Causes and consequences of exotic invasions in Wisconsin forests

Donald M. Waller

Dept. of Botany

University of Wisconsin – Madison

http://www.botany.wisc.edu/waller

University of Wisconsin Plant Ecology Laboratory

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

Wired *Magazine*

Admire
Invaders??

9 Great Invasive Species Worth Admiring

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

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Science News *... from universities, journals, and other research organizations*

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.

A pollinating insect on a Carpobrotus affine acinaciformis flowerhead. (Credit: SINC / Ignasi

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Biological invasions (species transported by humans outside their region of origin to other regions where these species become

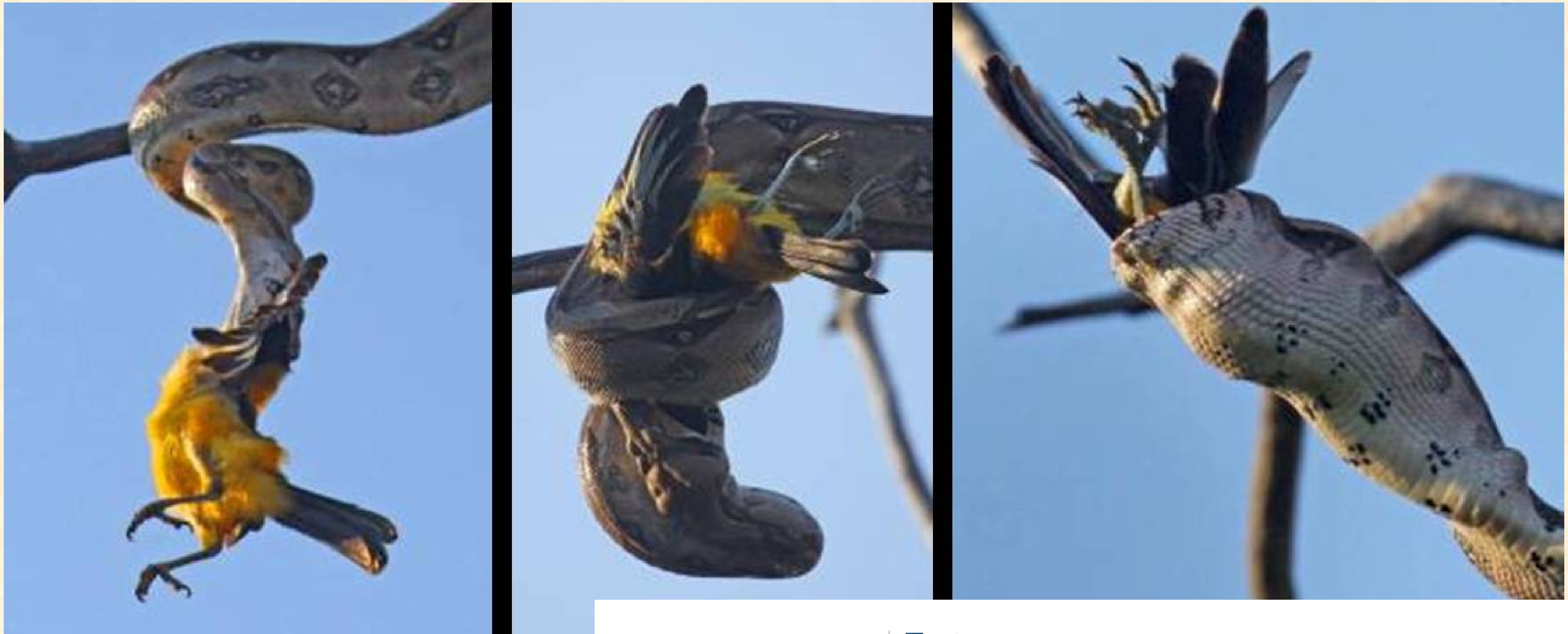
24 FEB 2011: **REPORT**

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.

January 27, 2011, 3:21 PM | 7 Comments

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 pouch 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

30,000 Pythons in the Everglades, Florida

“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.”

Will Snakes Inherit the Earth?
NT Times, Oct. 2012
By DIANE ACKERMAN

ELSEVIER
Opinion TRENDS in Ecology and Evolution Vol.19 No.9 September 2004
Full text provided by www.sciencedirect.com
SCIENCE DIRECT

Are invasive species a major cause of extinctions?

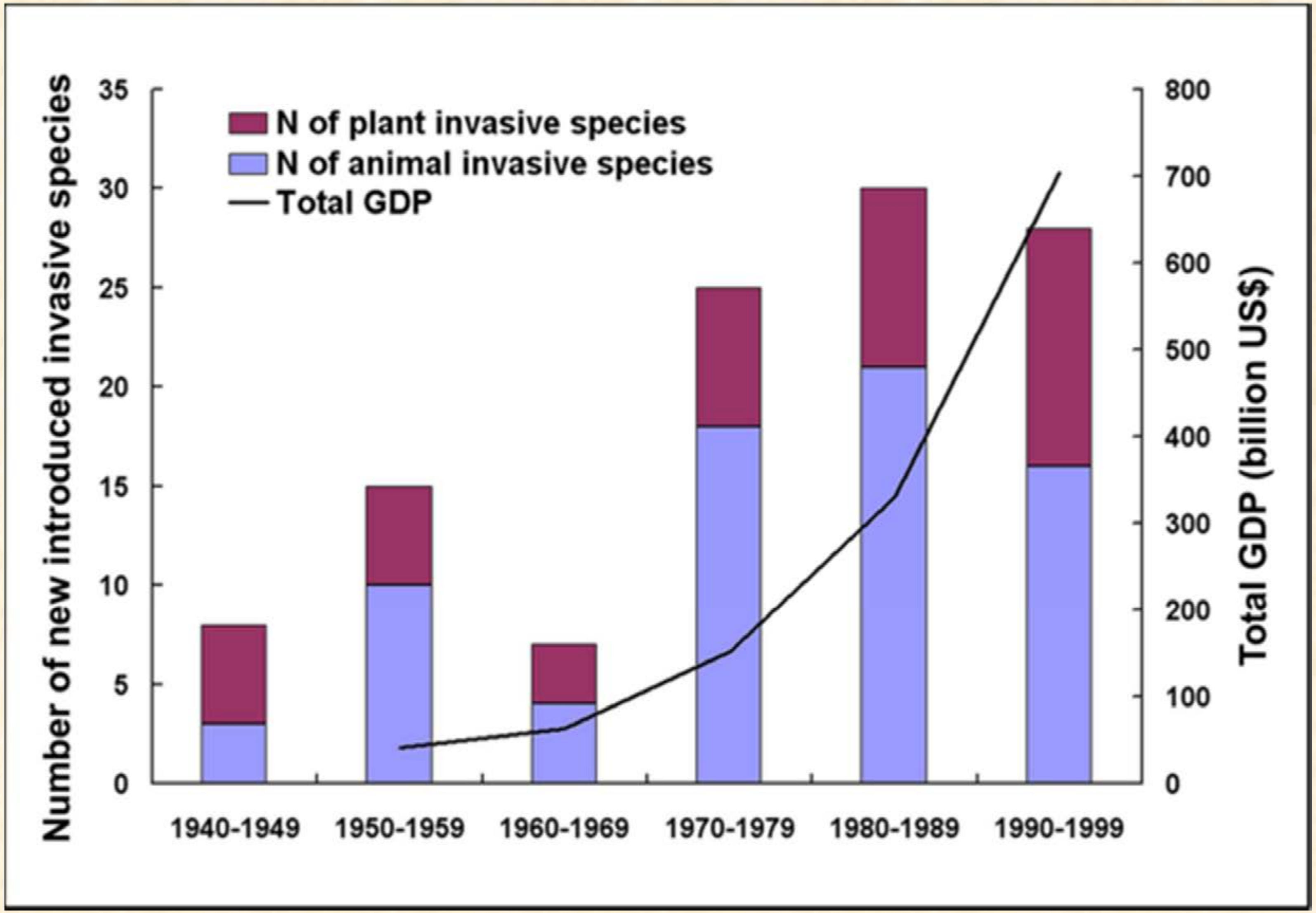
Be skeptical about invader impacts?

Jessica Gurevitch and Dianna K. Padilla

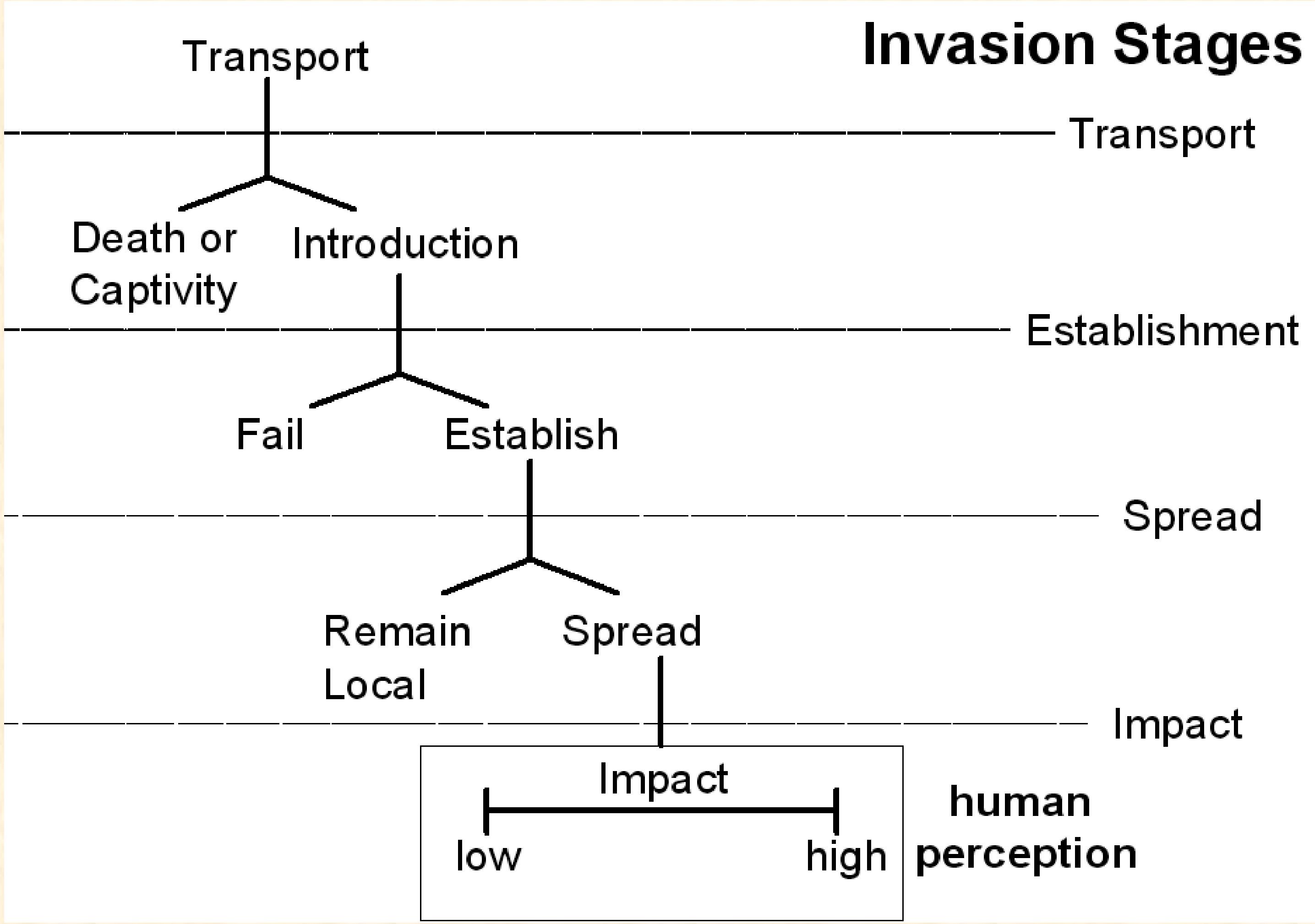
Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794-5245, USA

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.



