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Research

Sustainability of Human Ecological Niche Construction

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ABSTRACT. Humans influence and depend on natural systems worldwide, creating complex societal-ecological feedbacks that make it difficult to assess the long-term sustainability of contemporary human activities. We use ecological niche theory to consider the short-term (transient) and long-term (equilibrium) effects of improvements in health, agriculture, or efficiency on the abundances of humans, our plant and animal resources, and our natural enemies. We also consider special cases of our model where humans shift to a completely vegetarian diet, or completely eradicate natural enemies. We find that although combinations of health, agriculture, and efficiency improvements tend to support more people and plant resources, they also result in more natural enemies and fewer animal resources. Considering each of these improvements separately reveals that they lead to different, and sometimes opposing, long-term effects. For example, health improvements can reduce pathogen abundances and make it difficult to sustain livestock production, whereas agricultural improvements tend to counterbalance these effects. Our exploratory analysis of a deliberately simple model elucidates trade-offs and feedbacks that could arise from the cascading effects of human activities.

Key Words: *agriculture; human health; niche theory*

INTRODUCTION

Humans are influencing natural systems worldwide (Chapin et al. 1997, 2000, Vitousek et al. 1997, Tilman 1999) and humans depend on natural systems (Daily 1997, Millennium Ecosystem Assessment 2005, Kareiva et al. 2011). One great challenge of our time is to understand these feedbacks enough to determine a safe operating space for a rapidly growing human population on a finite planet (Daily et al. 2009, Rockström et al. 2009, Foley et al. 2011, Tilman et al. 2011, Ehrlich et al. 2012). For example, it is estimated that crop production would need to double by 2050 to keep up with human population growth, changes in diets, such as increased meat consumption, and increases in bioenergy use; and it has been proposed that agricultural improvements and diet shifts away from meat could accomplish this without devastating the environment (Foley et al. 2011, Tilman et al. 2011, Mueller et al. 2012). Here we use simple ecological models to consider both short-term transient dynamics, which could indicate the contemporary consequences of such changes in human behavior, and long-term equilibrium dynamics, which could indicate sustainability constraints operating over the course of human history.

Simple ecological models have offered unique insights and general rules regarding the long-term dynamics of many complex systems (May 1976, Tilman 1982, Leibold 1996, Holt and Polis 1997, van Nes and Scheffer 2004, Loreau 2010, Kylafis and Loreau 2011). We build on previous ecological theory considering omnivory (Holt and Polis 1997) and niches (Leibold 1996, Kylafis and Loreau 2011) to explore the cascading effects, long-term consequences, and limits of human niche construction. We consider a deliberately simple model to rigorously explore a few cascading effects and feedbacks between humans and the species with which humans most strongly interact.

There are multiple schools of thought regarding global human carrying capacity (Cohen 1995). First, the "fewer forks" school emphasizes that decreases in population growth may be necessary to ensure that we do not exceed biophysical limits. For example, it may be necessary to reduce fertility rates (Ehrlich et al. 2012) by expanding and improving education (Lutz and K.C. 2011) to avoid exceeding planetary boundaries (Rockström et al. 2009). Second, the "bigger pie" school emphasizes that improvements in technology may allow continued population growth without exceeding biophysical limits. For example, as George H. W. Bush, the 41st President of the United States, pointed out, "every human being represents hands to work, and not just another mouth to feed" (Cohen 1995). Many previous investigations of human carrying capacity have ignored either physical limits or technological improvements (Cohen 1995). Furthermore, most approaches for considering human carrying capacity are static (Cohen 1995), and thus do not allow consideration of negative or positive system feedbacks. Ecological niche construction theory provides a dynamic framework for considering how humans might use technology, or otherwise change behavior, to increase human carrying capacity within biophysical constraints.

Modern ecological niche construction theory considers both the influence and dependence of a species on its environment. Early niche concepts focused either on species requirements (Grinnell 1917) or species impacts (Elton 1927). Modern niche theory has bridged these early niche concepts to consider both species responses to, and influences on, ecosystems (Leibold 1995, 1996, Chase and Leibold 2003). This theory has recently been extended to consider ecological niche construction, which can be defined as a process by which an organism improves its environment to enhance its growth and persistence (Kylafis and Loreau 2011). Although human niche construction has been rigorously considered in anthropology (Laland and O'Brien 2010, Riel-Salvatore 2010, Kendal et al. 2011, Lansing and Fox 2011, Riede 2011, Smith 2011, Vigne 2011) and evolutionary biology (Odling-Smee et al. 2003, Laland and Sterelny 2006, Odling-Smee 2010), it has not yet been explored within the current theoretical framework for ecological niche construction. Doing so may provide a predictive framework for considering the influence and

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dependence of humans on natural systems, allowing consideration of both technological improvements and biophysical limits.

We begin to develop a theoretical framework that could be used to consider the complex feedbacks between humans, our plant and animal resources, and our natural enemies. We determine how improvements in agriculture, health, or resource use efficiency influence the abundances of humans, plant resources, animal resources, and enemies. We also consider special cases of our model where humans shift to a completely vegetarian diet, completely eradicate natural enemies, or share natural enemies with animal resources, such as zoonotic infections. First, we include humans in a simple, analytically tractable ecosystem model to explicitly describe the influence and dependence of humans on the other biotic components of natural systems. Second, we define constraints on the human ecological niche, including both its fundamental and realized components. Third, we consider the consequences of human ecological niche construction for human carrying capacity, and for human birth and death rates.

