A New Human Predation Model for Late Pleistocene Megafaunal Extinction Patterns in North America

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Pleistocene Background

- Many megafaunal species present before humans arrived in North America
- By c. 10,000 years ago, most North American megafauna were extinct
- Was human hunting (“overkill”) responsible? Climate? Both?

Overview

Although Late Pleistocene extinctions were especially tough on larger mammals, smaller mammals were also lost

No satisfactory explanation for that pattern

We offer the first attempt in that direction, testing our hypothesis via a deterministic six-prey, one-predator model

Ecological Modeling

- Humans are the predators
- Assumption: human predation could have caused the extinctions
- Assumption: altering functional response choice might improve the match to historical survival-extinction outcomes

Functional Response

- The rate at which predators capture prey under circumstances of changing prey and predator density

- A critical component of predator-prey models (e.g., Skalski and Gilliam 2001; Fenlon and Faddy 2006)

Functional Responses Tested

- **Holling Disc Equation** ("Holling Type II")

  excludes predator interference

- **Beddington-DeAngelis**

  includes gradations of predator interference, ***i***

- **Ratio-Dependence**

  assumes complete sharing of prey among predators

What's the mark to beat?

Alroy (2001): works slightly better than separating mammals into two groups based on mass and assuming that all species above the cutoff went extinct while all below it survived

Single-line method predicts 30 of 41 (73%) of actual survival-extinction outcomes

Alroy (2001) model predicts 32 of 41 (78%) of actual outcomes

Alroy's 41 Prey Species

SPECIES	WEIGHT (KG)	STATUS
Capromeryx minor	**21**	E
Pecari tajacu	**30**	S
Oreamnos harringtoni	**45**	E
Platygonus compressus	**53**	E
Stockoceros conklingi	**53**	E
Stockoceros onusrosagris	**54**	E
Rangifer tarandus	**61**	S
Tetrameryx shuleri	**61**	E
Antilocapra americana	**68**	S
Mylohyus fossilis	**74**	E
Oreamnos americanus	**91**	S
Ovis canadensis	**91**	S
Odocoileus virginianus	**107**	S
Odocoileus hemionus	**118**	S
Navahoceros fricki	**223**	E
Hemiauchenia macrocephala	**238**	E
Paleolama mirifica	**245**	E
Ovibos moschatus	**286**	S
Equus conversidens	**306**	E
Holmesina septentrionalis	**312**	E
Tapirus veroensis	**324**	E
Equus francisi	**368**	E

SPECIES	WEIGHT (KG)	STATUS
Bison bison	**422**	S
Equus complicatus	**439**	E
Alces alces	**457**	S
Cervacles scotti	**486**	E
Euceratherium collinum	**499**	E
Cervus elaphus	**500**	S
Bison priscus	**523**	E
Equus niobrarensis	**533**	E
Equus scotti	**555**	E
Equus occidentalis	**574**	E
Nothrotheriops shastensis	**614**	E
Glyptotherium floridanum	**666**	E
Bootherium bombifrons	**753**	E
Camelops hesternus	**995**	E
Megalonyx jeffersonii	**1320**	E
Paramylodon harlani	**1990**	E
Mammuthus primigenius	**3174**	E
Mammut americanum	**3298**	E
Mammuthus columbi	**5827**	E

Surviving (Extant) = S
Extinct = E

One-Line Method

SPECIES	WEIGHT (KG)	STATUS
Capromeryx minor	21	E
Pecari tajacu	30	S
Oreamnos harringtoni	45	E
Platygonus compressus	53	E
Stockoceros conklingi	53	E
Stockoceros onusrosagris	54	E
Rangifer tarandus	61	S
Tetrameryx shuleri	61	E
Antilocapra americana	68	S
Mylohyus fossilis	74	E
Oreamnos americanus	91	S
Ovis canadensis	91	S
Odocoileus virginianus	107	S
Odocoileus hemionus	118	S
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Paleolama mirifica	245	E
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Equus conversidens	306	E
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Camelops hesternus	995	E
Megalonyx jeffersonii	1320	E
Paramylodon harlani	1990	E
Mammuthus primigenius	3174	E
Mammut americanum	3298	E
Mammuthus columbi	5827	E

Surviving (Extant)	=	S
Extinct	=	E

Where We Can Do Better

For species > 500 kg, both Alroy's simulation and the single-line method do well. This makes ecological sense (e.g., Johnson 2002).

But both the single-line method and the Alroy simulation fall short among species weighing less than 55 kg-75 kg.

A cluster of extinctions occurs amongst these lighter species.

Extinction Cluster

SPECIES	WEIGHT	STATUS
Capromeryx minor	21	E
Pecari tajacu	30	S
Oreamnos harringtoni	45	E
Platygonus compressus	53	E
Stockoceros conklingi	53	E
Stockoceros onusrosagris	54	E
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Equus conversidens	306	E
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Surviving (Extant)	=	S
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Extending Intuition

An analysis of ratio-dependent parameter space by Berezovskaya, Karev, and Arditi (2001) extends ecological common sense, predicting increased risk of extinction both at higher and lower prey mass.

Extending Intuition

BKA Space suggests a refinement of the one-line method: draw two lines, predicting extinctions both above the higher and below the lower mass thresholds.

The consequence: a simple, transparent prediction of extinction patterns.

Two-Line Method

SPECIES	WEIGHT	STATUS
Capromeryx minor	21	E
Pecari tajacu	30	S
Oreamnos harringtoni	45	E
Platygonus compressus	53	E
Stockoceros conklingi	53	E
Stockoceros onusrosagris	54	E
Rangifer tarandus	61	S
Tetrameryx shuleri	61	E
Antilocapra americana	68	S
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Paramylodon harlani	1990	E
Mammuthus primigenius	3174	E
Mammut americanum	3298	E
Mammuthus columbi	5827	E

Surviving (Extant)	=	S
Extinct	=	E

Testing Intuition

BKA Space describes a single-predator, single-prey system

More complex systems may not follow this pattern: the math doesn’t exist for us to tackle this question

But we can address it via simulations

Testing Intuition

Any model of these interactions must assign parameter values for extinct species and vanished human societies

A significant challenge — how best to constrain the values we assign?

