

The Evolution of an Ecosystem: Pleistocene Extinctions

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Abstract

It is generally assumed that evolution is an issue of looking at how a species fits into its environment. This over-constrains our thinking; we should look at how the species and the ecosystem evolve together.

The current theories of the Pleistocene extinction (Climate change and Overkill by H. sapiens) are inadequate. Neither explains why: (1) browsers, mixed feeders and non-ruminant grazer species suffered most, while ruminant grazers like bison generally survived, (2) surviving mammal species, including both subspecies of bison, were sharply diminished in size; and (3) vegetative environments shifted from plaid to striped (Guthrie, 1980).

In addition, climate change theories do not explain why mammoths and other megaherbivores survived changes of similar magnitude. Although flawed, the simple overkill hypothesis does link the extinctions and the arrival of H. sapiens. However, it omits the reciprocal impact of prey decline on H. Sapiens; standard predator-prey models, which include this effect, demonstrate that predators cannot hunt their prey to extinction without themselves succumbing to starvation.

*An alternate scenario and computer simulation (download at <http://quaternary.net>) characterized by a boom/bust population pattern is presented. It suggests H. sapiens reduced **predator** populations, causing a herbivore population boom, leading to overgrazing of trees and grass, resulting in environmental exhaustion and extinction of herbivores. If true, bison survival and differentiation into two subspecies, (B. bison bison [plains bison] and B. bison athabasca [woodland bison,] through the Pleistocene may be accounted for thus: environmental exhaustion selectively favors animals that could extract maximum energy from low quality forage to survive and reproduce the split into sub species is a reflection of the new vegetative environment.*

Background

At the end of the last ice age, the Pleistocene, the New World experienced a severe extinction of large animals. Mammoths, mastodons, giant beavers and giant ground sloths went extinct. New world horses and camels though not as large also went extinct.

There are two theories put forward to explain these extinctions – climate change and overkill by humans. Neither is satisfactory. Climate change theories are unsatisfactory because the animals survived previous changes of similar magnitude. The overkill theory is unsatisfactory because predators cannot hunt their prey to extinction without starving themselves.

There are also observations about the pattern of extinction that cannot be accounted for by either theory.

A shift in the vegetation pattern from plaids – patchy mixed woodland – to stripes – closed canopy forest near the mountains, unbroken grassland in the center and tundra in the north of the continent (Guthrie, 1989).

A bias in favor of small size and for ruminants observed in many species including bison.

The extinction of cecal digesters, like horses, that should not have suffered from climate change, since they can live in the environment today.

And, the extinction of animals that were not hunted by *H. sapiens* – the Shasta ground sloth (*Nothrotheriops shastensis*). Hansen's (1978) study of sloth dung and the surrounding environment from Rampart cave shows no evidence of climate change but does show that the diet of the sloth changed showing less and less of its staple, globemallow (*Sphaeralcea ambigua*), and more and more Mormon tea (*Ephedra navadensis*), its less preferred food. Globemallow is used by other herbivores and Mormon tea is not.

Hypothesis

Imagine the following scenario:

Homo sapiens enters the New World. The introduction of a new predator, *H. sapiens*, reduces the number of herbivores available to each of the existing predators.

Predators who are unable to find enough to eat and who have no experience with *H. sapiens* prey on *H. sapiens*.

***H. sapiens* reduces predator populations**

In revenge and to cut down on competition, *H. sapiens* establishes a policy of killing predators. Through this policy, predator populations are reduced below the level where they are able to control herbivore populations. Herbivore populations boom.

H. sapiens populations expand, but more slowly than the predators they kill because humans recruit more slowly. *H. sapiens* does not control herbivore populations as well as the now scarce predators did formerly.

Herbivores boom and exhaust the environment

Herbivore populations overgraze the environment. Herbivores are forced to eat their less preferred foods. Mammoths and mastodons knock over trees, eventually turning mixed parkland into grassland (Wing and Buss, 1970).

Without sufficient food, herbivore populations crash (Leader-Williams, 1980; May, 1973; Scheffer, 1951).

As *H. sapiens* populations begin to experience food stress and competition with non-human predator becomes more important, predator killing increases.

In the denuded environment, herbivores that can get the most nutrition and reproduce soonest from resources which recruit quickly are selectively favored – bison. *H. sapiens* populations have been decimated. Relict groups establish new life ways. The new Holocene equilibrium is established (Whitney-Smith, 1995).

