Causes and consequences of exotic invasions in Wisconsin forests

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Outline

• Are invasive species benign or serious?
• Factors driving long-term ecological change
  – Are invasive species “passengers” or “drivers”? 
• Study system – Forests in Wisconsin
• Causes of invasion?  Local or Landscape?
• Do deer and Alliaria interact to affect natives?
• Consequences of invasion?
  – Coarse vs. fine-scale associations
• Conclusions
9 Great Invasive Species Worth Admiring

By Brandon Keim  November 4, 2010 | 7:00 am | Categories: Animals

Admire Invaders??

(Wired Magazine)
Native Plants Can Also Benefit From The Invasive Ones

ScienceDaily (May 21, 2008) — Using empirical tests, a pioneering study shows how plant species, such as the prickly pear, invade Mediterranean ecosystems, and can either rob the native plants of pollinating insects, or, surprisingly, can attract them, thus benefiting the whole plant community, such as in the case of balsam. The research contradicts the hypothesis of the “floral market” whereby only the invasive flowers are seen to benefit and the native flowers are no longer visited by pollinating insects.

Alien Species Reconsidered: Finding a Value in Non-Natives

One of the tenets of conservation management holds that alien species are ecologically harmful. But a new study is pointing to research that demonstrates that some non-native plants and animals can have beneficial impacts.

BY CARL ZIMMER
Why study invasive species?

According to Aruba Birdlife Conservation, boa constrictors kill more than 17,000 island birds per year.

Island Birds + Invading Boa = Trouble in Paradise

By Andrew C. Revkin

For thousands of years, human mobility has brought all manner of species to isolated islands and regions, with the result being powerfully disrupted ecosystems. As I’ve said before, in recent decades we’ve become something of a Waring blender for biology, for better or worse.
Invasive de jour...

Burmese Python

Thanks to its tropical climate, zoo-wrecking hurricanes and a greater-than-usual number of people with a hankering for fashionably exotic pets, Florida is an invasive-species mecca. Squirrel monkeys, capybara, Gambian pouched rats, scorpions, Butterfly Peacock fish, a menagerie of parakeets, the list goes on, and on and on.

But of all these newcomers, one stands out: the Burmese python. One of the world’s largest snakes, they run 12 feet long on average, move with equal ease between land, water and trees, and are known
“Alas, they’ve vanquished nearly all the foxes, raccoons, rabbits, opossums, bobcats and white-tailed deer in the park; also the three-foot-tall statuesque white wood storks. A survey conducted between 2003 and 2011, and published in PNAS reported that raccoons had declined 99.3%, opossums 98.9% and bobcats 87.5%. It also said that marsh rabbits and foxes had completely disappeared. Last year, one Burmese python was found digesting an entire 76-pound deer.”
Are invasive species a major cause of extinctions?

Jessica Gurevitch and Dianna K. Padilla

Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794-5245, USA

actual extinctions. A few widespread rat species, feral pigs (as in Hawaii, Box 1), several predatory snakes (particularly on islands), possibly annual Mediterranean grasses and several other plants, a few microbial pathogens and a finite list of other invaders might be responsible for most of the extinction risk posed by aliens. Alien plants might be more likely to cause displacement and community change rather than causing species extinctions. This is the
Increasing & costly problem in U.S.
Stages in invasion

Not every exotic species establishes or invades.
Invasion trajectory

• Note:
  – ‘Lag phase’
  – Exponential phase = acceleration
  – No plateau yet
Invasion trajectory – of publications

- Note:
  - ‘Lag phase’
  - Exponential phase = acceleration
  - No plateau yet
Invasives threaten native species

- The biological invasion of exotic plants, animals and pathogens is one of the greatest threats to the existence of native organisms and biodiversity, second only to the loss of habitat.

http://www.mda.state.mn.us/invasives/default.htm
Many invasive plant species

Species with origins outside USA:

- Plants 3,723
- Terrestrial vertebrates 142
- Insects and arachnids >2,000
- Fishes 76
- Mollusks (nonmarine) 91
- Plant pathogens 239
- Total >6,271