METHODS

Model and assumptions

We considered a simple model ecosystem in which humans are omnivores that consume plant and animal resources. Animal resources compete with humans for plant resources, for example, some crops are used for both food and feed. Plant resources exhibit logistic growth in the absence of consumers. Natural enemies, such as pathogens, reduce human population growth. Such a system can be described by the following dynamical equations:

$$\frac{dP}{dt} = P(r\left(1-\frac{P}{K}\right) - c_{pa}A - c_{ph}H) \tag{1}$$

$$\frac{dH}{dt} = H(c_{ph}f_{ph}P + c_{ah}f_{ah}A - c_{he}E - m_h) \tag{2}$$

$$\frac{dA}{dt} = A(c_{pa}f_{pa}P - c_{ah}H - m_a) \tag{3}$$

$$\frac{dE}{dt} = E(c_{he}f_{he}H - m_e) \tag{4}$$

where the state variables represent biomass compartments (Loreau 2010) for plant resources (*P*), humans (*H*), animal resources (*A*), and natural enemies (*E*); *r* and *K* are respectively the intrinsic growth rate and carrying capacity for plant resources; and biomass in compartment *i* is lost from the system at a rate m_i (which includes both mortality and basal metabolism), consumed by compartment *j* at a rate c_{ij}, and converted into compartment *j* at a rate c_{ij} f_{ij}, where f_{ij} indicates conversion efficiency. In this Lotka-Volterra human niche model, consumer growth is assumed to be proportional to the rate of consumption. Although other functional forms might better represent specific interactions between humans and a particular plant or animal resource, or a particular natural enemy, we consider a simple and generic representation of human interactions with these broad groups of species.

This model assumes that if a natural enemy is present, then it depends entirely on humans, and does so in a classical density-dependent way. This first assumption will not hold for zoonotic infections that are shared between humans and animal resources. Note, however, that although many emerging zoonotic infections have high case fatality rates, their absolute incidence remains low (World Health Organization 2012). Thus, this first assumption may be an acceptable initial approximation. The incidence of zoonotic infections may increase in the future if human behaviors that promote zoonotic infections, for example, bush-meat hunting, farming, and trade of wild animals, become increasingly common, or if new zoonotic infections continue to emerge. If this occurs, then it may be best to instead assume that humans and animal resources share natural enemies. We relax this first assumption and use numerical simulations to consider zoonotic infections. The first assumption will also not hold when human hosts are variably susceptible (S), infected (I), or resistant (R). Future studies could relax this assumption by considering multiple human compartments, such as assuming S-I-R dynamics for human hosts. Rather than precisely describing the dynamics of any particular natural enemy, such as a specific pathogen that is particularly important today or a specific predator that might have been important during early human history, here we consider a general and deliberately simple specification that roughly describes the total long-term effects of natural enemies.

This model also assumes that humans and animal resources depend entirely on the same plant resources. This second assumption will not hold when animal resources have plant resources that are not shared with humans, such as forage, nor when humans have plant resources that are not shared with animal resources. Note, however, that more than one-third of crops produced worldwide (on a mass basis) are used for animal feed (Foley et al. 2011), including major cereal grains such as maize. Thus, given that many plant resources are shared between humans and our animal resources, this second assumption may also be an acceptable initial approximation. Future studies could relax this assumption by considering multiple shared or nonshared plant resource compartments.

Analytically defining the human niche and simulating niche construction

We first analyzed the model analytically to identify factors with long-term effects on the abundances of humans, plant and animal resources, and natural enemies. We analytically determined the equilibrium abundances and feasibility conditions for all compartments at all equilibriums where humans were present. Boundary equilibriums were investigated in previous studies (Leibold 1996, Holt and Polis 1997). We also defined the conditions for the human fundamental niche, as was previously done for nonhuman species (Leibold 1995, 1996, Chase and Leibold 2003). We used the Solve, D, and Reduce functions in Mathematica 8 (Wolfram Research Inc., Champaign, Illinois, USA) to obtain these analytical results.

We also numerically simulated various types of human ecological niche construction, including improvements in agriculture, health, and the efficiency of resource consumption, to compare their short-term and long-term effects on the abundances of humans, plant, and animal resources, and natural enemies. We considered the consequences of improvements in health care by considering the effects of increasing the intrinsic mortality rate of enemies (m_e), such as by increased use of antibiotics, or of decreasing the rate that humans are attacked and converted to enemies ($c_{he}f_{he}$), such as by increased use of vaccinations. We considered the consequences of improvements in agriculture by considering the effects of increasing the plant intrinsic growth rate (r), such as by intensification of agriculture, or of increasing the plant carrying capacity (K), such as by the extensification of agriculture. We considered the consequences of humans consuming fewer resources per person by considering the effects of increasing the efficiency that plants (f_{ph}) or animals (f_{ah}) are converted to humans. Note that increasing these conversion efficiencies corresponds to more humans being produced by a given amount of resources, or, equivalently, to fewer resources producing a given amount of people. After considering the case assuming no zoonotic infections, we repeated these human niche construction simulations with shared natural enemies between humans and animal resources. We did so by adding the term $c_{ae}f_{ae}AE$ to equation (4), and subtracting the term $c_{ae}AE$ from equation (3), considering cases where humans were either more ($c_{ae} > c_{he}$) or less ($c_{ae} < c_{he}$) able to resist natural enemies than animal resources. A full stability analysis of the interior equilibrium was intractable; however, we used numerical simulations to consider regions of parameter space that were known to lead to transitions between stable and unstable dynamics for the enemy-free web (Holt 1997, Holt and Polis 1997). We used the lsoda function in the deSolve package of R version 2.15.3 (R Core Team 2013) to obtain numerical simulation results.

RESULTS

Defining the human niche

A two-dimensional fundamental niche can be defined by the zero net growth isocline of the focal species (Leibold 1995, 1996, Chase and Leibold 2003, Kylafis and Loreau 2011). When there are three niche factors (E, P, A), a plane (rather than a line) describes zero net growth of the focal species in niche space, i.e., state space of niche factors, and the fundamental niche can be defined as the volume (rather than the area) on the side of this zero net growth isoplane (ZNGI) where population growth is positive. As in a two-dimensional niche, the ZNGI describes the abundances of the niche factors (E, P, A) when the focal species (H) is at equilibrium. We obtained the human ZNGI by setting the dynamical equation for humans (equation 2) to zero. This allowed us to define the human fundamental niche as the set of conditions where the density of enemies is sufficiently small compared to the density of plant and animal resources:

$$E \leq \frac{c_{ph}f_{ph}P + c_{ah}f_{ah}A - m_h}{c_{he}} \quad (5)$$

Thus, the human population can persist only where and when the negative effects of enemies on human population growth are small compared to the positive effects of plant and animal resources on human population growth. Intuitively, this also suggests that health and agricultural improvements could be considered human niche construction to the extent that they promote persistence, i.e., non-negative growth at positive abundance, of the human population.

