

# Variation in species interaction outcomes

**Scott Chamberlain**

**Simon Fraser University**

**My website <http://bit.ly/schamber>**

**28 September 2012**

**Follow along with this talk <http://bit.ly/ucalgarytalk>**

Shortcuts:

M = G =



# Collaborators

**Jennifer Rudgers** - ([website](#))



**Judith Bronstein** - ([website](#))



# Bronstein 1994 TREE

## Conditional outcomes in mutualistic interactions

Judith L. Bronstein

Mutualisms are interspecific interactions in which both partners experience a net benefit. Mutualisms are ubiquitous in nature, as well as extremely diverse<sup>1,2</sup>. They range from species-specific, obligate, coevolved associations to looser and more generalized ones, and include relationships both between free-living species (e.g. plants and their pollinators) and species living in close association for their entire lifetimes (e.g. mammals and their gut bacteria). The more intimate mutualisms are often considered separately as 'symbioses', adding to a confusion of terminology that has long plagued the study of beneficial interactions (Box 1). In recent years, however, efforts have been made to identify ecological and evolutionary patterns that cut across diverse forms of mutualism<sup>3–8</sup>.

One such generality is that in most mutualistic associations, one partner performs some action (a service) that benefits its associate, and receives some payoff (a reward) for doing so<sup>7</sup>. These rewards are often costly to produce:

**Interspecific interactions are traditionally displayed in a grid in which each interaction is placed according to its outcome (positive, negative or neutral) for each partner. However, recent field studies consistently find the costs and benefits that determine net effects to vary greatly in both space and time, inevitably causing outcomes within most interactions to vary as well. Interactions show 'conditionality' when costs and benefits, and thus outcomes, are affected in predictable ways by current ecological conditions. The full range of natural outcomes of a given association may reveal far more about its ecological and evolutionary dynamics than does the average outcome at a given place and time.**

---

Judith Bronstein is at the Dept of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA.

---

leading to what have conditional outcomes<sup>14,15</sup>. Here, I focus on conditional outcomes of mutualistic interactions, reviewing their origins, patterns of occurrence and evolutionary significance.

either the costs or the benefits change in magnitude, then the degree to which an association is mutually beneficial will change as well. Hence, any interaction might be considered to occupy a potentially dynamic position along a continuum of possible outcomes, ranging from beneficial to progressively more antagonistic (Box 2). It is increasingly clear that over evolutionary time, certain interactions have shifted away from antagonism towards commensalism and even mutualism<sup>5</sup>. Researchers are beginning to delineate the genetic and life-history conditions that predispose such evolutionary transitions<sup>11,12</sup>; some of these transitions are being studied with great success in laboratory cultures<sup>13</sup>. Costs and benefits also frequently vary, however, over ecological time and space for a single interaction, recently been referred to as conditionality<sup>16</sup>.

# Species interactions

# Species interactions

- Species interact in a variety of ways

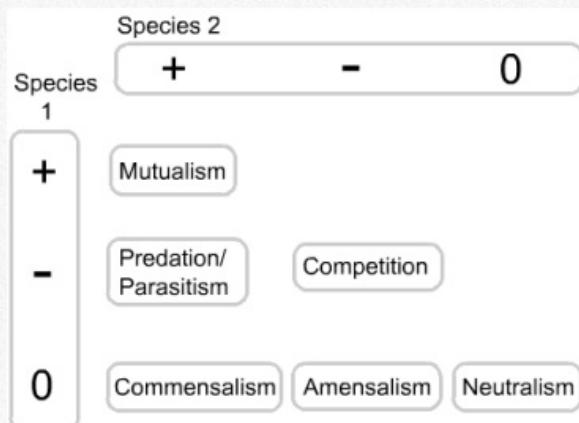


# Species interactions

- Species interact in a variety of ways



- Outcomes of species interactions range from - to +



Source: [Principles of Animal Behavior](#)

# **Interaction outcomes are important for:**

- Individual growth and reproduction - e.g., herbivory
- Population growth - e.g., fox and hare
- Formation and dynamics of food webs - e.g., interaction strengths important for stability
- Evolution - e.g., interactions alter traits important for interaction

# Mean interaction outcomes

Vol. 140, No. 4

The American Naturalist

October 1992

## A META-ANALYSIS OF COMPETITION IN FIELD EXPERIMENTS

JESSICA GUREVITCH, LAURA L. MORROW, ALISON WALLACE,  
AND JOSEPH S. WALSH\*

## RESOURCE COMPETITION MODIFIES THE STRENGTH OF TRAIT-MEDIATED PREDATOR-PREY INTERACTIONS: A META-ANALYSIS

DANIEL I. BOLNICK<sup>1,2,4</sup> AND EVAN L. PREISSER<sup>2,3</sup>

## DIRECT AND INTERACTIVE EFFECTS OF ENEMIES AND MUTUALISTS ON PLANT PERFORMANCE: A META-ANALYSIS

WILLIAM F. MORRIS,<sup>1,12</sup> RUTH A. HUFFBAUER,<sup>2</sup> ANURAG A. AGRAWAL,<sup>3</sup> JAMES D. BEVER,<sup>4</sup> VICTORIA A. BOROWICZ,<sup>5</sup>  
GREGORY S. GILBERT,<sup>6</sup> JOHN L. MARON,<sup>7</sup> CHARLES E. MITCHELL,<sup>8</sup> INGRID M. PARKER,<sup>9</sup> ALISON G. POWER,<sup>3</sup>  
MARK E. TORCHIN,<sup>10</sup> AND DIEGO P. VÁZQUEZ<sup>11</sup>

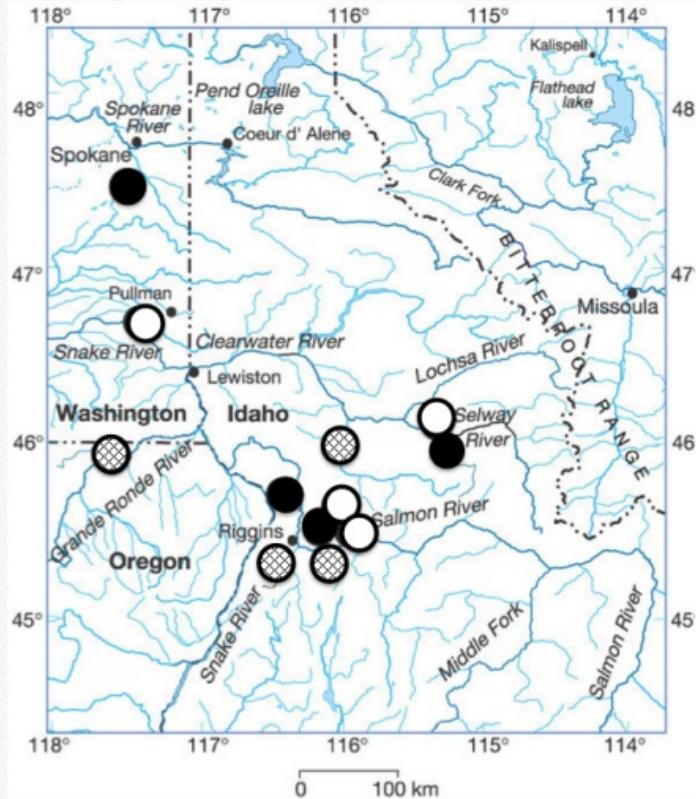
VOL. 155, NO. 2 THE AMERICAN NATURALIST FEBRUARY 2000