Allometric Constraints/Assumptions

Parameter	Allometric Power Assumed	Source
r_m (maximal intrinsic rate of population increase)	- 0.36	Caughley and Krebs 1983
K (carrying capacity)	- 0.75	Damuth 1987
e (conversion efficiency)	1.0	Assumption: all herbivore flesh has equal per kg nutritional value
h (handling time)	1.0	Assumption: time to prepare and digest herbivore flesh is proportional to its mass
a or α (capture efficiency)	Unknown	The parameter our model explores

Capture Efficiency 1 of 3

Capture efficiency, *a* or α, presents a challenge

No allometry describes the relationship between prey mass and predator capture efficiency

Nor can we estimate capture efficiency from archaeological evidence or observation of extant hunter-gatherer societies

Capture Efficiency 2 of 3

So we designed our model to explore capture efficiency

Analogous in biological meaning between functional response forms but due to differing units, not directly comparable:

Holling II and Beddington-DeAngelis:

$$\frac{1}{time \times individual}$$

Ratio Dependence:

$$\frac{1}{time}$$

Capture Efficiency 3 of 3

$$a = C_a m_i$$

PowerCE

$$\alpha = C_\alpha m_i^{PowerCE}$$

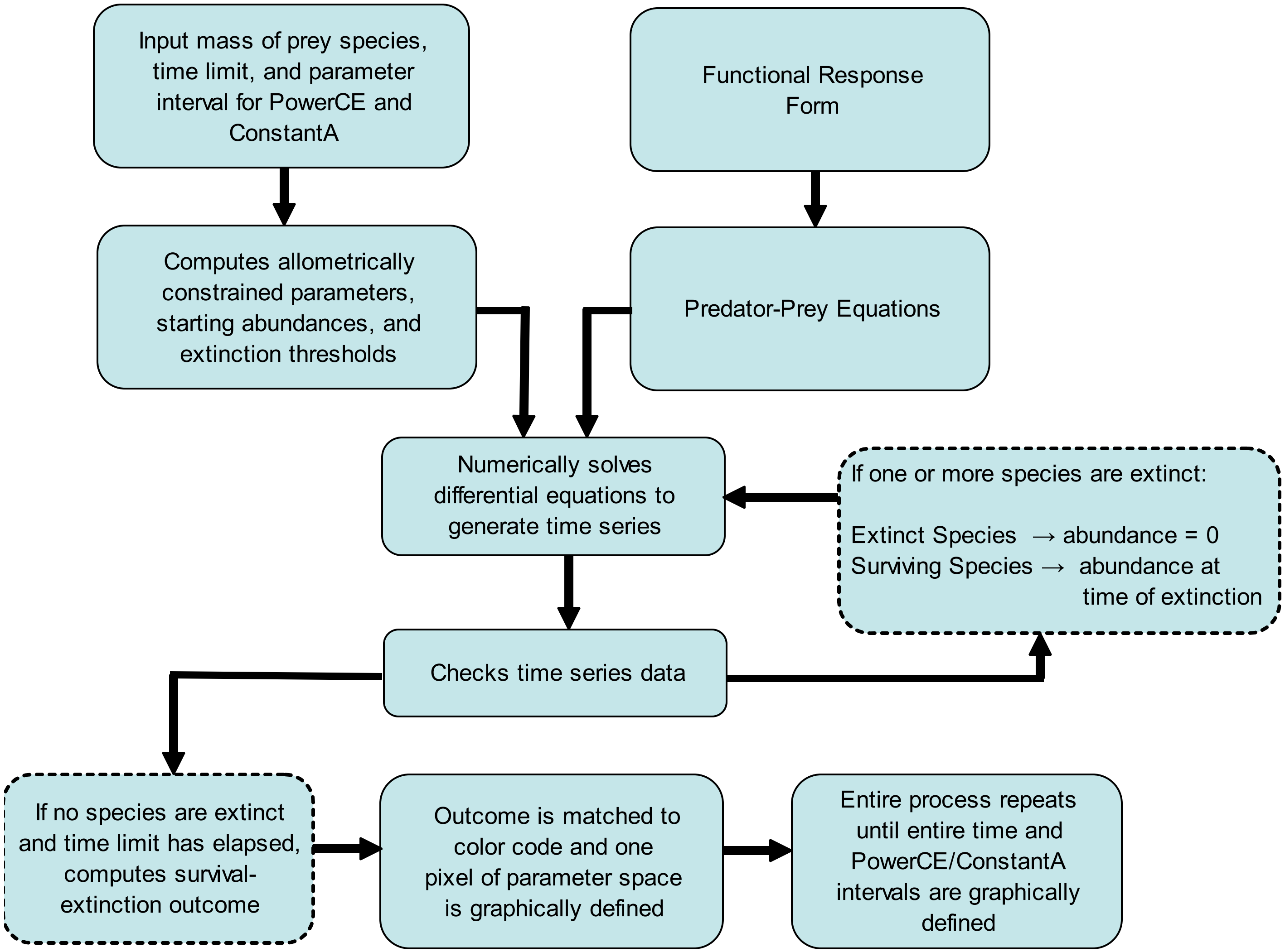
C is the constant of each allometry and represents hunting pressure; m_i the mass of the species; and *PowerCE* the power of the allometry and represents relative susceptibility of prey species to human hunters.

Constants differ between functional response forms, but the power of the allometry remains unchanged.

