Evolutionary Processes in Biological Invasions

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Talk outline

- Invasion biology
- Evolutionary processes in invasion
- *Daphnia lumholtzi*
- Experimental design

The scope of biological invasions

- Environmental costs
  - Second only to habitat destruction as a cause of global extinctions
- Economic costs
  - Estimated to cost the US over $100 billion/year
  - Global cost estimated at over $1.4 trillion/year, or about 5% of the global economy

What is an invasive species?

- An alien species that has a negative impact on its new environment
- Invasive species cause harm by
  - Killing native species
  - Competing with native species for food and space
  - Spreading new diseases and parasites to native species
  - Hybridizing with native species

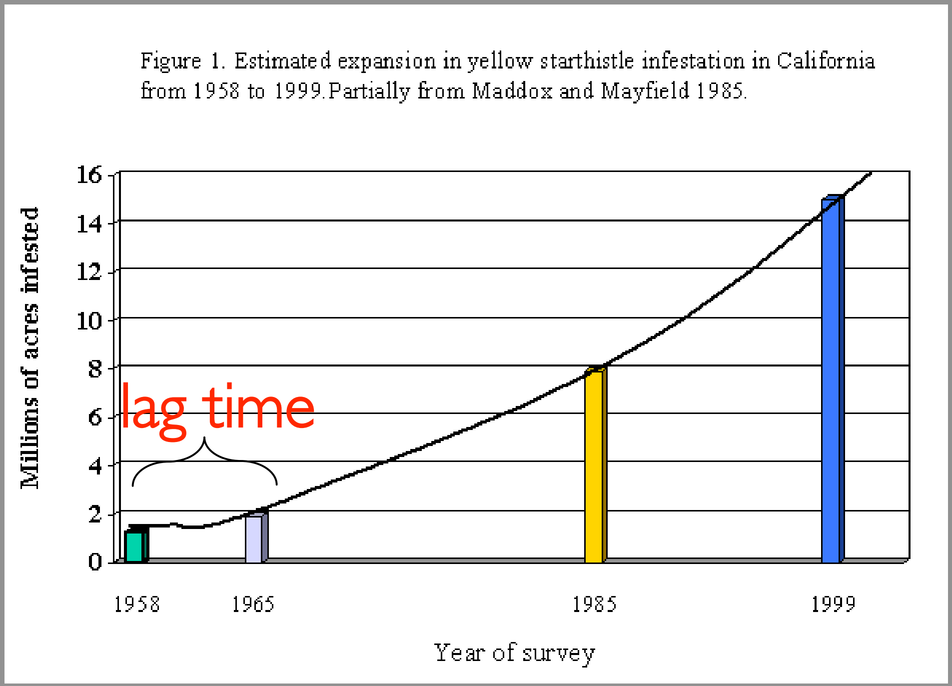
Studies of invasive species

- Which habitats are vulnerable?
  - Disturbed ecosystems
- What makes a good invader?
  - Broad physiological tolerance
  - High rate of vegetative growth
  - Rapid/high reproductive output
  - Competitive advantage (allelopathy)
  - Ability to thrive in disturbed habitat

Rate of invasion

- Invasive populations often exhibit a lag time before spreading

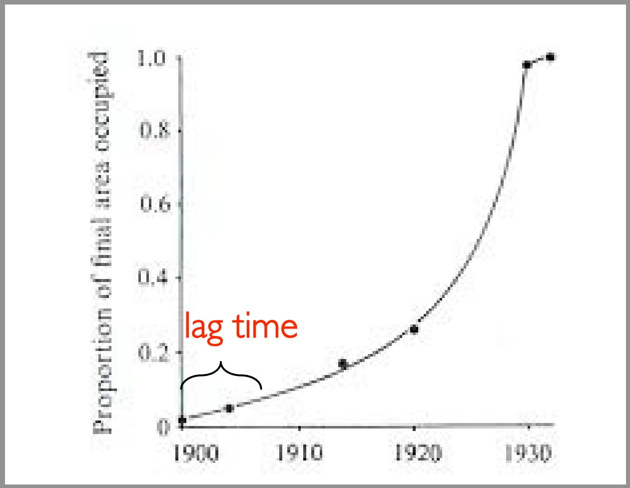
Yellow Starthistle
(Centaurea solstitialis)