## Trophic Cascades in Terrestrial Systems: A Review of the Effects of Carnivore Removals on Plants

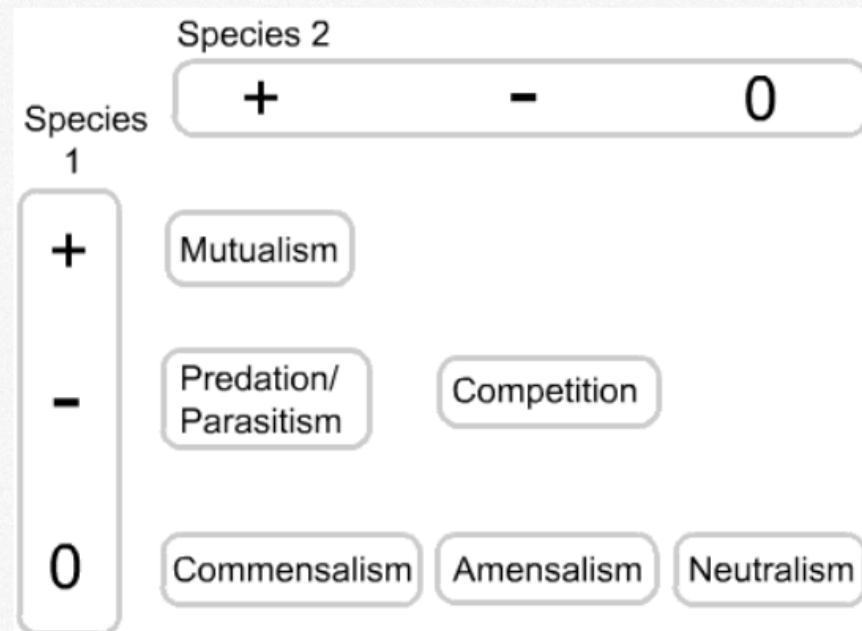
Oswald J. Schmitz,<sup>1,2,\*</sup> Peter A. Hambäck,<sup>1</sup> and Andrew P. Beckerman<sup>1</sup>

# What about variation in outcomes?

# Species interaction outcomes vary a lot



# Within a species interaction, outcomes are not just +, 0, or -

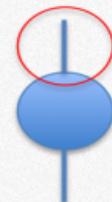


***Outcomes within a species interaction can range from - to +***

# What is meant by variation in interaction outcomes?

# What is meant by variation in interaction outcomes?

- Not error variation in outcome in one context



Site 1

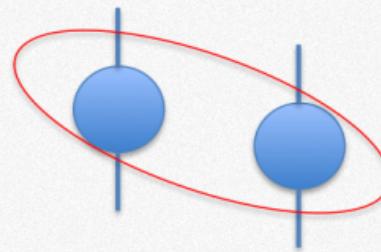
# What is meant by variation in interaction outcomes?

- Not error variation in outcome in one context



Site 1

- The variation in outcomes among more than one context



Site 1      Site 2

# Variation in interaction outcomes - example

# Variation in interaction outcomes - example

- Not error variation in outcome in one context



*C. mimosae* (RRB)

# Variation in interaction outcomes - example

- Not error variation in outcome in one context



*C. mimosae* (RRB)

- The variation in outcomes among more than one context



*C. sjostedti* (AB)



*C. mimosae* (RRB)



*C. nigriceps* (BBR)



*T. penzigi* (TP)

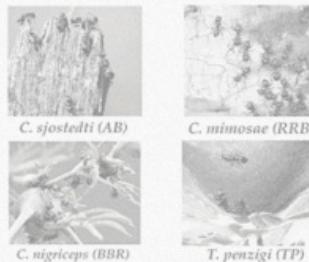
# Variation in interaction outcomes - example

- Not error variation in outcome in one context



*C. mimosae* (RRB)

- The variation in outcomes among more than one context



- And so on for other types of contexts: time, space, etc.

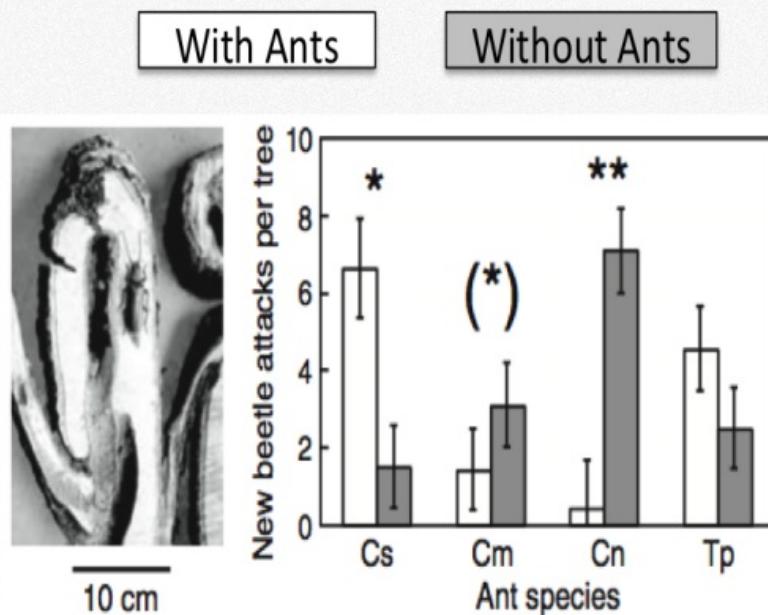
## **Two points:**

- 1. Variation in outcomes is common**
- 2. Variation in outcomes is important**

# Variation in outcomes is common

## Mutualism

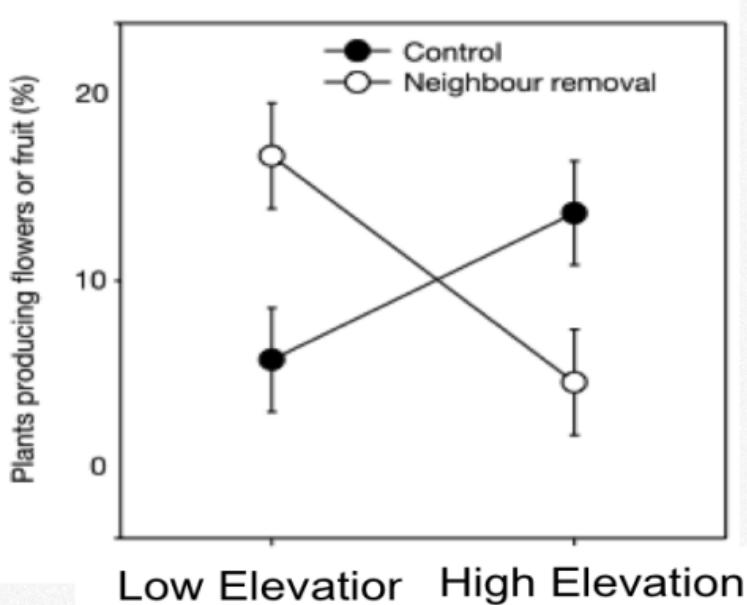
Herbivory outcome for *Acacia* trees varies with ant species identity  
**(Palmer et al. 2008)**



# Variation in outcomes is common

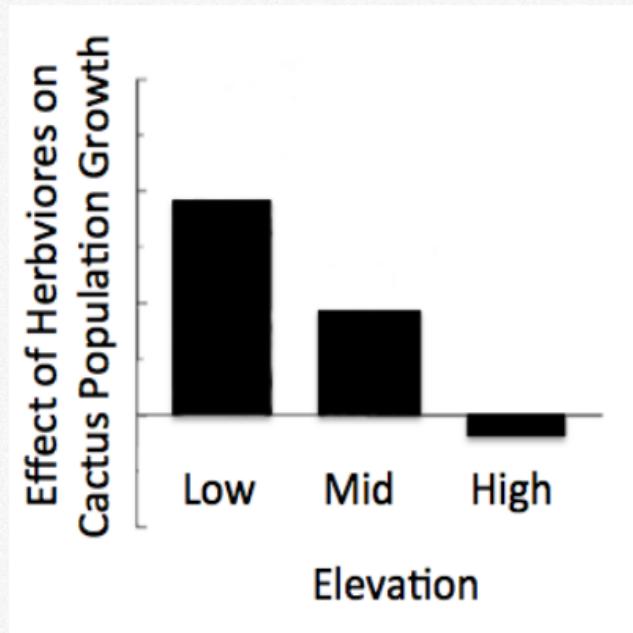
## Competition/facilitation

Outcomes vary from competition at low elevation to facilitation at high elevation ([Callaway et al. 2002](#))