Methods

Two system dynamics computer models were designed as a test of the hypothesis presented above. Assumptions: (1) ecosystems are generally in equilibrium, (2) vegetation continues to grow until it fills up the available area, (3) each sector of the ecosystem (predator, herbivore, *H. sapiens*) is dependent upon its food source, and (4) the food source is depleted by the populations which use it.

The steps in the simulation are: 1 – Establish an equilibrating ecosystem with three sectors; Plants, herbivores, and predators, 2a – Introduce *H. sapiens* as a second predator, 2b – Link the *H. sapiens* sector and the predator sector to simulate *H. sapiens* killing predators – (Second Order Overkill), 3 – Build a model with vegetation partitioned into big and small trees, high and low quality grass; herbivores partitioned into browsers, mixed feeders and ruminants and non-ruminant grazers.

Values used in these simulations: are based directly on those used by Whittington and Dyke (1989). Some of the values have had to be modified to fit the model. For example, Whittington and Dyke (1989) use a 0.25 recruitment rate which is represented by a birth and death rate which results in a 0.25 recruitment rate.

The hunting rate used in the simulation presented in this paper is based on food needed per pound of predator per year. Data from extant predators suggests 20 pounds of food per pound per year (International Wolf Center, 1996; Cat House, 1996; Petersen, 1977; Schaller, 1972). It is assumed that *H. sapiens* requires half the amount of meat that an obligate predator needs. A number of values were derived by running the model with approximated values until the model reached equilibrium. The initial division between trees and grass is arbitrarily set at 50%.

Modeling paradigm: Each of the sectors in all of the models take a similar form: The amount of stock in the sector at any given time is determined by the amount of stock in the sector at the previous time times some growth rate, discussed above, modified by the limit of that sector and minus the death rate and the hunting or consumption rate. Birth and death rates are modified by available resources for the members of the sector. Thus herbivores are limited by the amount of plants times the efficiency rate for that animal.

Hunting values are based on density of prey. If prey is sufficiently dense, predators it will kill all the prey they desire and reproduce at their biological maximum. If prey is

less dense than the predator population is not able to recruit at its biological maximum. Over time the system stabilizes where predator, prey and plant populations are in balance.

Results – Steps 1 & 2

The first step is to establish a stable ecosystem with three sectors; plants, herbivores, and carnivores (Figure 1a). Since the goal of this step is a stable ecosystem, the model was perturbed and subsequently returned to normal.

The second step is a model with a second predator, *H. sapiens*. It is broken into two parts.

Step 2a introduces *H. sapiens* as a second predator. *H. sapiens* enters the New World - 11500 BP, 100 years after the start of the model. Figure 1b shows the impact of a second predator – the overkill hypothesis.

Herbivores decreased less than predators, and food for predators increased. At the end of the model predator populations are 59% of what they were when the model started; Herbivore populations are 63% and Plants has increased to 103% of the starting value (there are fewer herbivores therefore there are more plants). It has been assumed that *H. sapiens* needs half the food per year per pound (10 lb.) than non-human predators. *H. sapiens* is considered to be as effective a hunter as are non-human predators. As in the Whittington and Dyke model *H. sapiens* is 200 individuals at year - 11500 BP. Each person is 100 lb. of biomass.

Step 2b is the position of the scenario presented above. It links the *H. sapiens* sector and the predator sector to simulate *H. sapiens* killing predators – (second order predation – 2op) (Figure 1c)

