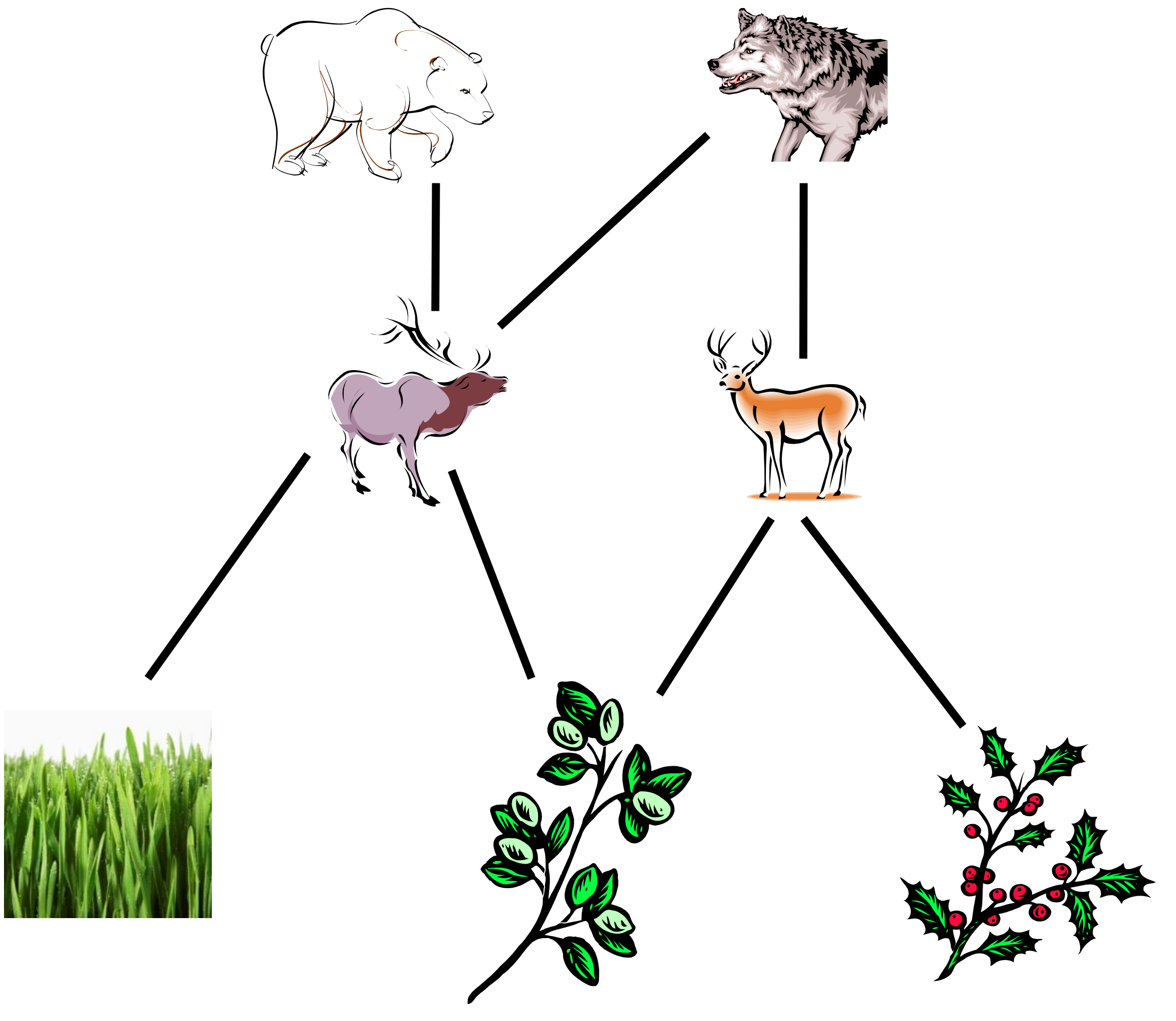
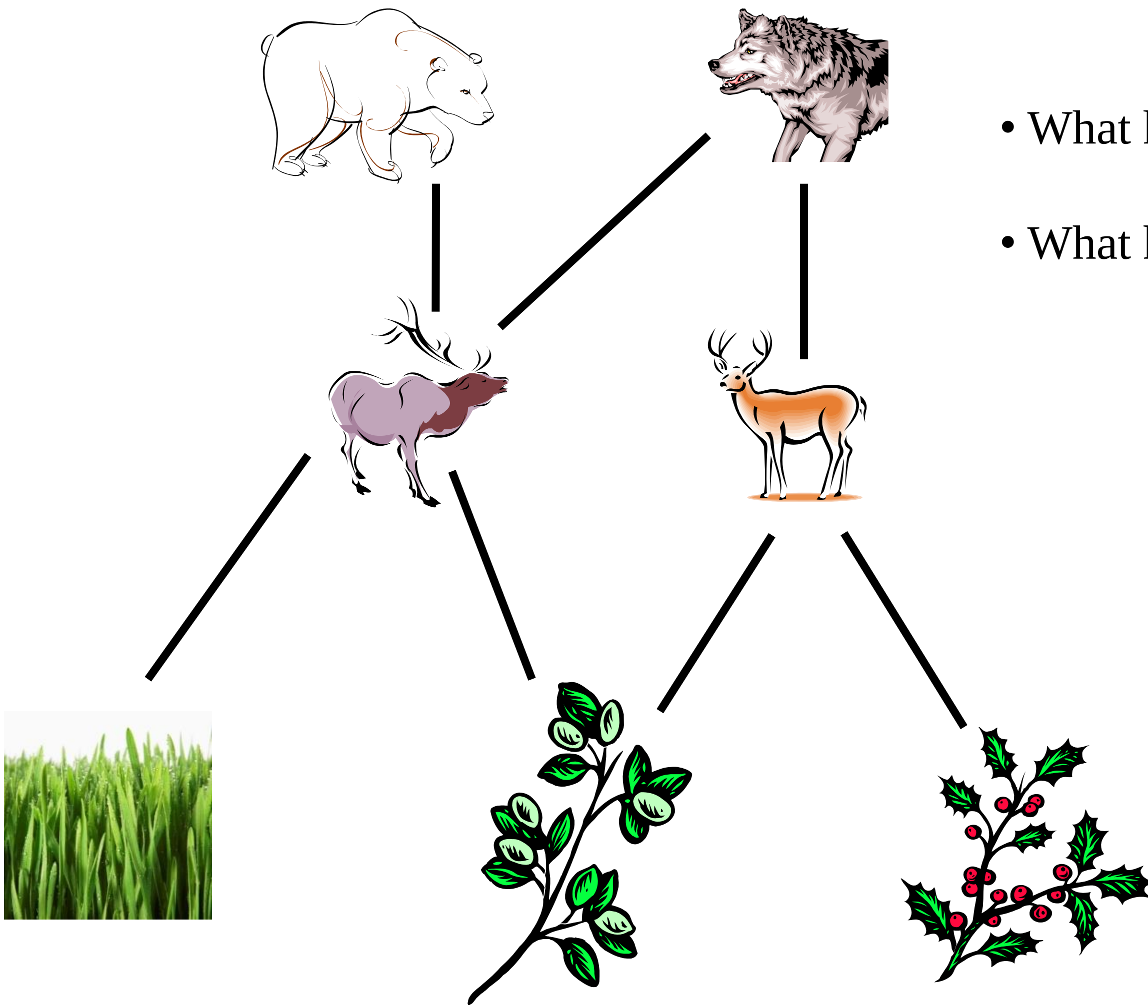
Food Webs and Trophic Cascades