# Variation in outcomes is important

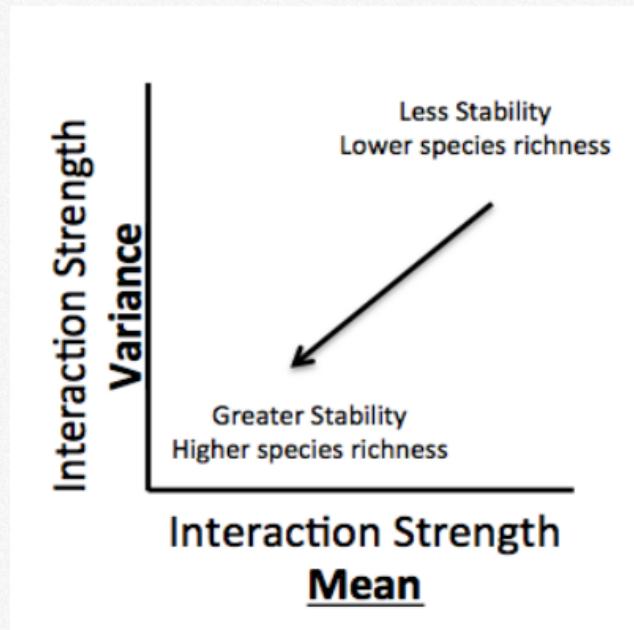
for populations



Miller et al. 2009

# Variation in outcomes is important

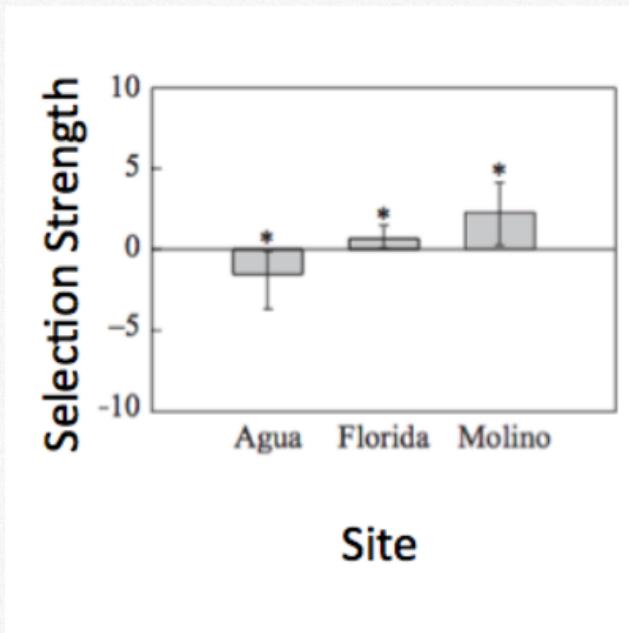
## for communities



Kokkoris et al. 2002

# Variation in outcomes is important

for evolution



Rudgers and Strauss 2004

# And people are calling for examination of variation

- “ To the extent that different biotic interactions are important contributors to different population dynamics within a species, variable interactions might be expected to be a powerful such source. - Joseph Travis 1996 AmNat
- “ The full range of natural outcomes...may reveal far more about...ecological and evolutionary dynamics than does the average outcome. - Judith Bronstein 1994 TREE
- “ ...understanding context-dependency is critical for such reconciliation [of variation in species interaction outcomes]. - Anurag Agrawal et al. 2007 FREE

# Questions

- 1. How do different species interaction types differ in variation in outcomes?**
- 2. What are the relative importance of drivers of variation in outcomes?**
- 3. Does variation in outcome differ by ecosystem type?**

**Two major distinctions can be made:**

- 1. Types of species interactions, and**
- 2. Gradients along which interaction occur**

# **How do different species interaction types differ in variation in outcomes?**

# How do different species interaction types differ in variation in outcomes?

- Mean strength
  - Mutualisms weaker than antagonisms (Morris et al. 2007)
  - General sense in literature that mutualisms less important because so variable (Sachs & Simms 2006)
  - Weak interactions the most variable (Berlow et al. 1999)

# How do different species interaction types differ in variation in outcomes?

- Mean strength
  - Mutualisms weaker than antagonisms (Morris et al. 2007)
  - General sense in literature that mutualisms less important because so variable (Sachs & Simms 2006)
  - Weak interactions the most variable (Berlow et al. 1999)
- Interaction complexity
  - Predation more specialized than mutualism (Gomez et al. 2010)
  - Strength greater with fewer interactions (Edwards et al. 2010)

# Gradients that drive variation in interaction outcome

# Gradients that drive variation in interaction outcome

- Same two species
  - Abiotic: Nutrients
  - Space: Across sites
  - Time: Across hours, days, or years
  - Third party presence: Two species w/ or w/o a third species

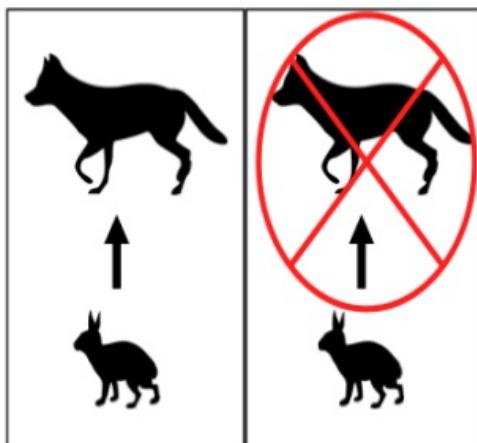
# Gradients that drive variation in interaction outcome

- Same two species
  - Abiotic: Nutrients
  - Space: Across sites
  - Time: Across hours, days, or years
  - Third party presence: Two species w/ or w/o a third species
- Just one species is the same
  - Species identity: Sp. A interacts with either sp. B or sp. C

# Meta-analysis

- Web of Science search
- Experimental studies only
- Interaction outcome w/ & w/o competitor, predator, or mutualist
- Error estimates & sample sizes available
- Response variables: abundance, population growth, reproduction, etc.
- Responses measured over >1 year, population, or species, etc.

# E.g. Getting data from a single study



Site A



Site B

Site C

Site D

Site E

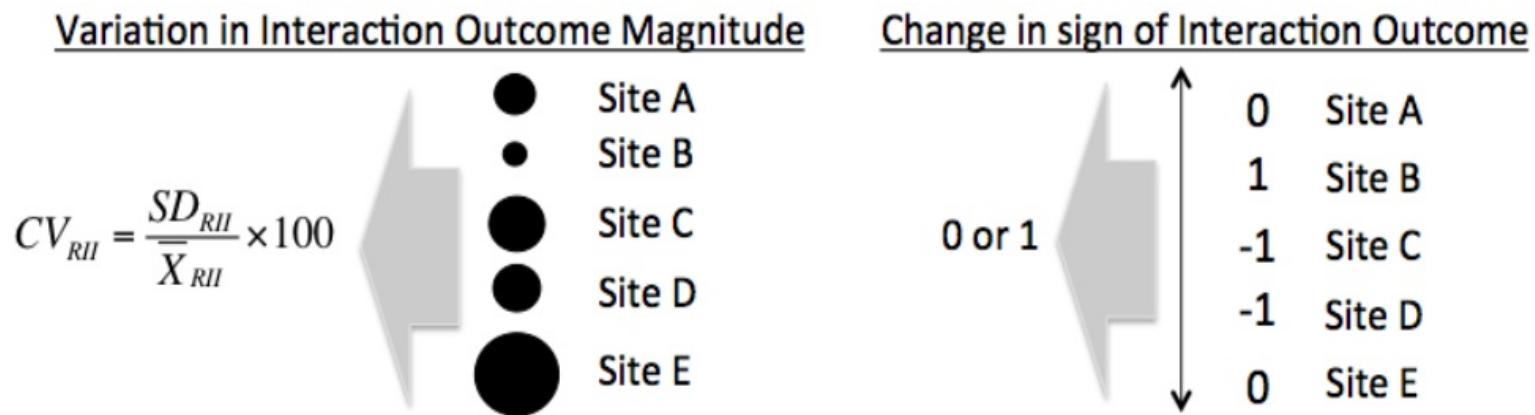
Mean Interaction Outcome  
from Armas *et al.* (2004)