Humans will persist under only some of the conditions included in the human fundamental niche if other competing species are also present. A species' realized niche is constrained by the requirements and impacts of its competitors with respect to shared resources and enemies (Leibold 1995, 1996, Chase and Leibold 2003, Kylafis and Loreau 2011). That is, other species may constrain the areas of the human fundamental niche where resources are sufficient for humans by decreasing resources, increasing enemies, or both. In our model ecosystem, animal resources compete with humans for plant resources. Thus, the long-term abundance and persistence of humans may depend on the requirements and impacts of animal resources with respect to shared plant resources. Furthermore, humans might coexist with animal resources that compete for plant resources under only some of the conditions included in the human realized niche. We next analytically consider such constraints on the human fundamental and realized niches by determining feasibility conditions for relevant equilibriums in our model (Table 1).

At the interior equilibrium in the full web, the human and plant resource compartments will always have a positive abundance (here and henceforth, we assume that all parameters are positive; Table 1). In this case, feasibility for the animal resource compartment further requires a sufficiently large intrinsic plant growth rate:

$$r > \frac{c_{ph}KH_f^*}{K - P_f^*} \quad (6)$$

and sufficiently large intrinsic plant carrying capacity in the absence of consumers:

$$K > P_f^* \quad (7)$$

Feasibility for the enemy compartment further requires a sufficiently small human loss rate:

$$m_h < c_{ah}f_{ah}A_f^* + c_{ph}f_{ph}P_f^* \quad (8)$$

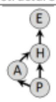
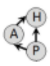
The interior equilibrium will be feasible when all of these conditions (inequalities 6-8) are met. The stability of the interior equilibrium will be discussed below, in the context of human niche construction.

The boundary equilibrium in the enemy-free web represents the special case where humans have completely eradicated all natural enemies (Table 1). This omnivory, or intraguild predation, web has been well studied (Holt and Polis 1997). In this case, feasibility for the plant compartment requires an efficient indirect pathway of resource flow from plant resources to humans through animal resources, as indicated by:

$$f_{ah} > \frac{c_{pa}m_h}{rc_{ah} + c_{ph}m_a} \quad (9)$$

and:

Table 1. Abundances of humans, plant resources, animal resources, and natural enemies at four equilibriums where humans are present.

	Web structure	Humans (H*)	Plant resources (P*)	Animal resources (A*)	Enemies (E*)
Full web (f)		$H_f^* = \frac{m_e}{c_{he} f_{he}}$	$P_f^* = \frac{c_{ah} H_f^* + m_a}{c_{pa} f_{pa}}$	$A_f^* = \frac{r(K - P_f^*) - c_{ph} K H_f^*}{c_{pa} K}$	$E_f^* = \frac{c_{ah} f_{ah} A_f^* + c_{ph} f_{ph} P_f^* - m_h}{c_{he}}$
Enemy-free (u)		$H_u^* = \frac{c_{pa} f_{pa} P_u^* - m_a}{c_{ah}}$	$P_u^* = \frac{K(r c_{ah} f_{ah} + c_{ph} f_{ah} m_e - c_{pa} m_h)}{r c_{ah} f_{ah} + K c_{pa} c_{ph} (f_{ah} f_{pa} - f_{ph})}$	$A_u^* = \frac{m_h - c_{ph} f_{ph} P_u^*}{c_{ah} f_{ah}}$	0
Vegetarian (v)		$H_v^* = \frac{m_e}{c_{he} f_{he}}$	$P_v^* = K\left(1 - \frac{c_{ph} H_v^*}{r}\right)$	0	$E_v^* = \frac{c_{ph} f_{ph} P_v^*}{c_{he}} - \frac{m_h}{c_{ph}}$
Enemy-free Vegetarian (uv)		$H_{uv}^* = \frac{r}{c_{ph}}(1 - \frac{P_{uv}^*}{K})$	$P_{uv}^* = \frac{m_h}{c_{ph} f_{ph}}$	0	0

$$f_{pa} \geq \frac{f_{ph}}{f_{ah}} \tag{10}$$

Alternatively, if the resource flow from plant resources to humans via animal resources is inefficient (i.e., inequalities 9 and 10 are both unmet, which might occur if humans consume mostly beef, which is an inefficient source of calories and protein compared to other animal resources such as chicken), then plant resource feasibility requires a sufficiently large intrinsic plant carrying capacity:

$$K > \frac{r c_{ah} f_{ah}}{c_{pa} c_{ph} f_{ph} - c_{pa} c_{ph} f_{ah} f_{pa}} \tag{11}$$

If the plant compartment is feasible, then human persistence further requires a sufficiently large equilibrium abundance of plant resources:

$$P_u^* > \frac{m_a}{c_{pa} f_{pa}} \tag{12}$$

If the plant compartment is feasible, then feasibility for the animal resource compartment further requires a sufficiently small equilibrium abundance of plant resources:

$$P_u^* < \frac{m_h}{c_{ph} f_{ph}} \tag{13}$$

Thus, feasibility of the entire enemy-free web, which would allow humans to coexist with animal resources, and thus to continue eating meat, would require an intermediate equilibrium abundance of plant resources (inequalities 12, 13). When the equilibrium abundance of plant resources is too high (violating inequality 13), humans outcompete animal resources for shared plant resources; and when the equilibrium abundance of plant resources is too low (violating inequality 12), then animal resources outcompete humans. Satisfying both inequalities (12 and 13) requires that animal resources be superior competitors for shared plant resources, relative to their loss rate, as previously shown for intraguild predation (Holt and Polis 1997). This boundary equilibrium has domains of both stability and instability (Holt 1997, Holt and Polis 1997).

The boundary equilibrium in the vegetarian web represents the special case where humans do not eat meat (Table 1). This tri-trophic food web has also been well studied (Oksanen et al. 1981, Loreau 2010). In this case, humans will always have positive equilibrium abundance (Table 1). Feasibility for the enemy compartment in the vegetarian web requires a sufficiently large equilibrium abundance of plant resources:

$$P_v^* > \frac{m_h c_{he}}{c_{ph}^2 f_{ph}} \tag{14}$$

Feasibility for the plant compartment in the vegetarian web requires a sufficiently small equilibrium abundance of humans:

$$H_v^* < \frac{r}{c_{ph}} \tag{15}$$

Shifting to a completely vegetarian diet does not increase human carrying capacity because $H^*_f = H^*_v$ (Table 1).