Indirect Effects in Food Webs: Insights from studies of species removals



- What happens to elk if you remove wolves?
- What happens to grass if you remove elk?

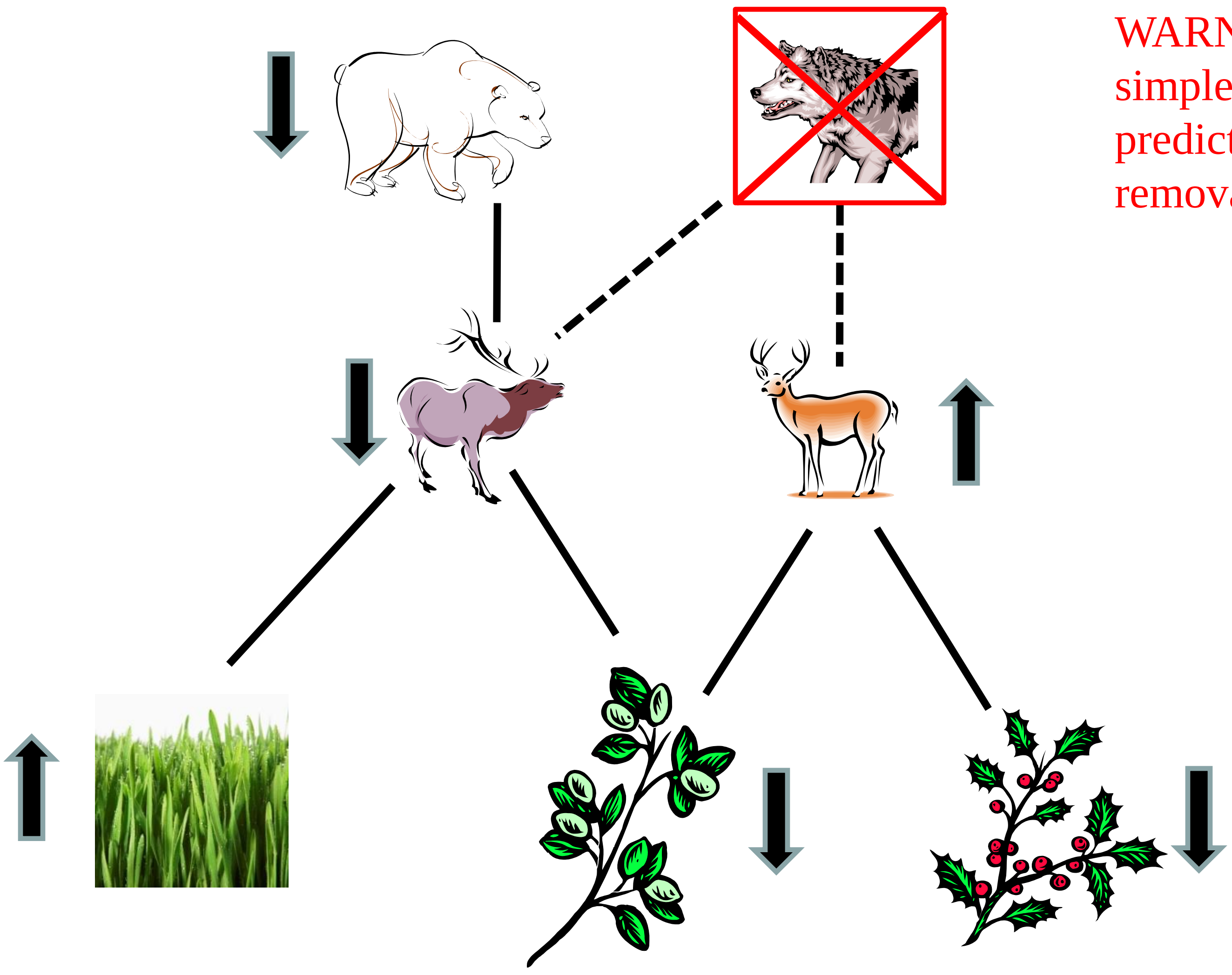
Indirect Effects in Food Webs

(Sih et al., 1985)

- Surveyed results of 100 experimental studies of predation
- In 66% of cases species removal had the “expected” result
- In 33% of cases, however, species removal had “unexpected” results