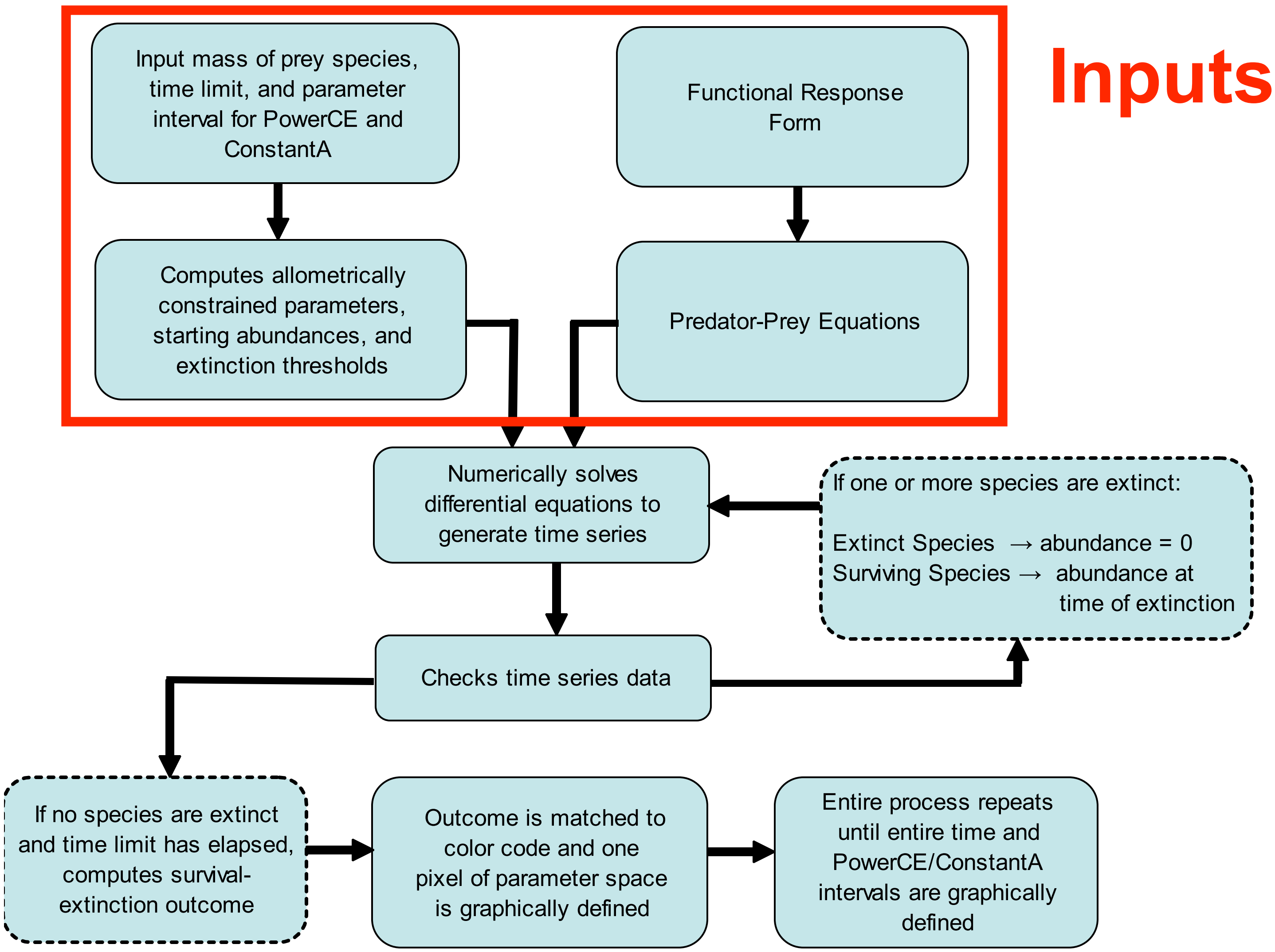
Prey Species Modeled

Species	Mass (kg)	Status
Capromeryx minor *(Dimunitive pronghorn)*	21	Extinct
Pecari tajacu *(Collared peccary)*	30	Surviving
Odocoileus hemionus *(Mule deer)*	118	Surviving
Equus conversidens *(Mexican horse)*	306	Extinct
Megalonyx jeffersonii *(Jefferson's ground sloth)*	1320	Extinct
Mammuthus columbi *(Columbian mammoth)*	5827	Extinct

Model Overview



Model Overview



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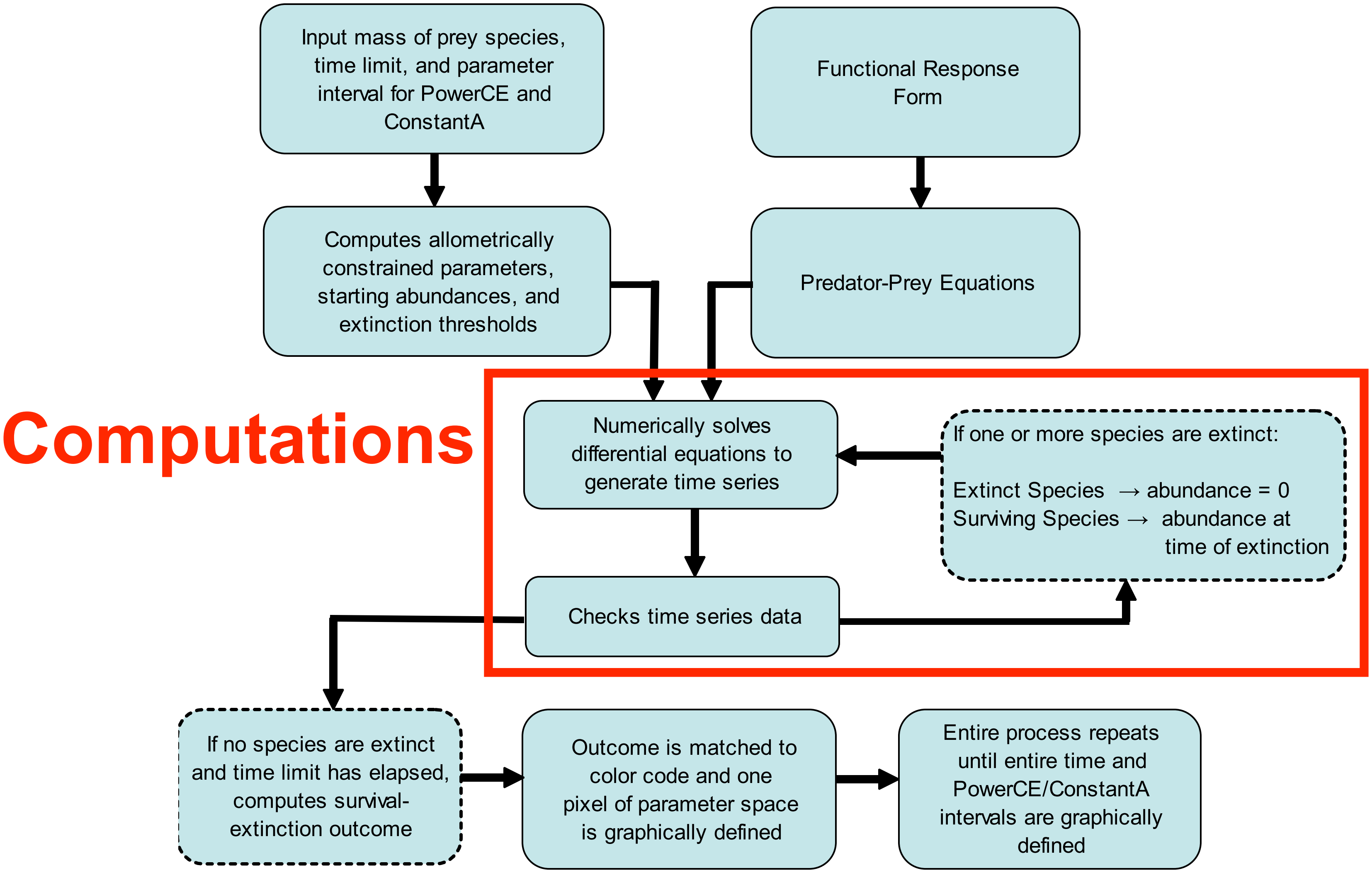