$$RII = \bar{X}_C - \bar{X}_E / \bar{X}_C + \bar{X}_E$$

Negative  $RII$  = better w/o predation

Positive  $RII$  = better with predation

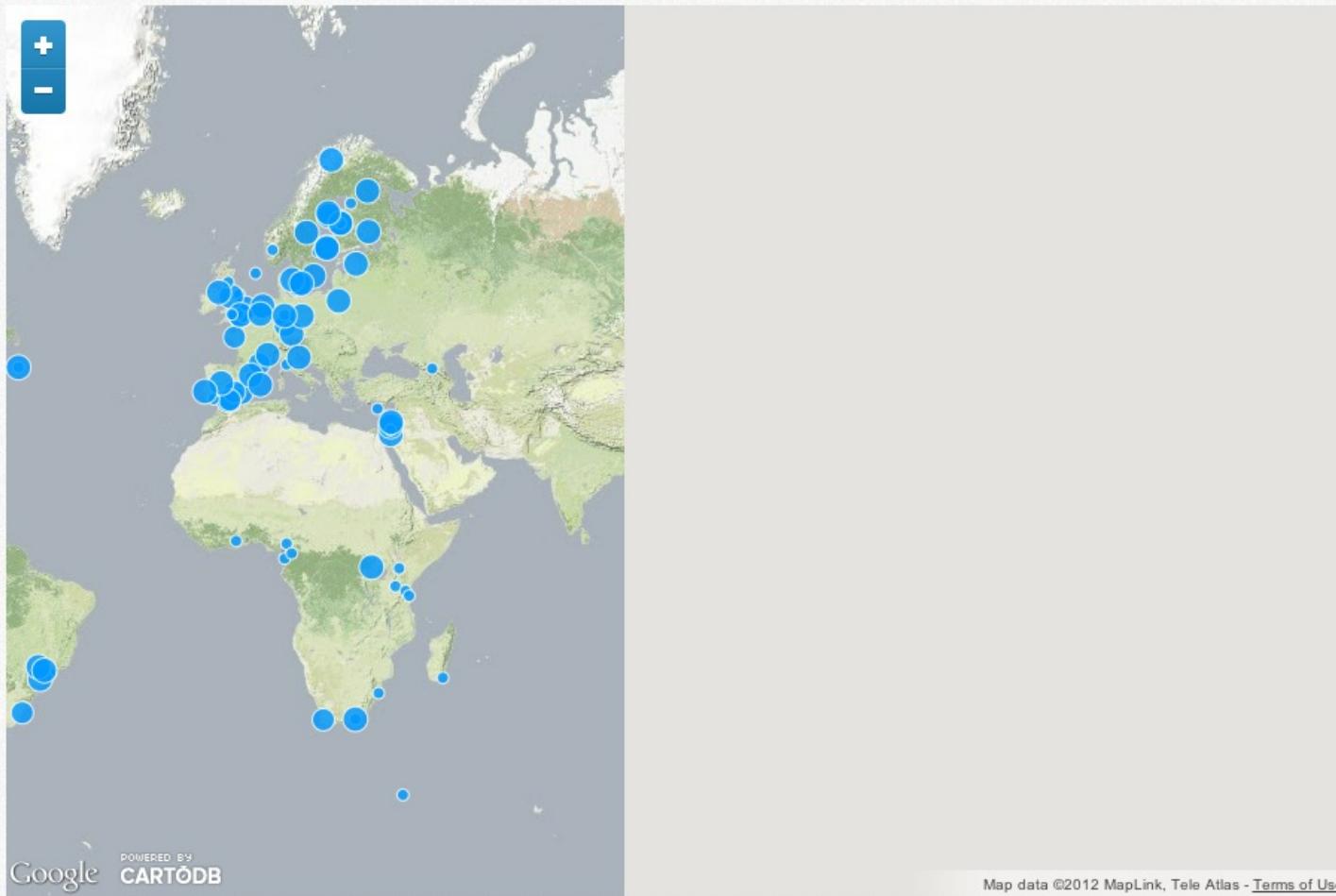
# E.g. Getting data from a single study..cont.



# Data analyses

- Weighted general linear models
  - Magnitude (CV)
    - $CV \sim \text{context type} + \text{species interaction type} + \text{err}$
    - $CV \sim \text{context type} + \text{species interaction type} + \text{ecosystem} + \text{err}$
  - Sign change
    - $\text{sign change} \sim \text{context type} + \text{species interaction type} + \text{err}$
    - $\text{sign change} \sim \text{context type} + \text{species interaction type} + \text{ecosystem} + \text{err}$

# Final dataset - 353 papers



# How do different species interaction types differ in variation in outcomes?



P

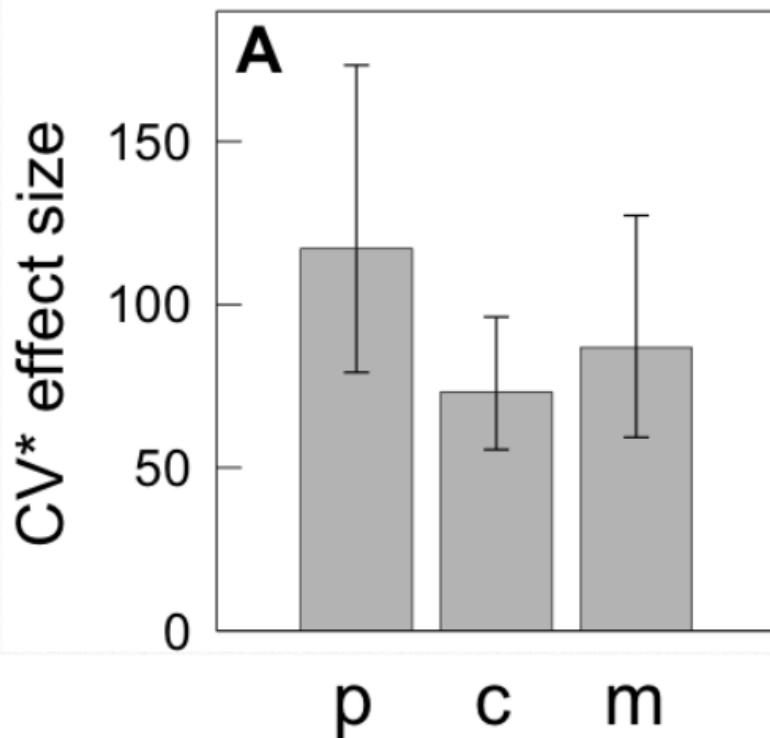


C

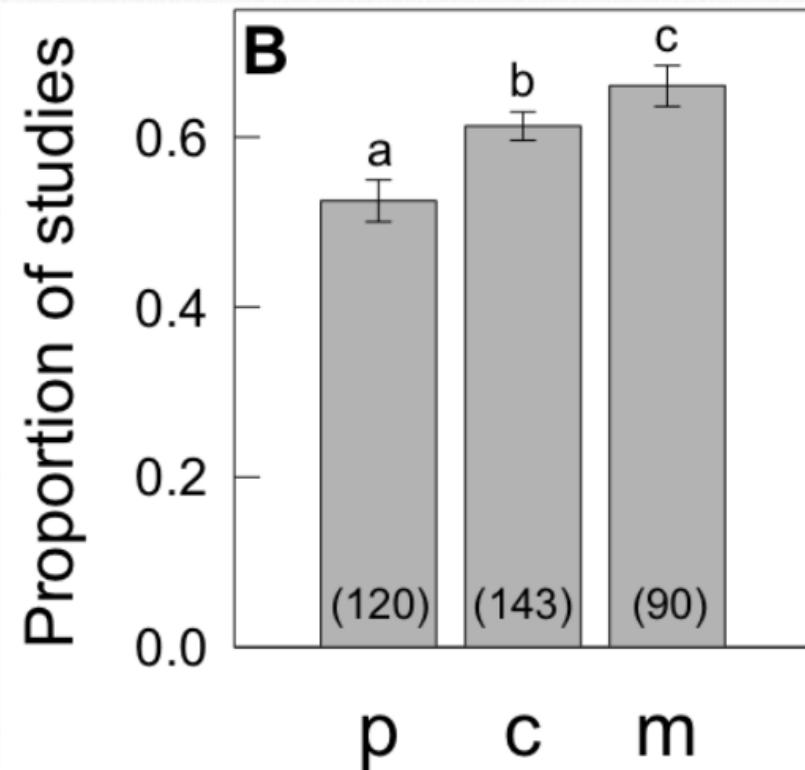


M

# How do different species interaction types differ in variation in outcomes?



# How do different species interaction types differ in variation in outcomes?



# Why is mutualism more variable?

# Why is mutualism more variable?

- I don't know, but...