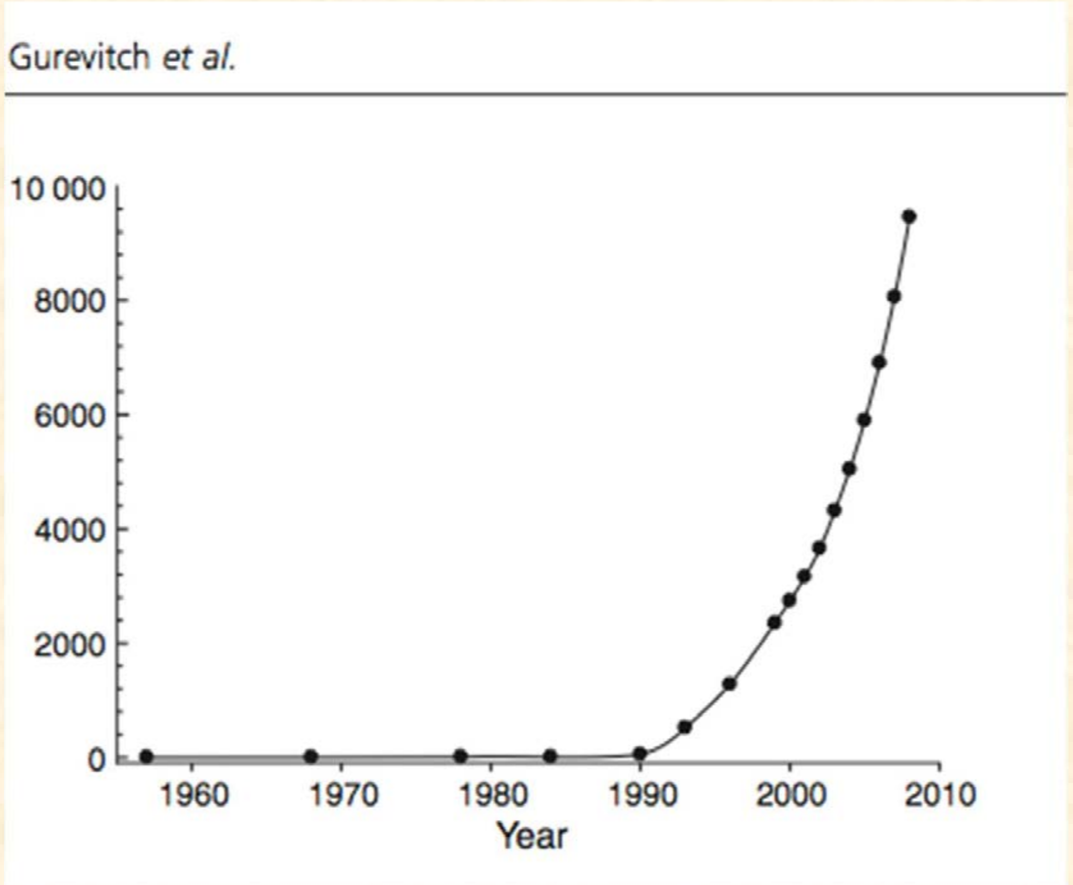
Stages in invasion



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

408 J. Gurevitch *et al.*

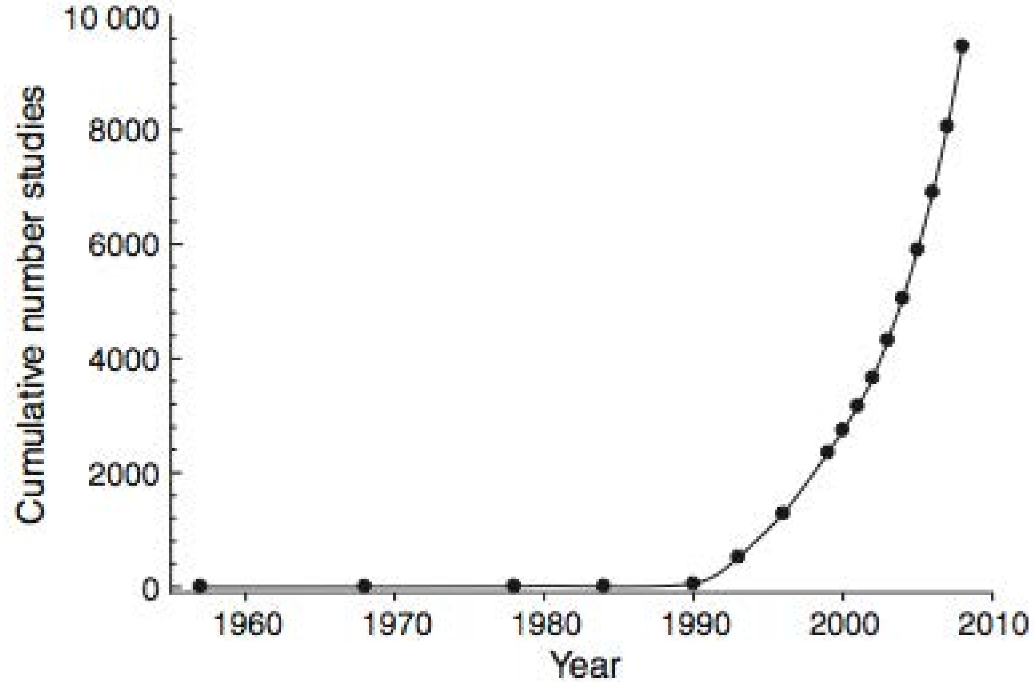
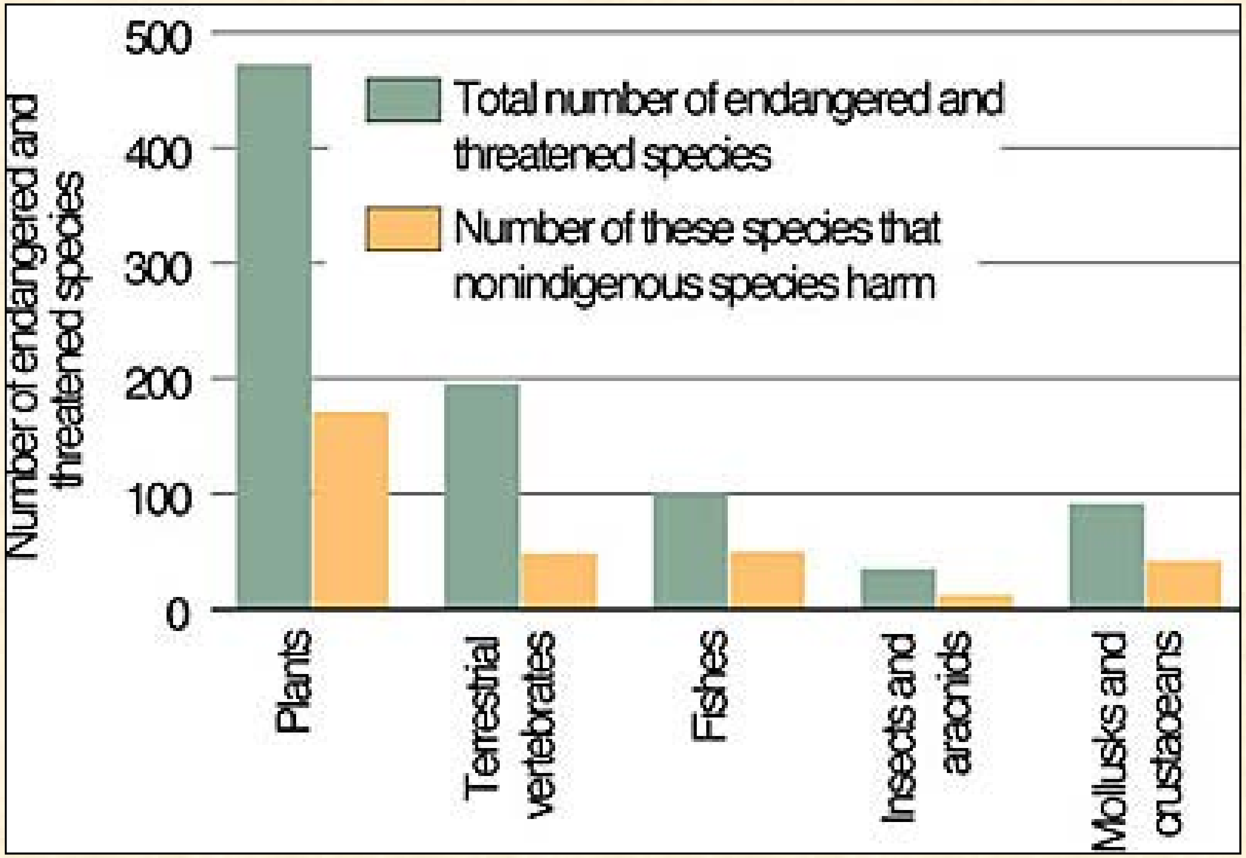


Figure 1 Cumulative number of studies in invasion ecology from 1958 to 2008 from a Web of Science search on key terms ‘inva*’ and ‘(ecol* or plant or invert*)’ after eliminating all non-ecological subject categories (engineering, oncology, etc.), for 10-year intervals through 1978, 5-year intervals from 1987 to 1990, 3-year intervals to 1999 and 1-year intervals from 2000 to 2008.

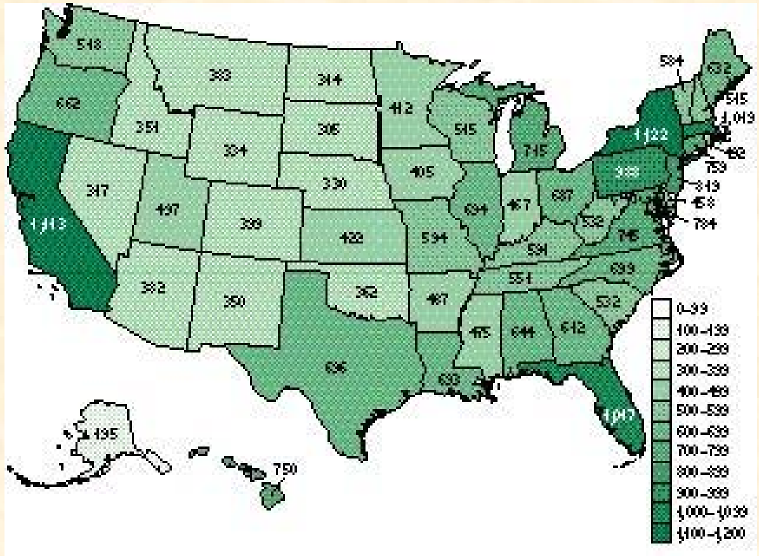
Invasives threaten native species

- 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**

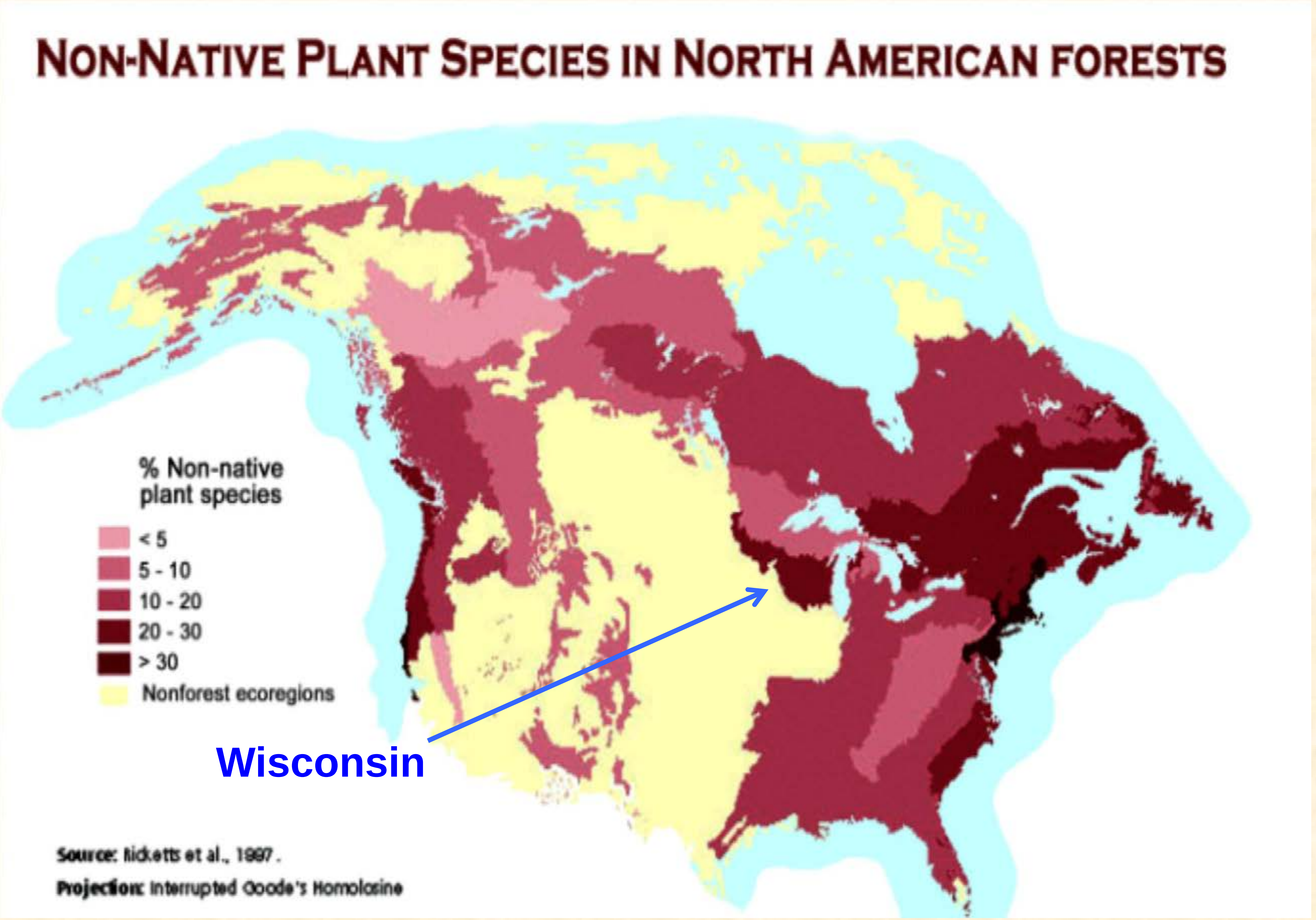


Number of nonindigenous plant species (from outside the United States) introduced into each state (data on number of native and introduced species from a phytogeographic data summary in preparation by J. T. Kartesz, Biota of North America Program of the North Carolina Botanical Garden, Raleigh).

Species with origins outside USA:

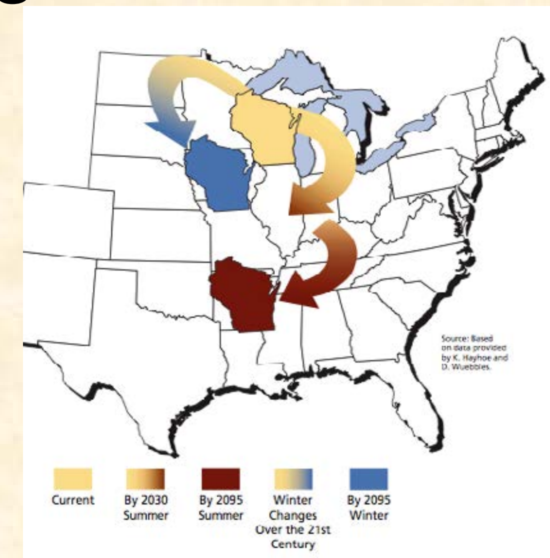
• Plants	3,723
• Terrestrial vertebrates	142
• Insects and arachnids	>2,000
• Fishes	76
• Mollusks (nonmarine)	91
• Plant pathogens	239
• **Total**	**>6,271**

Plants invading forests



Factors driving ecological change

- Massive changes in **land use**
  - **Habitat fragmentation** from
    Intensified **urbanization** & **agriculture**
- Global and regional **climate change**

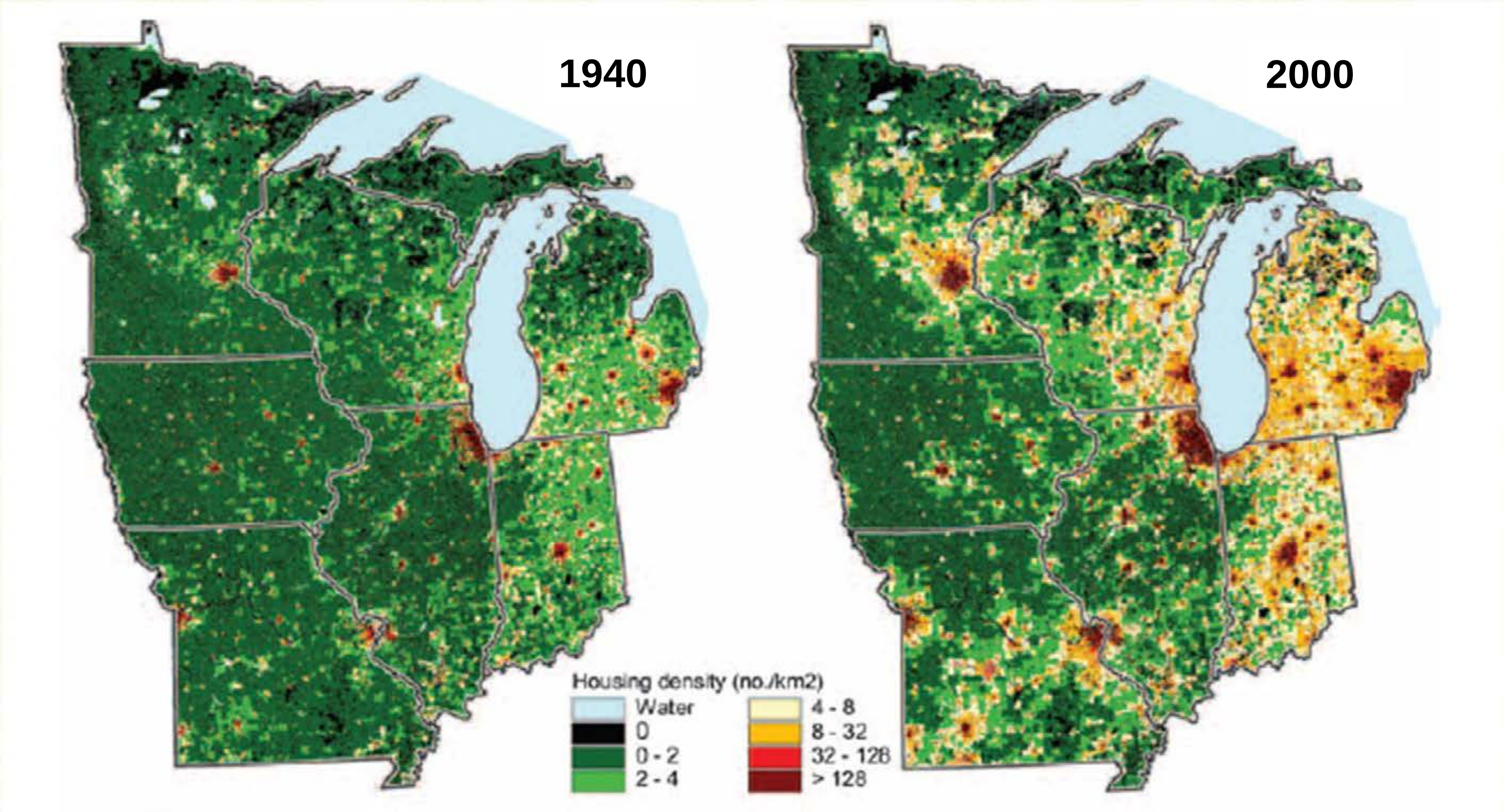


- Acid rain & **N deposition**
- Overabundant **deer**

- Species losses &
  Biotic **homogenization**

Landscape change:

Habitat Fragmentation & Urbanization



Radeloff, V.C., R. B. Hammer, S. I. Steward. 2005. Rural and suburban sprawl in the U.S. Midwest from 1940 to 2000 and its relation to forest fragmentation. Conservation Biology 19(3) 793-805.

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?

?

?