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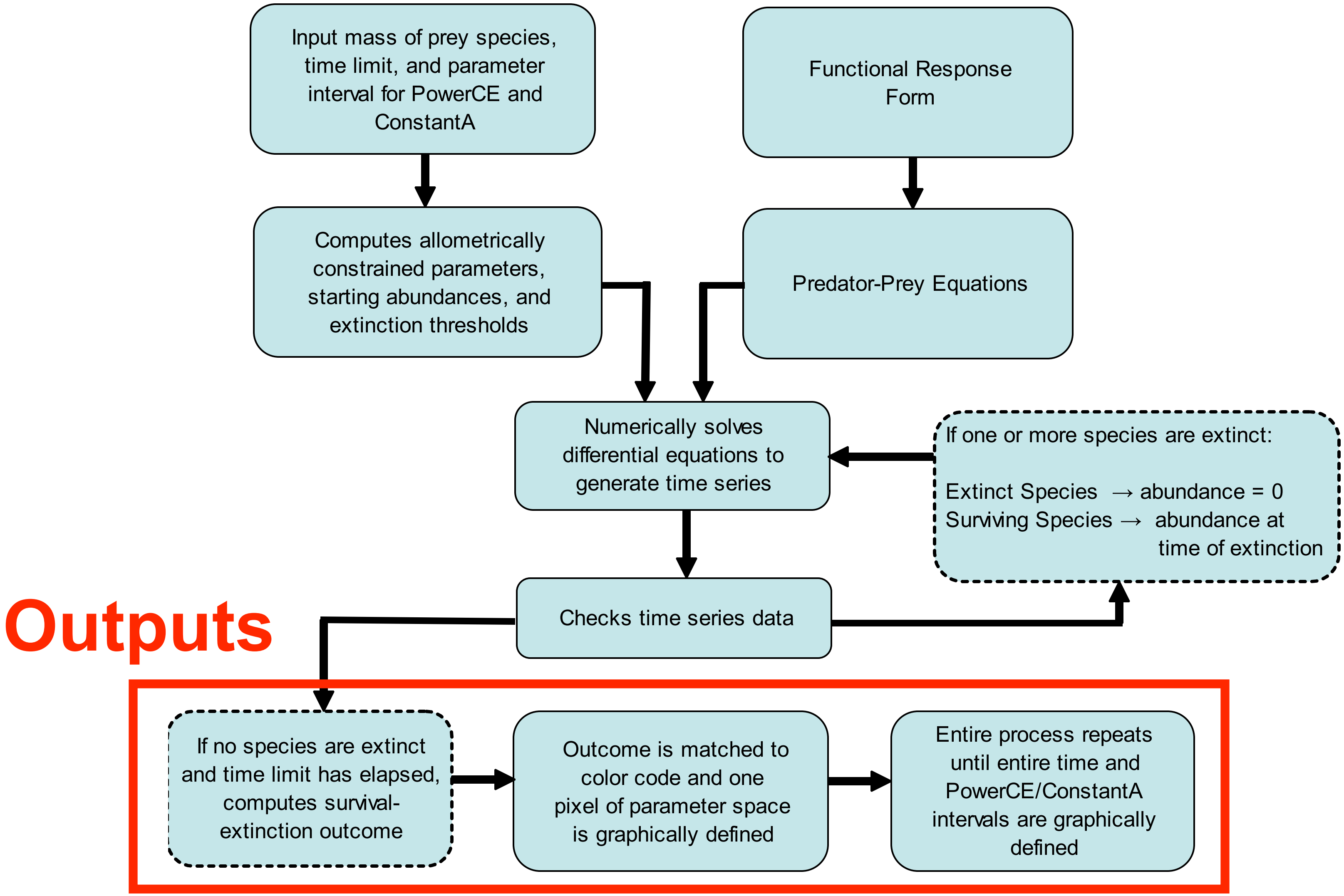

Results

No qualitative differences in survival-extinction patterns result from changes in functional response

Outcomes depend on the combined absolute magnitudes of hunting pressure (C_a or C_α) and the relative susceptibility of prey species to human hunters, *PowerCE*

Survival-Extinction Outcomes

Bracketed numbers represent, from left to right, six prey (in order of increasing mass) and one predator species, humans

0 = extinct
1 = surviving

	Outcome
black	None of the below
red	{0, 0, 0, 0, 0, 0, **0**}
pink	{0, 0, 0, 0, 0, 1, **1**}
gray	{0, 0, 0, 0, 0, 1, **0**}
magenta	{0, 0, 0, 0, 1, 1, **1**}
purple	{0, 0, 0, 1, 1, 1, **1**}
indigo	{0, 0, 1, 1, 1, 1, **1**}
blue	{0, 0, 1, 1, 1, 1, **1**}
light blue	{0, 1, 1, 1, 1, 1, **1**}
cyan	{1, 0, 0, 0, 0, 0, **1**}
green	{1, 1, 0, 0, 0, 0, **1**}
yellow-green	{1, 1, 1, 0, 0, 0, **1**}
yellow	{1, 1, 1, 1, 0, 0, **1**}
gold	{1, 1, 1, 1, 1, 0, **1**}
orange	{1, 1, 1, 1, 1, 1, **1**}
salmon / white	Any predator extinction other than above

Survival-Extinction Outcomes

Bracketed numbers represent, from left to right, six prey (in order of increasing mass) and one predator species, humans