# Why is mutualism more variable?

- I don't know, but...
- A few possibilities:
  - Conditionality seems to be discussed more in the mutualism literature, but perhaps just what mutualism people are interested in?
  - Possible that species interactions are misidentified? -> Predation is likely predation, whereas not so for mutualism and competition
  - Mutualism is just more variable = but what is it that makes this so?  
Any ideas?

# **What are the relative importance of drivers of variation in outcomes?**

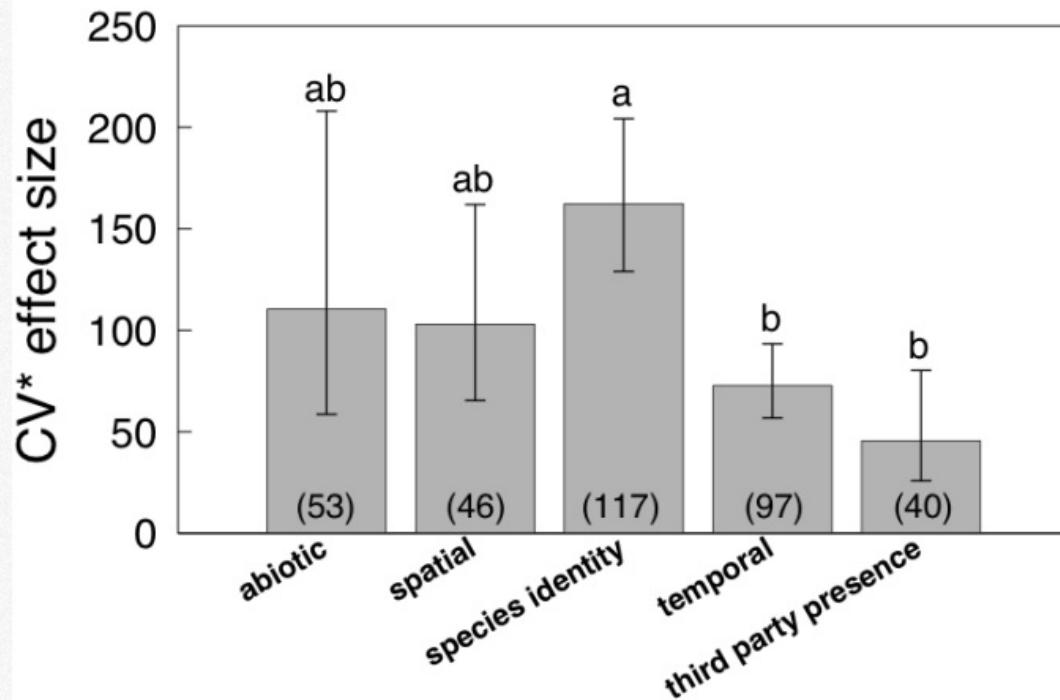
# What are the relative importance of drivers of variation in outcomes?

- Same two species
  - Abiotic: Nutrients
  - Space: Across sites
  - Time: Across hours, days, or years
  - Third party presence: Two species w/ or w/o a third species

# What are the relative importance of drivers of variation in outcomes?

- Same two species
  - Abiotic: Nutrients
  - Space: Across sites
  - Time: Across hours, days, or years
  - Third party presence: Two species w/ or w/o a third species
- Just one species is the same
  - Species identity: Sp. A interacts with either sp. B or sp. C

# What are the relative importance of drivers of variation in outcomes?



\*\* No difference for sign change

# What does this mean?

# What does this mean?

A few observations

# What does this mean?

A few observations

**Species identity > third party presence**

- Perhaps it's really species identity that matters when considering community context

# What does this mean?

A few observations

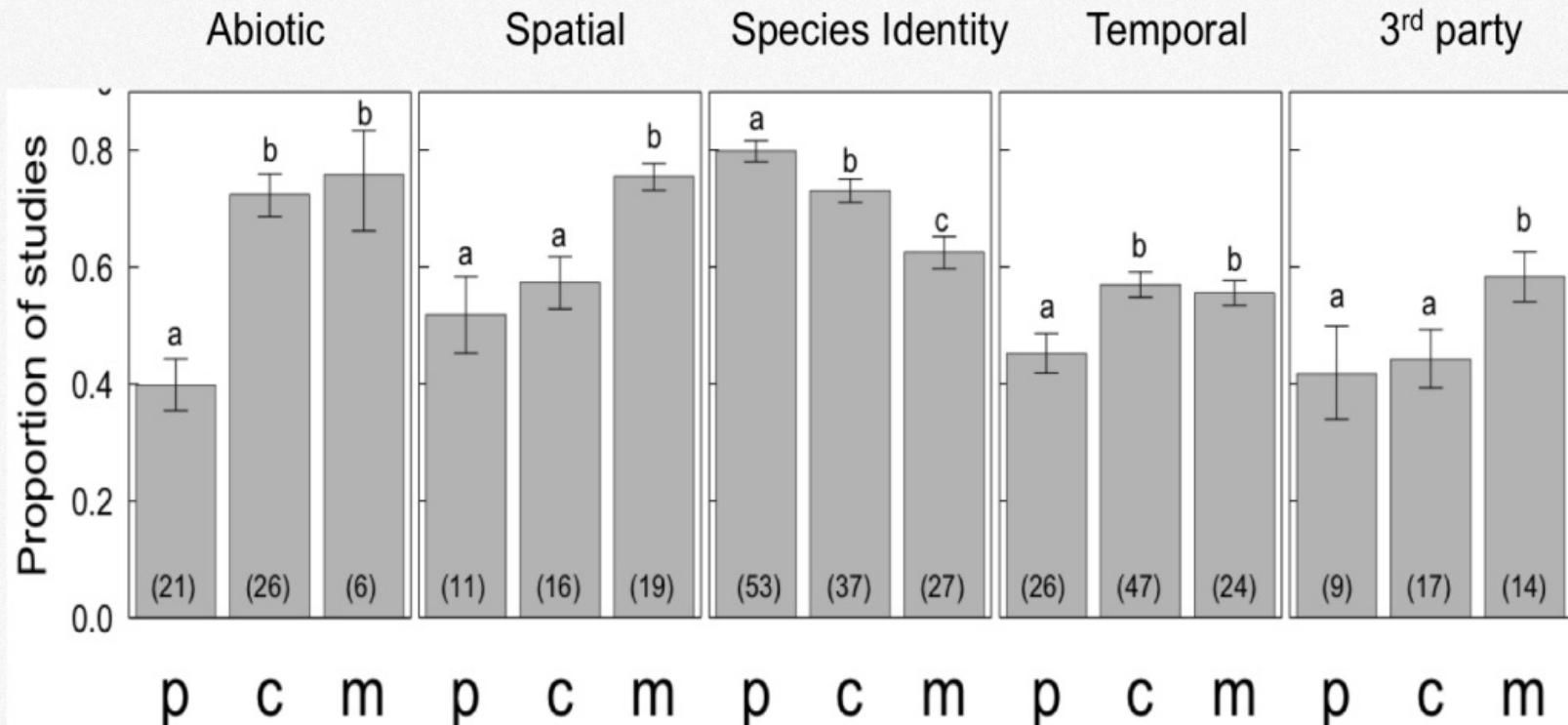
**Species identity > third party presence**

