Theory Building with System Dynamics: Ice Age Extinctions

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Abstract

A recently developed system dynamics model specifies a new hypothesis for the extinctions at the end of the Pleistocene – Second Order Predation – and compares it with the overkill hypothesis (see http://quaternary.net/extinct2000). It provides a quantitative description of the interrelationships between four plant stocks, four herbivore stocks, carnivores, and H. sapiens. Different assumptions regarding H. sapiens *in-migration, hunting of prey or predators, can be simulated. Second Order Predation: i.e.* H. Sapiens *killing of other carnivores, leads to herbivore overpopulation, environmental degradation, and differential extinction of herbivores. The paper suggests thinking about whole system evolution and calls for additional models that will support comparison of competing hypotheses, allow precision in quantities and timing, and exhibit internal dynamics. It challenges scientists conversant with models to simplify models to encourage their use by their colleagues.*

Background

Climate change theories put forward to explain the extinctions at the close of the Pleistocene are unsatisfactory because the animals in question (mammoths, mastodons, horses) survived previous changes of similar magnitude. The overkill theory is unsatisfactory because predators cannot hunt their prey to extinction without starving themselves. Combining the theories, without a proposed mechanism, is incomplete and inadequate. All current models assume animal populations decrease monotonically to extinction. An alternate scenario and computer simulation characterized by a boom/bust population pattern is presented. It suggests that *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 through the Pleistocene may be accounted for thus: herbivore population explosion created a condition of scarcity in which there was selective pressure favoring animals that could extract maximum energy from low quality forage to survive and reproduce.

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*.
>
> 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.
>
> 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, they strengthen their policy to exterminate any remaining predators who are now more serious competition.

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

Methods

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

The steps in the process of 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 grazers, 4 - Build a model with grazers partitioned into ruminants and non-ruminant herbivores.

Values used in these simulations: Table 1 shows the values used in the simulations based directly on those used by Whittington and Dyke (1989) .

Table 1- Values based directly on Whittington and Dyke (1989)

Description of Variable	Baseline	Source

Human population size	200	Budyko 1967, 1974
Human population growth rate	0.0443	Birdsell 1957

Table 2 below shows values used as starting values and modified to fit the modeling paradigm

Table 2 - Whittington and Dyke (1989) values, changed in this model - all based on Mossiman and Martin (1975)

Description of Variable	Baseline	Variation
Prey carrying capacity a.u.*	25	Changed to the amount of Plants per square mile.
Prey biomass replacement a.u.*	0.25	Used as base recruitment rate: Birth rate -(average death through hunting by predators + natural death rate) = 0.25

*Animal Units = 1K lb. of herbivore

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 year per pound of predator (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.

Running the model with approximated values until the model reached equilibrium derived a number of values. The division between trees and is arbitrary and 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. Available resources modify birth and death rates for the members of the sector. Thus herbivores are limited by the amount of Plants times the efficiency rate for that animal.

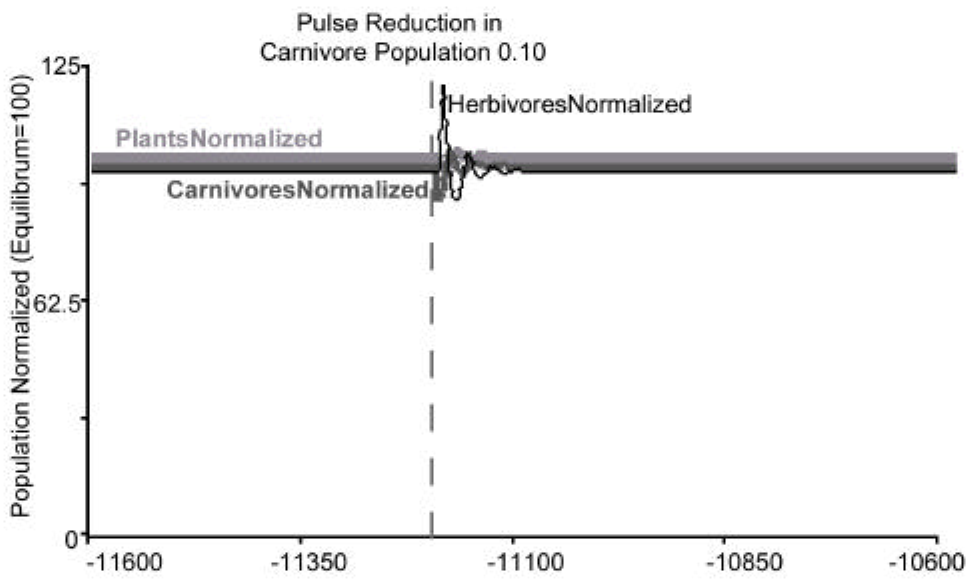
Hunting values are based on density of herbivores. It is assumed that an average predator can cover a hunting range of 2 miles per day and if prey is sufficiently dense it will kill all the prey it desires within that radius. If prey is less dense then the predator population is not able to recruit at its biological maximum. Since populations rarely recruit at their biological maximum this has the effect of reducing the effective reproduction rate. Hence populations of predators are dependent on a certain density of herbivores. Over time the system stabilizes where predator, prey and food populations are in balance.