Rate of invasion

- Invasive populations often exhibit a lag time before spreading

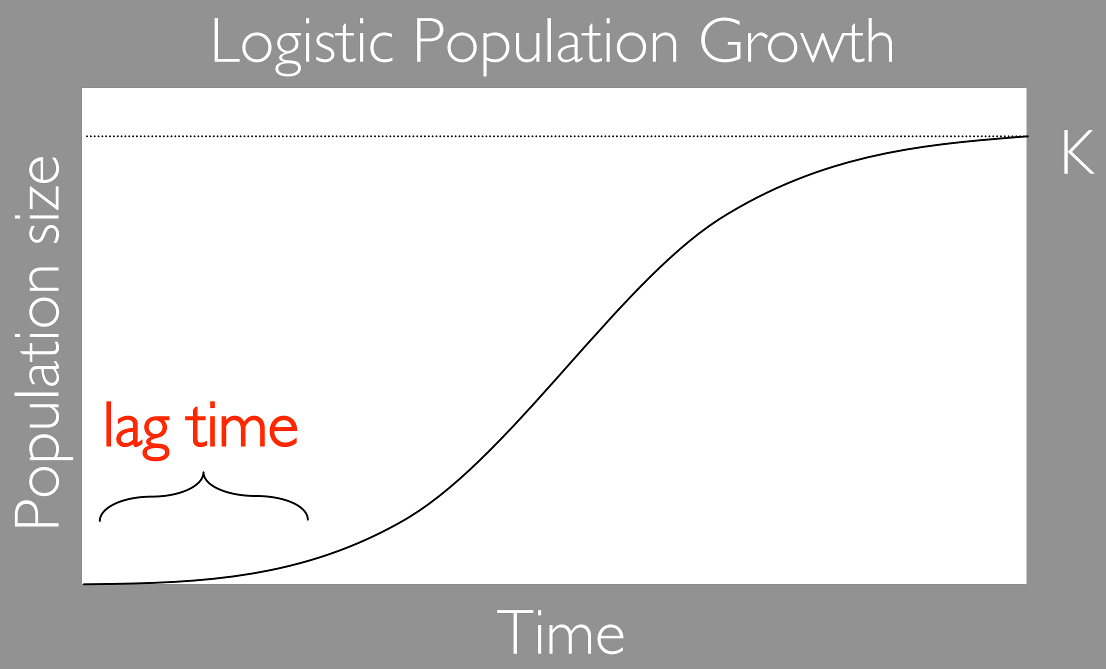
Cheatgrass
(*Bromus tectorum*)



Spread of cheatgrass through Great Basin of North America

Rate of invasion

- Invasive populations often exhibit a lag time before spreading
- Ecological explanation:



Evolution and biological invasions

- Do evolutionary processes play a role in invader success?
- Are natives exhibiting an evolutionary response to invaders?
- Recent studies say: yes to both!

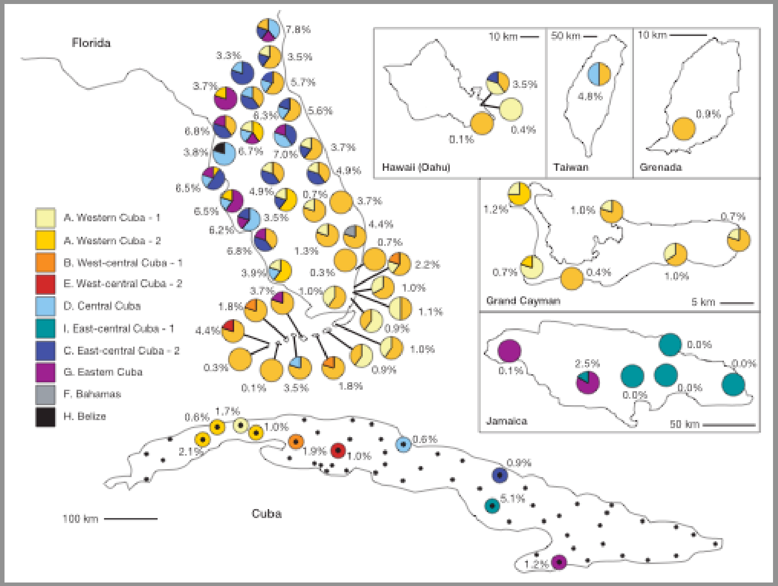
Case 1: Adaptive evolution

- EICA: in absence of native enemies, plants rapidly evolve to be less defended but more competitive
- 45 studies have compared quantitative traits in native vs introduced populations via common garden or greenhouse experiments, or herbivore bioassays
  - 56% found increased growth in introduced populations
  - 55% found decreased resistance to herbivores
  - Little conflicting evidence