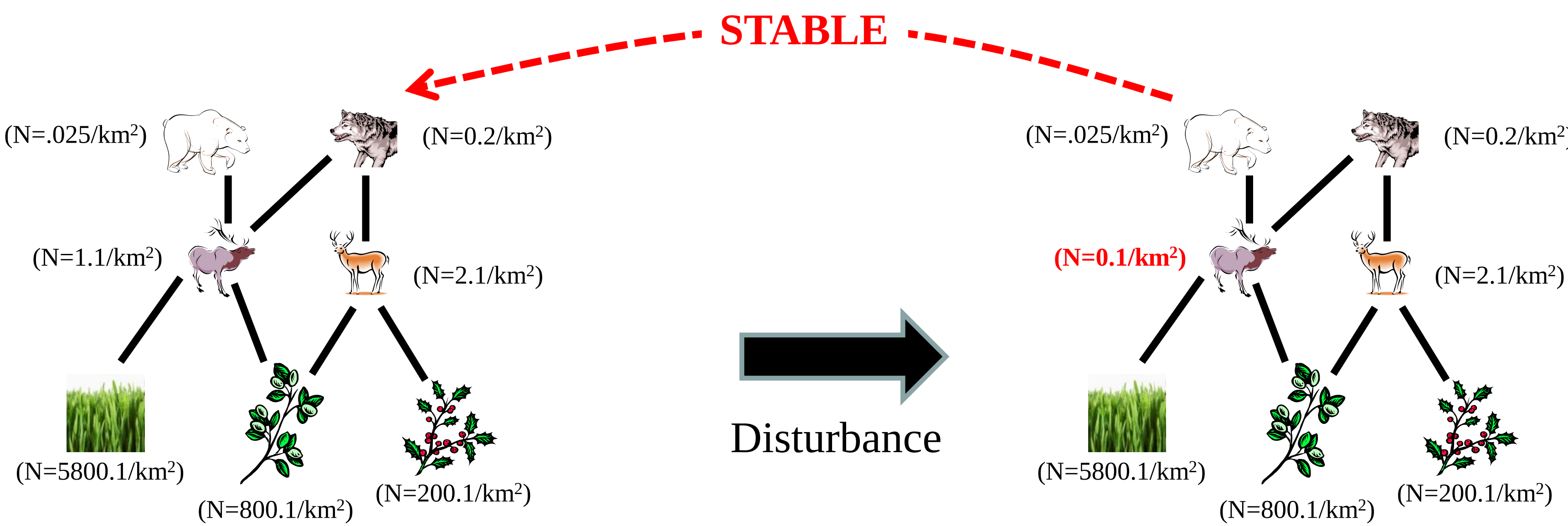
Why do we get unexpected results?

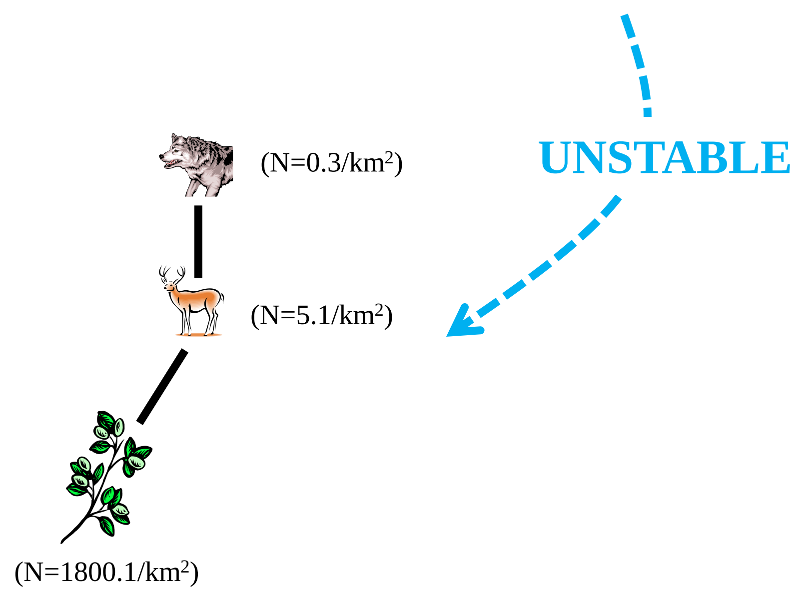
Indirect Effects can yield unexpected results



WARNING: In only the very simplest of systems can we predict the impact of species removals or additions!!!

Stability of Food Webs





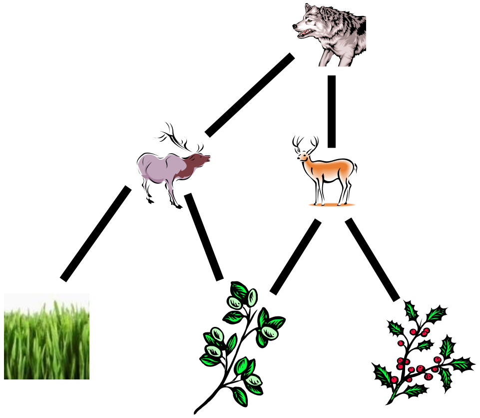
What determines stability?

The role of complexity in stability

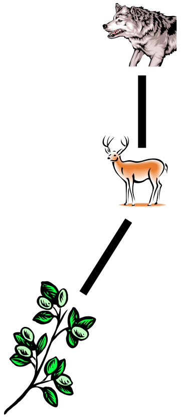
• MacArthur (1955) argued that increasing the complexity (number of species) in a food web would increase its stability

• His logic was based on the idea that increasing complexity increases redundancy

Stable to removal of lower trophic levels



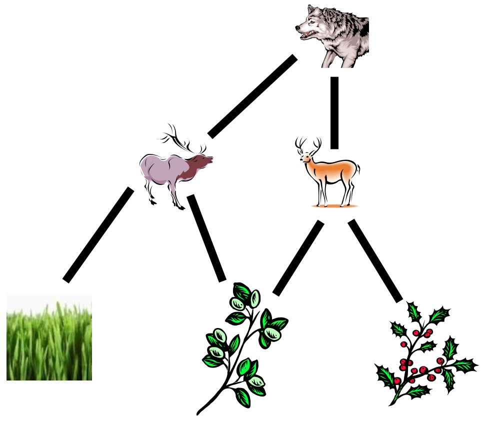
Unstable to removal of lower trophic levels



Stability of Food Webs

- May (1972) developed mathematical models to investigate MacArthur's ideas

- These models were based on the following parameters:
  1. The number of interacting species, S
  2. The fraction of all possible species pairs that interact directly, "connectance", C
  3. The effect of species i's density on species j's growth rate β_{ij}



<u>In this example:</u>

S = 6
C = 6/(6 choose 2) = 6/15

Stability of Food Webs

• May (1972) then drew β values at random

• Found that communities would be stable only if:

$$\beta\sqrt{SC} < 1$$

β is the average magnitude of interaction strengths within the web

➔Contradicts MacArthur's ideas. As S and C increase, both of which measure complexity, stability goes down!