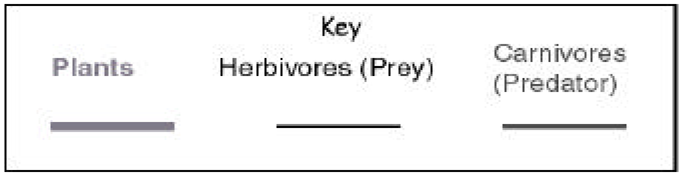
In the Three Herbivore model hunting rates were based on gross density rather than subtracting the actual density from the preferred density as in the base model. It became apparent in simulations of the base model that it was possible to base hunting rates directly on density. Since this conceptualization of the model is simpler it was decided to use it in both the Three and Four Herbivore models.

Results

The first step - Establish a stable ecosystem with three sectors; Plants, herbivores, and predators - produced the graph shown below (Figure 1). Since the goal of this step is a stable ecosystem, the model was perturbed and subsequently returned to normal. This is the base model from which all subsequent models are derived.

Figure. 1. Graph of the base model

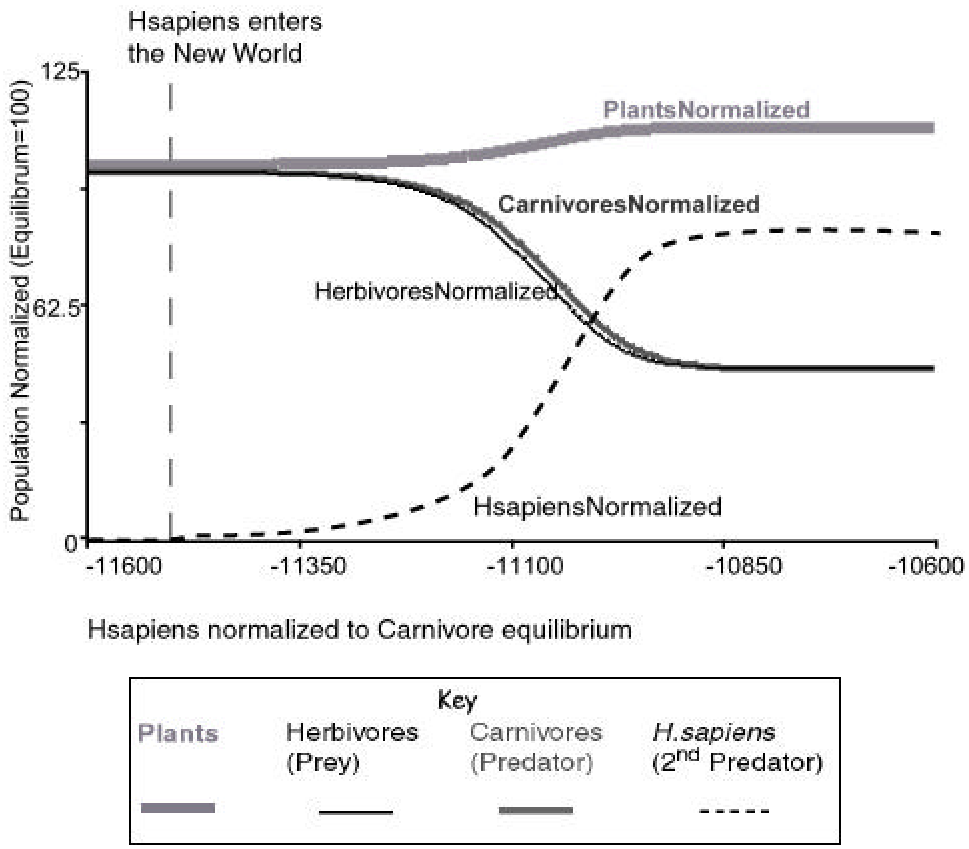




The second step is a model with a second predator, *H. sapiens.* It is broken into two parts.