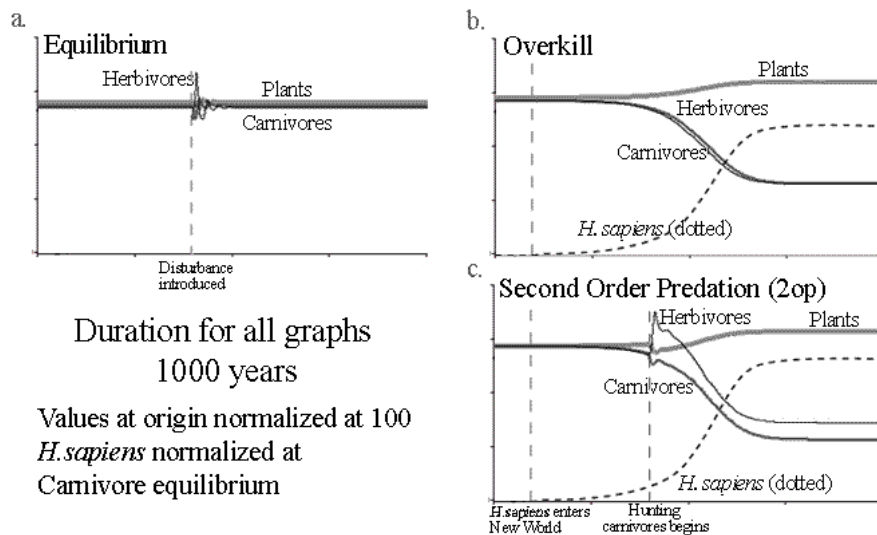


Figure 1 – Graphs of the base model results.

In the second order predation (2op) run of the base model, 400 years after *H. sapiens* enters the New World predator populations are reduced by 1.5%. This destabilizes the system. Herbivore populations escape from predator control. This creates a population boom. Herbivores eat Plants faster than they can be replaced. Ultimately herbivores crash allowing plants to recover. The system then stabilizes. At the end there are fewer herbivores and carnivores than with the overkill run and there are more plants and *H. sapiens*.

Discussion

The highly aggregated base model shows that second 2op leads to a boom and bust but doesn't show extinction *per se*. We may speculate that during the boom phase of the run less efficient herbivores perished in the competition for scarce resources but this is not conclusive. It is necessary to disaggregate the model to see if extinctions are actually occurring during the boom phase. In addition, this version of the model doesn't explain the pattern or extinction or the changes in the vegetation pattern identified above.

Results – Step 3

Step 3 is to build a model with vegetation partitioned into big and small trees, high and low quality grass; herbivores partitioned into browsers, mixed feeders and ruminant and non-ruminant grazers. Test equilibrium, overkill and 2op in this model.

The reduction in carnivore populations is based on carnivores killed per *H. sapiens* per year. The reduction in carnivore populations is a factor of carnivore density and kills per *H. sapiens*. At maximum density a 100 lb *H. sapiens* kills 2.5 lbs. of carnivore per year. As carnivore densities fall kills per unit of *H. sapiens* drop off to zero.

The stable ecosystem graph is like the stable ecosystem in the Base Model (Figure 1a) presented above. The only difference is that the increase in size and stability of a more complex system made it necessary to perturb the predator sector with a pulse reduction of 3% before any disturbance of the system was observable.

In the four herbivore model the introduction of *H. sapiens* causes very little disturbance to any of the sectors. Populations are 90% of starting values. Predator populations are reduced relatively more than Herbivores but only a fraction of a percent, and plants still increase slightly to 101% of its starting value (Figure 2a.).

In second-order predation mode, where *H. sapiens* hunts carnivores, first, as in the second order predation mode of the base model, herbivores increase, then crash; plants dip then recover; carnivores decline. With this version of the model after the first crash there is a leveling off and then a second crash of herbivores, carnivores, and *H. sapiens*, all leveling off at much lower levels and a second increase in plants with a leveling off at much higher levels. This is a new dynamic (Figure 2b).

The Herbivore graph Figure 2c shows ruminant grazers and browsers expand mixed feeders remain more or less level responding to competition from both grazers and browsers, non-ruminant grazers slump, responding more to competition from ruminants then to predation. Then mixed feeders crash followed by browsers. Ruminant grazers

dip as they bear impact of predation from both carnivores and *H. sapiens*. Non-ruminant grazers rebound. A temporary equilibrium is established but then non-ruminant grazers crash.

The vegetation graph (Figure 2d) shows the reason. During the boom phase, browsers and mixed feeders eat trees faster than trees can recruit, resulting in a complete crash of small trees, followed by near extinction of large trees as well. The loss of trees frees up more land for quickly recruiting grass and so grazers are relatively favored. Grass and grazer populations are stable for a while. Then trees, freed from predation by browsers and mixed feeders recover and begin to colonize new territory. The loss of grassland to trees coupled with the decline in predators (human and non-human) sets up a competitive situation between the grazer populations. Since non-ruminants are less efficient than ruminants the competition drives non-ruminants to final extinction.