Number of nonindigenous plant species (from outside the United States) introduced into each state (data on number of native and introduced species from a phytogeographic data summary in preparation by J. T. Kartesz, Biota of North America Program of the North Carolina Botanical Garden, Raleigh).
Plants invading forests

Non-Native Plant Species in North American Forests

Wisconsin
Factors driving ecological change

- Massive changes in land use
  - Habitat fragmentation from
    Intensified urbanization & agriculture
- Global and regional climate change
- Acid rain & N deposition
- Overabundant deer
- Species losses & biotic homogenization
Landscape change:
Habitat Fragmentation & Urbanization

Factors driving ecological change

- Massive changes in land use
  - Habitat fragmentation from intensified urbanization & agriculture

- Global and regional climate change

- Acid rain & N deposition

- Overabundant deer

- Species losses & Biotic homogenization

Invading exotic species

Cause or consequence?
Many invasive plant species

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Study system:
Wisconsin Forests
Southern Forests

**BEFORE:**
Mosaic of prairie, savanna & oak-hickory forests
Maintained by frequent fires

**NOW:**
Dominated by agriculture
Forests - small & fragmented
Selective logging, hunting and recreation
Southern Forests: 94 Stands

More forests & hills

More urban & agriculture

Relative Abundance
- 0.000 - 0.011
- 0.011 - 0.029
- 0.031 - 0.061
- 0.063 - 0.105
- 0.109 - 0.154
- 0.169 - 0.243
Baseline data - J.T. Curtis et al.

- John T. Curtis & colleagues sampled extensively across Wisconsin from 1942-1956
- Detailed, quantitative data from >1000 sites (~300 forested)
- Classic work to test ecological continua - published in the *Vegetation of Wisconsin* (1959)
- Carefully archived data

Provides exceptional baseline
Changes in Southern Forests

Local **diversity has** declined

80% of sites lost herb diversity

Species density declined:

- 25% / 1 m²
- 22.4% / 20 m²

Lack of fire & ‘mesification’

Declines in among site (b) diversity are associated with increases in exotics
Decreasing diversity = convergence = community ‘homogenization’

Both among quads within sites and among sites

But NOT driven by invasions – reflects in common native species
Herb Losers

- Bloodroot
- Nodding Trillium
- Wild Yam
- Yellow violet
- Tick-seed Trefoil
- Sweet Cicely
- Lopseed
- Bedstraw (4 spp)
- Bellwort
- Nodding Trillium
- Wild Yam
- Tick-seed Trefoil
Winners: Common Natives

Circea luteiana

Geranium maculatum

Parthenocissus spp
# Winners: Exotic Taxa

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>IV</th>
<th>Sites</th>
<th>Avg Freq</th>
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<tr>
<td>Alliaria petiolata</td>
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<td>bladder campion</td>
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<td>Glechoma hederacea</td>
<td>creeping-Charlie</td>
<td>0.2417</td>
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</table>
3 Eurasian invaders

- **Alliaria petiolata** - biennial herb introduced to the U.S. mid-1800’s. Most abundant exotic herb in these forests (45 / 94 sites) - mean frequency **30%**.

- **Rhamnus cathartica** – large understory shrub invaded North America in the mid-1800’s. Most common woody exotic occurring (45/ 94 sites) – mean frequency **11.7%**.

- **Lonicera x bella** – Asian hybrid shrub in 38 / 94 sites with mean frequency **3.7%**.

- These invasive species thrive in disturbed landscapes & fragmented forests.

- They efficiently intercept resources and produce allelochemicals that interfere with the growth of nearby plants and alter soil processes & nutrient cycling
Exotic species invading S forests

26% of stands had exotics in 1950 vs. 82% now

Increased in both range & abundance within sites:

6x increase in the abundance of exotics when present
Invasions into S Wisconsin Forests

Strong signal for analyzing causes & consequences . .
Causes of invasion? Local

• Supply **PUSH** - plant invasions reflect many seeds from invaders with high **fecundity** and wide **dispersal** and the right **traits**:
  – Invasives ‘pre-adapted’ to invade **disturbed** sites
  – Invasives good at **colonizing** = r-selected
  – **Novel weapons** = chemical arsenal (allelopathy)
  – **Enemy release** → freed from co-evolved enemies
  – Evolution of **increased competitive ability** (EICA)