Step 2a is to introduce *H. sapiens* as a second predator. *H. sapiens* enters the New World -11500 BP, 100 years after the start of the model. Figure 2 shows the impact of a second predator. It is the position of the overkill hypothesis.

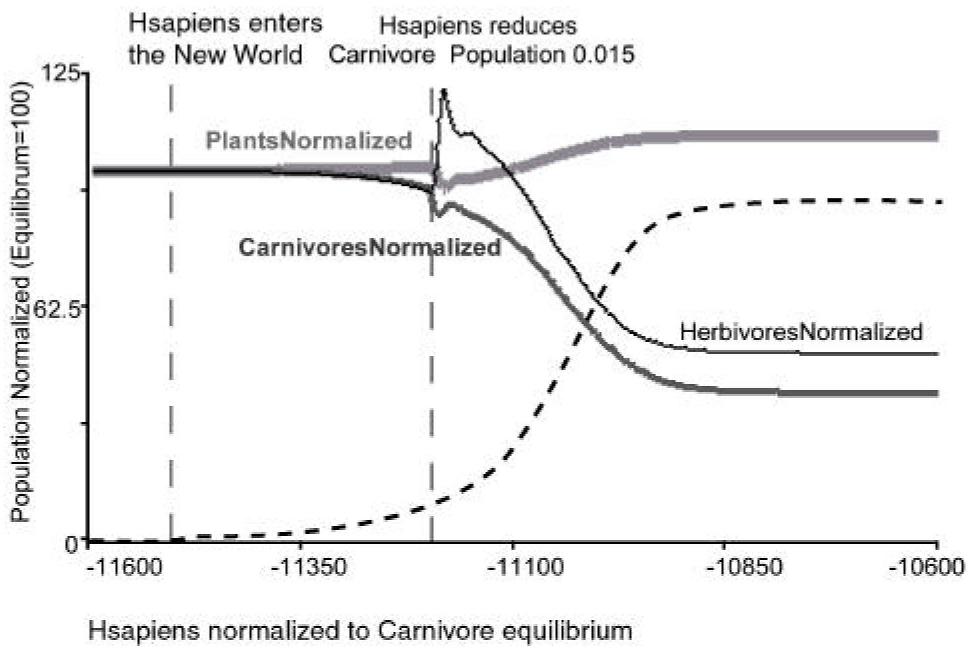
Fig. 2. Graph of the second predator (overkill) mode.



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 Overkill). The graph is presented below. (Figure 3)

Fig. 3. Graph of the second order predation model Key as in figure 2.



In this version 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 the Plants faster than it can be replaced. Ultimately herbivore populations crash. The crash in herbivore populations allows the Plants to recover. This boom / bust cycle is repeated with each cycle decreasing in amplitude. After several cycles the system stabilizes. During the boom bust cycles the animals that can survive on the fastest recruiting resource and who can extract maximum nutrition should be favored over those who cannot.

The task of the next steps in the modeling effort is to examine why some animals are favored over others.

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 grazers. 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 off kills per unit of *H. sapiens* drop off to zero.

The stable ecosystem graph (Figure 4) is like the stable ecosystem in the Base Model (Figure 1) 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 Three 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 5).

In second-order overkill mode, where *H. sapiens* hunts carnivores, results in a major crash of Herbivore and Carnivore populations after which populations level off. It is shown in Figure 6.

Consider the Herbivore sector. The graph below shows the behavior of browser, mixed feeder, and grazer populations (Figure 7). Browsers and mixed feeders expand and crash. Grazers, initially have a population slump, as they bear all the pressure of predation by both non-human predators and *H. sapiens*. As *H. sapiens* and predator populations diminish, grazers rebound, and stabilize.