The boundary equilibrium in the enemy-free vegetarian web represents the special case where humans have completely eradicated all natural enemies and do not eat meat (Table 1). These simple consumer-resource interactions have also been well studied (Tilman 1982, Loreau 2010). In this case, plant resources will always have positive equilibrium abundance (Table 1). Humans will persist when plant equilibrium abundance in the absence of humans (K) is larger than that in the presence of humans:

Table 2. Effects of human ecological niche construction on abundances of humans, plant and animal resources, and natural enemies. The first arrows indicate initial transient effects; the second arrows indicate long-term effects on equilibrium abundances. For example, improving agriculture (by increasing r and K in our model) initially increases human population (↑), but has no long-term effect on human population (→).

Type of niche construction:	Parameter changes	Humans	Plant resources	Animal resources	Enemies
Technological innovations					
Improve health	$\downarrow c_{he}$ & $\uparrow m_e$	↑↑	↓↑	↓↓	↓↓
•Immunizations	$\downarrow c_{he}$	↑↑	↓↑	↓↓	↓↑
•Antibiotics	$\uparrow m_e$	↑↑	↓↑	↓↓	↓↓
Improve agriculture	$\uparrow r$ & $\uparrow K$	↑→	↑→	↑↑	↑↑
•Intensification	$\uparrow r$	↑→	↑→	↑↑	↑↑
•Extensification	$\uparrow K$	↑→	↑→	↑↑	↑↑
Behavioral modifications					
Reduced resource consumption	$\uparrow f_{ph}$ & $\uparrow f_{ah}$	↑→	↓→	↓→	↑↑
•Efficient animal consumption	$\uparrow f_{ah}$	↑→	↓→	↓→	↑↑
•Efficient plant consumption	$\uparrow f_{ph}$	↑→	↓→	↓→	↑↑

↑, ↓, or → respectively indicate increases, decreases, or no net effect

$$K > P_{uv}^{*} \qquad (16)$$

See Table 1 for equilibrium abundances of all compartments at equilibriums where humans and plant resources were present.

Consequences of human niche construction

Improvements in health care (i.e., increasing m_e or decreasing c_{he}) increased the equilibrium abundances of humans and plant resources, but decreased that of animal resources in the full web (Tables 1, 2; Fig. 1a-c). In the vegetarian web, these changes increased the equilibrium abundance of humans, but decreased that of plant resources and enemies (Table 1).

Improvements in agriculture (i.e., increasing r or K) had no impact on the equilibrium abundances of humans or plant resources, but increased the equilibrium abundances of animal resources and enemies in the full web (Tables 1, 2; Fig. 1d-f). Although agricultural improvements led to a short-term increased pulse in human abundance, this benefit was later passed on to natural enemies (Fig. 1d-f). Thus, agricultural improvements may allow humans to eat meat (inequalities 6, 7), but may also inadvertently promote natural enemies (Fig. 1d-f). In the enemy-free web, however, extensification of agriculture (i.e., increasing K) increased the equilibrium abundances of humans and plant resources, and decreased that of animal resources (Table 1). In the vegetarian web, improvements in agriculture both increased the equilibrium abundances of plant resources and enemies, and had no effect on human carrying capacity (Table 1). In the enemy-free vegetarian web, improvements in agriculture both increased human carrying capacity and had no influence on the equilibrium abundance of plant resources (Table 1).

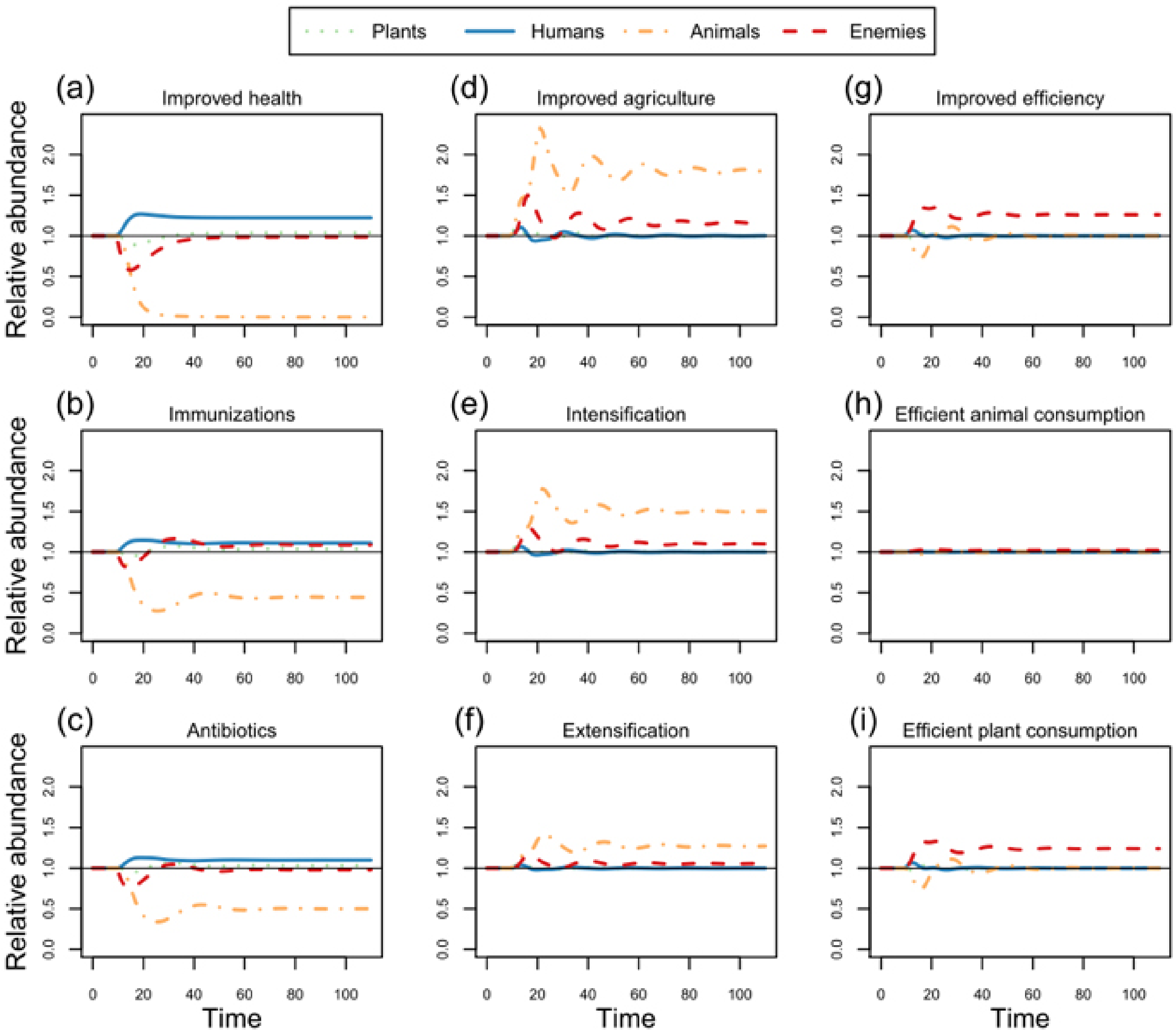
Increased human resource use efficiency (i.e., increased f_{ph} or f_{ah}) had no impact on the equilibrium abundances of humans, plant resources, or animal resources, but increased the equilibrium abundances of enemies in the full web (Tables 1, 2; Fig. 1g-i). Although increased human resource use efficiency initially increased human abundance, this benefit was later passed on to natural enemies (Fig. 1g-i). Increased resource-use efficiency would tend to make it easier for enemies to persist (inequality 8). In the enemy-free web, increased human resource use efficiency increased the equilibrium abundances of humans, but decreased that of animal resources (Table 1). In the vegetarian food web, increased human resource use efficiency increased the equilibrium abundance of enemies, and had no effect on that of humans and plant resources (Table 1). In the enemy-free vegetarian food web, these changes decreased the equilibrium abundance of plant resources, and increased that of humans (Table 1).