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Invading **exotic species**

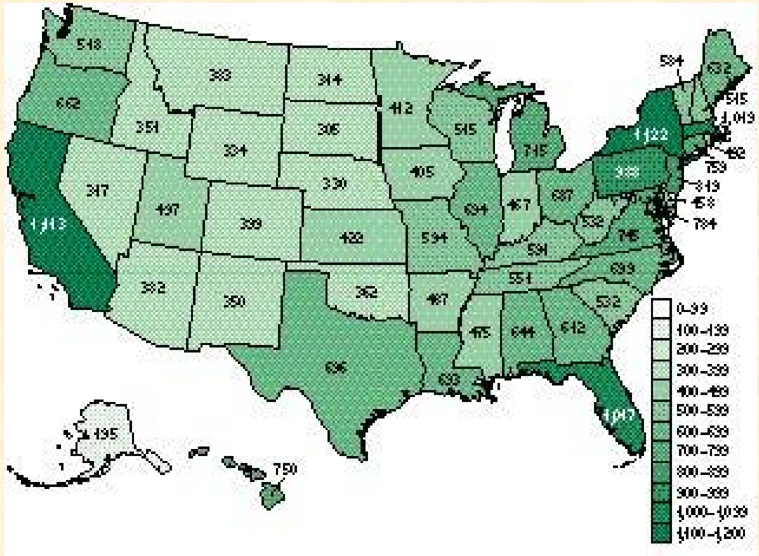
cause or consequence?

?

- Species losses &

  Biotic **homogenization**

Many invasive **plant species**



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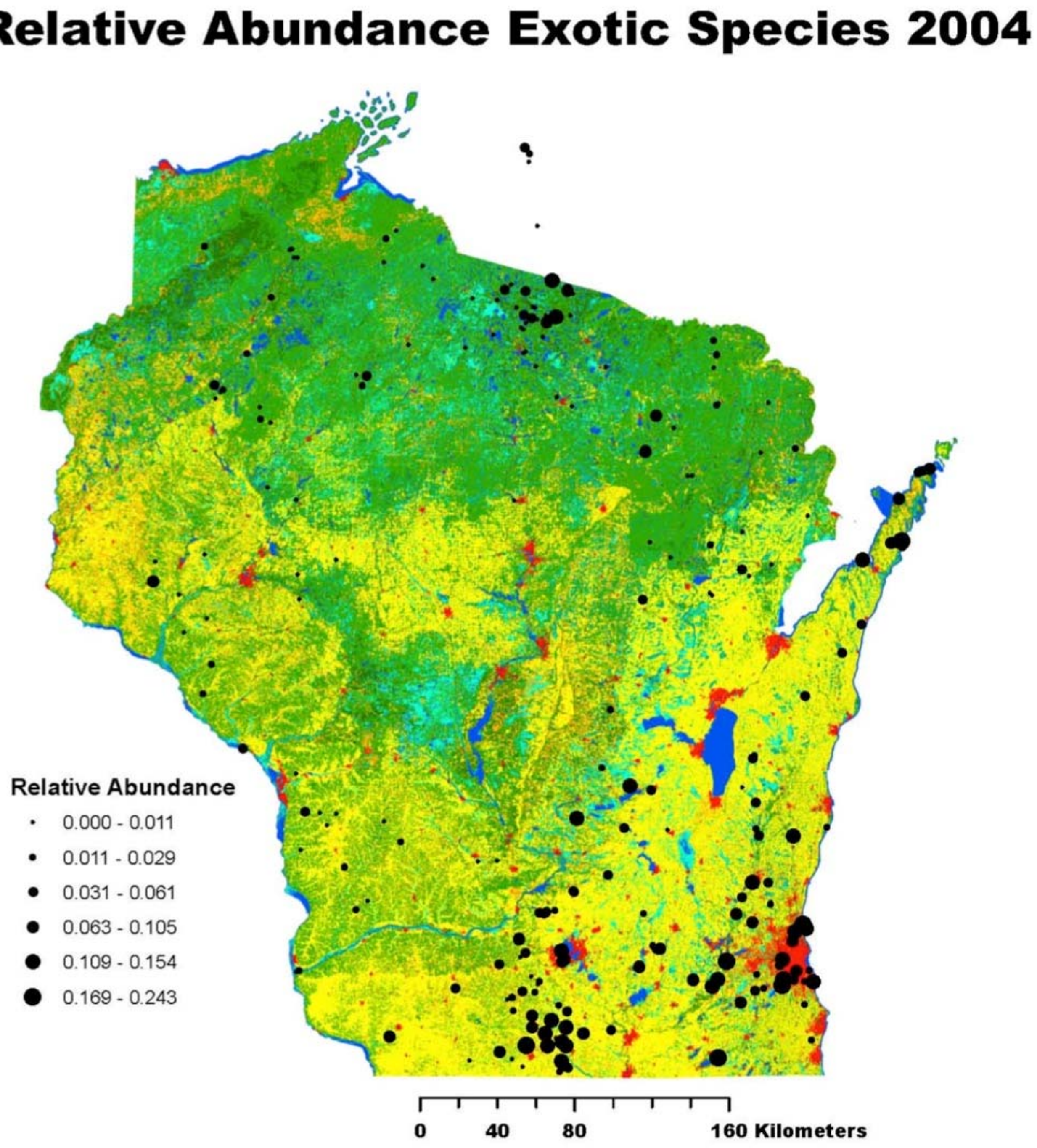
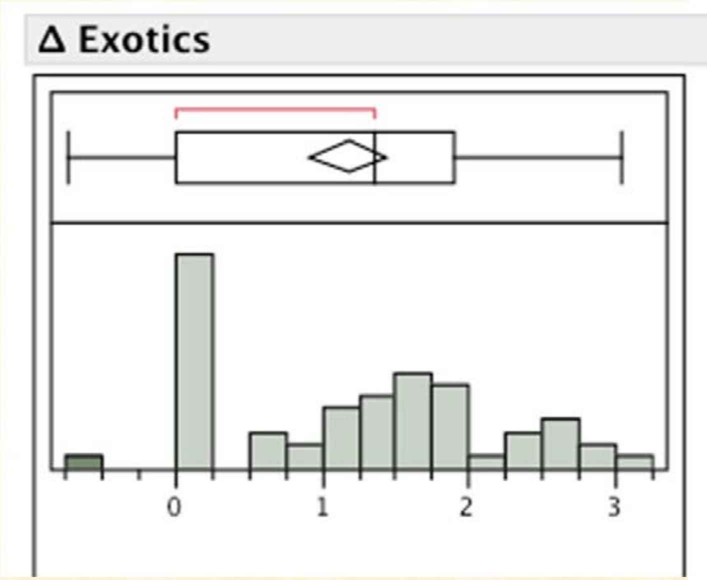
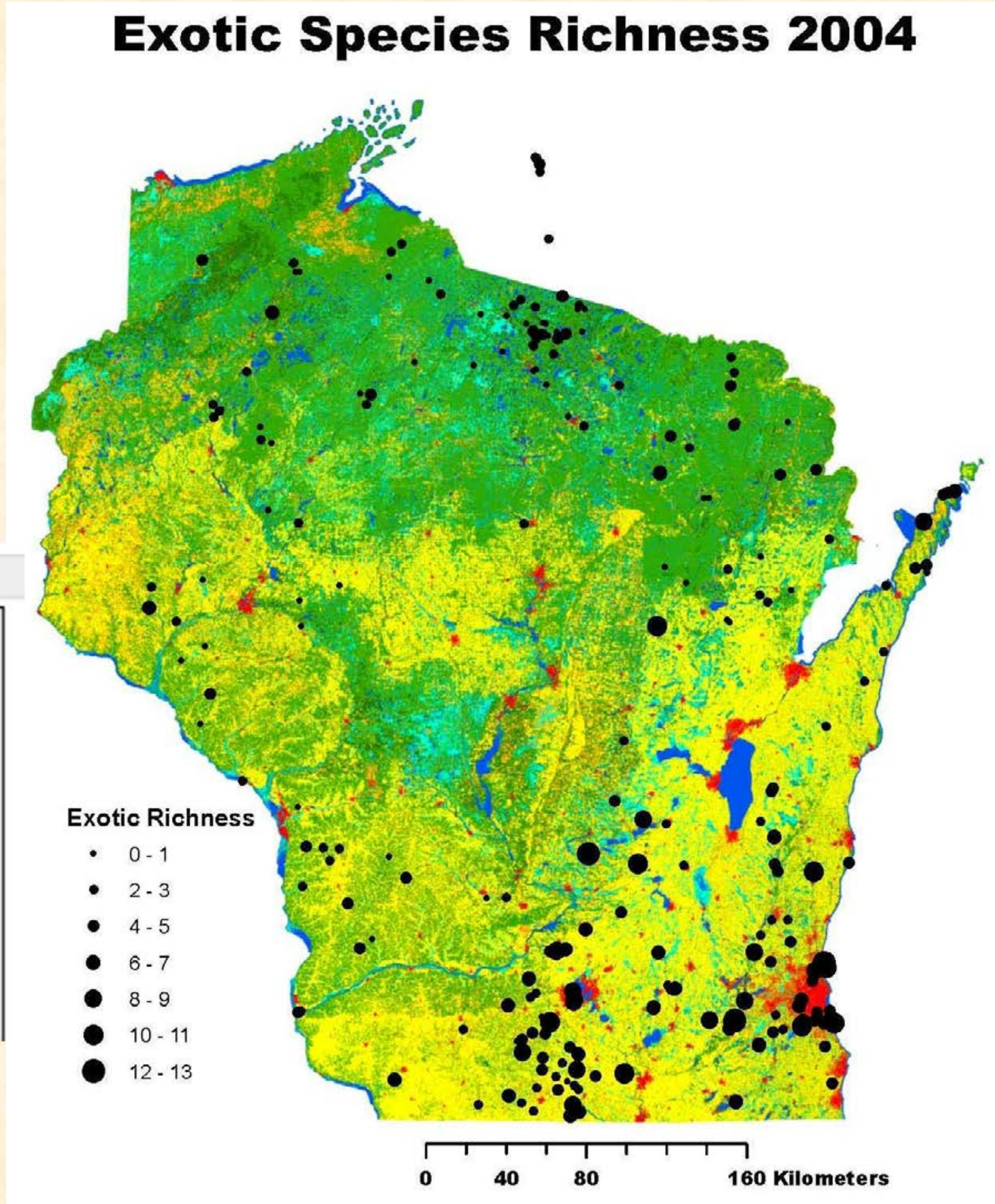
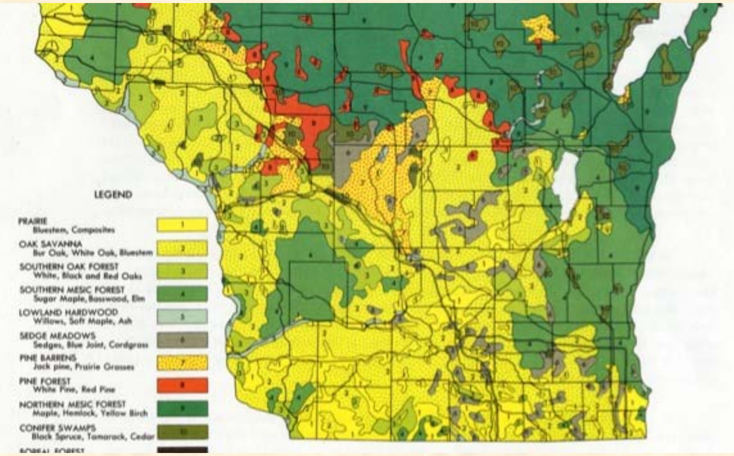
Study system:

Wisconsin Forests




Δ Exotics
0
1
2
3


Exotic Species Richness 2004
Exotic Richness
0 - 1
2 - 3
4 - 5
6 - 7
8 - 9
10 - 11
12 - 13
0
40
80
160 Kilometers



Southern Forests

<u>BEFORE:</u>

Mosaic of prairie, savanna & oak-hickory forests

Maintained by frequent fires

<u>NOW:</u>

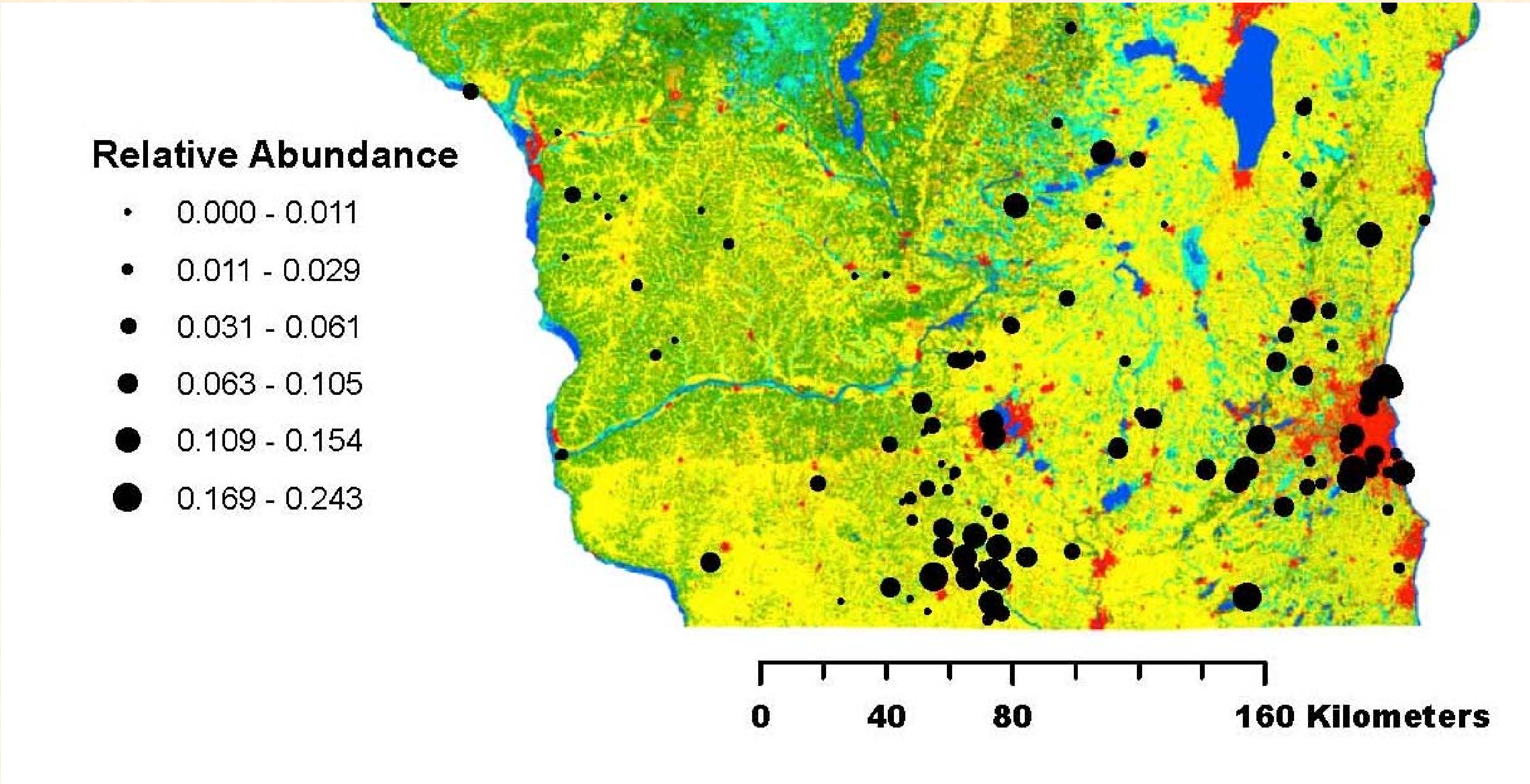
Dominated by agriculture

Forests - small & fragmented

Selective logging, hunting and recreation

Southern Forests: 94 Stands

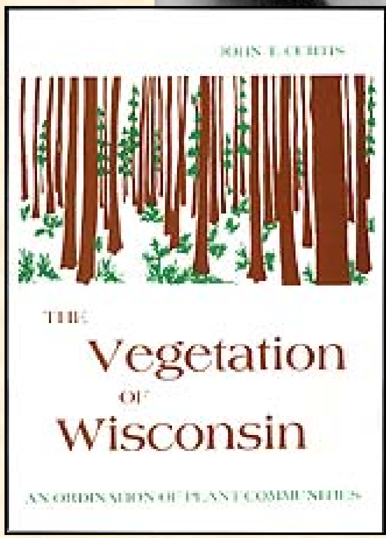
More forests & hills *More urban & agriculture*