Figure. 4. Equilibrium mode graph. Three herbivore model. Key as in figure 1

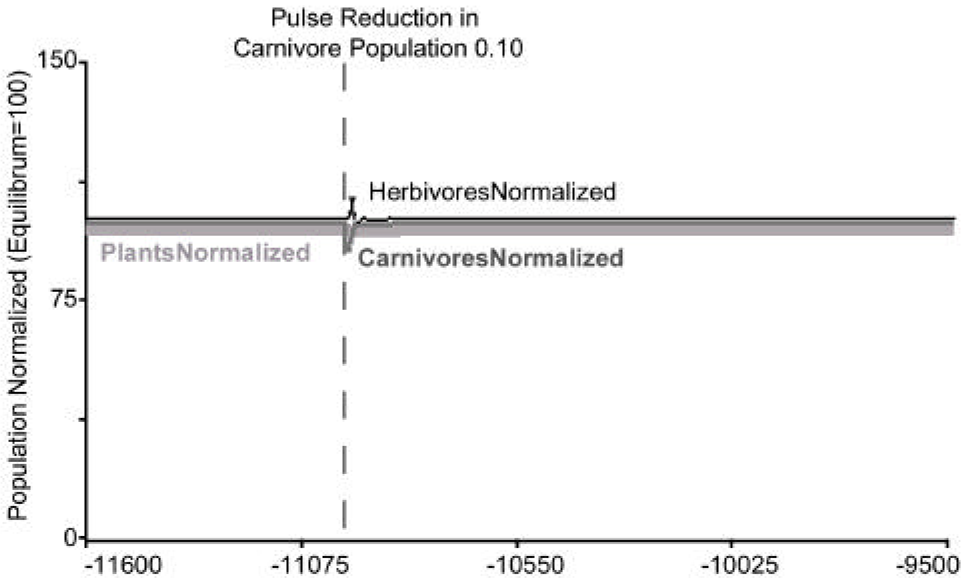


Fig. 5. - Second predator (overkill) mode, aggregated view. Key as in figure 2.

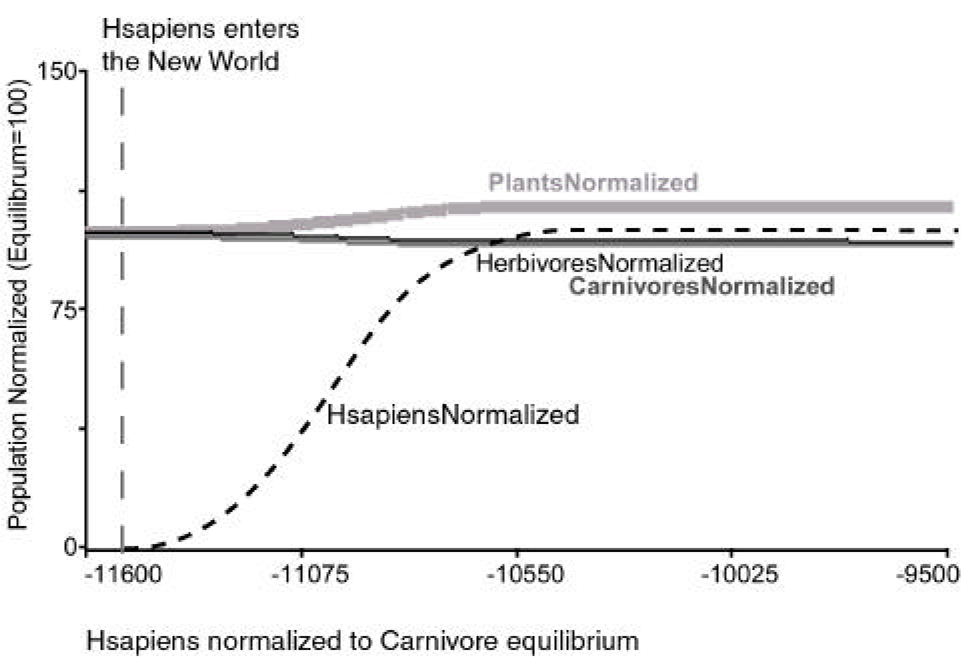


Fig. 6. Second-order predation, aggregated view. Key as in figure 2.