**Prediction:**
Invasions succeed at disturbed sites close to their existing populations / seed sources
Causes of invasion? Local

• Supply **PUSH** - plant invasions reflect a flood of seeds of invaders with high fecundity & wide dispersal – invasives ‘pre-adapted’ to invade
  – Prediction: Invasions will reflect proximity to existing populations / seed sources

• Demand **PULL** – plant invade “invadable” communities (‘empty niches’)
  Predict: **Diverse** communities better resist invasion
  but:
  “Invasion is *positively* associated with native species diversity and soil N and Ca.” J. Gurevitch
Predictors of Exotic Invasion

- Sites with fewer native species in 1950 experienced more invasions by exotic species
Do more diverse communities resist invasion?

Communities with more native plant diversity in the 1950s suffered fewer invasions of *Lonicera* and *Rhamnus* between the 1950s and 2000s.

Support for diversity resistance hypothesis?

Or artifact?

*Waller et al., submitted*
Land management affects invasions

$N = 98$  

** $P < .01$ for all comparisons

Δ Exotic Abundance

- **Hunting Allowed**
  - Yes: [Value]
  - No: [Value]

- **Public Access**
  - Yes: [Value]
  - No: [Value]

- **Trail Density**
  - Heavy: [Value]
  - Light: [Value]
Landscape Analyses

2000 Ortho-photo:
- Road Density
- Housing Density
- Patch Size
- Shape Index

2000 WISCLAND:
- % Forest Cover
- % Urban Cover
- % Agricultural Cover
- % Grassland Cover (mostly fallow land and road edges)
Paying the ‘extinction debt’

The species - area relationship is growing stronger:

Conclusions:

Isolation has started to take its toll

More extinctions are likely in the future

Rogers et al. 2009 Cons Bio
Are declines in diversity driven by urbanization?

YES!

This reflects many processes and drivers.
Effects of roads

Native species colonize few stands surrounded by roads:

Roads and urban areas act as barriers to block local re-colonizations

(preventing the ‘rescue effect’)

Adj. R² = 0.182, P < .001
Native Plant colonization

Landscape factors strongly affect the number of native species colonizing sites:
   Especially forest cover within 5 km

So site factors now appear less important than landscape effects
Exotics invading more in forests near urbanized areas
What drives EXOTIC plant colonization?

Urban cover (within 5 km) best predicts the number of EXOTIC species colonizing sites:

Landscape context matters more than local site factors.
Summary – Local vs. Landscape scales

- **Roads**, public access and trails all contribute to higher exotic richness and abundance.

- This suggests that life history traits (e.g. dispersal) may be more important than traits that increase competitive ability in intact forests.

- **Hunting** access decreased exotic invasions. This suggests that abundant deer may facilitate exotic invasions.

- Human induced changes to the landscape (e.g., road and trail densities) swamp out the effects of site conditions (N and P in soil) on exotic invasions.
N-loving species are increasing

N deposition is increasing both soil and leaf N in areas of high deposition.

Species with N-rich leaves have increased over the past 50 years.

*These include invasive species*
Is *Alliaria* invasion associated with N deposition?

**YES:**

Both soil N and N-deposition favor *Alliaria* invasions
Do deer play roles in invasion?

• Deer have several effects:
  – Spread seeds – endo & ecto-zoochory
  – Disturbance - Compact soil & disturb litter
  – Add N via urine & feces → fertilizer effect

• Deer can facilitate invasions if they prefer to browse on native plants
  – Deer favor invaders via ‘apparent competition’

• Deer also appear to facilitate earthworm invasions . .
Biodiversity, exotic plant species, and herbivory: The good, the bad, and the ungulate

Marty Vavra *, Catherine G. Parks, Michael J. Wisdom

Pacific Northwest Research Station, USDA, Forest Service, La Grande Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, United States

Les cerfs
Eurasian Earthworms Invasion “cascade”?

- Forest duff layer disappears
- Plant cover & diversity decline
- Shifts in soil nutrients - N & P availability
- Mycorrhizal colonization declines

Nielson & Hole 1964; Marinissen & van den Bosch 1992; Gundale 2002; Hale et al. 2005

worm-free understory

worm-infested understory

(Minnesota Worm Watch Web)
Do deer and garlic mustard interact to affect native plants?