0 = extinct
1 = surviving

	Outcome
	None of the below
	{0, 0, 0, 0, 0, 0, **0**}
	{0, 0, 0, 0, 0, 1, **1**}
	{0, 0, 0, 0, 0, 1, **0**}
	{0, 0, 0, 0, 1, 1, **1**}
	{0, 0, 0, 1, 1, 1, **1**}
	{0, 0, 1, 1, 1, 1, **1**}
	{0, 0, 1, 1, 1, 1, **1**}
	{0, 1, 1, 1, 1, 1, **1**}
	{1, 0, 0, 0, 0, 0, **1**}
	{1, 1, 0, 0, 0, 0, **1**}
	{1, 1, 1, 0, 0, 0, **1**}
	{1, 1, 1, 1, 0, 0, **1**}
	{1, 1, 1, 1, 1, 0, **1**}
	{1, 1, 1, 1, 1, 1, **1**}
	Any predator extinction other than above

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	{0, 0, 0, 0, 0, 1, **1**}
	{0, 0, 0, 0, 0, 1, **0**}
	{0, 0, 0, 0, 1, 1, **1**}
	{0, 0, 0, 1, 1, 1, **1**}
	{0, 0, 1, 1, 1, 1, **1**}
	{0, 0, 1, 1, 1, 1, **1**}
	{0, 1, 1, 1, 1, 1, **1**}
	{1, 0, 0, 0, 0, 0, **1**}
	{1, 1, 0, 0, 0, 0, **1**}
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	{1, 1, 1, 1, 0, 0, **1**}
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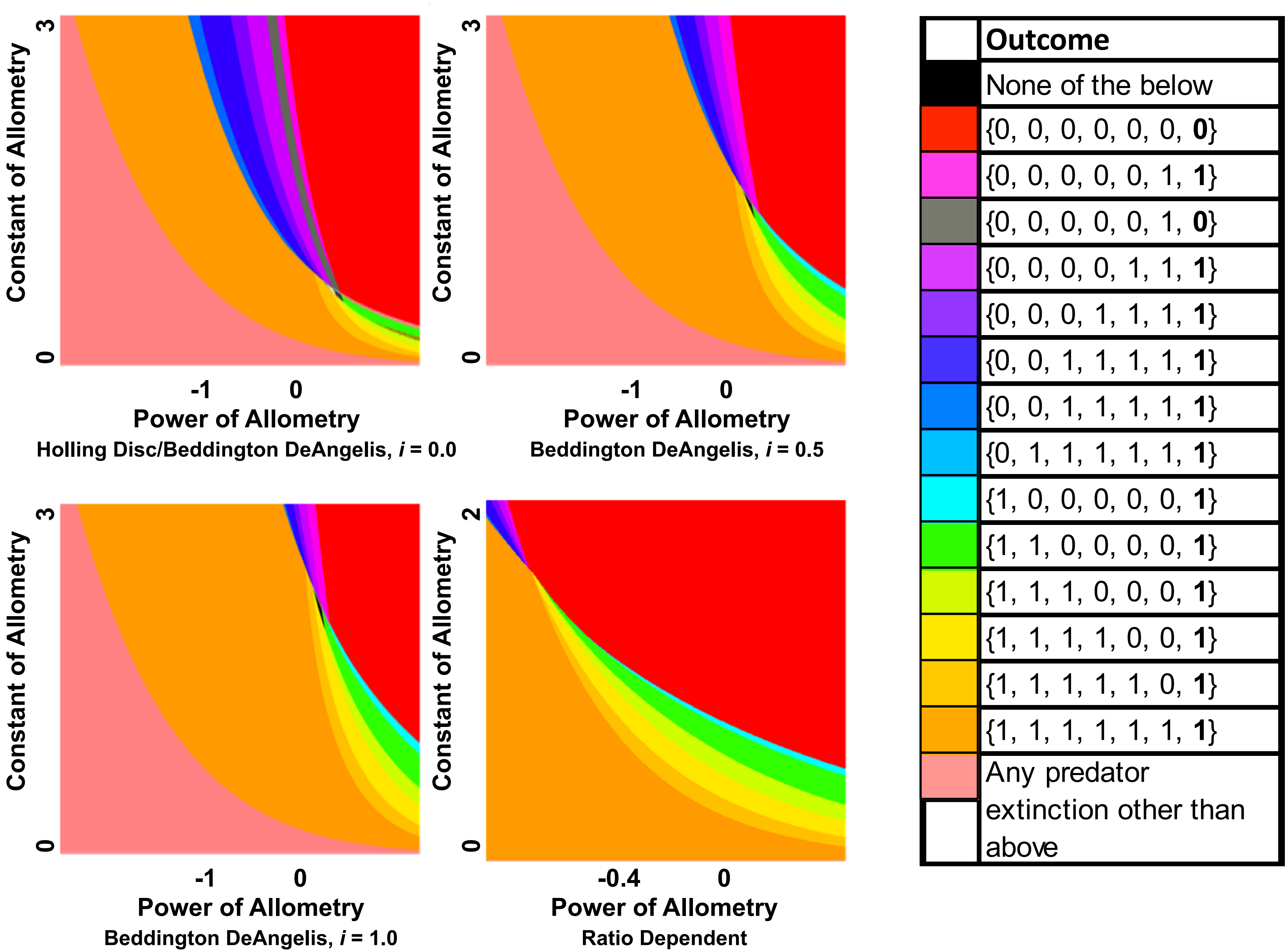
	Any predator extinction other than above

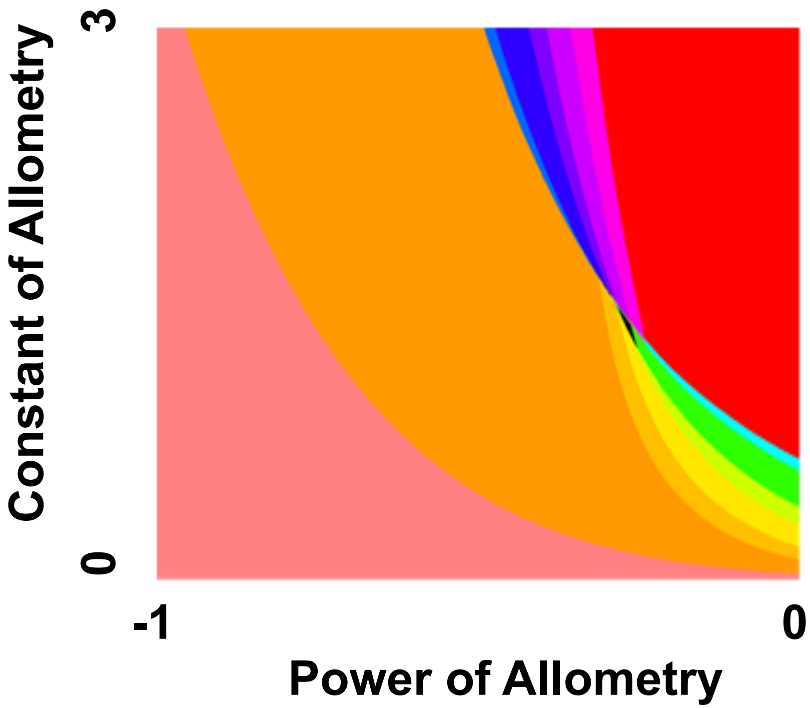
Survival-Extinction Outcomes. Bracketed numbers represent, from left to right, six prey and one predator species; 0 = extinct and 1 = surviving.