- Perhaps it's really species identity that matters when considering community context

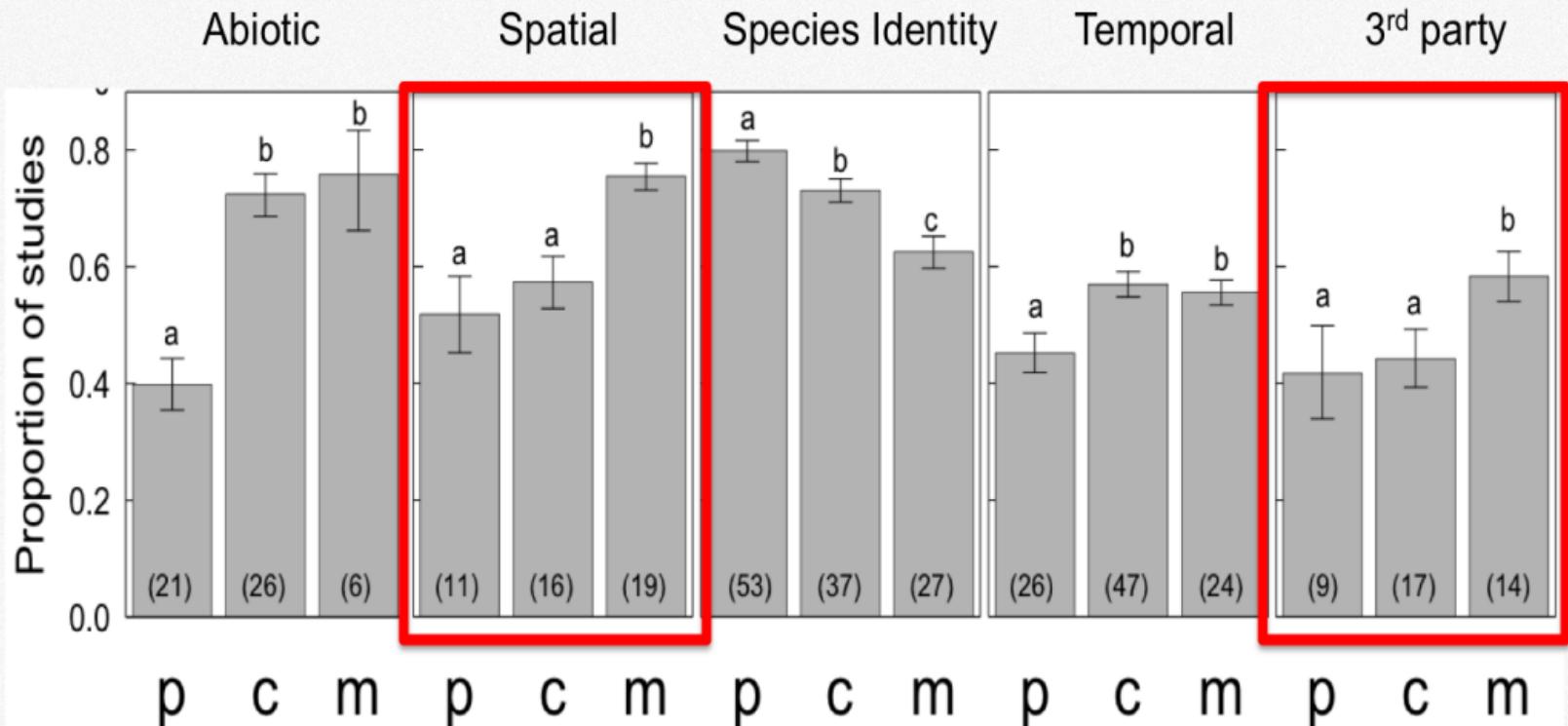
**Spatial tended to be > temporal variation, but not significant**

- Interesting that just as much variation in interactions can occur in space as in time

# Drivers of variation in outcomes X interaction type? - Sign



# Drivers of variation in outcomes X interaction type? - Sign



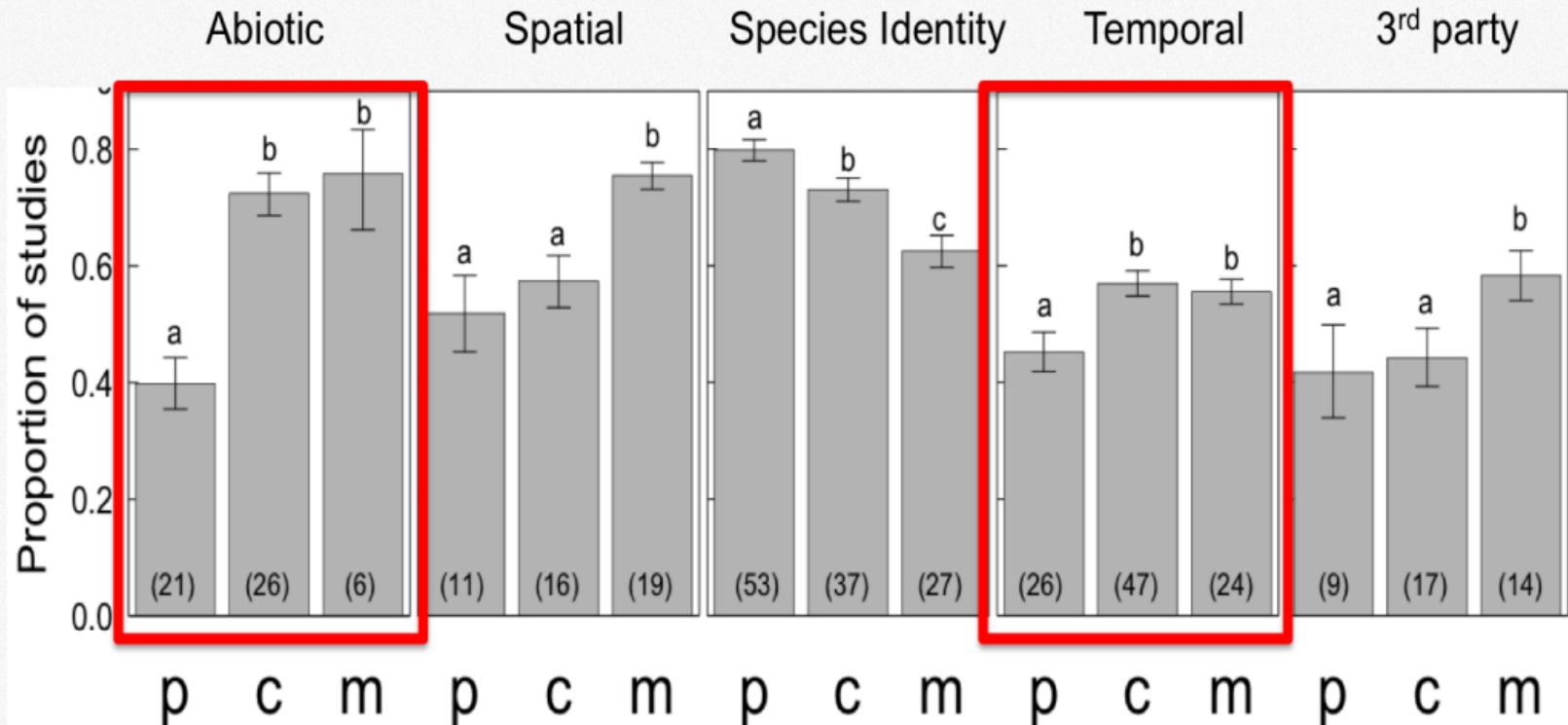
**Mutualism > predation & competition  
along spatial and 3rd party axes**