Combinations of improvements increased the equilibrium abundance of humans and decreased that of animal resources, except when there were no health improvements (Fig. 2). Combinations of improvements always increased the equilibrium abundance of natural enemies (Fig. 2). Improvements in health, agriculture, and efficiency supported more people and plant resources, but also more enemies and fewer animal resources (Fig. 2d).

Health improvements increased human carrying capacity by decreasing death rates before birth rates (Fig. 3a). Thus, there was a shift to a higher carrying capacity during the demographic transition from higher to lower birth and death rates (Fig. 3a). Simultaneously improving health and increasing consumption (i.e., increasing c_{ph} and c_{ah}) reduced this time lag between declines in death and birth rates, and led to a smaller increase in human carrying capacity during this demographic transition (Fig. 3b).

Combinations of niche constructing improvements had qualitatively similar effects when we allowed zoonotic infections and assumed that animal resources were superior to humans at resisting shared natural enemies (Fig. A1.1). In contrast,

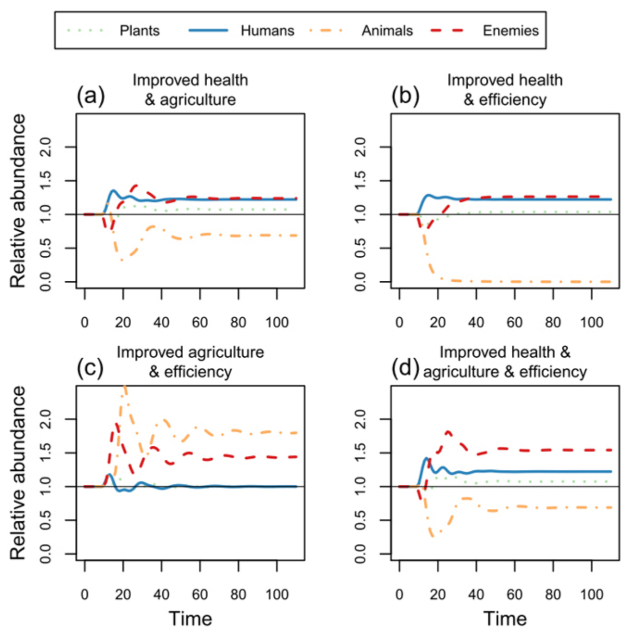
Fig. 1. Effects of improvements in health (a-c), agriculture (d-f), or efficiency (g-i) on the abundances of humans, plant and animal resources, and natural enemies. All state variables were at equilibrium from time 0 to 10, and are shown relative to these equilibrium values. Initial parameter values satisfied the feasibility conditions: c_{he} = 2, c_{pa} = 4, m_h = 0.25, c_{ah} = c_{ph} = f_{ah} = f_{he} = f_{pa} = f_{ph} = m_a = m_e = r = K = 1. At time 10, and thereafter, parameters of interest were changed by 10%. For example, c_{he} was decreased from 2 to 1.8 to consider the effects of decreasing the rate that humans were attacked by enemies (b), or m_e was increased from 1 to 1.1 to consider the effects of increasing the mortality rate of enemies (c), or both health improvements occurred simultaneously (a). All other parameters remained constant over time. Table 2 indicates parameters of interest and direction of change for each scenario.



combinations of improvements had qualitatively different effects when we allowed zoonotic infections and assumed that humans were better able to resist shared natural enemies (Fig. S2). In this case, niche construction more strongly favored humans over animal resources (Fig. A1.2) compared to the case where we assumed no zoonotic infections (Fig. 2). In both cases where we allowed zoonotic infections, transient dynamics following niche constructions were more quickly damped (Figs. A1.1, A1.2) than when we assumed no zoonotic infections (Fig. 2).

Some types of human niche construction and changes in human behavior might destabilize population dynamics. Numerical simulations showed unstable dynamics for the full web in approximately the same region of parameter space where they have been previously reported for the enemy-free web (Holt 1997,

Fig. 2. Effects of combinations of improvements in health, agriculture, and resource use efficiency on the abundances of humans, plant and animal resources, and natural enemies. All state variables were at equilibrium from time 0 to 10, and are shown relative to these equilibrium values. Initial parameter values satisfied the feasibility conditions: $c_{he} = 2$, $c_{pa} = 4$, $m_h = 0.25$, $c_{ah} = c_{ph} = f_{ah} = f_{he} = f_{pa} = f_{ph} = m_a = m_e = r = K = 1$. At time 10, and thereafter, relevant parameters were changed by 10% to consider the effects of combinations of improvements. Parameters were changed as in Figure 1. For example, improvements in agriculture and efficiency (c) consisted of a 10% increase in four parameters (r, K, f_{ah}, f_{ph}) from 1.0 to 1.1, while other parameters remained constant values.