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

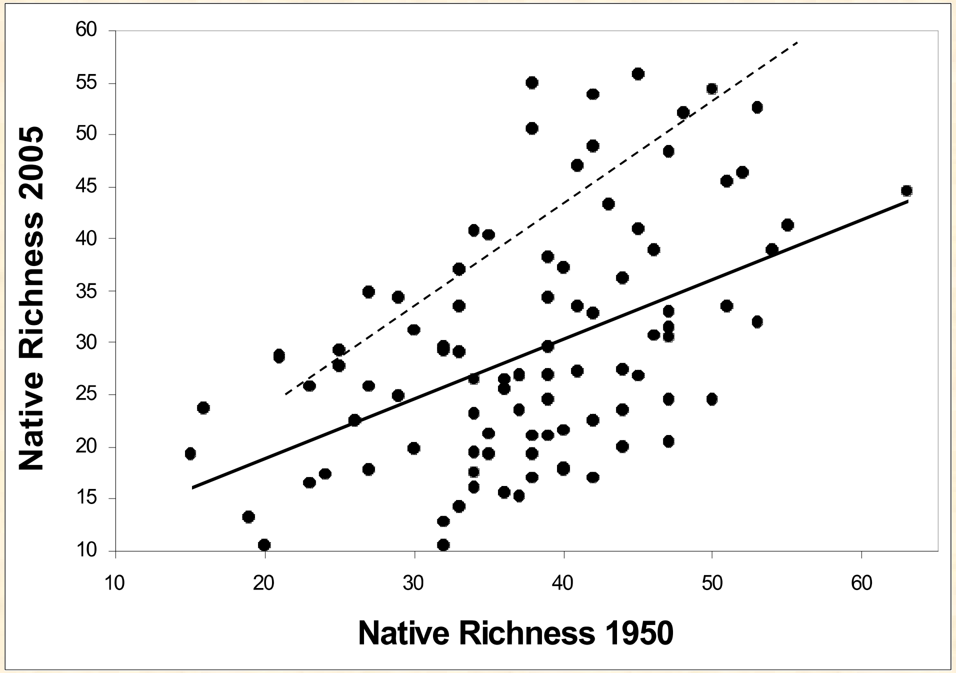
Local **diversity has** declined

80% of sites lost herb diversity

Species density declined:

25% / 1 m^2

22.4% / 20 m^2

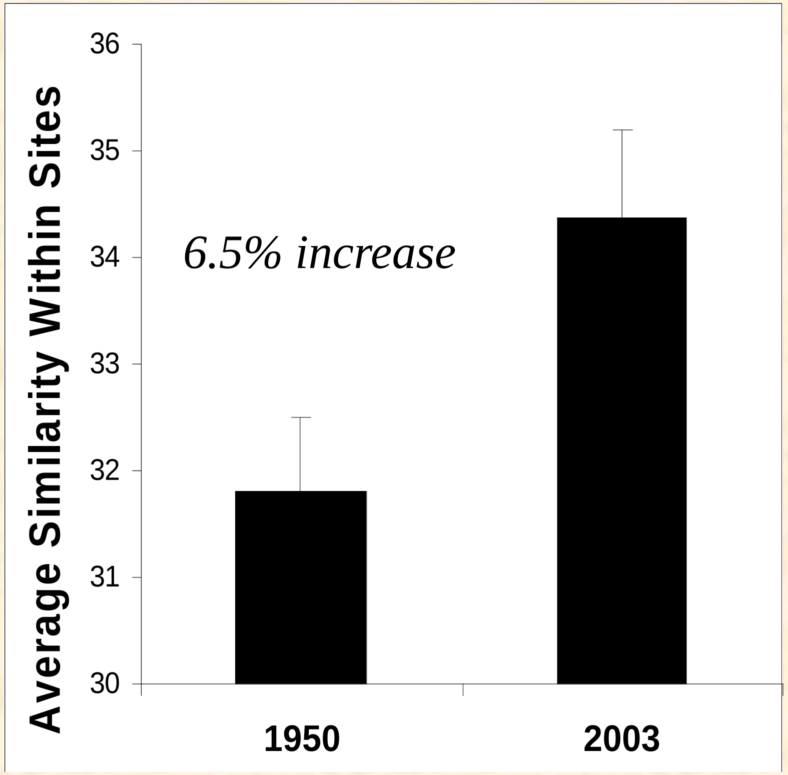


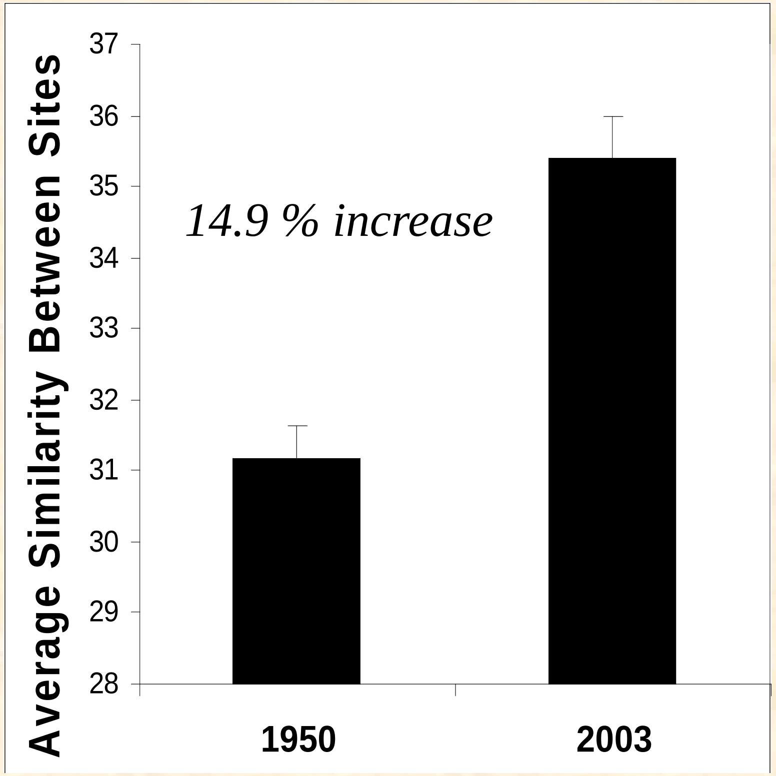
Declines in among site (b) diversity are associated with increases in exotics

Lack of fire & 'mesification'

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

Winners: Common Natives

Winners: Exotic Taxa

Species	Common Name	IV	Sites	Avg Freq
Alliaria petiolata	garlic mustard	19.1256	60	0.32
Rhamnus cathartica	common buckthorn	7.5730	60	0.13
Taraxacum officinale	common dandelion	4.6323	90	0.05
Lonicera x bella	Bell's honeysuckle	1.6960	48	0.04
Solanum dulcamara	bittersweet nightshade	1.2921	39	0.03
Arctium minus	common burdock	0.8905	46	0.02
Rosa multiflora	multiflora rose	0.8559	36	0.02
Leonurus cardiaca	lion's-tail	0.7408	11	0.07
Chenopodium album	lamb's-quarters	0.6753	21	0.03
Hesperis matronalis	dame's rocket	0.6708	13	0.05
Cirsium arvense	Canada thistle	0.4819	8	0.06
Cirsium vulgare	bull thistle	0.4483	17	0.03
Acer platanoides	Norway maple	0.3933	7	0.06
Poa pratensis	Kentucky bluegrass	0.3688	19	0.02
Morus alba	white mulberry	0.3578	14	0.03
Berberis thunbergii	Japanese barberry	0.2653	11	0.02
Silene latifolia	bladder campion	0.2625	2	0.13
Polygonum persicaria	spotted lady's-thumb	0.2614	8	0.03
Euonymus alata	winged burning-bush	0.2491	12	0.02
Glechoma hederacea	creeping-Charlie	0.2417	9	0.03

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

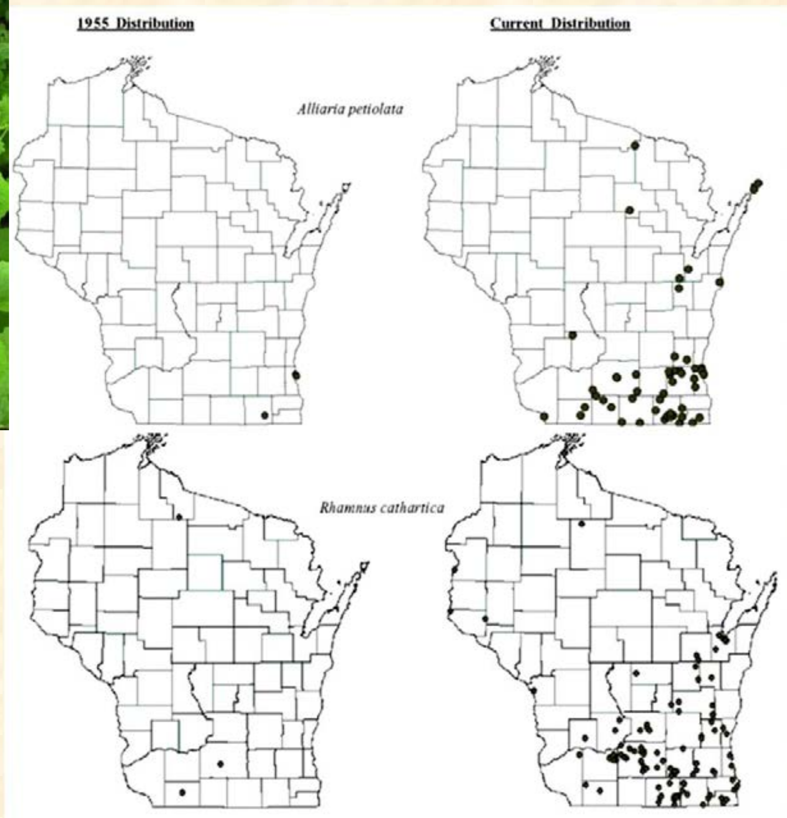
Exotic species invading S forests

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

Increased in both range & abundance within sites:

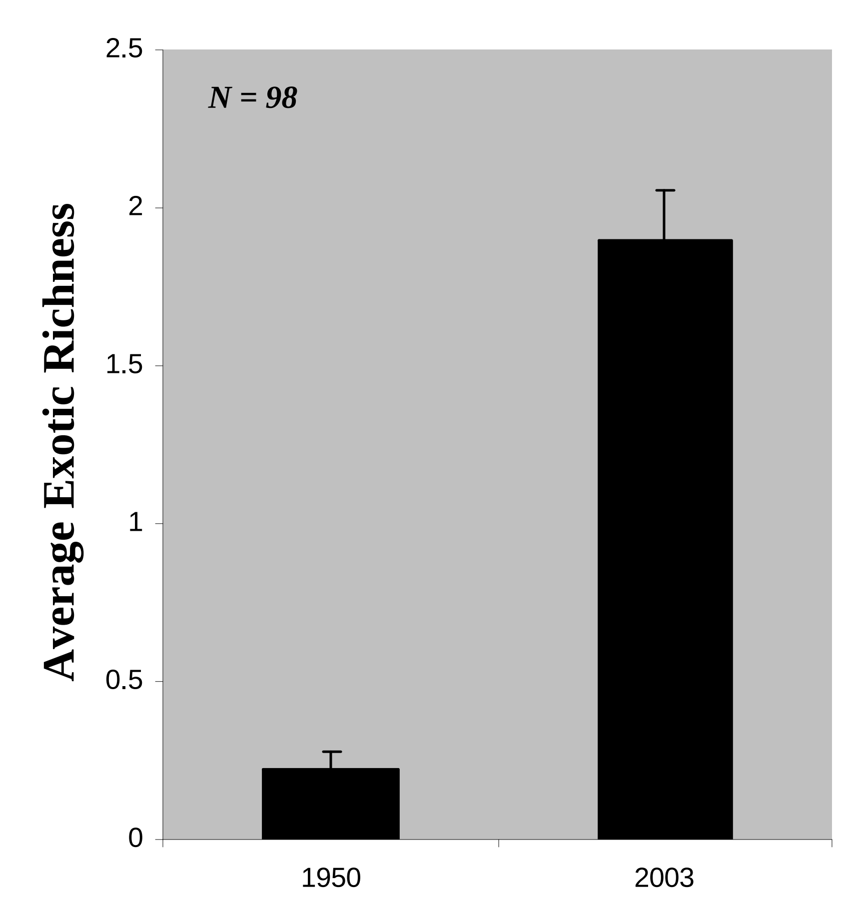
6x increase in the abundance of exotics when present

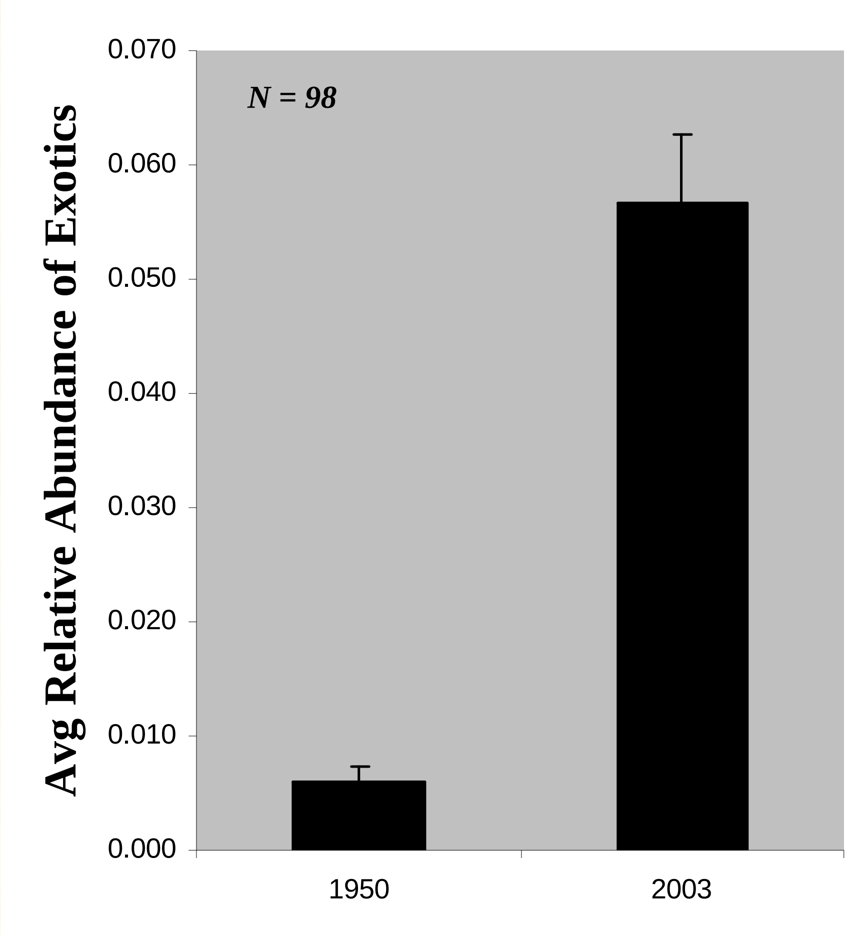
Then: **Now:**



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

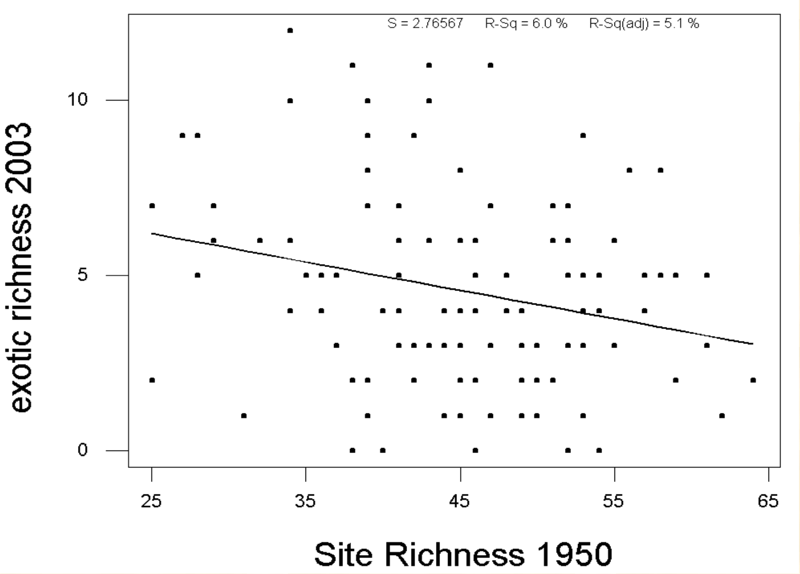
- Supply **PUSH** - plant invasions reflect a flood of seeds of invaders with high fecundity & wide dispersal – invasives ‘pre-adapted’ to invade
  - Prediction: Invasions will reflect proximity to existing populations / seed sources
- Demand **PULL** – plant invade “invadable” communities (‘empty niches’)

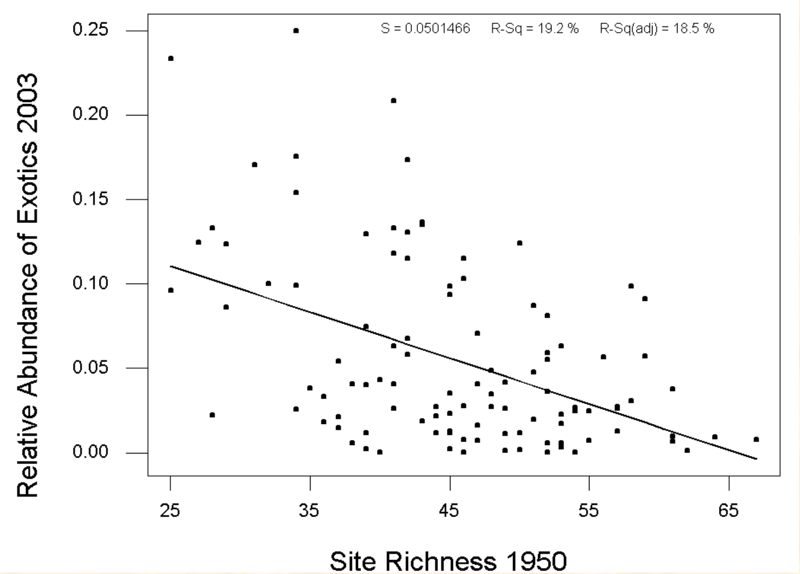
Predict: Diverse communities better resist invasion

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?