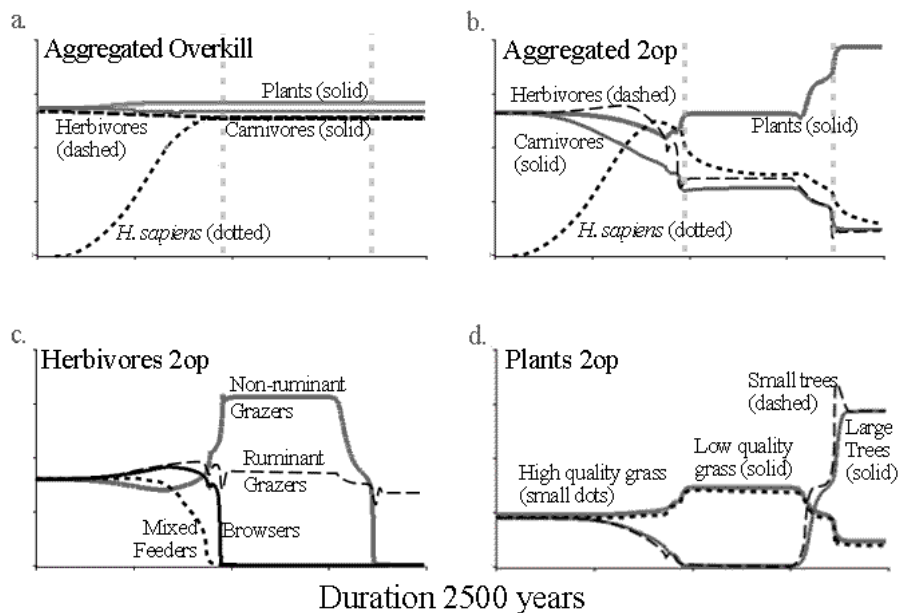


Figure 2 – Four Herbivore model results

Discussion

An unspoken assumption by scientists has been that population levels of the species which went extinct declined monotonically to zero. We see in the models presented here that the path of extinction is more likely to include recovery and overshoot as well as decline.

This research effort begins with the assumption that North American ecosystems were in equilibrium prior to the arrival of *H. sapiens*. This modeling paradigm forces

an understanding of the web of relationships that support equilibrium. Only then are we able to come to grips with the perturbations associated with the migration of *H. sapiens*.

In this modeling effort, the more complex four herbivore model has shown the impact of *H. sapiens* in the overkill mode is much less severe than in the simple, base model. In the second order predation mode, the more complex model shows much greater impact with very little reduction in predator populations. These results are both due to the interactions between herbivore species and their respective environments.

In the more complex model as one kind of herbivore or plant type is reduced other herbivores or plant types take their place so that the impact of predation (human or non-human) is buffered allowing the herbivore or plant type to recover – a complementary interaction. However, in the boom situation, due to loss of population control through predation, animals are in competition for scarce resources and an increase in one kind of herbivore means there is less available for others.

Given the assumption of equilibrium, Overkill has been shown to be inconsistent with extinction. Second Order Predation (*H. sapiens* reducing predator populations) has been shown to be more consistent with extinctions.

The boom and bust created environmental exhaustion – a period of extreme vegetation scarcity. This accounts for some of the observations which are not accounted for by either climate change or overkill.

This model accounts for the shift from plaids to stripes (Guthrie, 1989) mentioned above. During the time of scarcity mammoths would knock down the trees in the mixed woodland to get at the leaves at the top. Bison, mammoths and all the extant herbivores ate everything in sight. Then once the number of animals had been reduced, trees were able to re-invade from mountain refugia. Bison, which by that time had evolved into the smaller, obligate grazers of today bison kept the woodland from encroaching on the plains and thus preserved the prairie. The shift, in turn, suggests why two ecophenotypes or two sub-species of bison emerged – *B. bison bison*, grazers of the prairie and *B. bison athabascae*, mixed feeders of the woodland. *B. bison*

During the boom bust period there would have been a bottleneck of vegetation. Scarcity favors smaller animals over larger animals and ruminants (bison, elk, deer) and against cecal digesters (mammoth, mastodons, horses). The bottleneck accounts for the extinction of mid-size mixed feeders – North American camels – who were in competition with both grazers and browsers.

Environmental exhaustion accounts for the extinction of ground sloth. It explains the data from Hansen's (1978) study of Rampart cave. Scarcity from herbivore population growth put the sloth in competition with more efficient herbivores and forced the ground sloth to eat its less preferred food – Mormon tea.

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