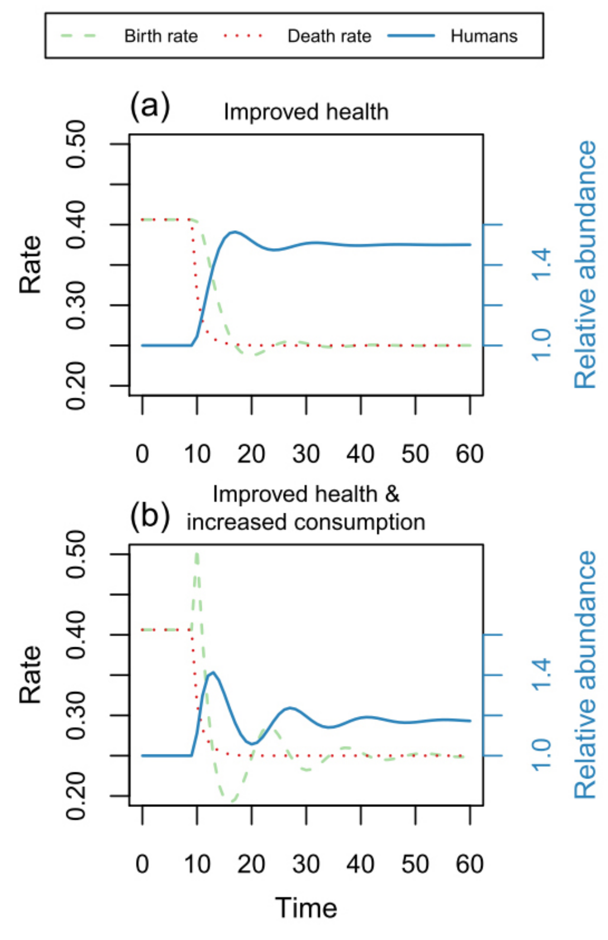


Holt and Polis 1997; Fig. 4). Thus, adding a natural enemy to the intraguild predator will not necessarily stabilize dynamics in food webs with intraguild predation. For example, increasing human plant consumption (increasing c_{ph}), after extensification of agricultural (increasing K), can destabilize dynamics, resulting in large amplitude fluctuations in the abundances humans, our plant and animal resources, and our natural enemies (Fig. 4).

DISCUSSION

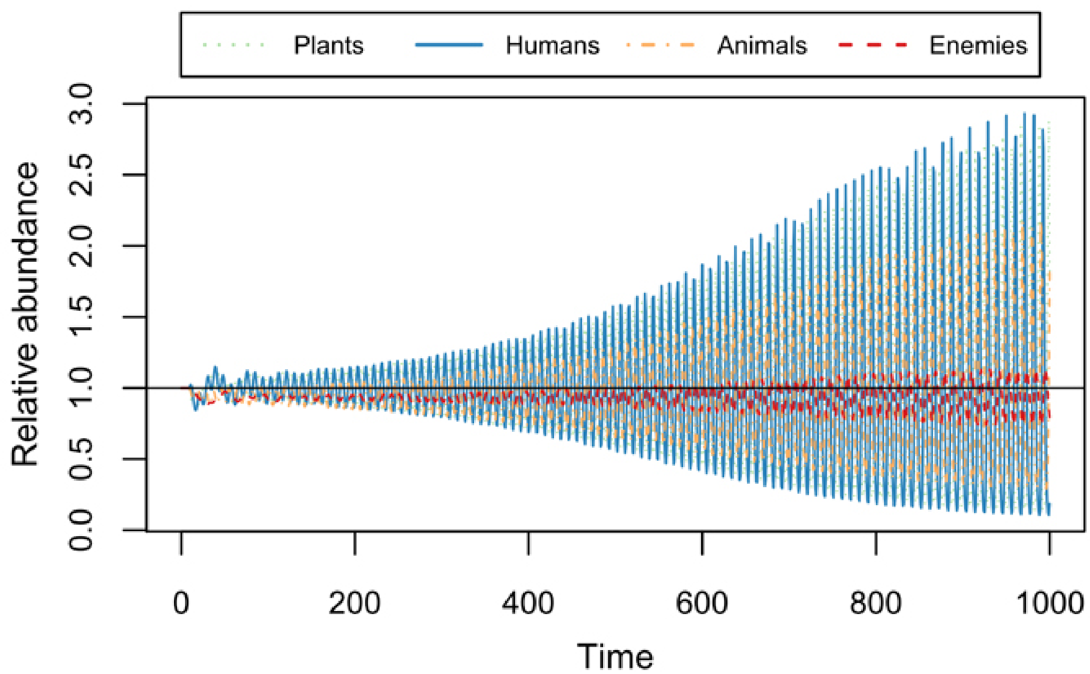
Our results reveal trade-offs and feedbacks that could arise from the cascading effects of human activities. Although it is unlikely that humans would knowingly continue with activities that shift the system toward undesirable outcomes, such as wild population fluctuations or competitive exclusion, human activities could inadvertently shift the system toward undesirable outcomes. Thus, investigations such as ours, which begin to identify the conditions under which social-ecological systems shift toward desirable or undesirable outcomes, might help avoid undesirable outcomes and minimize the need for compensatory actions in the future. Optimal control theory might then be used to identify time-dependent management actions that support sustainability objectives (Shastri et al. 2008).