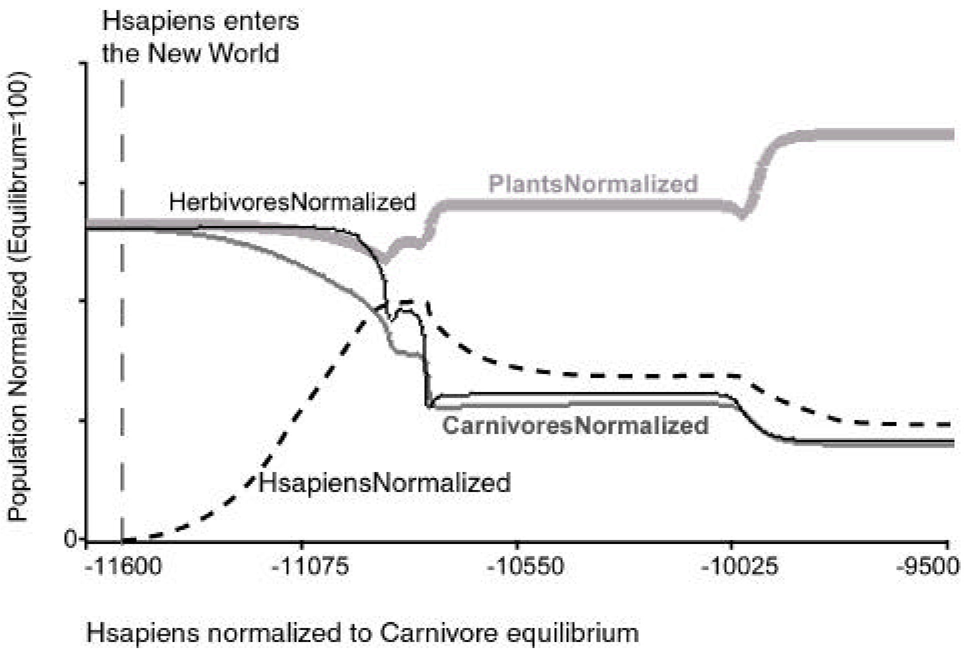


Fig. 7. Second-order predation, herbivores