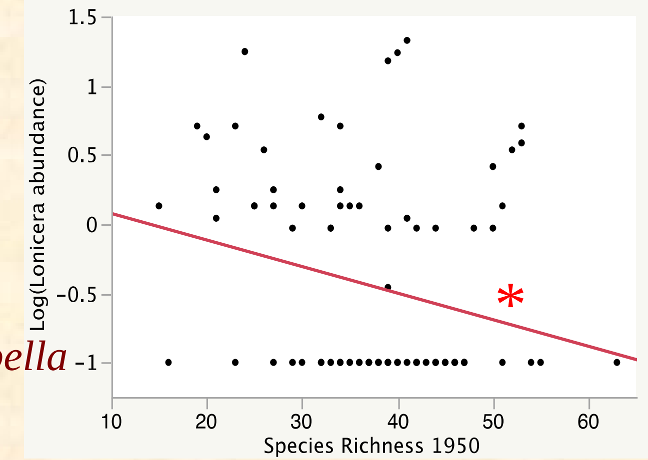
Communities with more native plant diversity in the 1950s suffered fewer invasions of *Lonicera* and *Rhamnus* between the 1950s and 2000s.

Support for diversity resistance hypthesis?

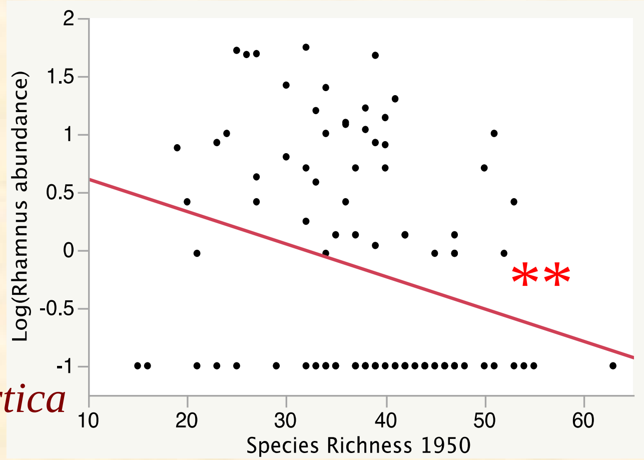
Or artifact?

Alliaria petiolata

Lonicera x bella

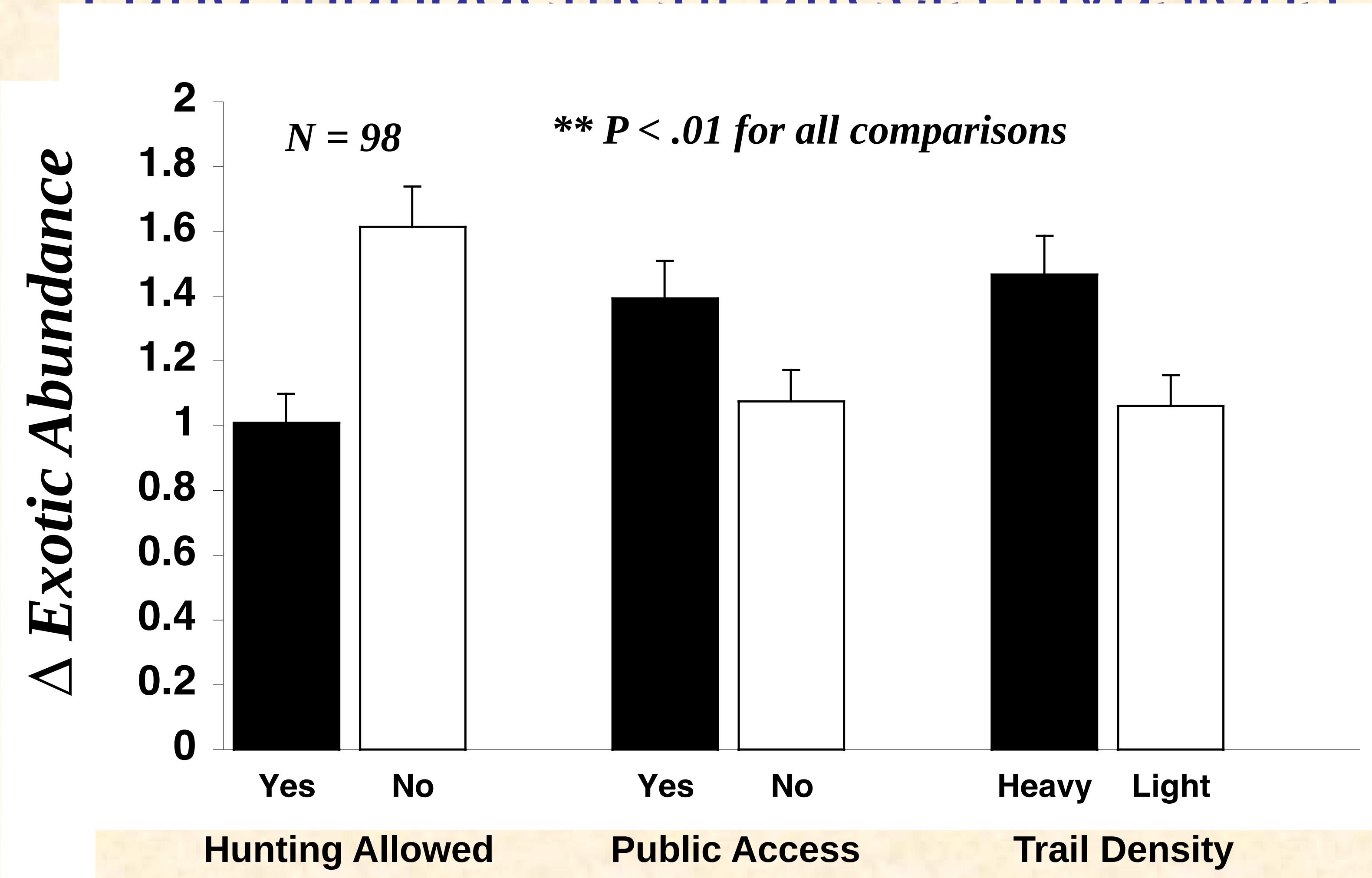


Rhamnus cathartica

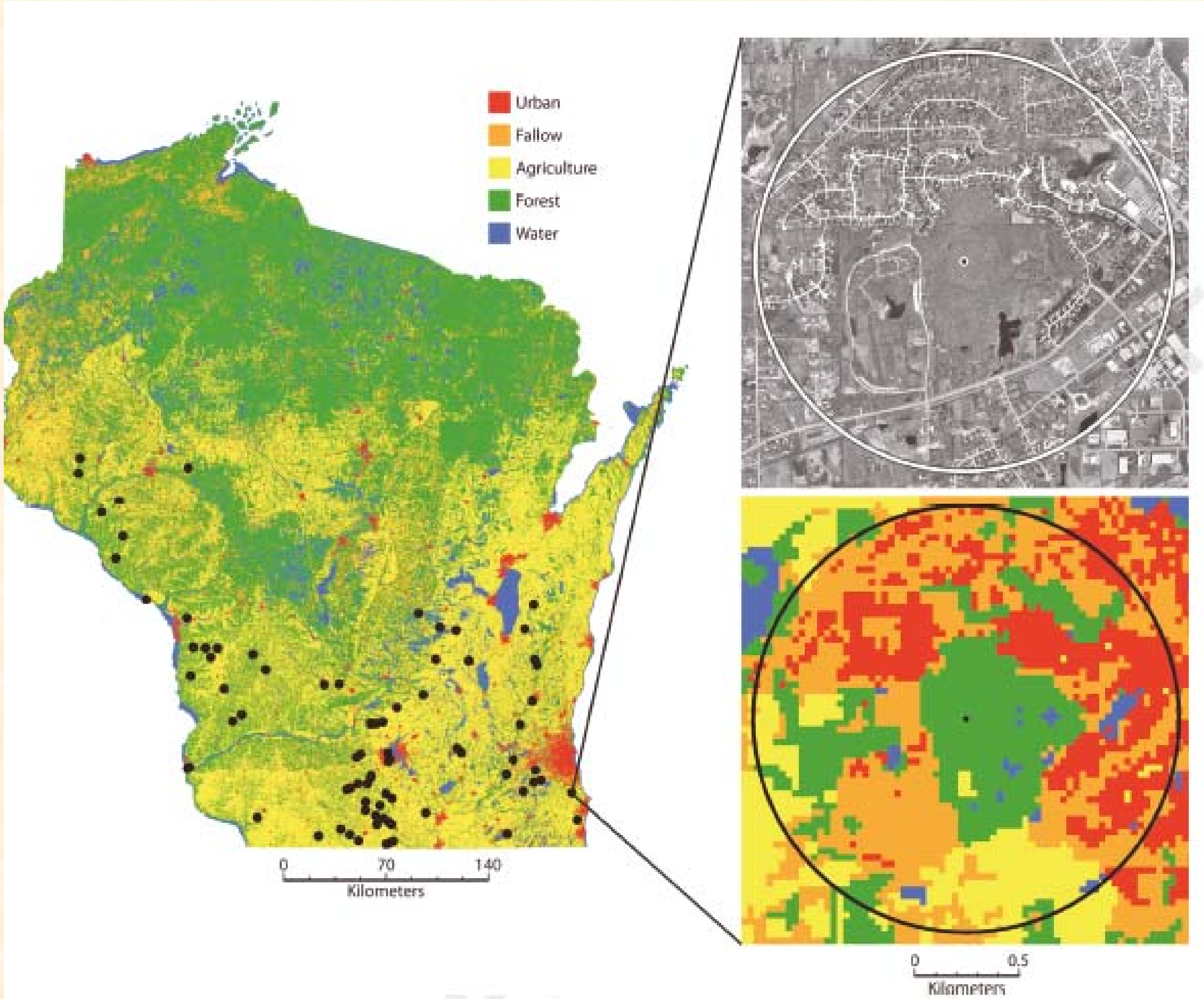


Waller et al., submitted

Land management affects invasions



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)

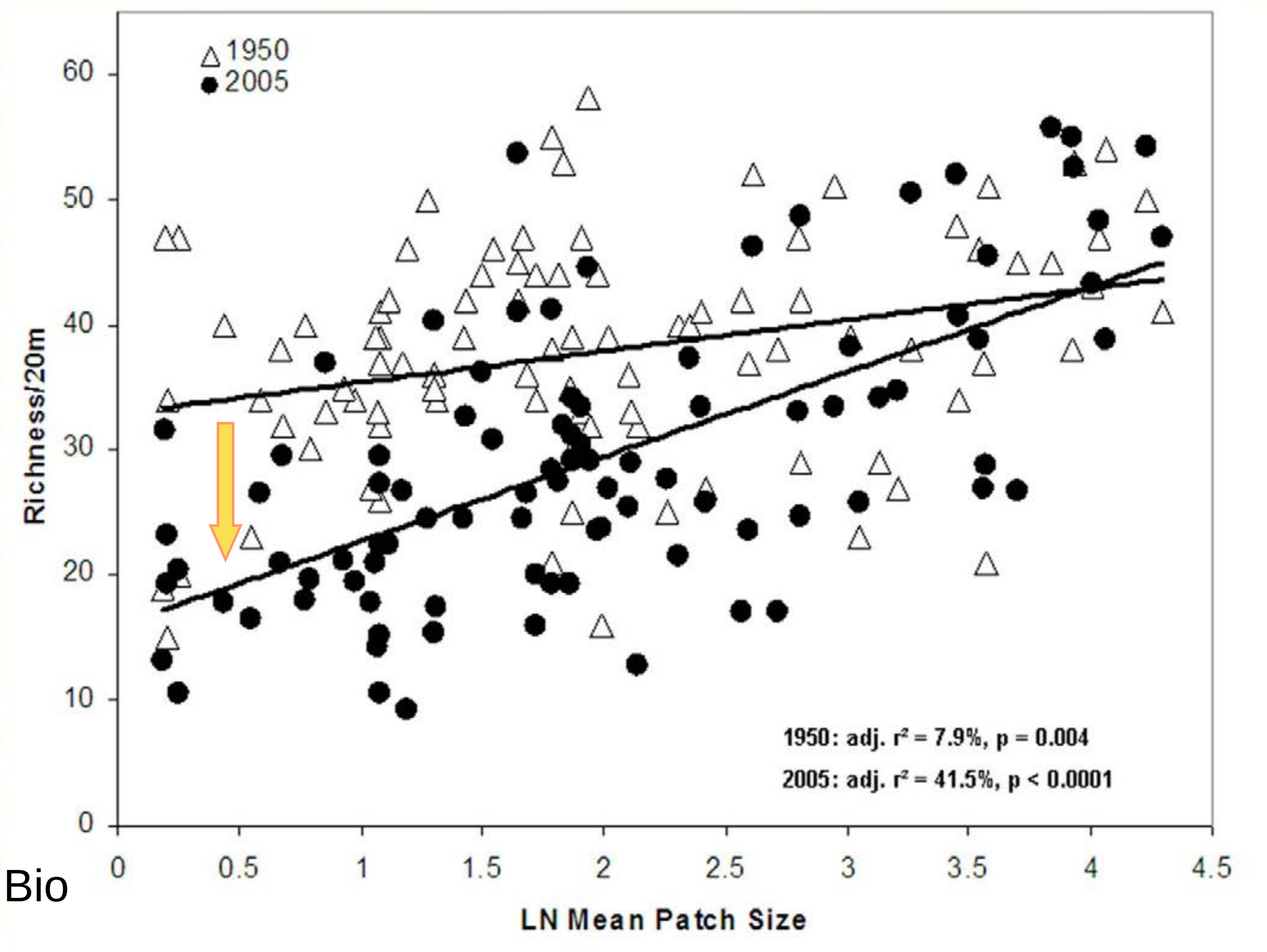
Paying the ‘extinction debt’

The **species - area** relationship is growing stronger:

Conclusions:

Isolation has started to take its toll

More **extinctions** are likely in the future

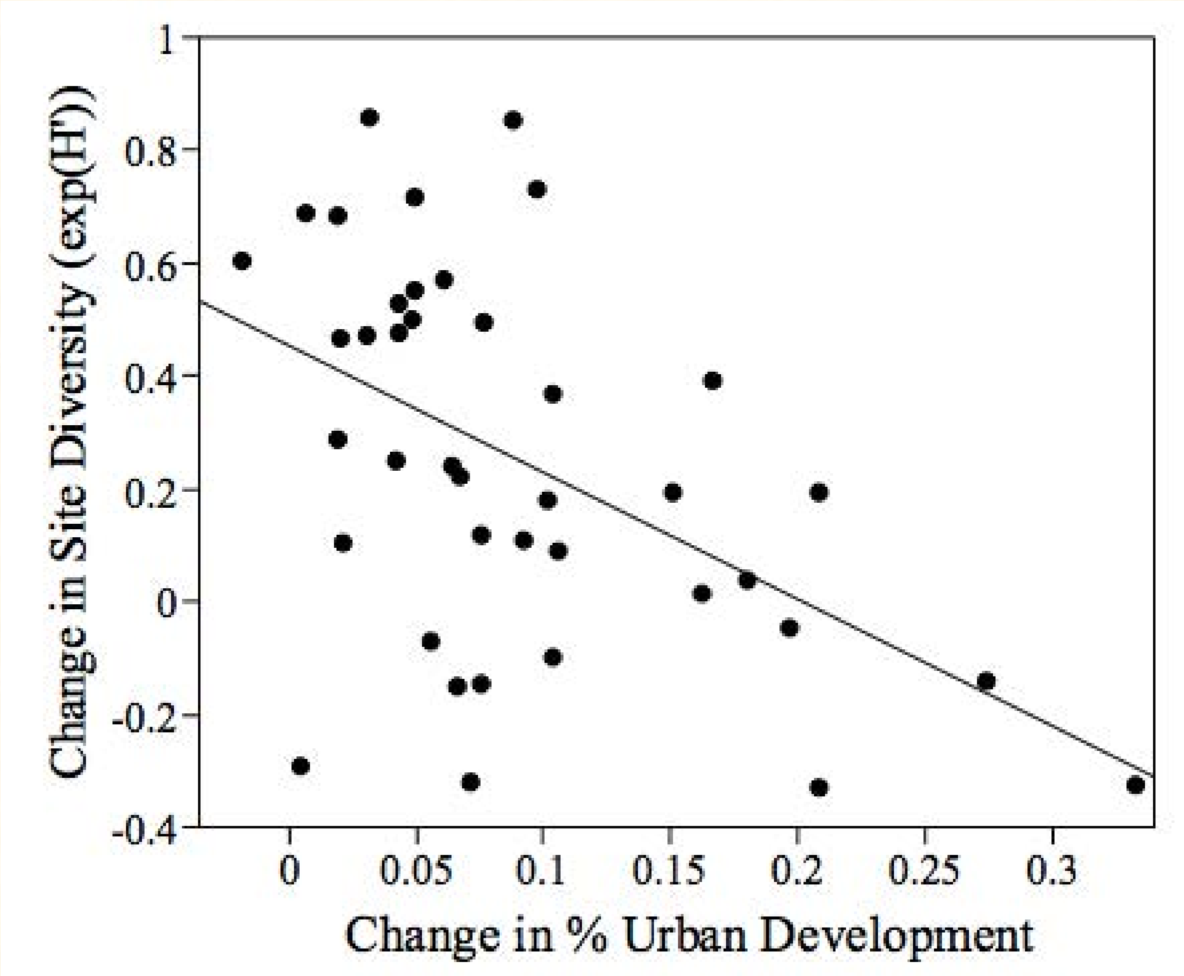


Rogers et al. 2009 Cons Bio

Are declines in diversity driven by urbanization?

YES!

This reflects many processes and drivers

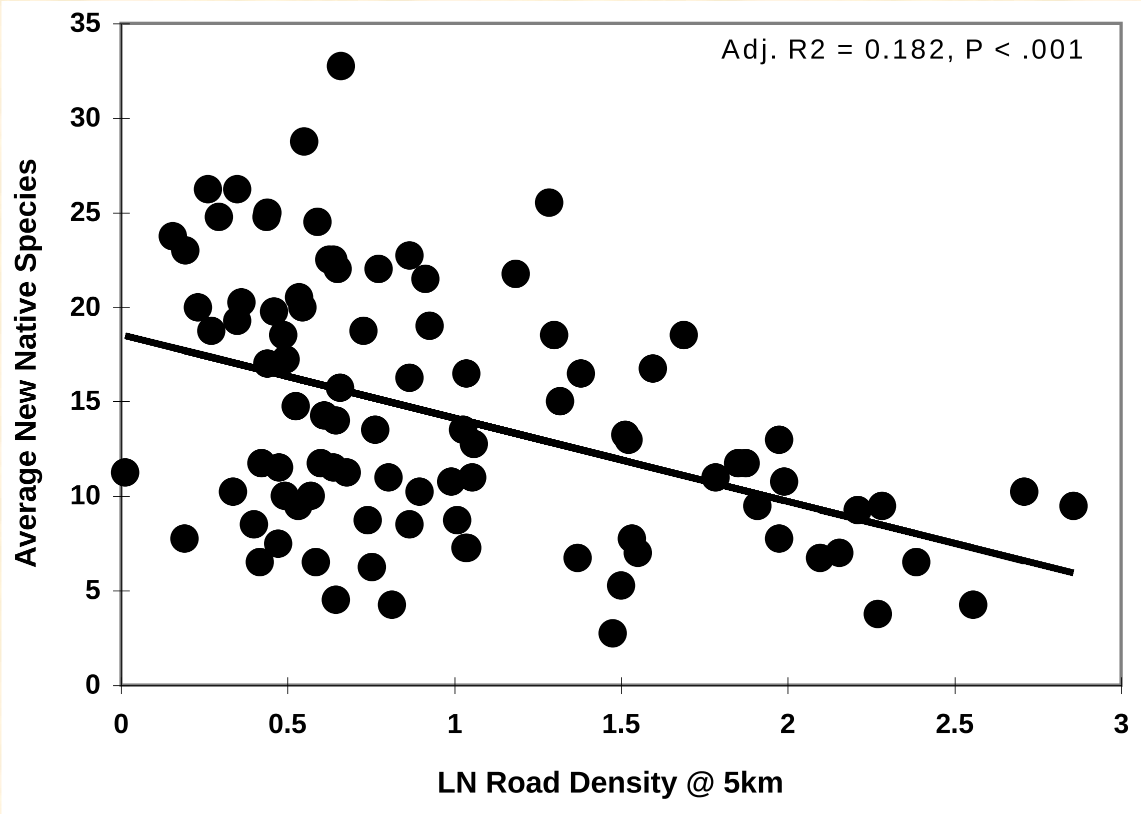


Effects of roads

Native species colonize few stands surrounded by roads:

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

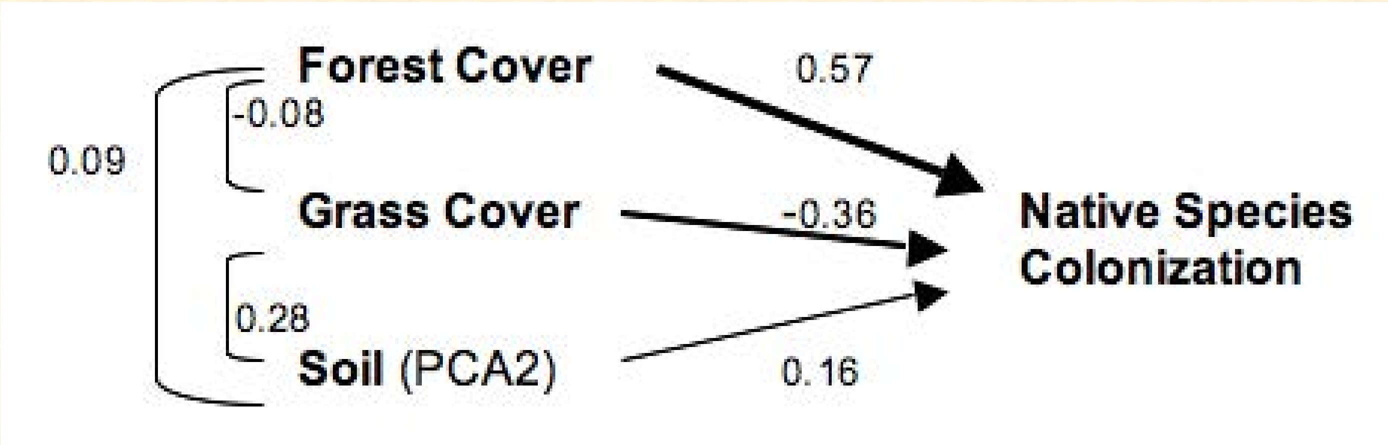
(preventing the 'rescue effect')



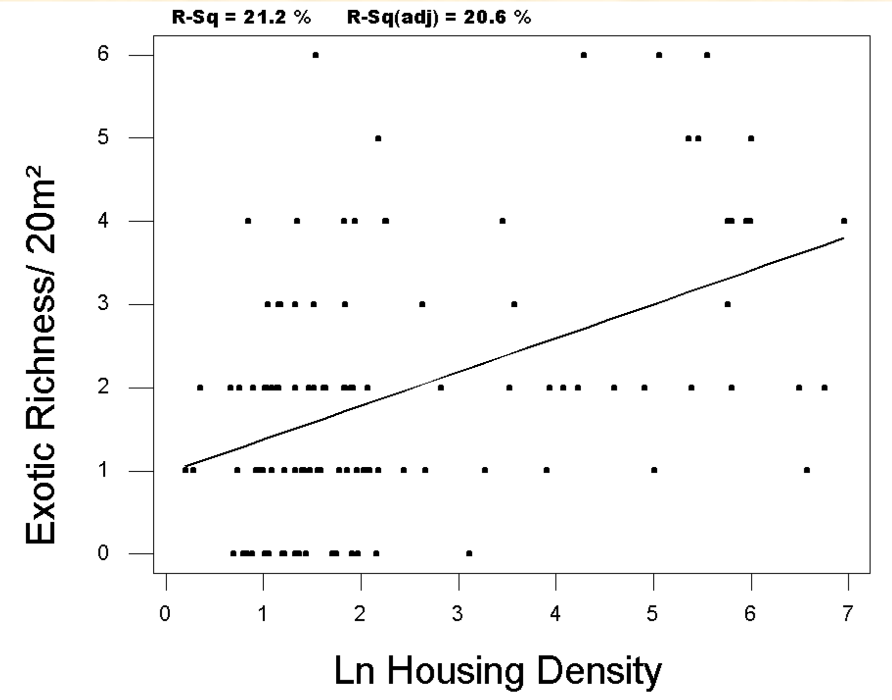
Native Plant colonization

Landscape factors strongly affect the *number* of native species colonizing sites:

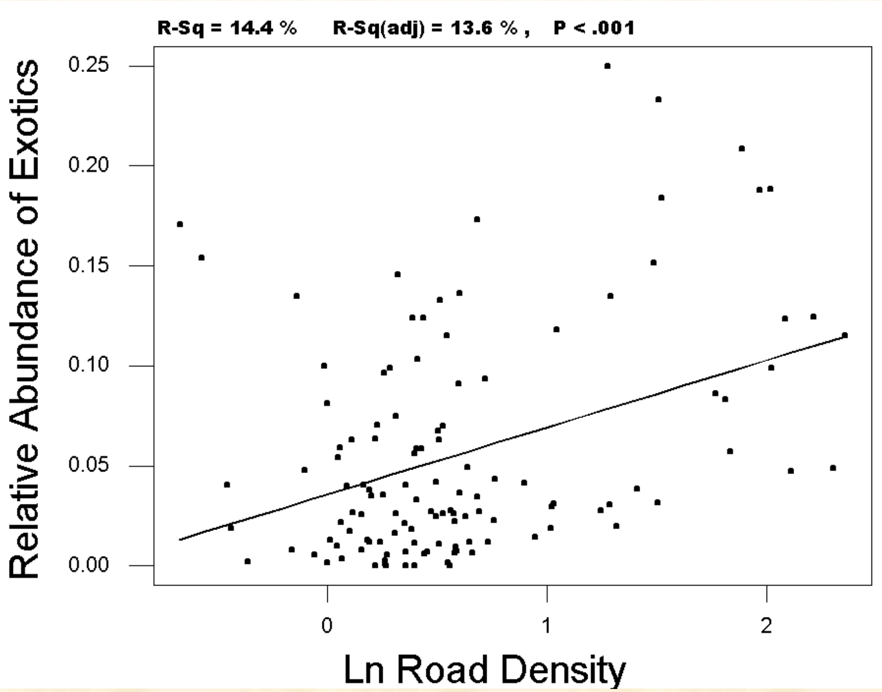
Especially **forest cover** within 5 km

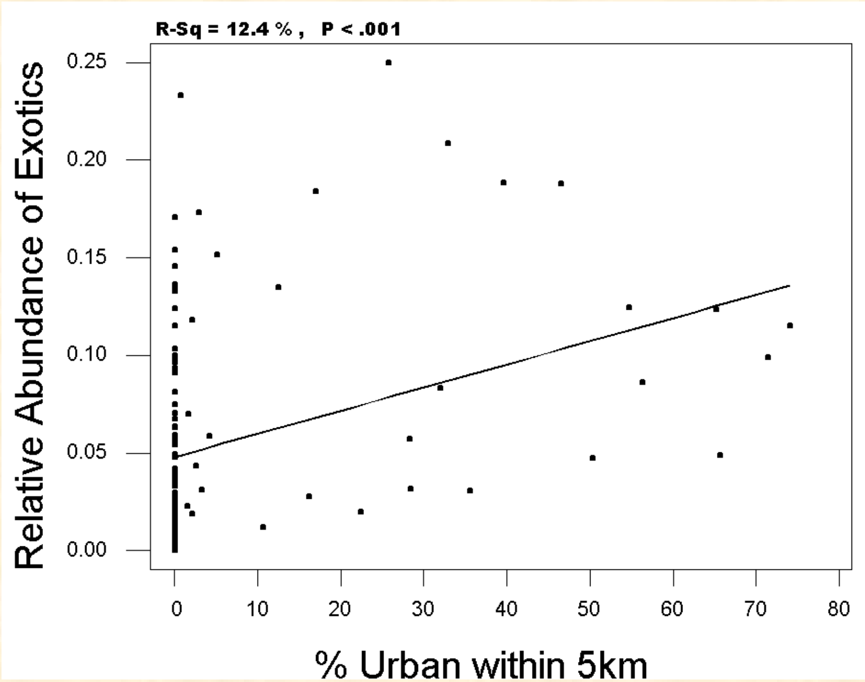


*So **site factors** now appear less important than **landscape effects***



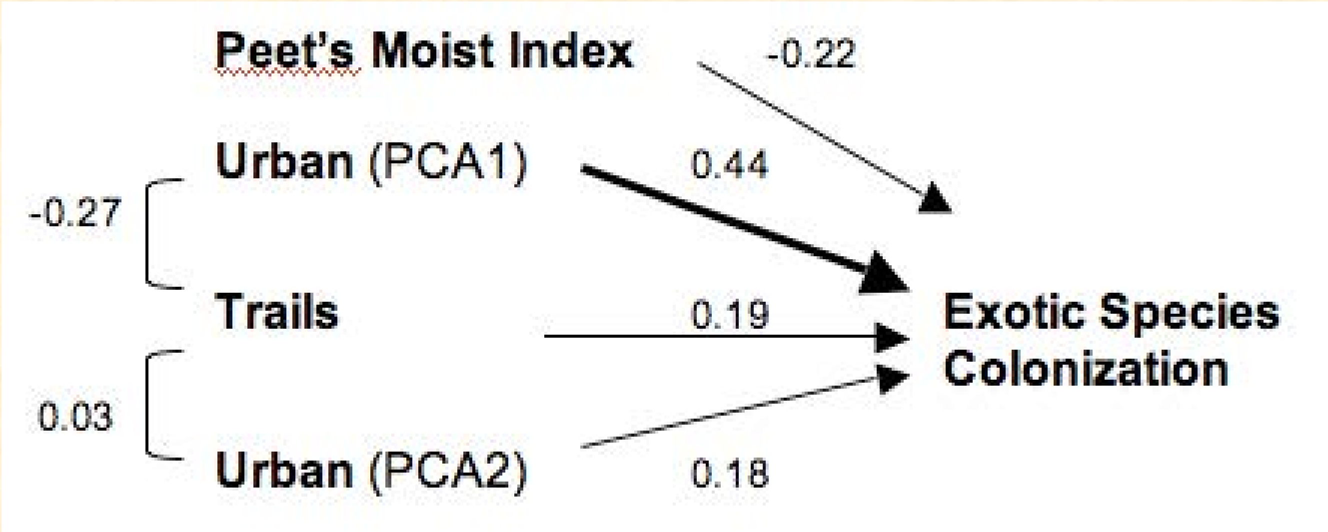
Exotics invading more in forests near urbanized areas