Case 2: Outbreeding

- Invasions often proceed only after multiple introductions

Brown anole
Anolis sagrei



Expanding populations feature greatest genetic variation

Case 2: Outbreeding

- Hybridization with native species can lead to invasiveness

Replacement of California cordgrass (*Spartina foliosa*) by *S. alterniflora* hybrids

Native (left) vs hybrid (right) *Spartina*

Case 3: Inbreeding

- Inbreeding can also lead to invasiveness

Argentine ant
Linepithema humile

Worldwide spread via
"super colony" formation

Case 4: Evolution in the invaded

- Do native organisms evolve in response to invasive species?

- Australian snakes at risk from cane toad toxins have exhibited:
  1. Increase in body size
  2. Decrease in head size
- Degree of change correlated to species' risk

Lag time in invasions

- Evolutionary explanations
  - Spread of adaptive alleles already present at low frequencies in the invasive founder population
  - Development and spread of superior recombinant genotypes via outbreeding
    - Multiple introductions
    - Hybridization with natives
  - Rise and spread of new adaptive mutations

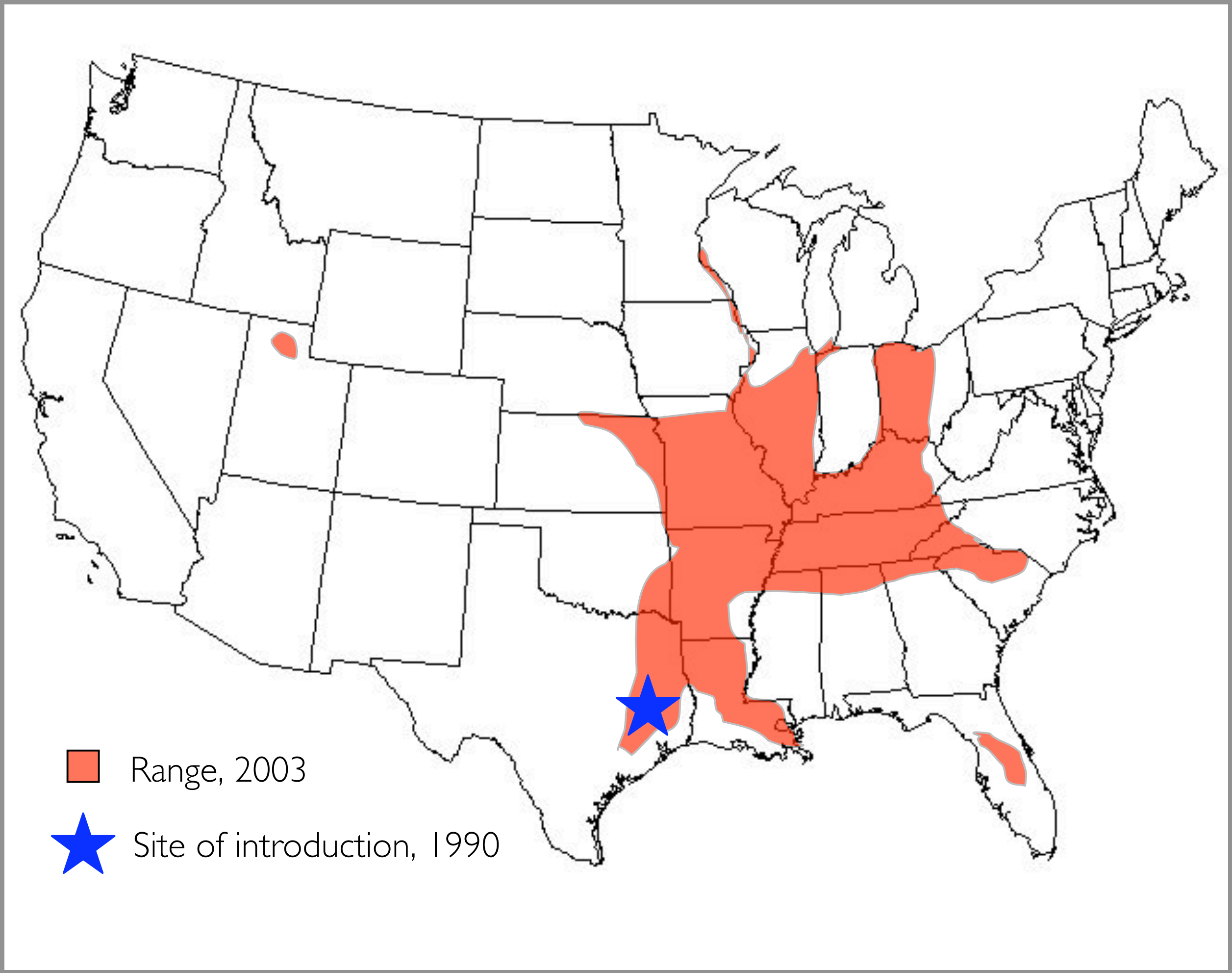
Evolutionary processes in biological invasions