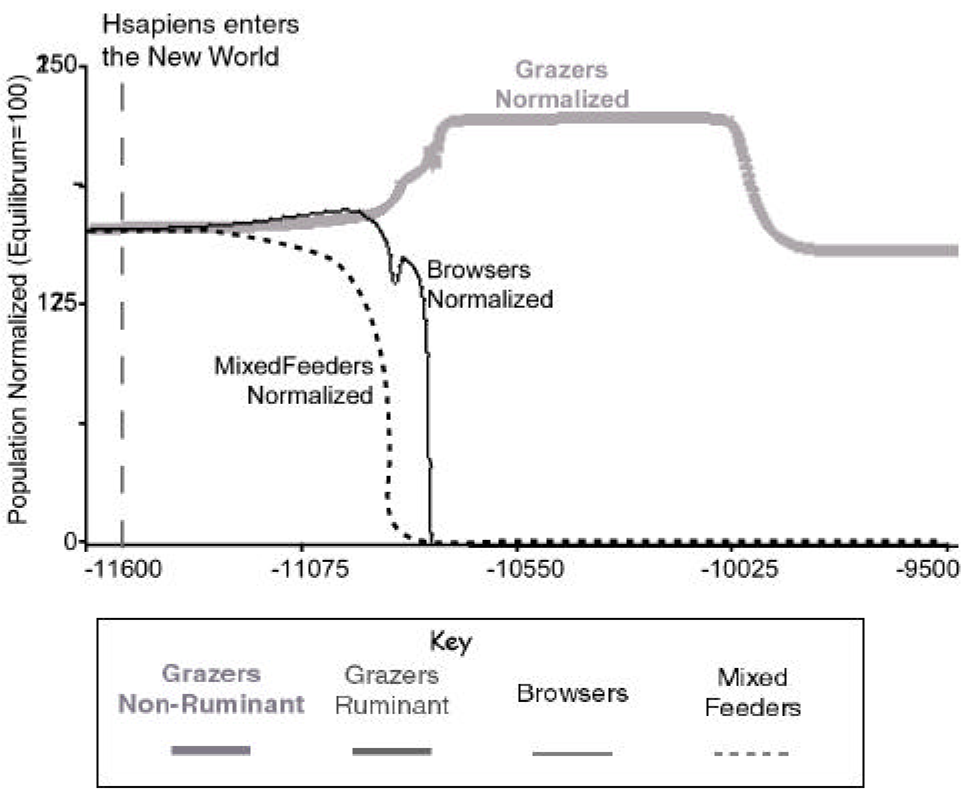
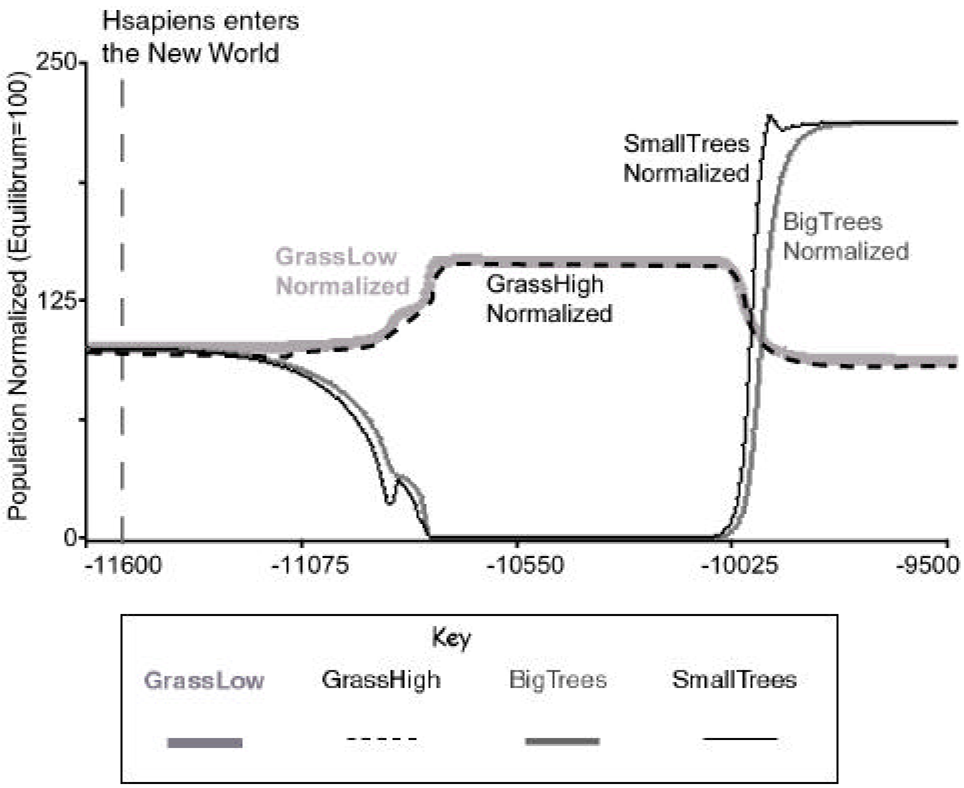