Fig. 3. Effects of health improvements (a), or both health improvements and increased resource consumption (b), on human birth rate ($c_{ph}f_{ph}P + c_{ah}f_{ah}A$), death rate ($c_{he}E + m_h$), and relative abundance. All state variables were at equilibrium from time 0 to 10, and human abundance is shown relative to its initial equilibrium value. Initial parameter values satisfied the feasibility conditions: $c_{he} = 2$, $c_{pa} = 4$, $m_h = 0.25$, $c_{ah} = c_{ph} = f_{ah} = f_{he} = f_{pa} = f_{ph} = m_a = m_e = r = K = 1$. At time 10, and thereafter, relevant parameters were changed by 40% to consider health improvements (i.e., decrease c_{he} from 2 to 1.2 and increase me from 1.0 to 1.4) (a), or both health improvements and increases in consumption (i.e., decrease c_{he} from 2 to 1.2; increase c_{ah} from 1.0 to 1.4; increase both c_{ah} and c_{ph} from 1.0 to 1.4) (b).



During early human history, resources and natural enemies were likely primary factors limiting human population growth (Finch 2010). That is, human births required sufficient consumption of resources and human deaths were often due to natural enemies, such as pathogens, parasites, or predators. Although these biophysical constraints have been relaxed in more recent human history (Finch 2010), the abundances of resources and natural enemies continue to influence human population growth and well-being. For example, childhood malnutrition and vaccine-preventable diseases are respectively the underlying cause of an estimated 35% and 20% of all deaths among children under five

Fig. 4. Effects of increased human consumption of plant resources on population dynamics. All state variables were at equilibrium from time 0 to 10, and are shown relative to these equilibrium values. Initial parameter values satisfied the feasibility conditions: c_{he} = 0.5, ch_{ph} = 0.01, f_{ph} = 0.3, m_h = 0.5, m_a = m_e = 0.1, K = 10, c_{ah} = c_{pa} = f_{he} = f_{ah} = f_{pa} = r = 1. At time 10, and thereafter, human consumption of plant resources was increased (c_{ph} = 0.3), while other parameters remained constant values. This particular region of parameter space, and particular change in parameter values, corresponds to those previously considered for intraguild predation (Holt 1997, Holt and Polis 1997).



years of age (World Health Organization 2012). Thus, we considered human niche construction mostly as the tweaking of parameters within our model over time, rather than as more substantial structural changes in our model. We also considered boundary equilibriums as special cases of structural changes to our model that may apply to certain enemy-free or vegetarian populations. We encourage future studies to consider how other models and functional responses might better represent these or other limiting factors, such as education, violence/interference, and how incorporating spatial structure and temporal fluctuations might further extend our results and conclusions. The benefits of incorporating such complexity often come at the expense of generality, though, and thus we chose to begin with an exploratory analysis of a deliberately simple model. A potentially useful next step would be to bridge human ecological niche construction theory with slightly more complex models developed to investigate optimal control for sustainable environmental management (Cabezas et al. 2005, Shastri et al. 2008).

Improvements in health and agriculture will likely continue. Between 2000 and 2010, the estimated number of measles deaths decreased by 74%, accounting for about 20% of the overall reduction in child mortality during this time period (World Health Organization 2012). However, there remains room for further improvement because about half of the world's population remains at risk for malaria (World Health Organization 2012); and such vector-borne and parasitic diseases continue to undermine economic development, particularly in tropical countries (Bonds et al. 2012). Between 1960 and 2000, global cereal yields more than doubled (Tilman et al. 2002), and they will need to approximately double again by 2050 to keep up with human population growth, changes in diets, for example, increased meat consumption), and increases in bioenergy use (Foley et al. 2011, Tilman et al. 2011). Our model provides a way to explore some potential short- and long-term consequences of further human niche construction.

What might be some short-term consequences of further improvements in health and agriculture? Our results suggest that improvements in health and agriculture will tend to increase human population in the short-term. The somewhat controversial idea that further agricultural improvements will promote short-term human population growth, rather than simply allowing humans to keep up with demographically inevitable demand for food (Foley et al. 2011, Tilman et al. 2011), may deserve further consideration. Childhood malnutrition is currently the underlying cause of an estimated 35% of all deaths among children under five years of age (World Health Organization 2012). Increasing food production could promote short-term population growth by decreasing such deaths, and by increasing the associated births that result from these individuals surviving until reproductive maturation. If so, then agricultural improvements might be better viewed as short-term strategies for supporting more people than as long-term solutions for sustainably meeting resource needs. On the other hand, if childhood malnutrition is not so severe that it results in mortality, but severe enough to stunt physical and mental development, then such agricultural improvements might be essential for escaping a poverty trap. Our simple ecological models do not consider such social feedbacks, which could strongly reinforce or offset the biophysical feedbacks explored here.

What might be some long-term consequences of further improvements in health and agriculture? Our results suggest that health improvements could increase human carrying capacity, and could also result in a lasting decrease in human birth and death rates. At the two equilibriums where enemies were present, health improvements increased human carrying capacity (Table 1). This occurred by decreasing human death rates before decreasing human birth rates, resulting in a transient period of rapid human population growth (Fig. 3a). Thus, our process-based model shows one mechanism by which the demographic transition can occur in human populations (Davis 1945).

Our results also suggest that agricultural improvements might not increase human carrying capacity, except in the special cases where humans completely eradicate natural enemies. When enemies are present, agricultural improvements could be passed through humans to natural enemies. Thus, agricultural improvements could produce a pulse of people that subsequently produces a sustained increase in enemies (Fig. 1d-f). More generally, human trophic position likely has a strong influence on human carrying capacity, because equilibrium abundances tend to be highest when a species (or trophic level) is at the top of a food chain, and lowest when it is just below the top (Hairston et al. 1960, Carpenter et al. 1985, Loreau 2010). Our results highlight the importance of considering trophic cascades and trophic positions (Hairston et al. 1960, Carpenter et al. 1985, Loreau 2010) when investigating human population growth and human carrying capacity, and when including humans in ecosystem models to investigate sustainability (Cabezas et al. 2005).

Although agricultural improvements might not increase human carrying capacity, they could allow people to continue eating meat. At the two equilibriums where animal resources were present (Table 1), agricultural improvements promoted persistence of animal resources (inequalities 6, 7). Humans are omnivores, and thus the benefits from improving plant resources are shared with animal resources. The relative competitive abilities of humans and animal resources for shared plant resources determine how much improvement in agriculture is needed to ensure that humans do not outcompete animal resources. For example, health improvements could shift the competitive advantage in the favor of humans over animal resources (Fig. 1a-c), and compensatory agricultural improvements may then be needed to sustain meat production (Fig. 2a). These relative competitive abilities also depend on intrinsic species-specific stoichiometric constraints, and on more plastic decisions regarding how much land is allocated to produce food or feed, which in turn depends on production costs and demand for meat and dairy products. Our results highlight the importance of considering complex biophysical feedbacks that can occur in systems with omnivores (Holt and Polis 1997) when investigating the long-term consequences of agricultural improvements.