- Definitely important in invasions
- Offer unique opportunity to study fundamental evolutionary processes
  - Plasticity vs genetic adaptation: tolerance or evolution?
  - Sex and adaptation: recombination vs 2x cost of sex, lottery-winning genotype
  - Source of genetic raw material for adaptive evolution: mutation vs standing genetic variation
  - Coevolution

System shopping list

- Ideal invasive species for studying these questions would:
  1. Be easily moved between lab/field
  2. Exhibit sexual/asexual reproduction
  3. Have rapid reproductive rate for manipulative experiments
  4. Feature existing genetic tools
  5. Bonuses?

Daphnia lumholtzi



Daphnia lumholtzi

D. lumholtzi

D. pulex

Daphnia lumholtzi

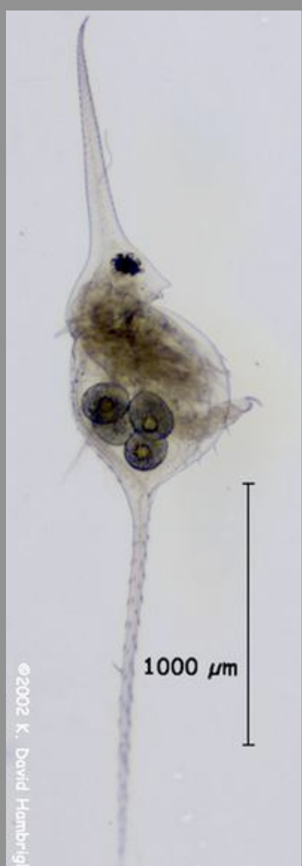
- Native to tropical Africa, Asia, and Australia
- Has higher temperature optimum than native US Daphnia
- May threaten native fish
  - Bluegill juveniles lose weight when exposed to *D. lumholtzi*

System shopping list: *D. lumholtzi*

1. Easily moved between lab/field
2. Reproduces clonally and sexually
3. Rapid reproductive rate
   1. First brood at ~6 days, produces ~40 offspring total
   2. Life span of about 20 days
4. Genetic tools
   1. *Daphnia pulex* sequence completed two weeks ago
   2. Thousands of microsatellites and other tools
5. Bonuses?
   1. Numerous interesting phenotypes
      - Defenses, phototaxis, rate of sexual reproduction, physiology
   2. Whopping bonus: Resting egg production (ephippia)

Reproductive cycle of *D. lumholtzi*

Clonal, diploid ♀ egg production



Stress →

Production of ♂s + 2 haploid ♀ eggs

Sex →

Fertilization: 2 diploid ♀ eggs

Death →

Dormancy until conditions improve

Reproductive cycle of *D. lumholtzi*

Benefits

1. Clonal reproduction: testing for genetic adaptation vs plastic responses
   - Can raise genetic clones in range of conditions to measure degree of plasticity for a given genotype, and compare means and variances of phenotypes between clone lines
2. Ephippia production: testing for rate of sexual reproduction
   - Rate of ephippia production equals rate of sex
3. Ephippia dormancy: looking at change over time
   - Ephippia from sediment cores at lake bottom can be hatched to look directly at phenotypic and genetic change over time

I'm sold! Getting started

- Wanted: *D. lumholtzi* - $100 bounty
- Keeping them alive

Food: CP
Belton
From: Dec. 5,05/Nov.29
Made: Jan. 5,06
indiv 10
Water change 1/19
add indiv. from Ori 1/19

Experiment 1: Cold tolerance

- Does the northern spread of *D. lumholtzi* represent a plastic response to colder temperatures, or genetic adaptation?

