Desire, disappointment, surprises, and food webs: melding conservation and ecological perspectives to better understand animal-invasive plant interactions.
• **Start to “tie it all together”**
  – By “it” I mean plant-animal interactions (i.e. weeds and wildlife)

• **How am I going to do this?**
  – **Broad overview**
    • Look at history and early assumptions of the interactions
    • Put the interactions in a general ecological framework
  – **Specific example**
    • Fennel – terrestrial vertebrate interactions on Santa Cruz Island (1990-1999)
  – Look at some recent work being done on the interactions
  – Conclude with some food for thought and potential future directions
The Challenge

• Put talks from conference into a broader context...
• …but try not to get lost in the netherworld of abstract concepts...
• …while not to getting lost in specifics of individual case studies

Hmmmm...why did I let John Knapp talk me into this?
New “Hot” Topic On An Old Issue
A pertinent observation…

“Just as there is honor among thieves, so there is solidarity and co-operation among plant and animal pests. Where one pest is stopped by natural barriers, another arrives to breach the same wall by a new approach. In the end every region and every resource get their quota of uninvited ecological guests.”

Recognition of:
- barriers
- dispersal
- dispersal limitation
- multiple invaders

Aldo Leopold
Cheat Takes Over
A Sand County Almanac, 1949
Another pertinent observation...

“...the cheat-afflicted regions make a virtue of necessity and find the invader useful. Newly sprouted cheat is good forage while it lasts; like as not the lamb chop you ate for lunch was nurtured on cheat during the tender days of spring. Cheat reduces the erosion that would otherwise follow the overgrazing that admitted cheat. (This ecological ring-around-the-rosy merits long thought).”

Recognition of:
- trophic interactions
- conservation contradictions
Invasive Non-native Species: The Dominant Historic Perspective (1880-1995)

Non-native predators and native prey

- [Image of Non-native predators]
- [Image of Native prey]
- [Image of Other native prey]
Invasive Non-native Species: The Dominant Historic Perspective (1880-1995)

Non-native primary consumers and native plants
Invasive Non-native Species: The Dominant Historic Perspective (1880-1995)

Non-native plants, native plants, and native wildlife
Invasive Non-native Species: The Desired Management Outcome

Invasive Non-native Species: The Desired Management Outcome
But a funny thing happened on the way to the forum…

Fitzgerald 1988, Murphy et al. 1998
But a funny thing happened on the way to the forum…

...a mix of desirable...

...and surprising, often undesirable outcomes

Management outcomes are tremendously variable, complex, and often unpredictable
(Zavaleta et al. 2001, Zavaleta 2002)
But Should We Have Been Surprised?

• Numerous ecological examples of what we considered surprises
  – From predators to prairie dogs…
  – From the Kaibab to the Klondike…

• We knew about
  – Apparent competition
  – Prey release
  – Prey switching
  – Trophic cascades
So Why The Surprises?

• We first thought as conservationists and then as ecologists
• Our desire to do good got ahead of some ecological realities
• We focused on the “bad guy” and overlooked the rest
Invasive Non-native Species: The Reality

Many, if not most systems have:

- Multiple non-native species...
- ...at different trophic levels...
- ...interacting with native and non-native species in various ways...
- ...and filling different functional roles
  - Predators (including seeds)
  - Seed dispersers
  - Herbivores
  - Pollinators
- ...with a range of interaction strengths...
Grappling With The Reality

- Biological invasions are a special case of dispersal

Invasion is not a state. It is a *process*...

...where species are added to an ecosystem...

...and species identity & environmental conditions determine “equilibrium” abundance
Grappling With The Reality

Management is the process of removing an invasive species from an ecosystem or shifting the distribution of its interaction strengths.
Dealing With Complexity Requires Objectivity

• What is the range of effects an invader can have in an ecosystem?
• Fennel on Santa Cruz Island

Brenton and Klinger 1994, 2001; Erskine-Ogden and Rejmánek 2005; Klinger 2007, Klinger et al. in review
The Spread of Fennel

- Colonized SCI mid to late 1800’s
- Patchy establishment by early 1900’s
The Spread of Fennel

- Colonized SCI mid to late 1800’s
- Patchy establishment by early 1900’s
- Lag period
- Explosive spread 1990’s
- Spread into previously unoccupied areas
- Greatest increase in cover was in areas with heavy cattle use
The Spread of Fennel

100-year lag period followed by burst of exponential spread

Distribution and/or Abundance

1890 1990 2010
Ecological and Management Issues

Ecological

• Community Stability
  – Resistance
  – Resilience
  – Variability
  – Persistence

• Biodiversity
  – Species Richness
  – Species Diversity
  – Species Composition

Management

• Feasibility of Control
  – Effects on community
Fennel The Villain

• Such a dominant invader would have to be reducing native biodiversity, right?
Expectations

- Community Stability
  - Resistance depends on vegetation community
  - Low resilience
  - Relatively low variability
  - Relatively high persistence

- Diversity patterns
  - Decreased species richness
  - Low evenness
  - High beta diversity

Stable but much more simple community
Two-Pronged Approach

- **Monitoring**

- **Experiments**
  - Fennel control
    - Phase 2 (1993-1997)
    - Phase 3 (1996-2001)
  - Fennel as a resource for small mammals and birds
Vegetation