Discussion

Coexistence transition in the region of *PowerCE* = -0.35 represents a tipping point between the relative importance of prey r_m and predator capture efficiency

Discussion



Beddington DeAngelis, *i* = 0.5

	Outcome
	None of the below
	{0, 0, 0, 0, 0, 0, **0**}
	{0, 0, 0, 0, 0, 1, **1**}
	{0, 0, 0, 0, 0, 1, **0**}
	{0, 0, 0, 0, 1, 1, **1**}
	{0, 0, 0, 1, 1, 1, **1**}
	{0, 0, 1, 1, 1, 1, **1**}
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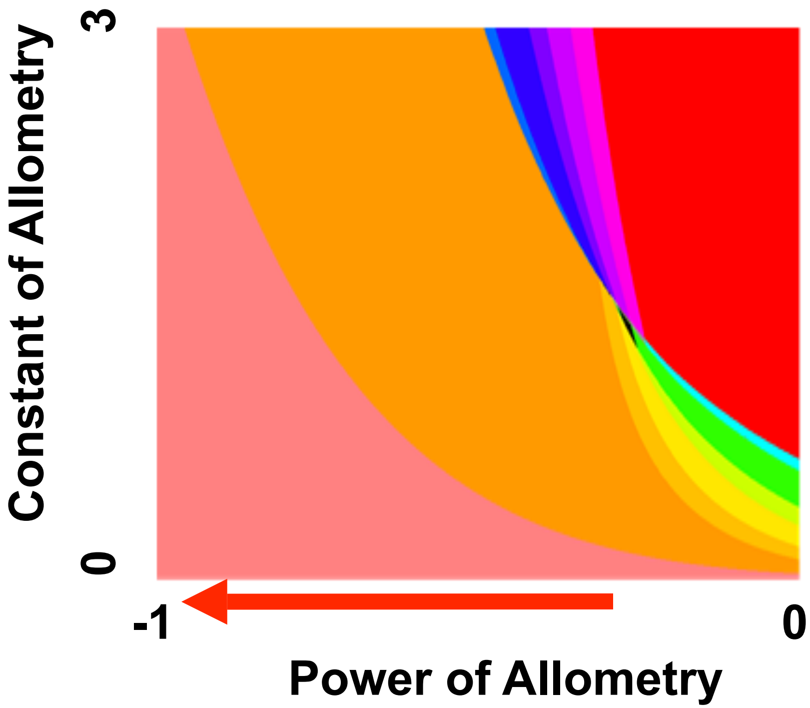
	{1, 0, 0, 0, 0, 0, **1**}
	{1, 1, 0, 0, 0, 0, **1**}
	{1, 1, 1, 0, 0, 0, **1**}
	{1, 1, 1, 1, 0, 0, **1**}
	{1, 1, 1, 1, 1, 0, **1**}
	{1, 1, 1, 1, 1, 1, **1**}
	Any predator extinction other than above

PowerCE < -0.35: difficult-to-capture larger prey persist despite relatively low r_m ; smaller prey eliminated despite relatively high r_m ; stepwise extinctions: smallest to largest

Discussion



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	{0, 0, 0, 0, 0, 1, **1**}
	{0, 0, 0, 0, 0, 1, **0**}
	{0, 0, 0, 0, 1, 1, **1**}
	{0, 0, 0, 1, 1, 1, **1**}
	{0, 0, 1, 1, 1, 1, **1**}
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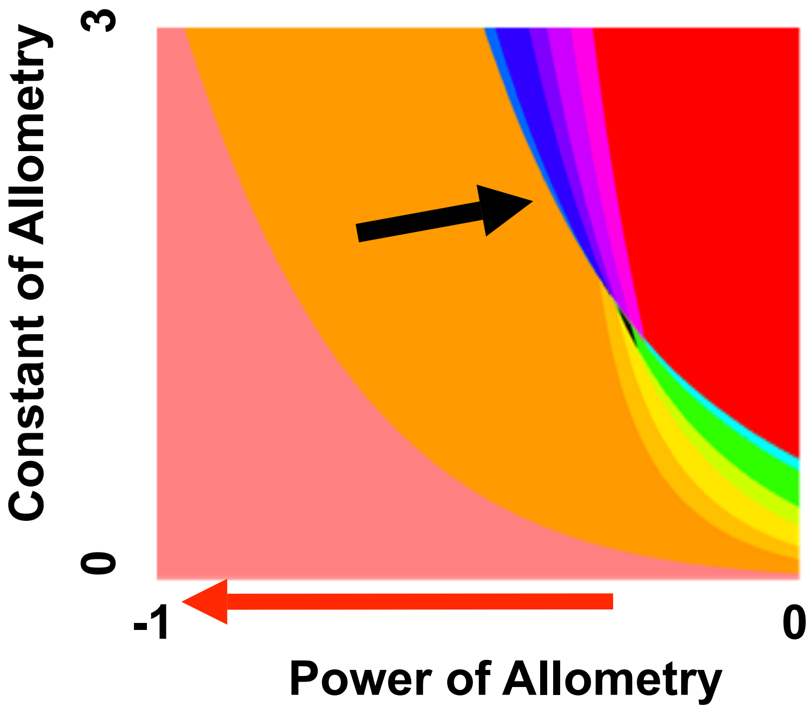