2 x 2 factorial experiment in 5 State Parks
  Deer Effect: Exclosure – IN or OUT?
  *Alliaria* Effect: Weeded or Not?
Evaluated effects on *Quercus*, *Geranium*, *Uvularia*, *Carex*
tracked survival & growth
Exclosures: ↓ soil compaction, soil N, & exotic earthworms
(so deer increase all 3)
Do deer and garlic mustard have *synergistic* effects on native plants?

What affects *Uvularia* growth & survival?

Most effects were additive – little interaction, but *Alliaria* sometimes protected palatable species from herbivory (reduced oak growth more with no deer)
Causes of invasion confirmed

- Massive changes in **land use**
  - **Habitat fragmentation** from
    - Intensified **urbanization & agriculture**
  - **Global and regional climate change**
  - **Acid rain & N deposition**
  - **Overabundant deer**
  - **Species losses & Biotic homogenization**

Invading **exotic species**

Driver or passenger??

cause or consequence?
Consequences of invasion?

• Coarse & fine-scale associations
  Do associations predict impacts?
Approach: Association analyses

- Evaluated effects on native species that increased (17) or decreased (53) over last 50 years
- Also rated for habitat specificity (Coef of Conservatism – C.C.)
- Used checkerboard (C) scores to evaluate + and – associations:
  \[
  C_{ij\text{-site}} = (r_i - S) \times (r_j - S) \quad \text{site}
  \]
  \[
  C_{ijk\text{-quad}} = (q_{ik} - Q_k) \times (q_{jk} - Q_k) \quad \text{quadrat}
  \]
- Evaluated effect sizes for these
Invasive exotic species are negatively associated with native species

Association sizes between the 3 most common invasive species and 70 native species across 94 sites

- Negative associations increase in more *urbanized* landscapes

Waller et al. submitted, *Biological Invasions*
Associations between Invasive and Native species at two scales

Mean co-occurrence (C-scores) between 3 common invaders and native species

a) Site-level C-scores are mostly negative for both increasing and decreasing native species

b) Quadrat-level C-scores show + associations between Alliaria and Rhamnus and increasing native species

Waller et al., submitted
Invasive-Native associations

Associations between invasive and declining native species become more **negative** as habitat specificity of native species (C.C.) increases

→ **Invasives not invading specialized habitats**

→ **Invasive impacts vary among species**

Waller et al., submitted
Conclusions: Causes

- Alien invasive species act as both passengers and drivers of ecological change
- Forests are more vulnerable to exotic invaders when:
  - Forest fragments are small and surrounded by dense human settlement
  - Visitation / use are high – trails, etc.
  - Deer are dense
  - Diversity & herb cover are low
  - Surrounding lands are infested
  - Earthworms have invaded
Causes & Consequences of invasion

Initial native diversity did not protect against invasions in this multivariate path model

Site soil conditions did not significantly affect either native or exotic dynamics

1950 Species Richness

Soil N

N-deposition

Deer

Road Density & urbanization

Forest Cover

1950 Species Richness

Soil N

N-deposition

Deer

Road Density & urbanization

Forest Cover

Abundance Richness

Exotic Species

Native Species

Abundance Richness

Abundance Richness

Causes

Consequences
Conclusions: Consequences

- Invasive species associate both + and – with native species
  - At site level, rarely significant
  - At 1m² quadrat level, + w. common species, but – with rare, declining, specialized species
- Negative exotic-native associations increase in landscapes with more roads and houses
- Analyzing local interactions among species gives us high statistical power.
- This may allow us to predict which invasive species most affect particular native species.
Merci à vous et

NSF USDA CSREES

Aldo Leopold

John Curtis

Dave Rogers
Bil Alverson

Shannon Wiegmann
Steve Horn

Sarah Johnson
Erika Mudrak

http://www.botany.wisc.edu/pel.htm
Dan Simberloff

Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both?

CONCLUDING REMARKS AND FUTURE DIRECTIONS

It is difficult to measure scientific credibility. I am unaware that invasion biology has lost credibility, in spite of this metaphor, the martial metaphors, and the few critics whose work I cite above. The problems associated with invasions have become so evident that the science continues to increase in prominence and activity, despite their writings.
Embrace Invaders?

