these traits are expressed relative to the nature of the environment, E, to determine the evolutionary success of that organism. As the equations show, the evolution of each and every component depends upon the state of all three.

The series of models that Odling-Smee *et al.* consider include a cultural trait with two variants, (niche constructing, E, and non-niche constructing, e), and a diploid genotype with two alleles (one favoured by high resource levels, A, and one favoured by low resource levels, R). The resource level at time *t* is defined as

$$R_t = \sum_{i=t-n+1}^{t} \pi_i x_i \tag{B.4}$$

where R_t is the state of the resource at time *t*. The right hand side of the expression sums the niche constructing activities over *t*-*n*+1 to t past generations. π_i is a weighting function (several are considered in different analyses) and x_i is the frequency of the niche constructing cultural type *E*. In this way environmental history is explicitly included in determining the future outputs of behavioural evolution.

Furthermore, the evolution of organisms is governed by the fitness of the six possible combinations of cultural type (E or e) and genotype (AA, Aa or aa). For example, the fitness of an EAA type (niche constructing high-resource homozygote) is

$$w_{11} = \alpha_1\eta_1 + \varepsilon R \tag{B.5}$$

and the fitness of the eaa type (non-niche constructing low-resource homozygote) is

$$w_{32} = \alpha_3\eta_2 + \varepsilon(1-R) \tag{B.6}$$

where the w_{ij} are the fitnesses of the *i*th genotype and *j*th culture type, α_j represents a component of fitness contributed by having the cultural variant *E* or e and η_i is the component fitness attributable to the genotypes. This first term on the right hand side, $\alpha_j\eta_i$ represents components of fitness independent of niche construction. The second term including ε represents the effect of niche construction. ε is a weighting factor that adjusts the strength of the niche construction effect. The models also include the possibility of biased cultural transmission. That is, considering only parent to child transmission for simplicity, Odling-Smee *et al.* analyse cases with pairs of parents of different cultural types (one is *E* and the other *e*) where the result is not the even average transmission of either *E* or *e* to their offspring with probability ½ but rather a biased transmission of *E* with probability *b* and *e* with probability 1-*b*, where *b*≠½.

Among the interesting results of models developed with this framework, cases arise in which cultural niche construction generates a counter selection that reverses the effect of independent selective forces. Examples of such cases are common. Cures for diseases allow selection to economize on costly adaptations needed to fight the disease. So long as malaria is controlled in North America the frequency of the gene responsible for sickle cell anemia will decrease. This is contrasted to parts of Africa where the frequency of the gene is high despite the near-lethal effects of the sickle cell gene on homozygotes because it protects against malaria in heterozygotes.

Appendix C

Logistic and Lotka–Volterra models

Standard logistic ecological models have been used to describe social dynamics by a number of authors (Richerson and Boyd 1998; Erickson and Gowdy 2000; Richerson *et al.* 2001; Turchin 2003). Here we present Turchin's (2003) model of the relationship between collective solidarity and geopolitical organization. The models used two coupled equations to represent collective solidarity, S, and scale of geopolitical organization, A. The change in the size of a state is described as $\dot{A}$,

$$\dot{A} = c_0 AS\left(1-\frac{A}{h}\right) - a \tag{C.1}$$

where c_0 is the effect of human capital or solidarity on geopolitical power of a state, *h* is the spatial scale over which geopolitical force is projected, and *a* is the geopolitical pressure from neighbouring groups, and assumed to be constant in this case. In this way the success of a state is a function of the size of the state and the capacity for collective action of its populace. Further defining the dynamics of that capacity S,

$$\dot{S} = r_0\left(1-\frac{A}{2b}\right)S(1-S) \tag{C.2}$$

where r_o is the maximum growth rate of solidarity, which Turchin argues usually occurs at the border or frontier region of a state, and *b* is the size of that frontier.

Turchin's model describes the expansion and collapse of empires based on the dynamics of the cultural variable of collective solidarity. Depending on values of *h* and *b*, a possible result is the initial growth of both solidarity and the state. The state soon runs into logistic limitations as the size of the state, A, increases over the limit, 2*b*, and solidarity, S, begins to decline. Declining solidarity leads to a weakened state, which begins to shrink and eventually collapses because it is no longer able to maintain geopolitical cohesion under pressure from outside polities, *a*. After a time, solidarity begins to rise again as conditions return to the frontier situation, and a new state may grow again. This scenario results from when $b < h/4$, or the size of the frontier is too small relative to the area over which political power is exercised to maintain a stable empire. Specifically empire size must be large in relation to frontier areas for boom–bust cycles to occur. Models such as this allow qualitative predictions that can be tested directly against historical data, and as they use the Lotka–Volterra framework, they can be easily coupled with environmental resource dynamics or species populations.