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Outcome
None of the below
{0, 0, 0, 0, 0, 0, **0**}
{0, 0, 0, 0, 0, 1, **1**}
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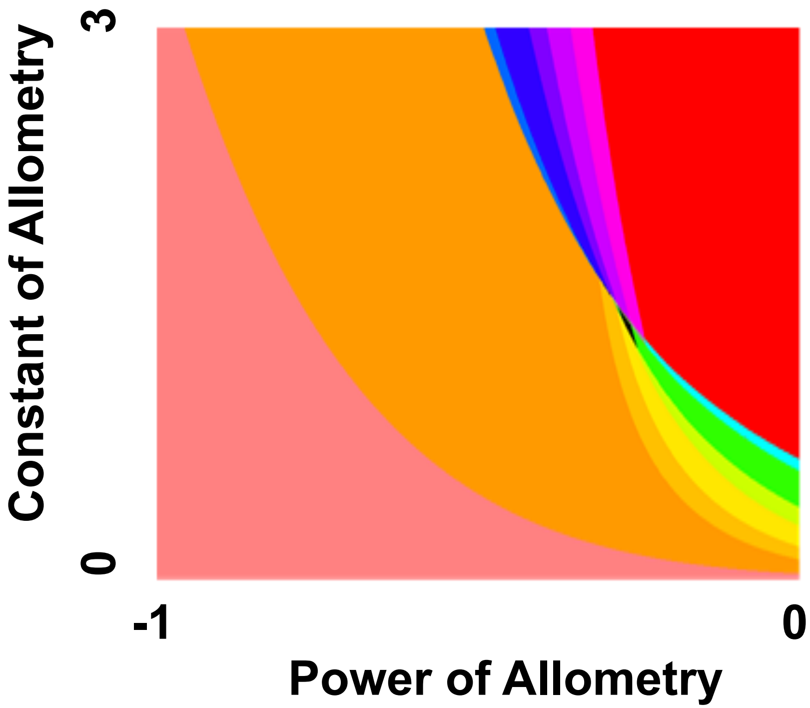

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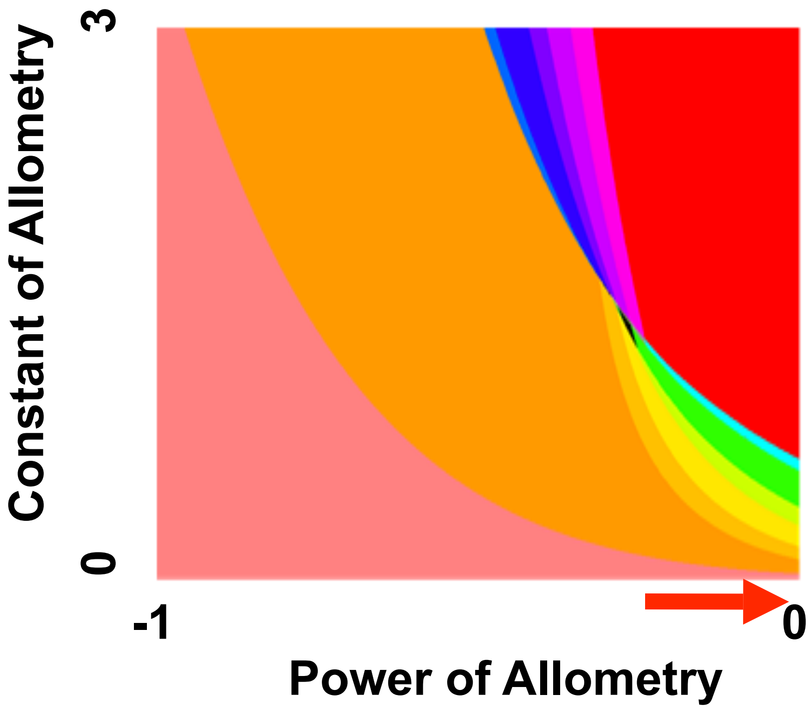
	Any predator extinction other than above

PowerCE > -0.35 and < 0: larger prey only marginally more difficult to capture than smaller and are extinguished; smaller prey persist despite hunting pressure due to their higher r_m ; stepwise extinctions: largest to smallest

Discussion



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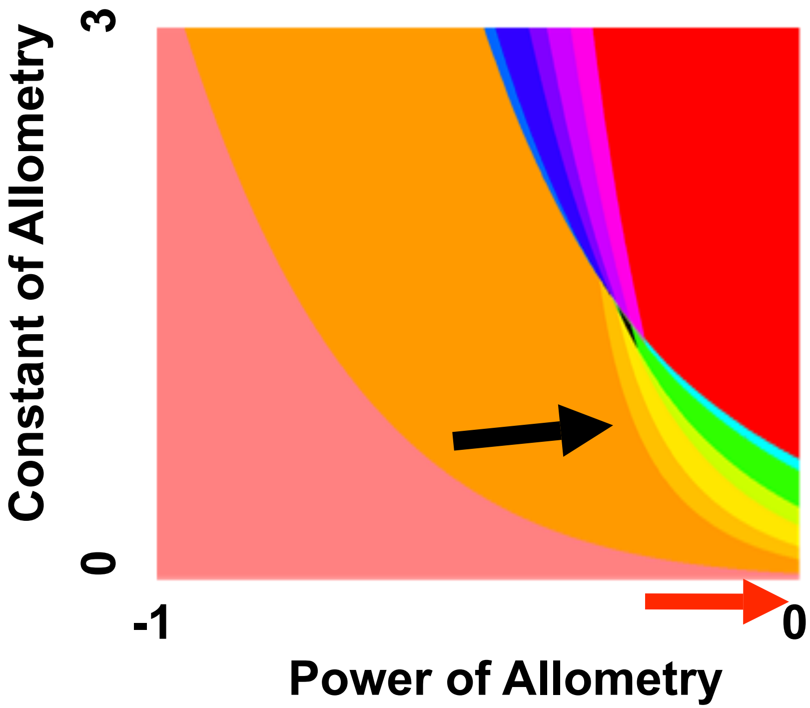

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	Outcome
	None of the below
	{0, 0, 0, 0, 0, 0, **0**}
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Discussion

- No support for the hypothesis that ratio-dependent functional response offers a superior explanation for Late Pleistocene extinction patterns

- Under all functional response forms, the “single-line” hypothesis could explain the extinction of larger ***or*** smaller species but not both simultaneously

Discussion

- The qualitative similarity in outcomes despite varied functional response forms is noteworthy
- This outcome may indicate that the functional response dynamics of obligate predator-prey systems (i.e., BKA) don’t apply to multi-prey systems

Discussion

- Functional response alone does not provide the hypothesized refinement
- But why?
- Possibly, predation alone cannot account for Late Pleistocene extinction patterns, which would lend credence to extinction scenarios involving predation along with other causes