➔ For the most part, subsequent theoretical studies qualitatively support May's result

➔ What about empirical studies?

An experimental test of complexity-stability theory

(McNaughton, 1977)

• Established species poor and species rich plots

• “Disturbed” plots by either a) adding nutrients or b) allowing grazing

• Both types of disturbance led to significant decreases in species diversity in species rich plots but not species poor plots

➔ **Supports May’s theoretical prediction**

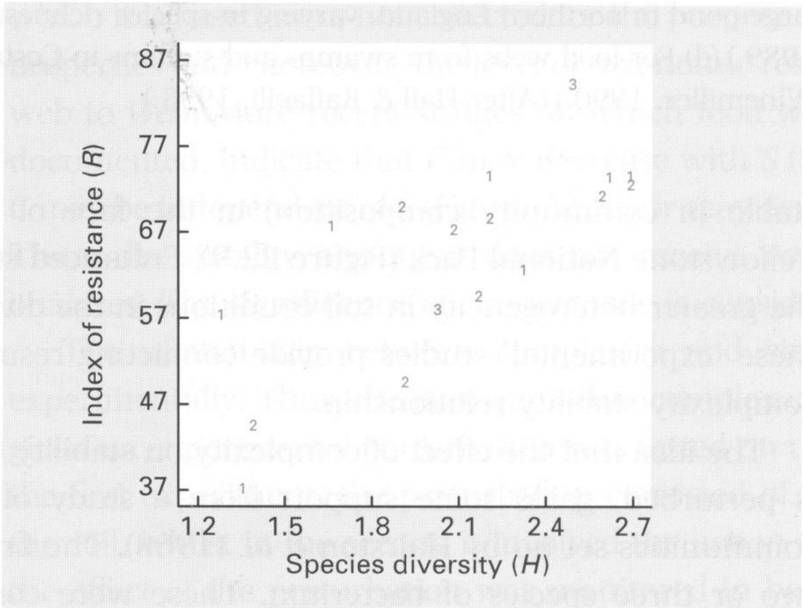
	Control plots	Experimental plots	Statistical significance
(a) *Nutrient addition*			
Species richness per 0.5 m^2 plot			
Species-poor plot	20.8	22.5	n.s.
Species-rich plot	31.0	30.8	n.s.
Equitability			
Species-poor plot	0.660	0.615	n.s.
Species-rich plot	0.793	0.740	$P < 0.05$
Diversity			
Species-poor plot	2.001	1.915	n.s.
Species-rich plot	2.722	2.532	$P < 0.05$
(b) *Grazing*			
Species diversity			
Species-poor plot	1.069	1.357	n.s.
Species-rich plot	1.783	1.302	$P < 0.005$

An experimental test of complexity-stability theory

(Frank and McNaughton, 1991)

- Studied 8 grassland communities in Yellowstone NP over the course of a severe drought
- Estimated species composition before and after drought
- Found that more diverse communities were MORE resistant to disturbance

➔ **Contradicts May's theoretical prediction**



Moving from random to real networks

(Yodzis 1981)

- May's result relies on the distribution of β_{ij} being random
- Yodzis estimated the distribution of β_{ij} for real networks
- These real networks were much more stable than May's random networks!

Why are real networks more stable than random networks?

Characterizing real food webs

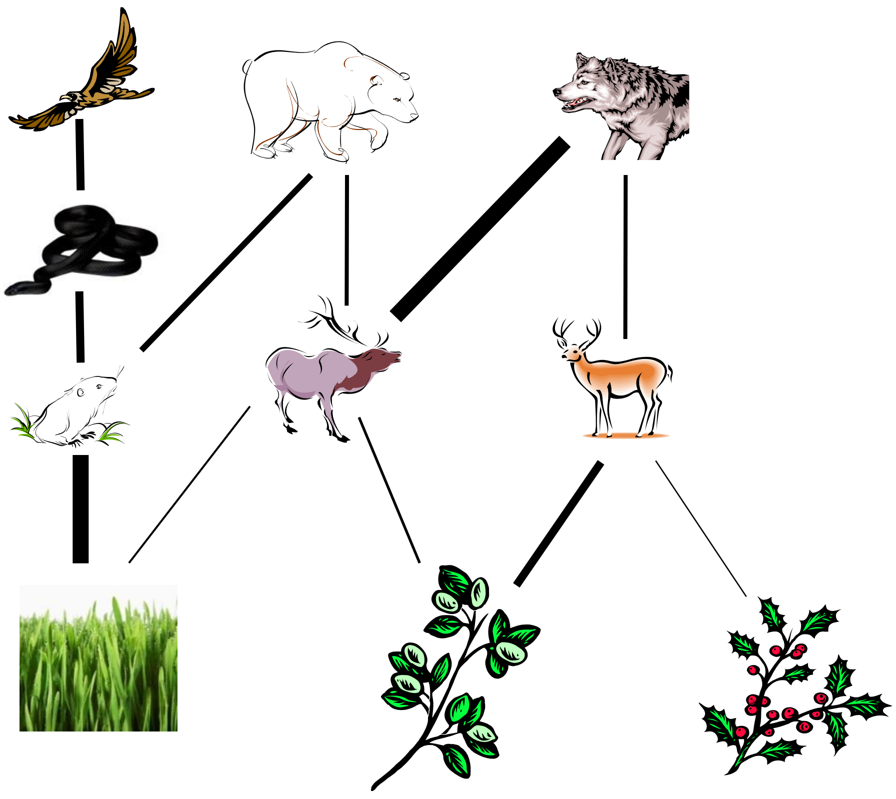
Paine (1992)