Figure 8 - shows why herbivore populations crashed. We see that the browsers and mixed feeders are eating trees faster than they can recruit, resulting in a complete crash of small trees, followed by near extinction of large trees as well. The dip in grazer populations after the extinction of browsers and mixed feeders allows the two grass sectors to boom until grazer populations equilibrate.

Fig. 8. Second-order predation, plants

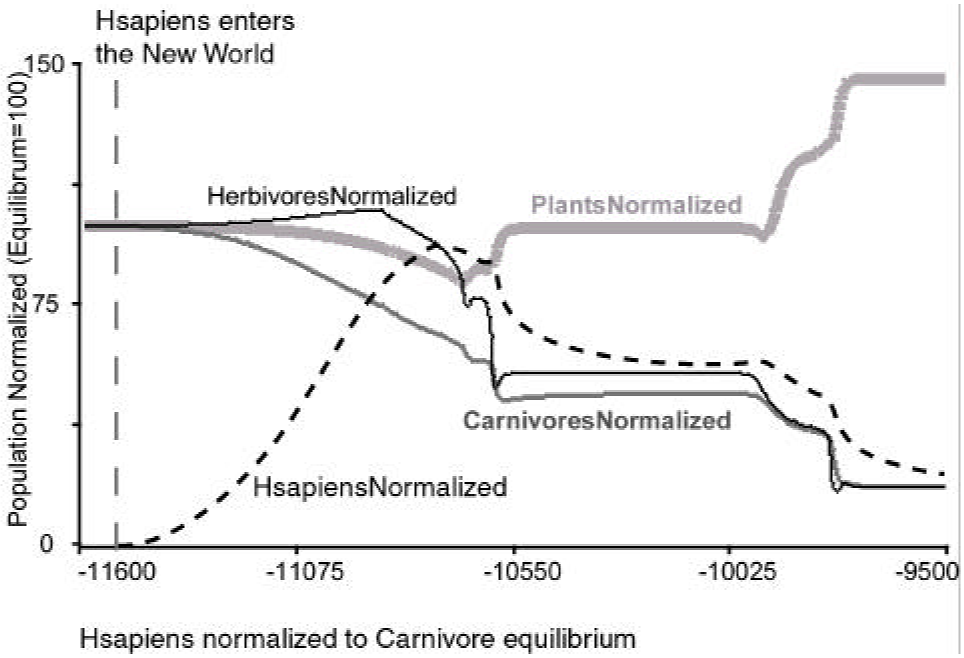


In the Four Herbivore model the Stable Ecosystem mode is the same as is the Stable Ecosystem mode of the Three Herbivore Model illustrated above. Like the Three Herbivore Model the only difference from the Base Model is that the stable ecosystem needed to be perturbed by a 5% pulse reduction before any difference could be observed.

The Second Predator mode of the Four Herbivore Model is the same as it is in the Three Herbivore model. There is little disturbance to either herbivores or predators.

The only difference between the Three Herbivore and Four Herbivore models is in the Second Order Overkill mode shown in Figure 9.

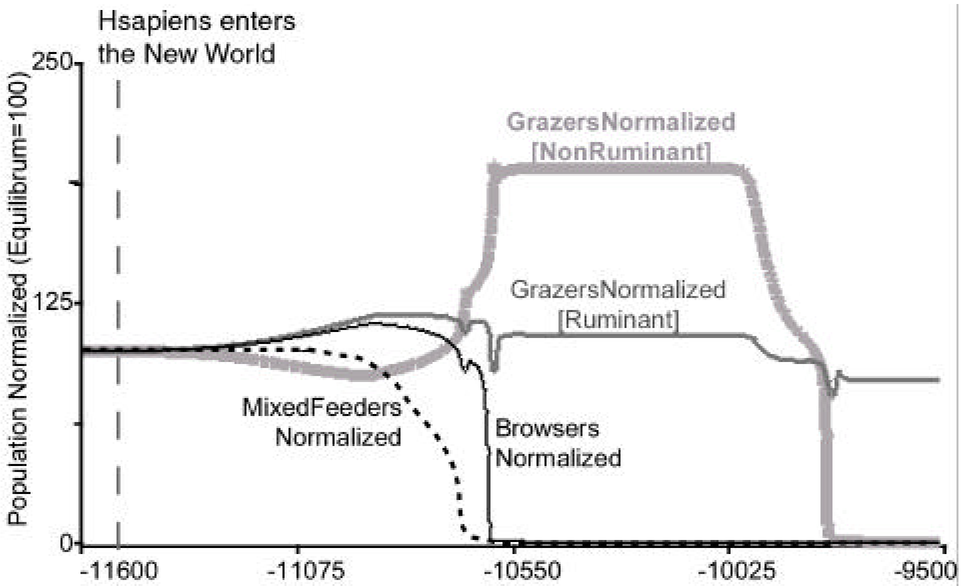
Fig. 9. Second-order predation, Four-herbivore model Key as in figure 2



The graph is very like the graph of the Second Order mode presented for the Three Herbivore Model until after the crash in all sectors. Then we see a further dip in Herbivores, Predators and *H. sapiens* populations. The crash in populations occurs later in the Four Herbivore Model than it does in the Three Herbivore Model.

In Figure 10 we see the reason for that dip. There are two interesting things about this graph. First, ruminant population levels impact non-ruminants more than they are by predation. Second, when ruminant populations fall, after the extinction of browsers and mixed feeders, non-ruminants boom. As ruminant populations recover, non-ruminant populations fall and eventually go extinct. Just as after the extinction of browsers and mixed feeders, ruminant populations dip as they are hit with the full weight of predation.