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

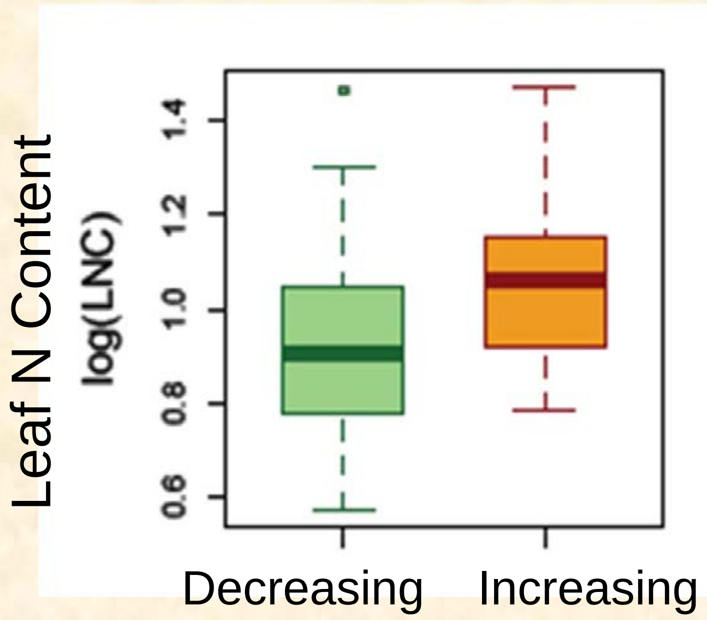
- **Roads**, public **access** and **trails** all contribute to higher exotic richness and abundance
- This suggests that life history traits (e.g. dispersal) may be more important than traits that increase competitive ability in intact forests.
- **Hunting** access decreased exotic invasions. This suggests 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

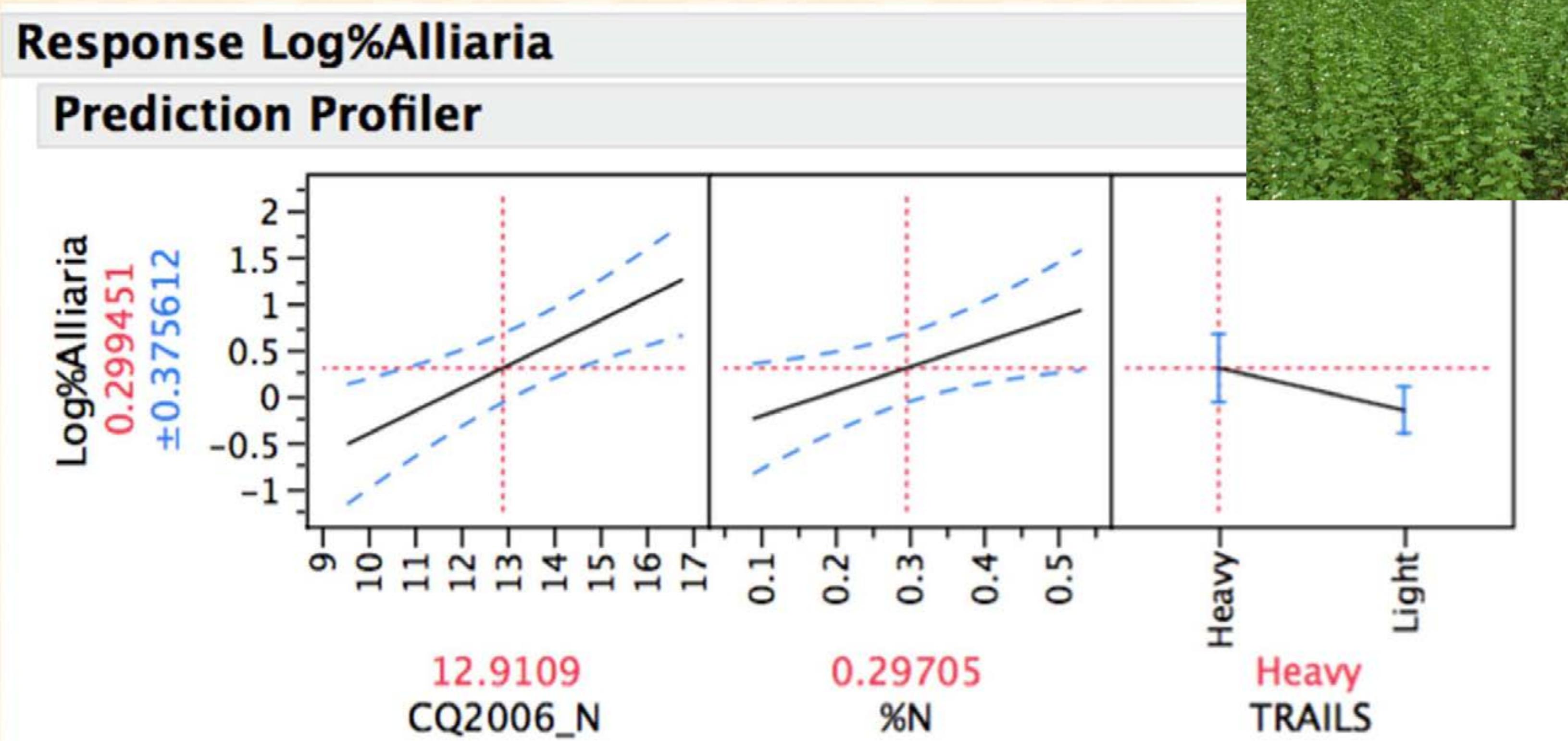
Species with N-rich leaves have increased over the past 50 years.

These include invasive species



Is *Alliaria* invasion associated with N deposition?

YES:



Aerial N deposition Soil Nitrogen

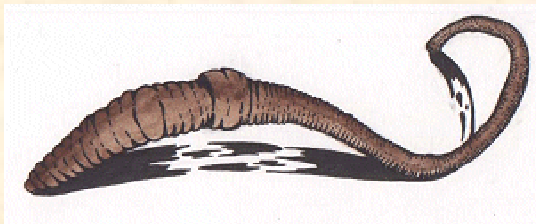
Both soil N and N-deposition favor *Alliaria* invasions

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 . .



Available online at www.sciencedirect.com

ScienceDirect

Forest Ecology and Management 246 (2007) 66–72

Forest Ecology and Management

www.elsevier.com/locate/foreco

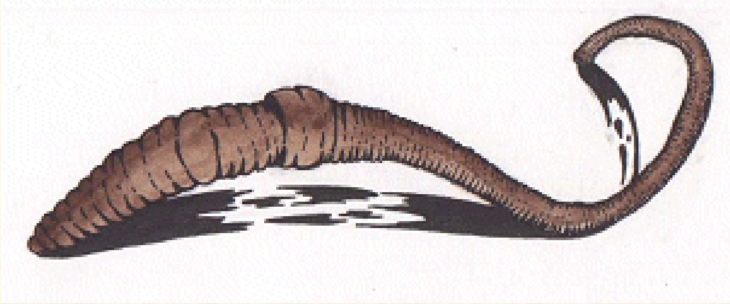
Biodiversity, exotic plant species, and herbivory: The good, the bad, and the ungulate

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)

ELSEVIER

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Do white-tailed deer and the exotic plant, garlic mustard interact to affect the growth and persistence of native forest plants?

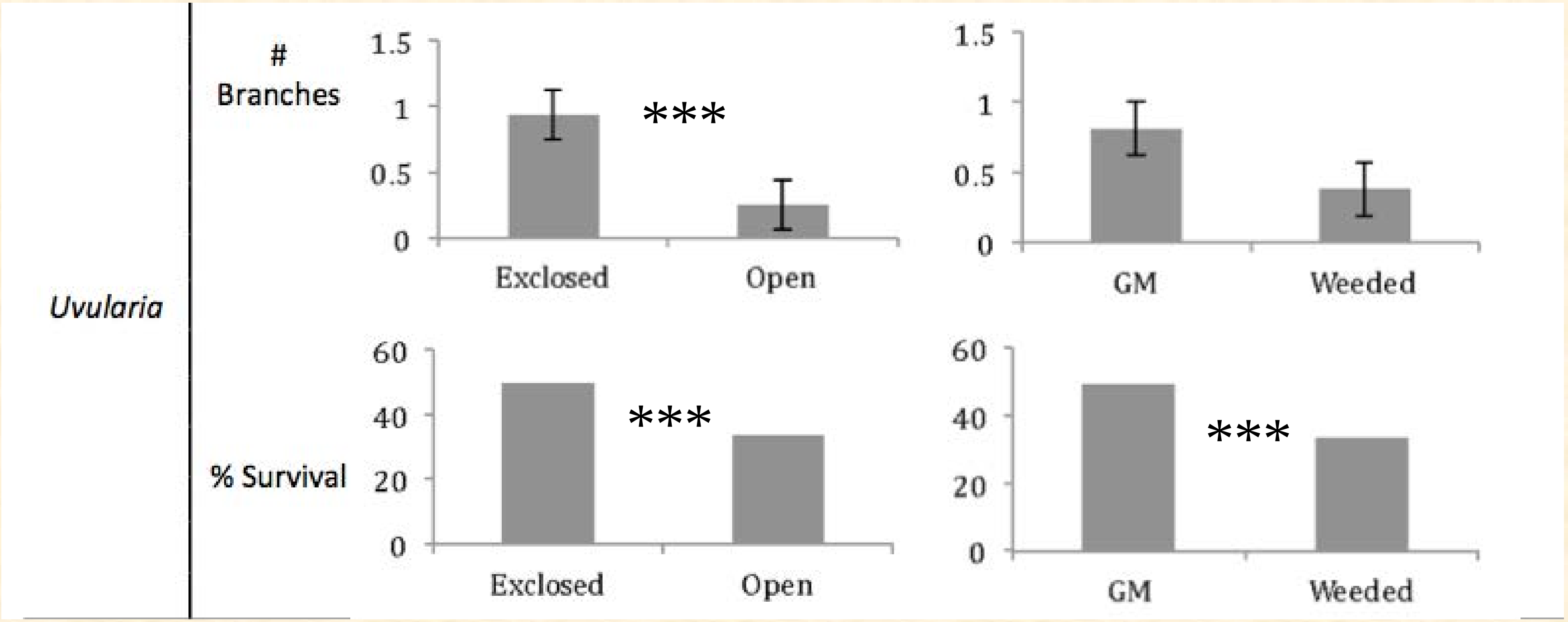
Donald M. Waller*, Lisa I. Maas

Department of Botany, University of Wisconsin-Madison, 430 Lincoln Drive, Madison, WI 53706, United States

Do deer and garlic mustard have **synergistic** effects on native plants?

What affects *Uvularia* growth & survival?

Deer ! *Alliaria* !



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**

✓ oui

?

✓ oui

✓ oui

Invading **exotic species**

Driver or passenger ??

- Species losses &
  Biotic **homogenization**

cause or consequence?

Consequences of invasion?

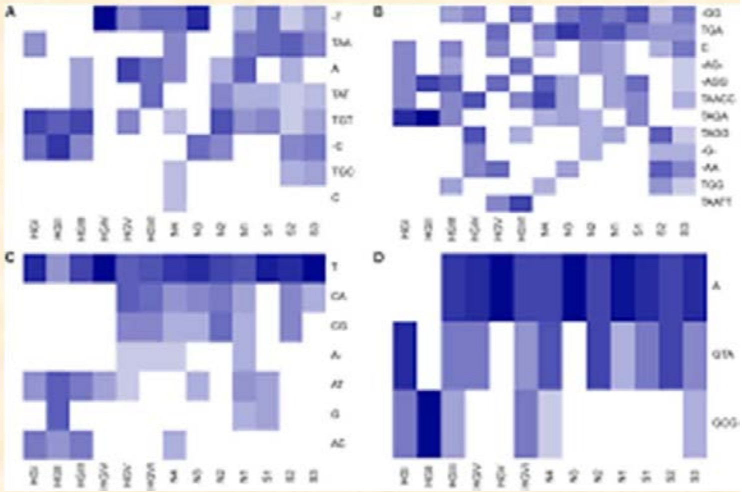
- Coarse & fine-scale associations
  Do associations predict impacts?

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:

$C_{ij\text{-}site} = (r_i - S) * (r_j - S)$ site

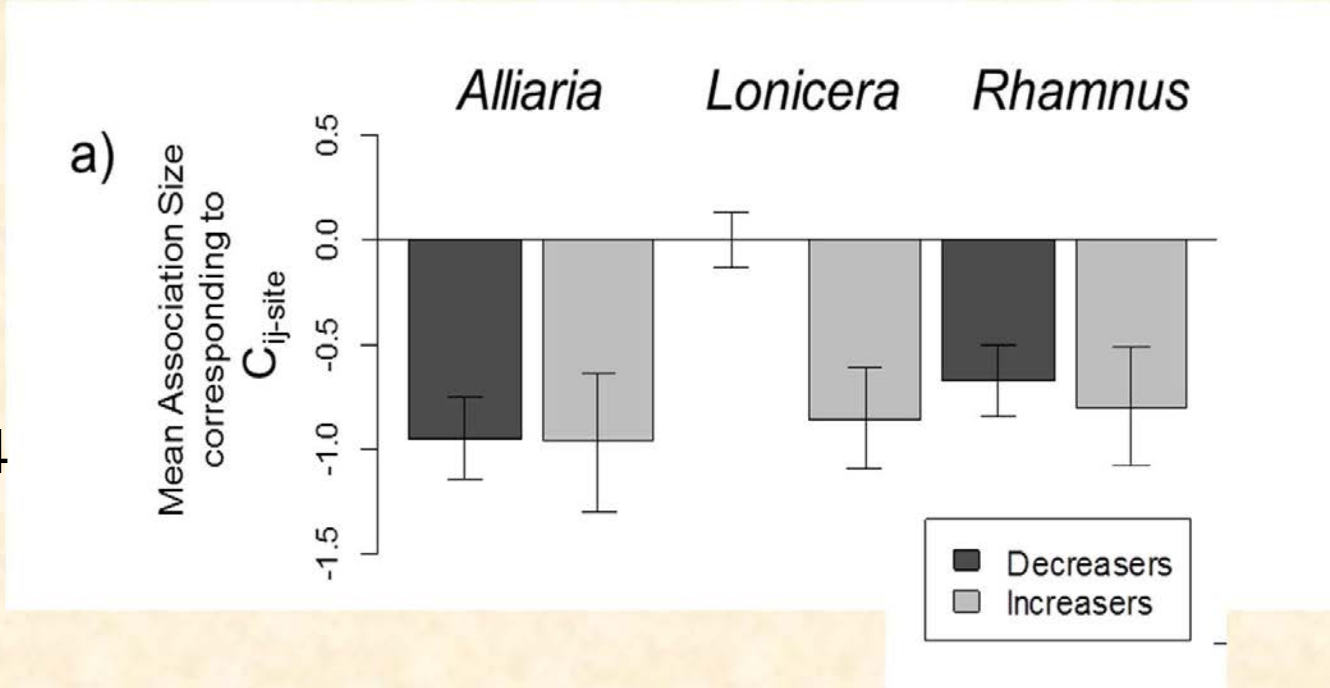
$C_{ijk\text{-}quad} = (q_{ik} - Q_k) * (q_{jk} - Q_k)$ quadrat