A forester engages in efforts to eradicate the velvet tree *Miconia calvescens* in Hawaii.

1996, only 4 have been successful. We must embrace the fact of ‘novel ecosystems’ and incorporate many alien species into management plans, rather than try to achieve the often impossible goal of eradicating them or drastically reducing their abundance. Indeed,

Don’t judge species on their origins

Conservationists should assess organisms on environmental impact rather than on whether they are natives, argue Mark Davis and 18 other ecologists.
Or fight invaders?
D. Simberlof

doi: 10.1111/j.1461-0248.2006.00939.x

**IDEA AND PERSPECTIVE**

Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both?

The minority of them (Simberlof 2003). The argument that introduced species are not so awful (Sagoff 1999, 2005; Rosenzweig 2001; Slobodkin 2001; Brown & Sax 2004) rests partly on the related, and equally false, charge that invasion biologists are not accounting for the benefits of some introduced species and the apparent harmlessness of most. It is just as misguided (Simberlof 2003, 2005).
### Stages in invasion

<table>
<thead>
<tr>
<th>Stage</th>
<th>Definition</th>
<th>Consequences of invasion</th>
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</thead>
<tbody>
<tr>
<td>3/Colonization</td>
<td>Survival of introduced plants enabling pioneer population to be self-sustaining</td>
<td>Harmful impact of species to ecology and economy</td>
</tr>
<tr>
<td>4/Naturalization</td>
<td>Survival and reproduction</td>
<td></td>
</tr>
<tr>
<td>5/Spread</td>
<td>Dispersal of propagules and spread of populations outside of area where first introduced PAB</td>
<td></td>
</tr>
<tr>
<td>6/Impact*</td>
<td>Combinations of PAB and spread</td>
<td></td>
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<tr>
<td>PAB</td>
<td>pAB</td>
<td></td>
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<tr>
<td>Local</td>
<td>Local and regional</td>
<td></td>
</tr>
<tr>
<td>Yes, but not essential</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Monitoring, detection and early eradication</td>
<td>Eradication and control of founding population; control of potential dispersal vectors</td>
<td>Dispersal and spread minimization; detection and eradication of satellite populations</td>
</tr>
<tr>
<td></td>
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<td>Population control; dispersal and spread minimization; impact alleviation</td>
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</table>
Evolution of increased competitive ability (EICA)


This could explain the observed 'lag' = time to adapt

From Gurevitch et al. 2011 Ecol Let 14: 407

Figure 3 Examples of how the synthetic invasion meta-framework (SIM) might be applied in three hypothetical invasion scenarios. (a) A simple case of enemy escape resulting in an invasion. (b) An example of the ecological and evolutionary components that may be involved in 'propagule pressure' (see text). (c) The hypothesis of the evolution of increased competitive ability (EICA) invokes many different components; the application of the SIM reveals the underlying complexity of the EICA. See text for explanation of the steps required for the EICA to be fully supported.
Too many theories?

Many theories about why species invade! reviewed by Catford, Jannson, & Nilsson 2009

**Methods** We review and synthesize 29 leading hypotheses in plant invasion ecology. Structured around propagule pressure (P), abiotic characteristics (A) and biotic characteristics (B), with the additional influence of humans (H) on P, A and B (hereon PAB), we show how these hypotheses fit into one paradigm. P is based on the size and frequency of introductions, A incorporates ecosystem invasibility based on physical conditions, and B includes the characteristics of invading species (invasiveness), the recipient community and their interactions. Having justified the PAB framework, we propose a way in which invasion research could progress.
✓ Surprisingly strong effect of N-dep in Wisconsin

$r^2 = 0.60$

Waller et al., unpublished

GLM across all sites
Deer as ‘keystone’ herbivore

Winter feeding

- Climate change (mild winters)
- Land use change (early successional)
- Landscape structure (fragmentation and edge)
- Predation pressure

Deer densities

- Tree regeneration
- Forest herb species richness
- Exotic species (worms and plants)
- Biotic homogenization

Forest canopy composition