Fig. 10. Second-order predation, herbivores. Key as in figure 7

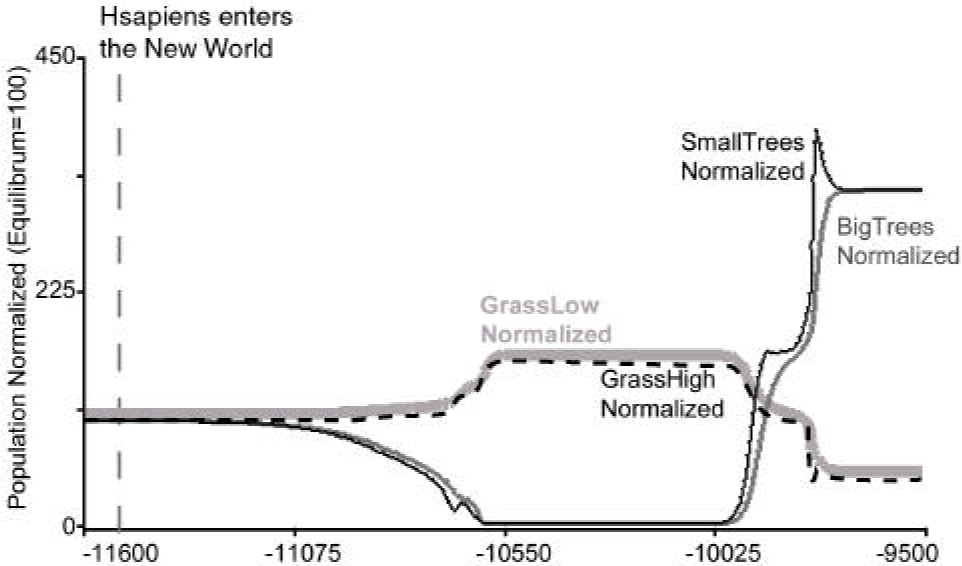


The vegetation graph below shows the reason, Figure 11. Browsers and mixed feeders eat trees faster than trees can recruit, resulting in a complete crash of small trees, followed by near extinction of large trees as well. The competition between the two grazer populations keeps grass stable Trees, freed from predation by browsers and mixed feeders 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.

Discussion

The major assumption of this research effort is 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*.

Fig. 11. Second-order predation, plants. Four-herbivore model



In this modeling effort as the models have become more complex and more like the real world, the impact of *H. sapiens* in the Second Predator - Overkill mode has been less and less severe. In the Second Order mode, as the models have become more complex, there have been more extinctions and greater overall change with little additional reduction in predator populations.

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 in an equilibrium system. The proximate cause of the extinctions is environmental exhaustion from destabilizing predator control of herbivore populations.

Environmental exhaustion as the proximate cause for extinctions suggests a period of extreme scarcity of vegetation. During that period ruminant digestors who extract the maximum nutrition and energy from their food would be selectively favored.

Environmental exhaustion would also account for the shift from plaids - patchy mixed woodland - to stripes - closed canopy forest near the mountain refugia and unbroken grassland in the center of the country (Guthrie, 1989). 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 bison* kept the woodland from encroaching on the plains by eating new trees and thus preserved the prairie.

Environmental exhaustion accounts for the bias in favor of small size observed in many species including bison and the extinction of animals that were not hunted by *H. sapiens* (e.g. ground sloths) and should not have suffered from climate change (e.g. horses).

Environmental exhaustion explains the data from Hansen's (1978) study of Rampart cave. There was apparently no evidence of climate change which would have reduced the food available to the Shasta ground sloth (*Nothrotheriops shastensis*) but in studying the evidence of diet in its dung Hansen found more and more Mormon tea (*Ephedra navadensis*) and less and less of its staple, globemallow (*Sphaeralcea ambigua*). Globemallow is used by other extant herbivores whereas Mormon tea is not. If the Second Order Overkill is correct the ground sloth would have been out-competed by more efficient herbivores in the time of extinction - the booms and busts.

Significance for evolution

The entire ecosystem evolved through the mechanism of extinctions. The extinctions being the result of an anthropogenic change in the relationship between carnivores and herbivores and thus changing the relationship between herbivores and plants.

Bison, being ruminant grazers made it through the bottleneck. The new "striped" Holocene environment gave two possibilities - grazing and mixed browsing. Living in one of the two stripes. Plains bison (*B. bison bison*) are obligate grazers whereas woodland bison (*B.bison athabascae*) are, as their name implies browsers and grazers. Both are significantly smaller than their Pleistocene forbears. Until they were hunted to near extinction during the 1880s, plains bison maintained the prairie as a grazing ground. Once they were removed trees began to encroach upon the long grass prairie. In the absence of farming, over time the increased number of trees would have changed the relative humidity through transpiration. This, in turn may have led to a decrease in continentality.

Significance for modellers

This project made a conscious effort to keep the model as simple as possible. Scientists who are not comfortable with complex models can see the utility of simple models that test one hypothesis against another. This is especially important for paleontologists and archaeologists who have little data and no other way of testing. Scientists who are conversant with models should make a concerted effort to bring their colleagues into the modeling community through the use of simple models.

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