Humans have a unique ability to make choices that optimize within biophysical constraints (Shastri et al. 2008). First, we might decide whether we wish to increase human carrying capacity. Our model suggests that we might do so by improving health care. Second, we might decide whether we wish to continue eating meat. Our results suggest that agricultural improvements might be necessary to sustainably continue consuming meat. Third, we might decide whether we wish to decrease both birth and death rates. We found that health improvements might do so, and that increased per capita consumption might further speed up the otherwise lagging decrease in birth rates. Together, these results suggest that a simultaneous combination of health improvements, agricultural improvements, and increased consumption might allow more people to sustainably consume more plants and meat, while experiencing lower birth and death rates; however, the associated cost might be large population fluctuations. We do not wish to promote this social agenda, and certainly not based on results from our single and simple model; however, we hope that extensions of our model can help inform such conversations in the future. Given the immense efforts underway worldwide to further improve agriculture and health, and to further increase consumption, we believe it is important to develop a theoretical framework for considering the long-term consequences of such activities. Further empirical work is needed to determine whether our model adequately represents reality, and which regions of parameter space are most relevant. Further theoretical work is needed to consider other models that might better represent reality. Together these studies could then provide insights regarding where contemporary human niche constructing activities might lead us in the future.

We emphasize that these anthropocentric decisions also have consequences for nonhuman species. For example, human niche constructing activities would likely result in a greater proportion of primary productivity being allocated to humans, consistent with recent trends (Vitousek et al. 1986, Imhoff et al. 2004, Haberl et al. 2007), thus reducing that available for the rest of life. In general, we suspect that activities that increase the equilibrium abundances of humans and our resources will tend to decrease that of other species, resulting in further biodiversity declines that will subsequently reduce the services that ecosystems provide for people (Balvanera et al. 2006). Further development of human ecological niche construction theory may provide a framework for investigating such trade-offs and the feedbacks of contemporary human activities on future human well-being.

Responses to this article can be read online at:
http://www.ecologyandsociety.org/issues/responses.php/6395

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Appendix 1. Sustainability of human ecological niche construction.

Supplementary figures considering human niche construction with zoonotic infections.

Figure A1.1. Effects of improvements in health, agriculture, and/or resource use efficiency on the abundances of humans, plant and animal resources, and shared natural enemies (e.g., zoonotic infections). As in Figure 2, except that the term $c_{ae}f_{ae}AE$ was added to equation 4 and the term $c_{ae}AE$ was subtracted from equation 3. Here we assume that humans were less able to resist the shared natural enemies ($c_{ae} = 1 < c_{he} = 2$).

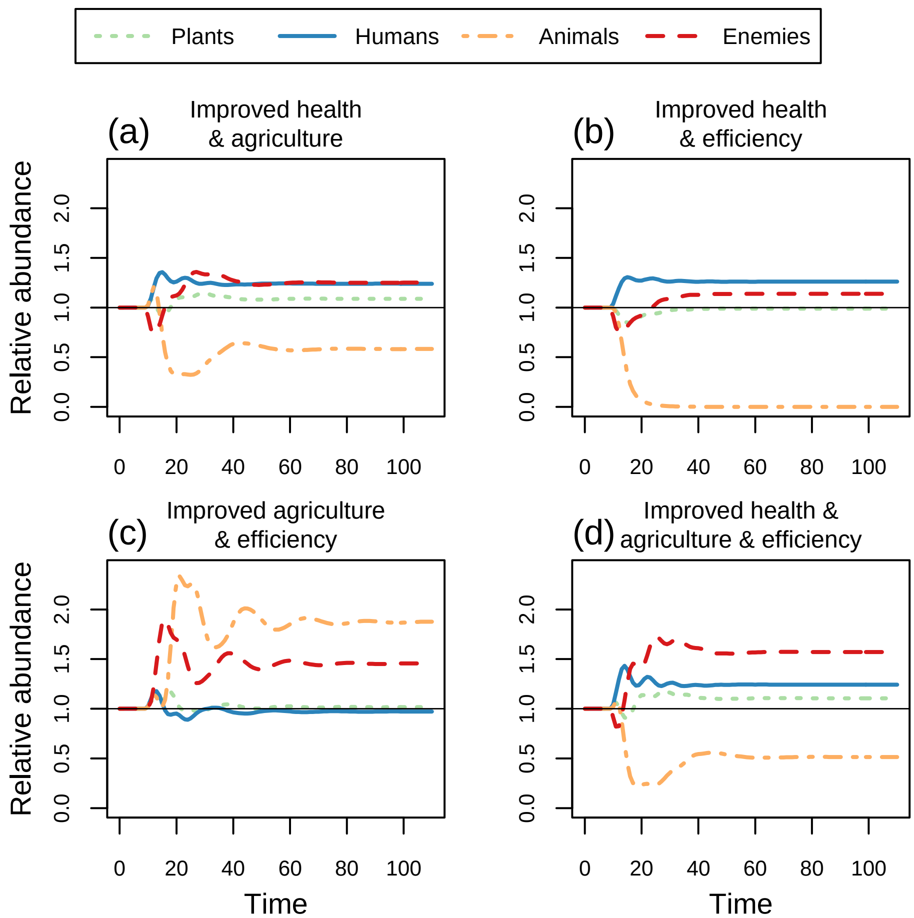

Figure A1.2. Effects of improvements in health, agriculture, and/or resource use efficiency on the abundances of humans, plant and animal resources, and shared natural enemies (e.g., zoonotic infections). As in Figure 2, except that the term $c_{ae}f_{ae}AE$ was added to equation 4 and the term $c_{ae}AE$ was subtracted from equation 3. Here we assume that humans were superior at resisting the shared natural enemies ($c_{ae} = 3 > c_{he} = 2$).