Experiment 1: Cold tolerance

- Performance experiment
  1. Raise clones from northern and southern populations at common temperature
  2. Expose clones to range of temperatures
  3. Measure physiological/behavioral performance
- Fitness experiment
  1. Raise clones from northern and southern populations at common temperature
  2. Expose clones to range of temperatures
  3. Count offspring per clone

Experiment 2: Sex and Adaptation

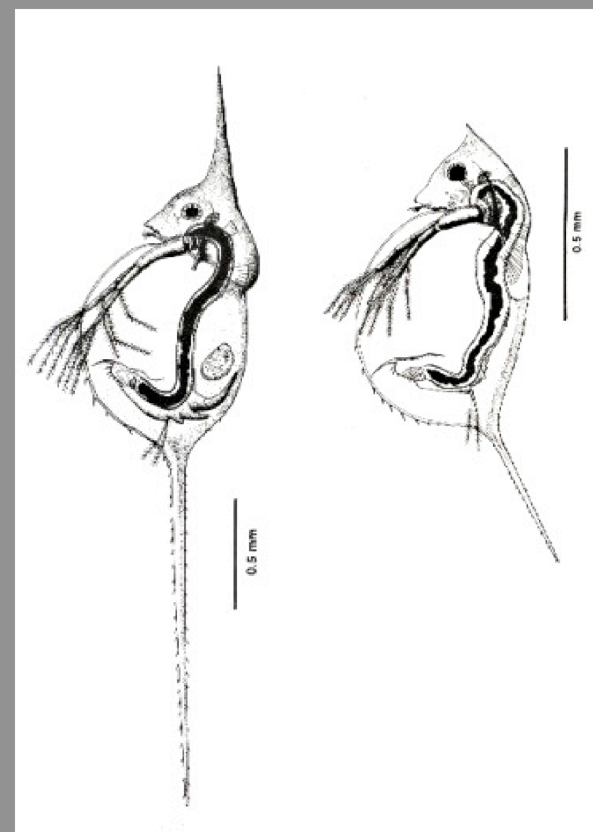
- Should we expect to see a higher or lower rate of sexual reproduction in populations encountering new environments?

Experiment 2: Sex and Adaptation

- Laboratory investigation
  1. Raise clones from northern and southern populations
  2. Measure rate of ephippial production
- Field investigation
  1. Measure number of ephippial females throughout season in N. American vs African populations

Experiment 3: Cost of plasticity

- *D. lumholtzi* has extreme inducible defenses. Is there a cost to maintaining the plasticity of this trait?

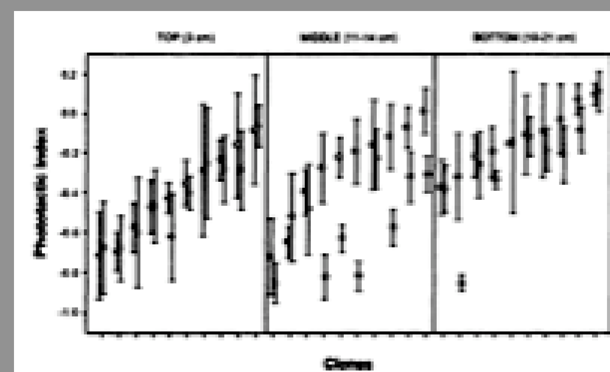


Experiment 3: Cost of plasticity

- Manipulative experiment
  1. Raise clones of *D. lumholtzi* from lakes with different predator densities (an alternative would be to produce your own lines of predator/nonpredator-exposed *lumholtzi* in the lab)
  2. Measure sensitivity/extent of inducible defenses for offspring of clones raised at different fish kairomone concentrations
  3. If differences in plasticity are found, is there an increase in fitness associated with loss of plasticity?

Other experiments

- Phototaxis
  1. Raise clones of *lumholtzi* from lakes with different predator densities
  2. Measure phototaxis
- Ephippia test
  1. Already been done!



Phototaxis response more plastic and more negative in clones hatched from ephippia produced in years with intense fish stocking

Long-term goals: genetics of adaptation

- Daphnia genome consortium
  1. Fully sequenced *D. pulex* genome
  2. Numerous genetic tools
- For traits that evidence genetic adaptation, look for genetic basis
  1. QTL mapping
  2. Comparative genomics
  3. Transgenics

Conclusions

- Invasive species pose a major conservation challenge
- Recognizing and understanding the role of evolutionary processes in biological invasions is important to meeting this challenge, and represents a valuable opportunity to study evolution in action