- Studied the distribution of β_{ij} in real communities

- Found that most interactions are WEAK and POSITIVE

Weak interactions and food web stability

- Weak interactions stabilize food webs, by preventing propagation of disturbance



Practice Question

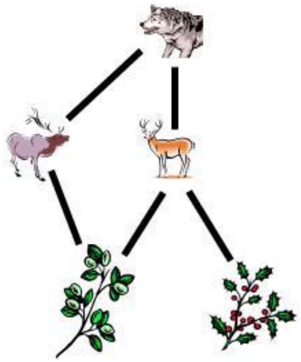
In 1955 MacArthur proposed that more complex communities should be more stable to perturbations because they have more redundancy in terms of trophic linkages between species. In 1972, May developed a mathematical model of MacArthur's idea and showed that a community would be stable to perturbations only if:

$$\beta\sqrt{SC} < 1$$

Where S is the number of species, C is the connectance, and β is the average magnitude of interaction strengths within the web.

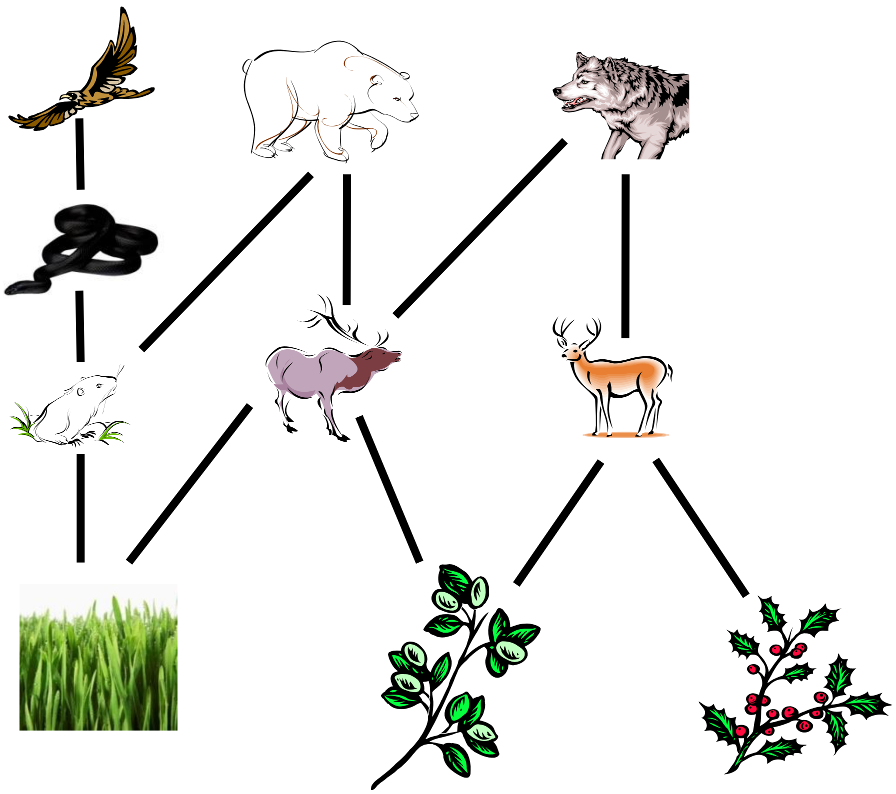
A (15pts). Does May’s result support MacArthur’s claim? Why or why not?

B (10pts). What are the values of S and C for the community shown below?



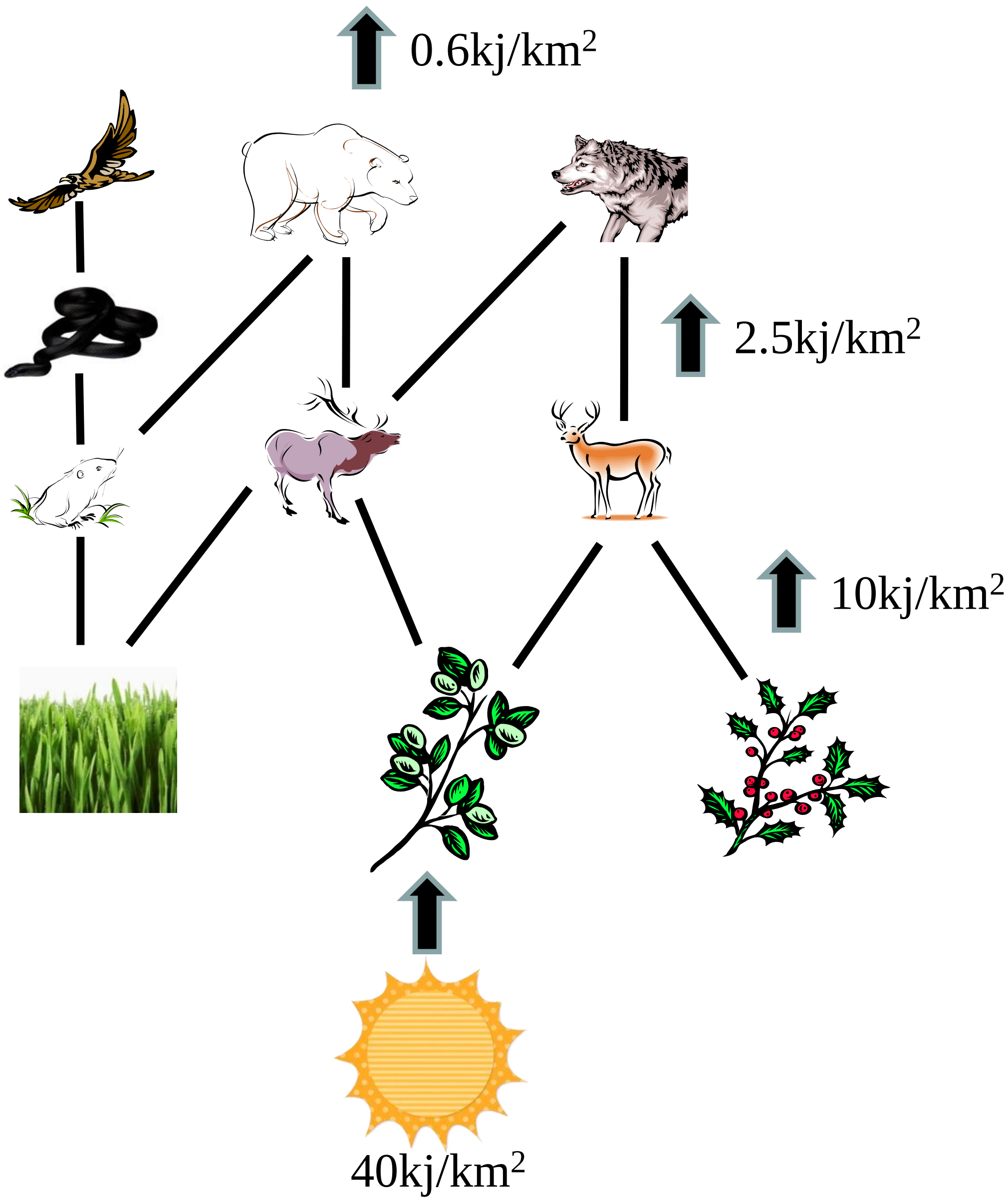
C (15pts). If β = .35, would the community shown above be stable using May’s mathematical criterion?