# Mutualism > predation & competition along spatial and 3rd party axes

- Makes sense at least in some mutualisms, e.g. ->



# Drivers of variation in outcomes X interaction type? - Sign

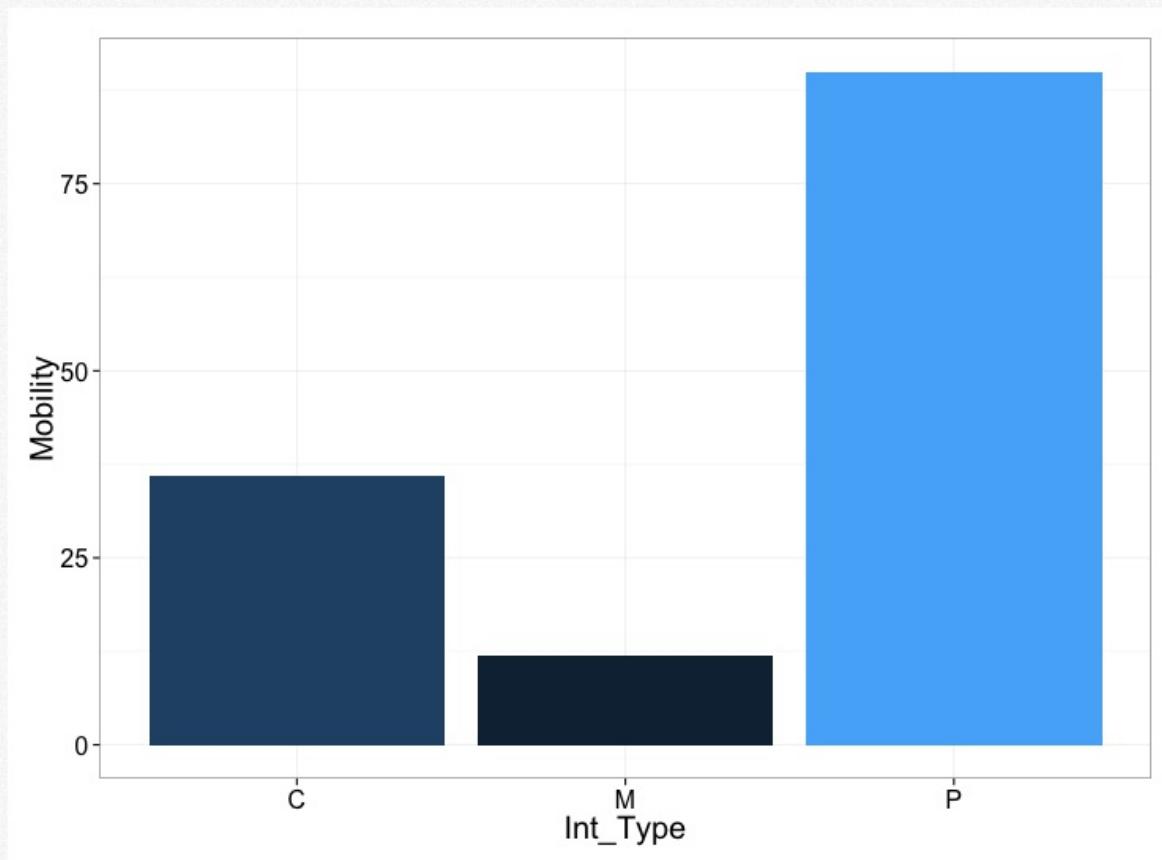


# Predation < competition & mutualism along abiotic and temporal axes

- Predator-prey with largely mobile species, escape abiotic constraints



# Mobility



**Results qualitatively the same when accounting for mobility**

# Does variation in outcome differ by ecosystem type?

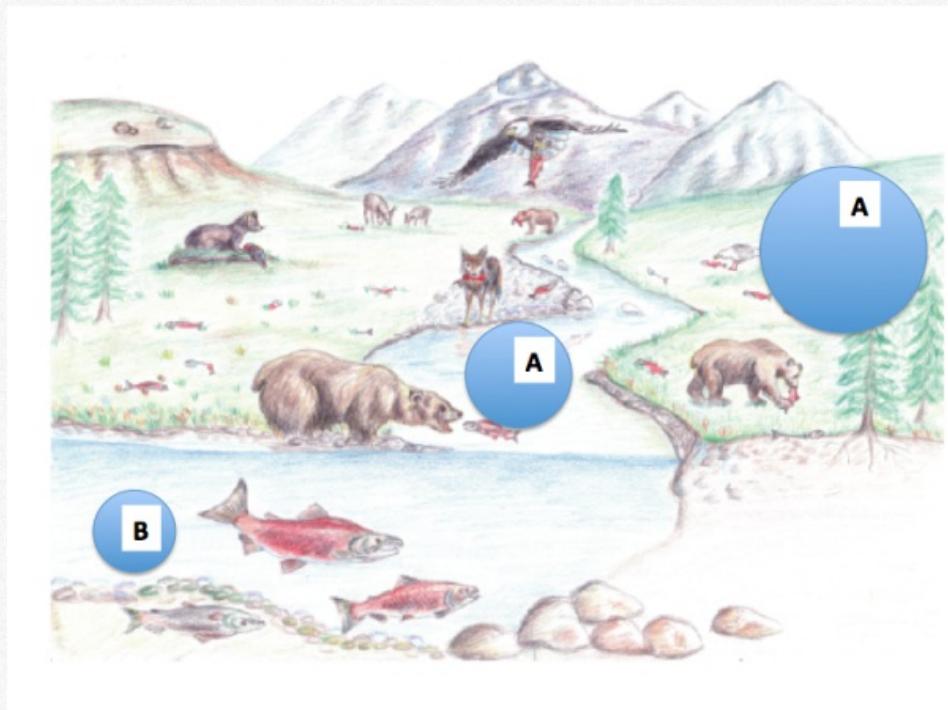


Image: <http://people.ucsc.edu/~trlevi/Projects.html>

# Reasoning for ecosystem differences

Oceans buffer abiotic variables more so than freshwater and marine

- Which could lead to less variation in interaction outcomes in oceans

Any ideas?

Reid et al. 2009

# Conclusions

# Conclusions

- **Types of species interactions differed in outcome variation**
  - We can't treat different species interactions as equivalent
  - In interaction webs, it may be most important to understand variation in mutualistic links

# Conclusions

- **Types of species interactions differed in outcome variation**
  - We can't treat different species interactions as equivalent
  - In interaction webs, it may be most important to understand variation in mutualistic links
- **Types of gradients differed in outcome variation**
  - Some sources of variation in species interactions should be given priority (i.e., species identity), especially in new study systems

# Conclusions

- **Types of species interactions differed in outcome variation**
  - We can't treat different species interactions as equivalent
  - In interaction webs, it may be most important to understand variation in mutualistic links
- **Types of gradients differed in outcome variation**
  - Some sources of variation in species interactions should be given priority (i.e., species identity), especially in new study systems
- **Types of ecosystems differed in outcome variation**
  - Outcome variation: terrestrial  $\geq$  freshwater > marine