High Resistance In Woody Communities

Low Resistance In Grasslands
Vegetation

Low resilience in grasslands

Distance-based redundancy analysis
Vegetation

Complex diversity patterns

Generalized additive models
Vegetation

Highly variable variability

More extreme decreases than increases

Species with wider distributions and greater abundance less variable
Vegetation

Persistence related to distribution

More restricted distribution = lower persistence

Natives significantly more restricted

Persistence varied among guilds

Natives had significantly lower persistence
Vegetation

Suppression or displacement of native species

Native forb species dramatically decreased as fennel cover increased

Woody species regeneration lower in fennel stands than grasslands
Birds

Low resilience

Distance-based redundancy analysis
**Birds**

- **Strong positive association with fennel**
  - Song sparrow
  - Red-winged blackbird
  - Lazuli bunting

- **Strong negative association with fennel**
  - Horned lark
  - Western meadowlark
  - Ash-throated flycatcher

Canonical correspondence analysis
• Diversity patterns
  – Increase in $\alpha$ diversity and abundance
  – $\alpha$ and $\gamma$ diversity as high or higher in fennel as all other vegetation types except chaparral
• Variability and Persistence
  - High variability but mostly positive
  - > 66% of species present 4 to 5 years
Small Mammals

- *Permyscus maniculatus* and *Reithrodontomys megalotis* occurred commonly in fennel stands.
- 2 – 8X higher proportion of captures of *P. maniculatus* in fennel.
Small Mammals

- Demographic contrasts between fennel and grassland (1996-1997)
  - Seasonally higher recruitment rates in grassland
  - Consistently higher survival rates in fennel (> 2.5x)

N = 6 grids (3 fennel, 3 grassland) trapped across six periods
Birds, Small Mammals & Fennel Seeds

• Seed removal experiment
  – Fennel vs. Grassland
  – Open vs. PVC tube
  – 5 stations/grid sampled each trapping period (50 seeds/station)

• Most fennel seeds in fennel stands removed by small mammals
• Most fennel seeds in grassland removed by birds

• Seed fate not determined
Expectations Revisited

- Stable but much more simple community?
  - Depends on measure of stability and taxa
The Fennel Ring-Around-The-Rosy
So Is Fennel A Villain?

- A native plant would probably say yes.
- A lot of native vertebrates would probably say no.
Recent Examples Of The Reality

Species deletions and trophic cascades in an insular high latitude ecosystem

Bergstrom et al. 2009
Recent Examples Of The Reality

Species deletions and trophic cascades in an insular high latitude ecosystem

Control of non-native predator leads to non-native dominated vegetation (*Poa annua*)

*Bergstrom et al. 2009*
Recent Examples Of The Reality

Species deletions and trophic cascades in an arid mainland ecosystem

Wallach et al. 2010
Recent Examples Of The Reality

Species deletions and trophic cascades in an arid mainland ecosystem

Control of native (more or less) predator leads to non-native dominated system

Wallach et al. 2010
Recent Examples Of The Reality

Species addition, apparent competition, habitat alteration, and diet switching in a coastal ecosystem

*Ammophila arenaria* appears to compete with endangered lupine.

*Dangremond et al. 2010*
Recent Examples Of The Reality
Species addition, apparent competition, habitat alteration, and diet switching in a coastal ecosystem

*Ammophila arenaria* appears to compete with endangered lupine. But suppression of lupine is actually due to pre-dispersal seed predation by native deer mouse.

*Dangremond et al. 2010*
The Message Is Sinking In

• Studies on invasive plant-wildlife interactions are becoming increasingly more grounded in an ecological context
• Initial assumption is to not just look for “impacts”, but interactions
• Two examples
  – Seed dispersal and diet selection
  – Species additions to suppress non-native
Frugivory And Invasion

Relationship between native frugivores, non-native trees, and food availability

Combination of observation and experimental approaches
Cheatgrass, Native Seed, & Rodent Interactions in Great Basin
Cheatgrass & Animal Community Composition

[Graph showing the relationship between Proportion Abundance and Rodent Species.]

[Figure illustrating the distribution and abundance of different rodent species in Cheatgrass and Sage habitats.]
Seed Exploitation: Native Cocktail vs. Cheatgrass

- Native seeds facilitated removal and caching of cheatgrass by rodents
- Depended on seed species
- Pattern varied between sage-dominated and cheatgrass communities

Quantified animal community structure then tied this to process (seed predation/dispersal)

Combination of observation and experimental approaches
Moving Ahead

- **Species additions**
- **Three questions to ask**
  - How long has the invader been in the system?
  - What is the range of their effects (positive as well as negative... i.e. “impacts”)?
  - Are they doing something a native species doesn’t do?
Moving Ahead

- Species deletions
- **Three questions to ask**
  - How long has the invader been in the system?
  - How many other invaders are in the system?
  - If you remove one invader will another replace it?
“Tying It Together”

• What did I see?
  – Clear progress since Monterey conference (February 2007)
  – More sophisticated perspectives and questions

• What did I hear?
  – Recognition of complexity and contradictions
  – A nod to realism
  – More “effects” than “impacts” (that’s a good thing folks!)
More Variety In Thinking

- Not so quick to believe our assumptions
- Not as prone to assume our desires will be met
- Expect surprises
  - Don’t let disappointment deter your efforts
- Thinking like ecologists first, then conservationists
  - Be patient
A Variety Of Approaches

- A lot of observation approaches
  - Realistic spatial and temporal scales
- Some experimental approaches
  - Strong on process and mechanism
- Some modeling
- Ideal is mix of all three

Murphy & Barrows. in progress
Dudley et al. in progress
That Is Progress