Structure of Food Webs: Food chain length



- This food web has a maximum food chain length of 4
- The majority of food webs studied have between 2 and 5 levels
- Why are there not food webs with more levels?

The energy flow hypothesis



Theory

•The sun provides a fixed amount of energy input

• Each trophic level above autotroph successfully incorporates only 1-30% of this energy

• Consequently, there may simply not be enough energy to support additional trophic levels

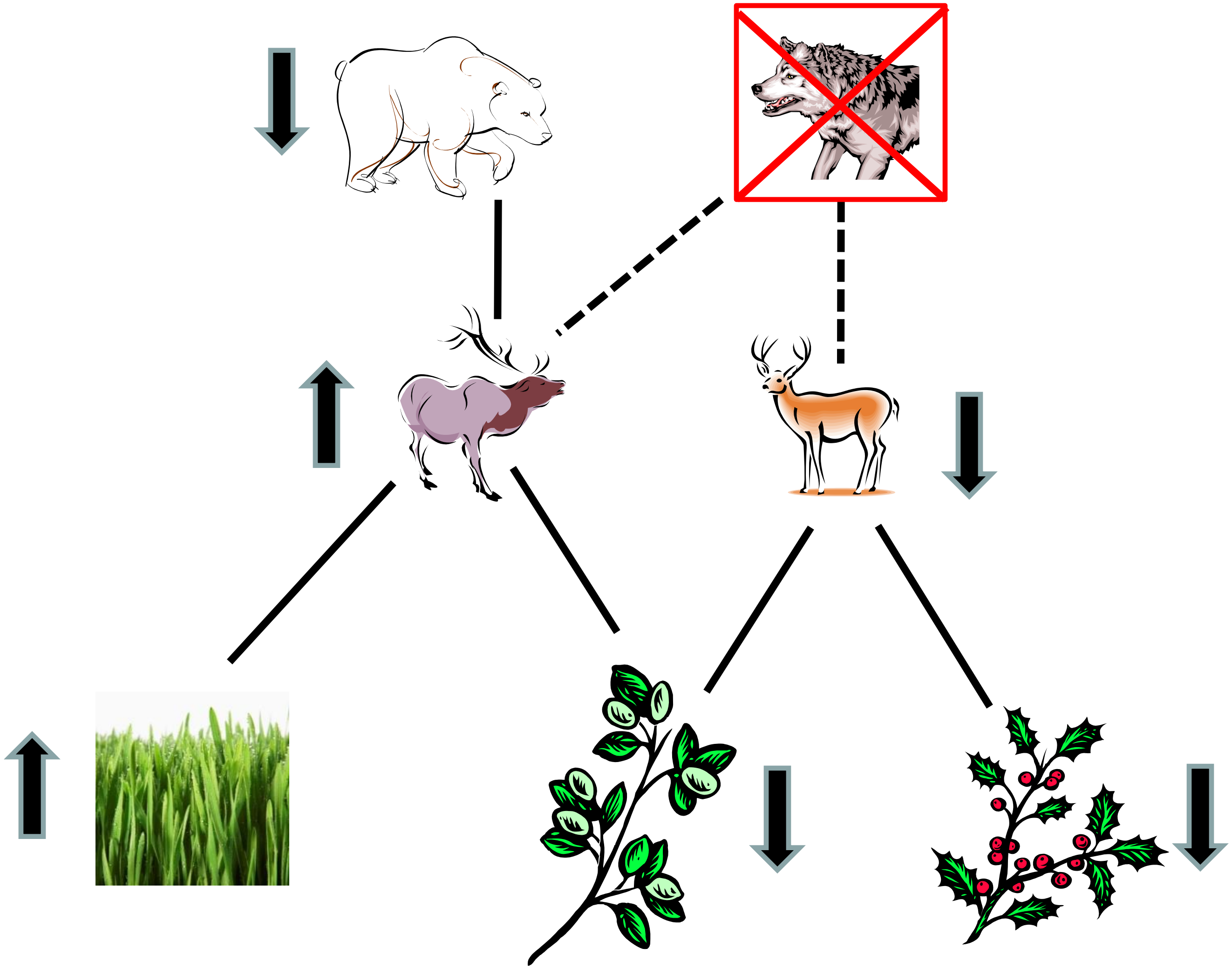
Empirical Studies

Food chains are no longer in tropical than presumably less productive temperate regions