# Future work

# Future work

- Add other species interaction types
  - Herbivory

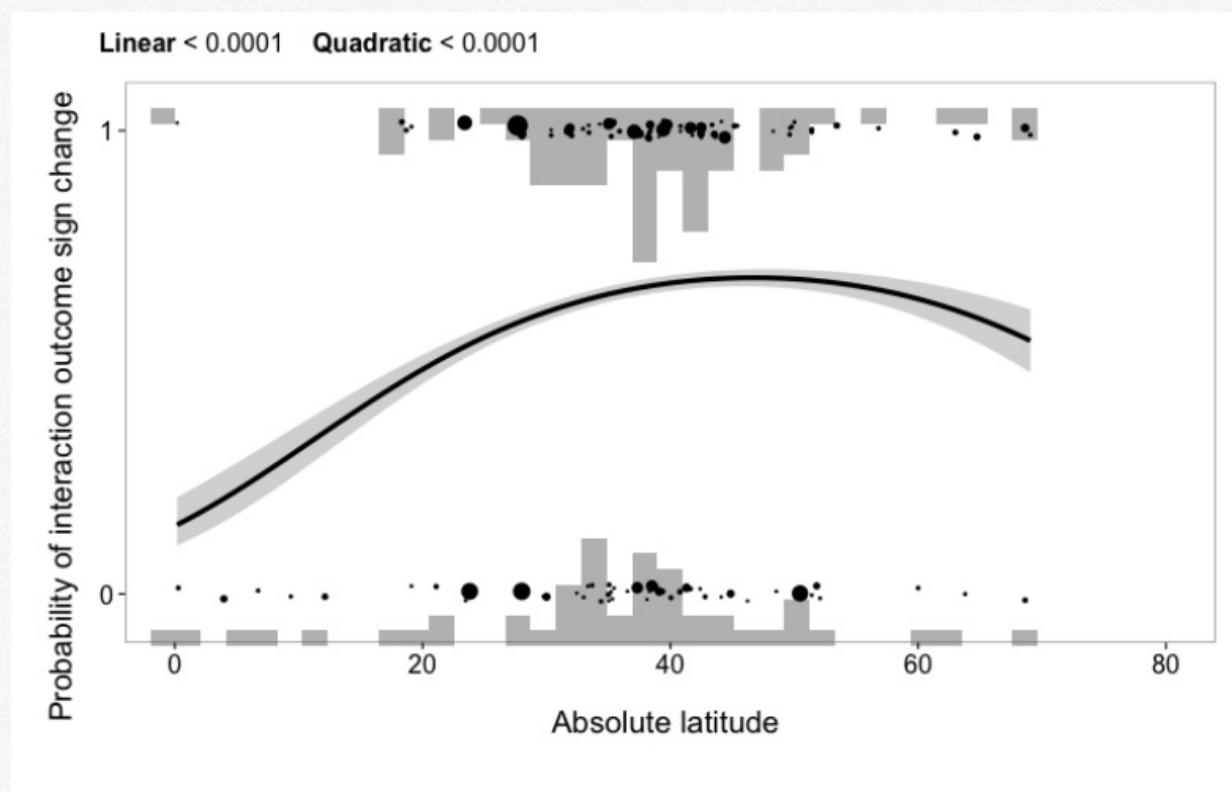
# Future work

- Add other species interaction types
  - Herbivory
- Do any variables correlate with variation in species interaction outcomes?
  - Do body size ratios predict variable outcomes?

# How does variation in outcome vary with latitude?

- Interaction outcomes are thought to increase in strength nearer the equator (**Schemske et al. 2009**)
  - Stronger biotic interactions nearer equator => Greater biodiversity
- What about variation?
  - Stronger mean interactions are thought to be associated with less variation (**Berlow 1999**)
    - Stronger mean nearer equator => less variable nearer equator

# How does variation in outcome vary with latitude? - Predation



# Latitude

# Latitude

- Variation may depend on latitude, or some variable correlated with latitude
  - Variation in outcomes may increase in some areas more than others with climate change

# Latitude

- Variation may depend on latitude, or some variable correlated with latitude
  - Variation in outcomes may increase in some areas more than others with climate change
- What about latitude is correlated with variation in interaction outcomes?
  - Exploring this question with Jeremy Kerr (Univ. Ottawa), looking at:
    - Temperature
    - Precipitation
    - Etc.

# **How can we test these findings in the field?**

# How can we test these findings in the field?

- What are the consequences of variation in outcomes?
  - Probably very difficult to manipulate variation in outcomes
  - Modeling perhaps?
  - Any ideas?

# How can we test these findings in the field?

- What are the consequences of variation in outcomes?
  - Probably very difficult to manipulate variation in outcomes
  - Modeling perhaps?
  - Any ideas?
  
- What are relative importance of mechanisms for variation in outcome?
  - A bit easier
  - Manipulate many gradients discussed here:
    - Abiotic gradients (e.g., nutrients)
    - Third party presence (e.g., presence of predator in plant-herbivore interaction)

# Thanks to...

- Data

**Tens of authors who provided data**

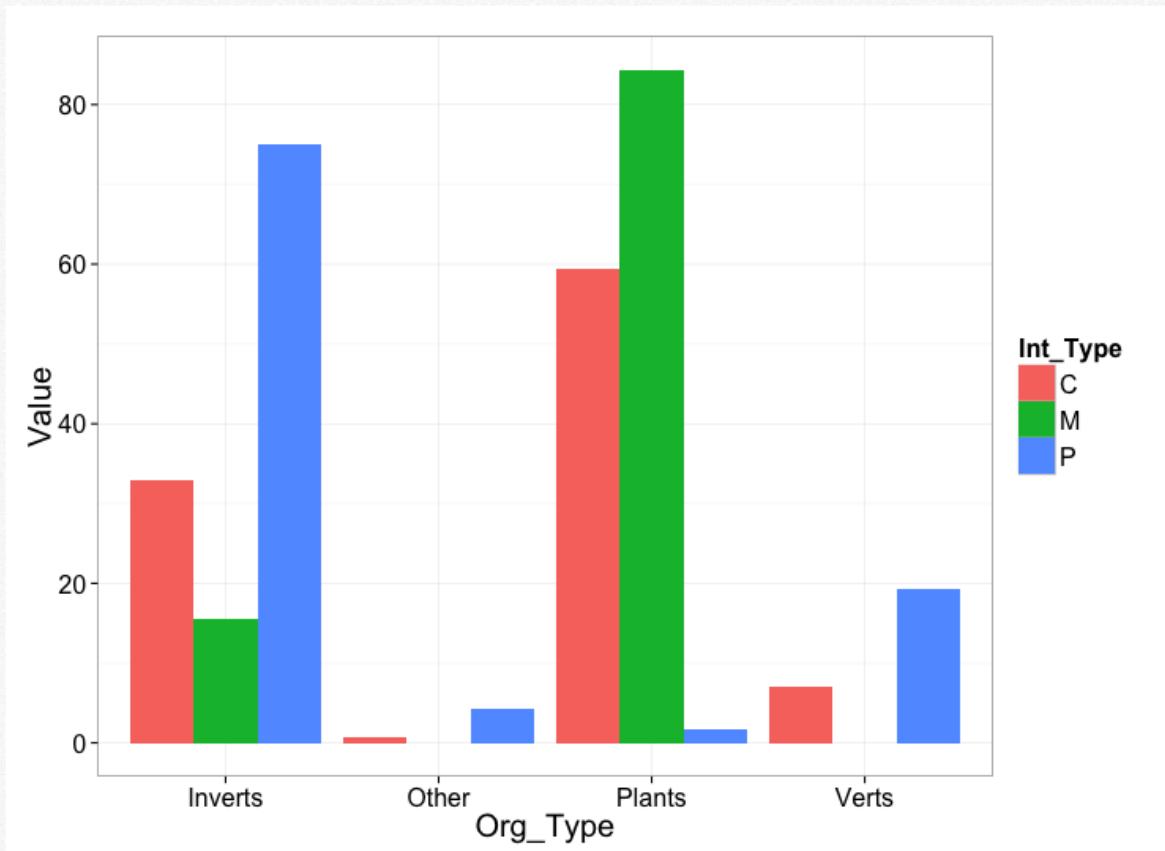
- Data collection

**Yosuke Akiyama, Neha Deshpande, Rohini Sigireddi, Prudence Sun,  
Edward Realzola, Rameez Anwar, Matt King, Roy Wu, Than Vu**

- Discussion

**The Rutgers-Whitney lab, Jennifer Rudgers, Ken Whitney, Volker  
Rudolf, Dennis Cox, Steve Hovick, Tom E.X. Miller, Elizabeth Elle,  
Lisandro Benedetti-Cecchi**

# Taxonomic bias



Though can't account for it due to lack of replication across levels