Discussion: Parameterization

- Our findings might expose the limitations of parameterization
- Allometric relationships between body mass and relevant life history traits provide the best available means of constraining parameter values

Discussion: Parameterization

- But they resolve in log-scale regressions, allowing for one to two orders of magnitude in uncertainty

- Such uncertainty allows for a wide range of plausible outcomes, regardless of functional response choice

Discussion: Parameterization

- Capture efficiency remains a problematic parameter
- Our model fails to illuminate it anywhere near as much as we would prefer

Conclusions

- Late Pleistocene extinction modeling should be subject to considerable skepticism, on at least two grounds
  - **Inability to explain survival-extinction patterns**
  - **Inability to support or refute particular extinction scenarios**
- Given parameteric uncertainty, models cannot differentiate between a variety of scenarios involving single or multiple causes

Conclusions

- Allometric constraint, while being the best constraint available, involves serious limitations — a novel observation

Conclusions

- We find no support for our hypothesis, but under the circumstances, we cannot differentiate between three possible explanations for our negative result

Conclusions

1. Our hypothesis is correct

Conclusions

1. Our hypothesis is correct

2. **Some other functional response form might better explain survival-extinction patterns**

Conclusions

1. Our hypothesis is correct

2. Some other functional response form might better explain survival-extinction patterns

3. **Observed survival-extinction patterns are unrelated to functional response**

Conclusions

Results consistent both with “overkill” and extinctions resulting from a range of anthropogenic factors, either in conjunction with or in isolation from climatic effects

This same caveat applies equally to other modeling efforts (e.g., Alroy 2001), which have been interpreted as supporting overkill

A New Human Predation Model for Late Pleistocene Megafaunal Extinction Patterns in North America

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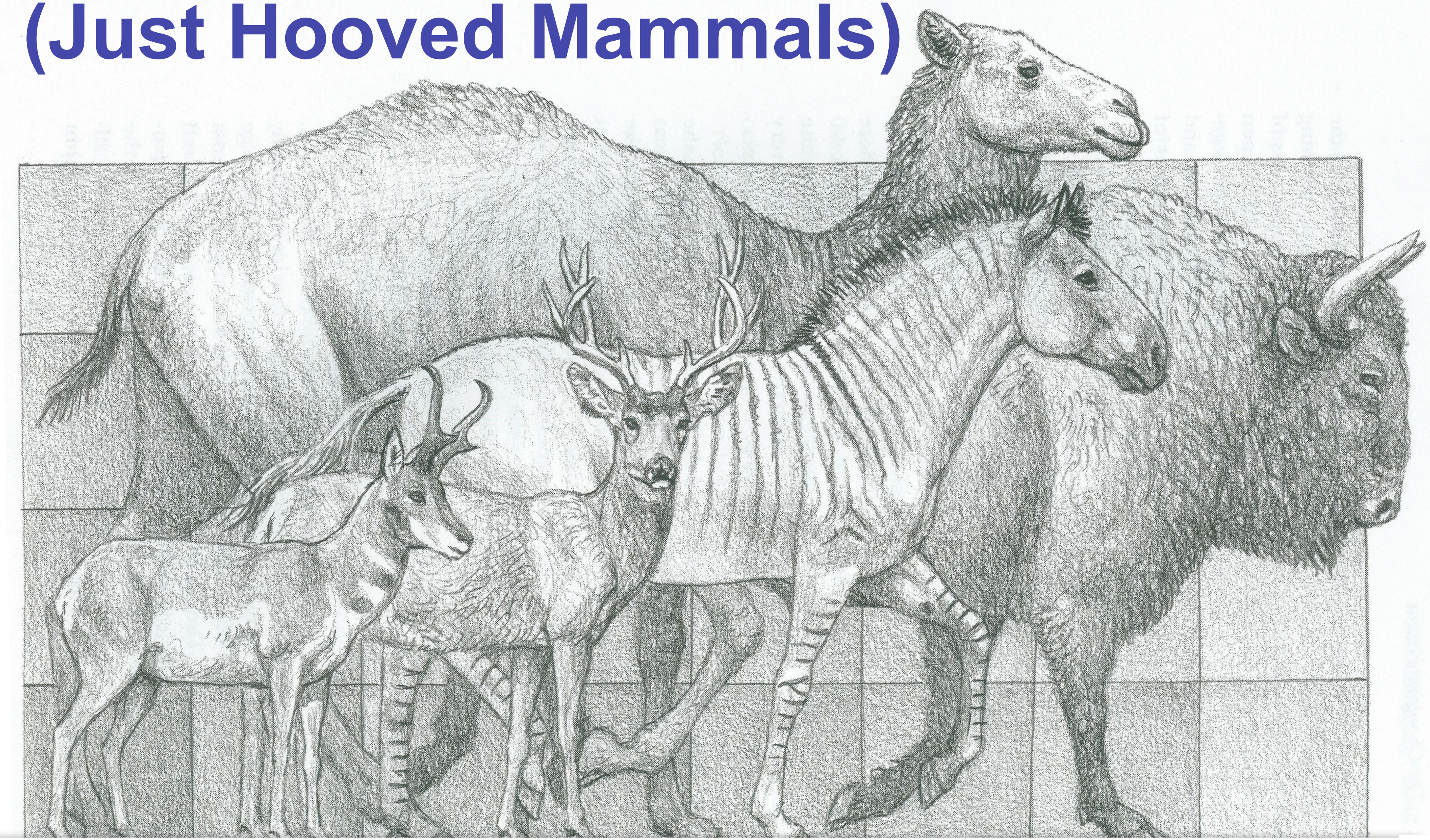
Pleistocene Rancho La Brean Prey (Just Hooved Mammals)



Ungulates Only, From Left to Right: Pronghorn (*Antilocapra*), Deer (*Odocoileus*), Giant Camel (*Camelops*), Horse (*Equus*), and Bison (*Bison*). Each square is 0.5 meters (about 1.5 feet) per side.

Prey Species Modeled

Species	Mass (kg)	Status
Capromeryx minor (Dimunitive pronghorn)	**21**	**Extinct**
Pecari tajacu (Collared peccary)	**30**	**Surviving**
Odocoileus hemionus (Mule deer)	**118**	**Surviving**
Equus conversidens (Mexican horse)	**306**	**Extinct**
Megalonyx jeffersonii (Jefferson's ground sloth)	**1320**	**Extinct**
Mammuthus columbi (Columbian mammoth)	**5827**	**Extinct**