➔Energy flow hypothesis not supported

➔ No strong support for other hypotheses

Trophic Cascades and indirect impacts of predation



Trophic Cascades

Trophic Cascade – Indirect effects of carnivores on plant populations or the progression of indirect effects by predators across successively lower trophic levels

Aspen in Yellowstone National Park

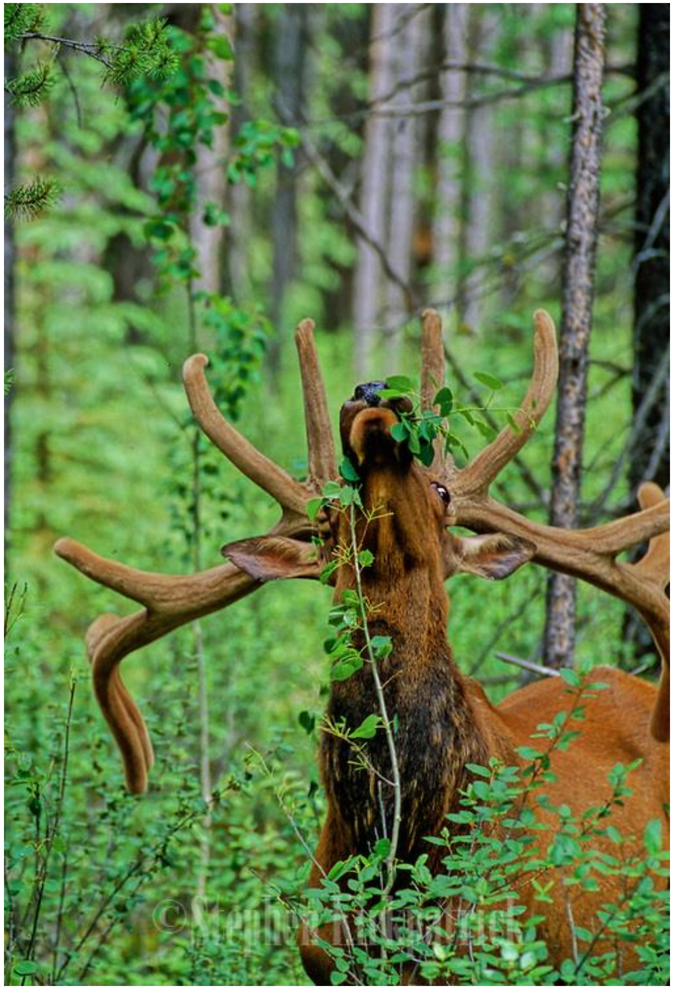
- Aspen are clonal with stands consisting of genetically identical individuals produced as suckers
- Historically, aspen covered 4–6% of the northern range of Yellowstone National Park
- Aspen now cover only 1%
- From 1930 on aspen recruitment in YNP ceased, except in sites protected from browsing.

Why are Aspen declining in Yellowstone National Park?

Interactions between elk and aspen

Elk eat the bark of aspen trees which can stress the plant and facilitate invasion by pathogenic fungi

Interactions between elk and aspen



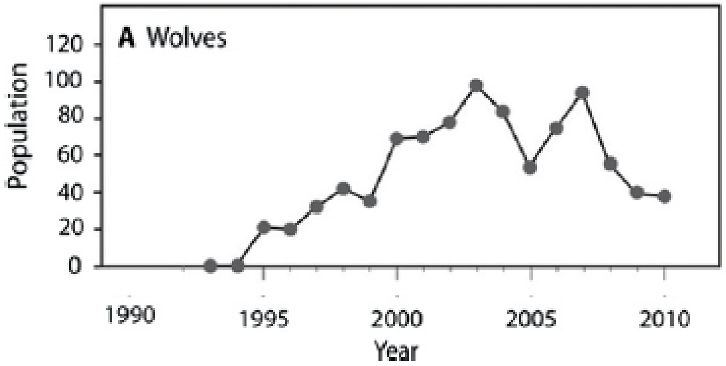
- Elk eat aspen suckers
- Elk eat juvenile aspen
- Together, this may inhibit recruitment and stand replacement

Wolves, Elk, and Aspen, a historical correlation

Dates	Wolf events	Aspen events
1914-1926	Wolves extirpated from YNP	
1930		Aspen overstory regeneration ceases
1995	Wolves reintroduced	
≈2000		Some Aspen stands in riparian areas begin to recover

Could wolf reintroduction have played a role?

Wolf reintroduction



- **Wolves were reintroduced into YNP in 1995**

- **By the end of 1998, 112 wolves lived in 11 packs in the greater Yellowstone ecosystem**

Impacts of wolf reintroduction on aspen

Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range

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- Established permanent plots in aspen stands in 1999

- Chose plots with aspen stands in high and low wolf-use areas

- Recorded number of elk pellet groups, aspen sucker heights and the percentage of suckers being browsed

Impacts of wolf reintroduction on aspen

- **Found significant differences in elk pellet groups**
- **Found significant differences in aspen sucker heights**

Habitat type	Low wolf-use areas					High wolf-use areas					
	n	Mean height (cm)	S.D.	Min.	Max.	*n*	Mean height (cm)	S.D.	Min.	Max	*P*-value
Mean aspen sucker heights (cm)[b]											
Xeric upland steppe	11	40.1	15.0	14.1	64.6	10	36.1	6.2	27.4	44.4	0.568
Mesic upland steppe	25	45.9	12.7	26.8	77.4	20	48.3	19.4	27.5	110.9	0.725
Riparian/wet meadow	15	37.2	17.3	13.0	75.4	26	49.3	18.5	26.1	93.1	0.019
All mesic types	40	42.6	15.0	13.0	77.4	46	48.9	18.7	26.0	110.9	0.120

➔ **Argued the data suggest high wolf-use causes a shift in elk habitat use and a subsequent recovery of aspen**

Elk behavioral change?

WOLVES INFLUENCE ELK MOVEMENTS: BEHAVIOR SHAPES A TROPHIC CASCADE IN YELLOWSTONE NATIONAL PARK

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- **Studied movement patterns of 13 female elk using data from radio collars**
- **Measured local wolf activity**
- **Measured local habitat characteristics**

Elk behavioral change?

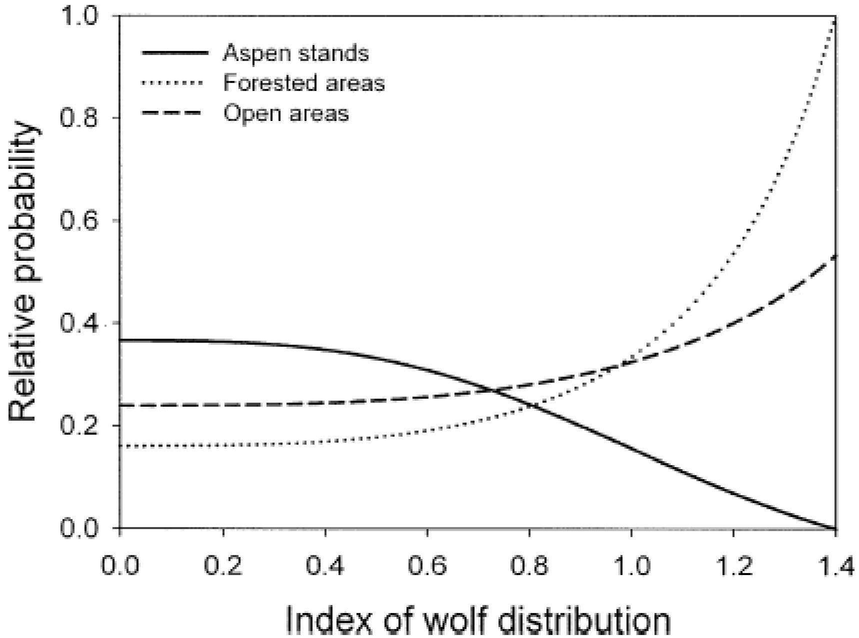

FIG. 3. Relative probability that elk select steps ending in various habitat types when traveling on their winter range, as a function of a wolf index averaged along the individual's step. Relative probabilities reflect the range of wolf indices 0–1.4 (i.e., from absence of wolves to high- and low-wolf-use areas) and were calculated from the SSF model provided in Table 1.

- **In the presence of wolves, elk moved toward forested areas**
- **In the absence of wolves, elk moved toward aspen stands**
- **Suggests wolves alter elk behavior in a way that reduces impacts on aspen**

Other indirect impacts of wolf reintroduction

Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction

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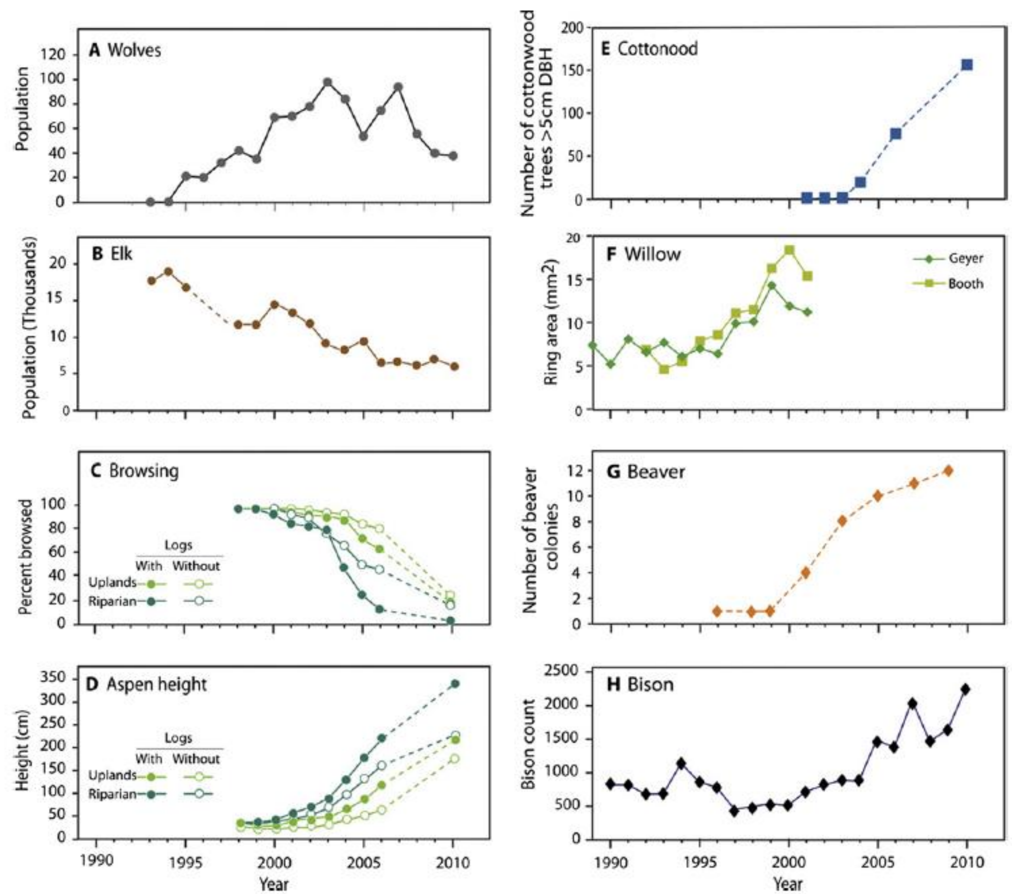

➔ Wolf reintroduction appears to be driving complex trophic cascades

Alternative explanations

Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade

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- **Increased aspen recruitment in riparian areas may be the result of climate change and altered snow melt patterns**

- **Wolf impacts on elk behavior may not be strong enough to save aspen**

- **Suggest that wolves are likely to save aspen only if they further reduce elk population size as grazing remains too intense for aspen regeneration**

- **We need replicated studies to tease these potential impacts apart**

A grand challenge in ecology