- 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

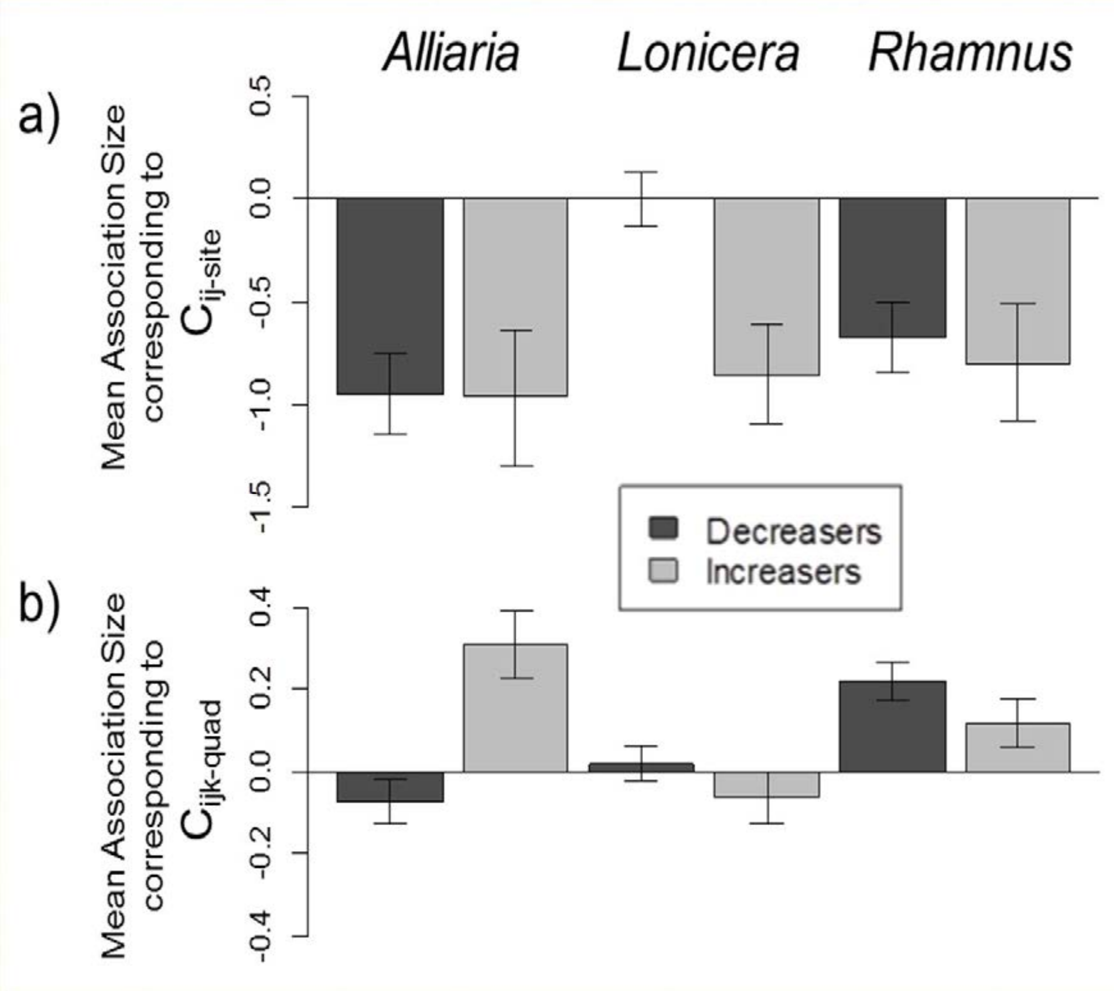
Waller et al. submitted, *Biological Invasions*

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



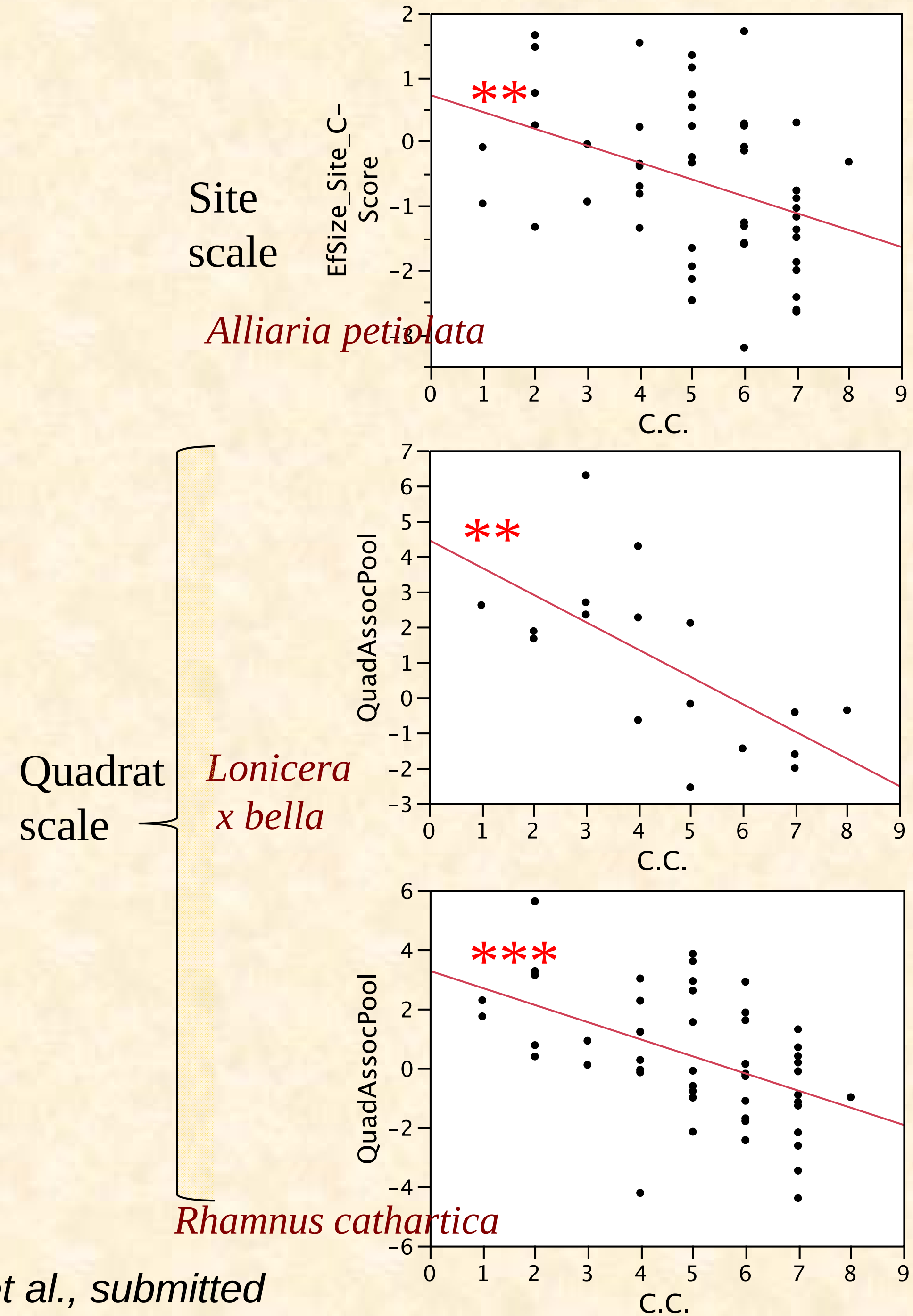
Waller et al., submitted

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*



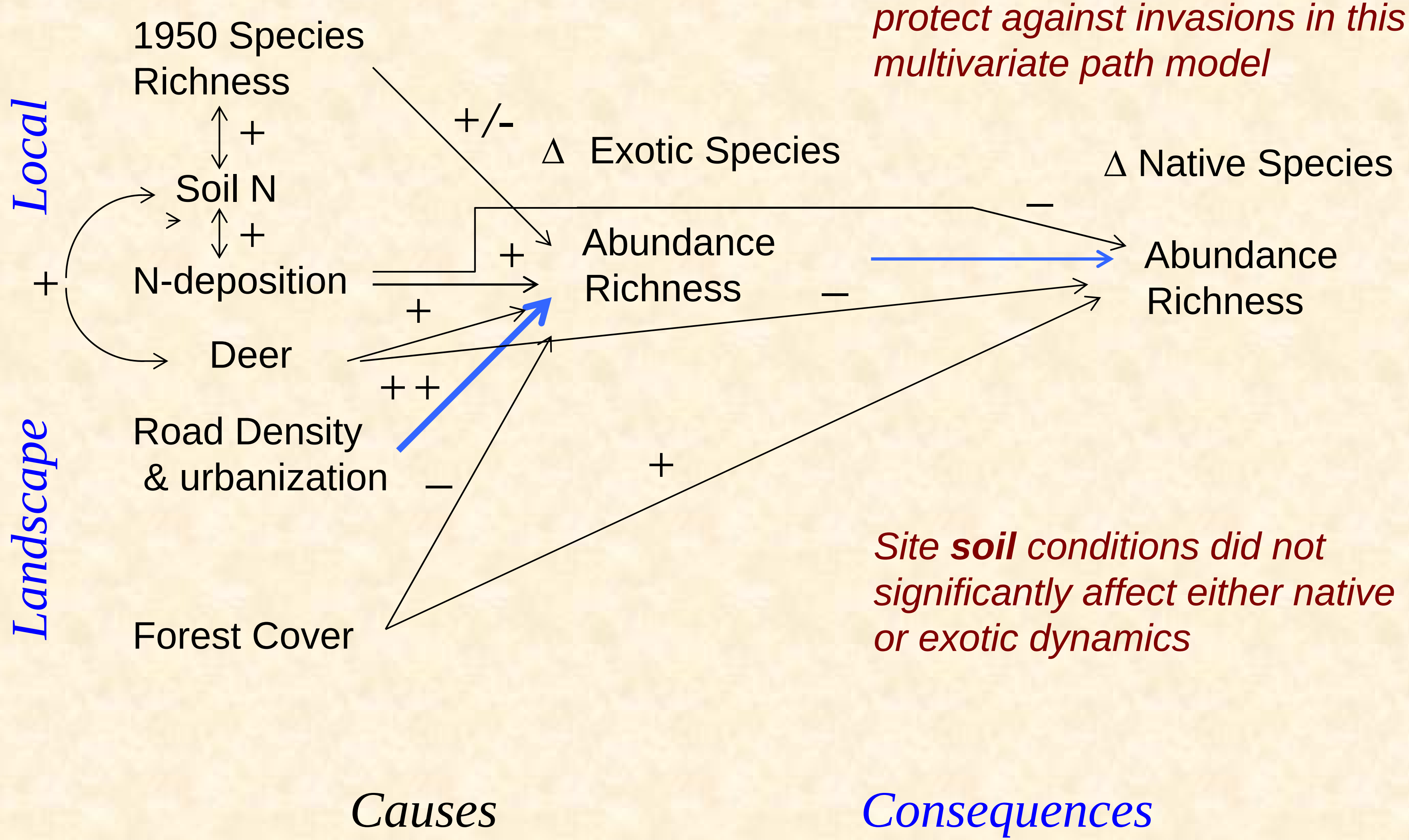
Waller et al., submitted

Conclusions: Causes

- Alein 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*

Conclusions: Consequences

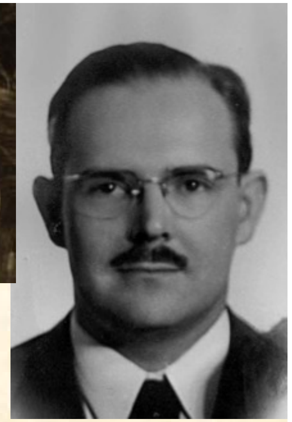
- Invasive species associate both + and – with native species
  - At site level, rarely significant
  - At 1m^2 quadrat level, **+** w. common species, but **–** with rare, declining, specialized species
  - Negative exotic-native associations increase in landscapes with more roads and houses
- Analyzing 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

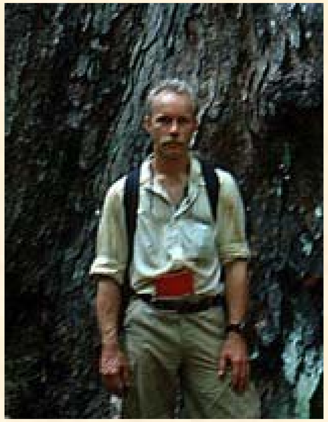
Aldo Leopold



John Curtis

Dave Rogers

Bil Alverson



Shannon Wiegmann

Steve Horn

Sarah Johnson

Erika Mudrak

Plant Ecology Laboratory

Plant Ecology Laboratory University of Wisconsin

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

Ecology Letters, (2006) 9: 912–919 doi: 10.1111/j.1461-0248.2006.00939.x

IDEA AND PERSPECTIVE

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?

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,

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

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. Simberloff

Ecology Letters, (2006) 9: 912–919 doi: 10.1111/j.1461-0248.2006.00939.x

IDEA AND PERSPECTIVE

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

minority of them (Simberloff 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 (Simberloff 2003, 2005).

Stages in invasion

nd definitions.

3/Colonization	4/Naturalization	5/Spread	6/Impact*
Survival of introduced plants	Survival and reproduction enabling pioneer population to be self-sustaining	Dispersal of propagules and spread of populations outside of area where first introduced	Harmful impact of species to ecology and economy
PAB	pAB	PAB	paB
Local	Local	Regional	Local and regional
Yes, but not essential	No	No, but can exacerbate	No
Monitoring, detection and early eradication	Eradication and control of founding population; control of potential dispersal vectors	Dispersal and spread minimization; detection and eradication of satellite populations	Population control; dispersal and spread minimization; impact alleviation

J. A. Catford et al.

Causes of invasion

Consequences of invasion

Evolution of increased competitive ability (EICA)

B. Blossey & R. Nötzold. 1995.

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

From Gurevitch et al. 2011 Ecol Let 14: 407

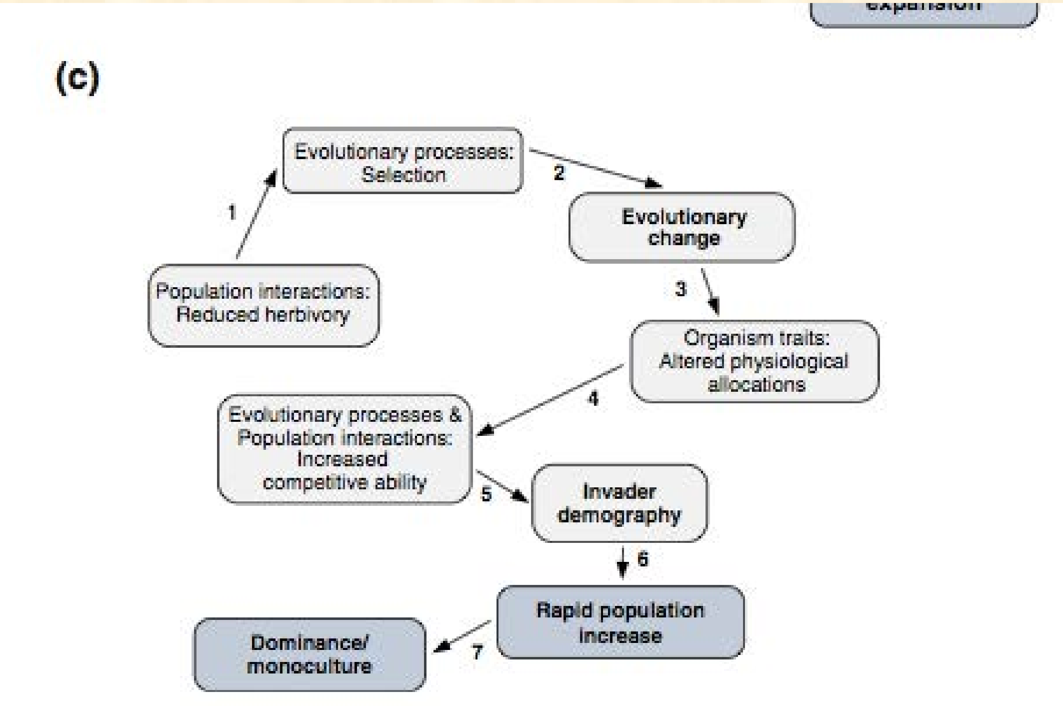


Figure 3 Examples of how the synthetic invasion meta-framework (SIM) might be applied in three hypothetical invasion scenarios. (a) A simple case of enemy escape resulting in an invasion. (b) An example of the ecological and evolutionary components that may be involved in 'propagule pressure' (see text). (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

Diversity and Distributions, (Diversity Distrib.) (2009) **15**, 22–40

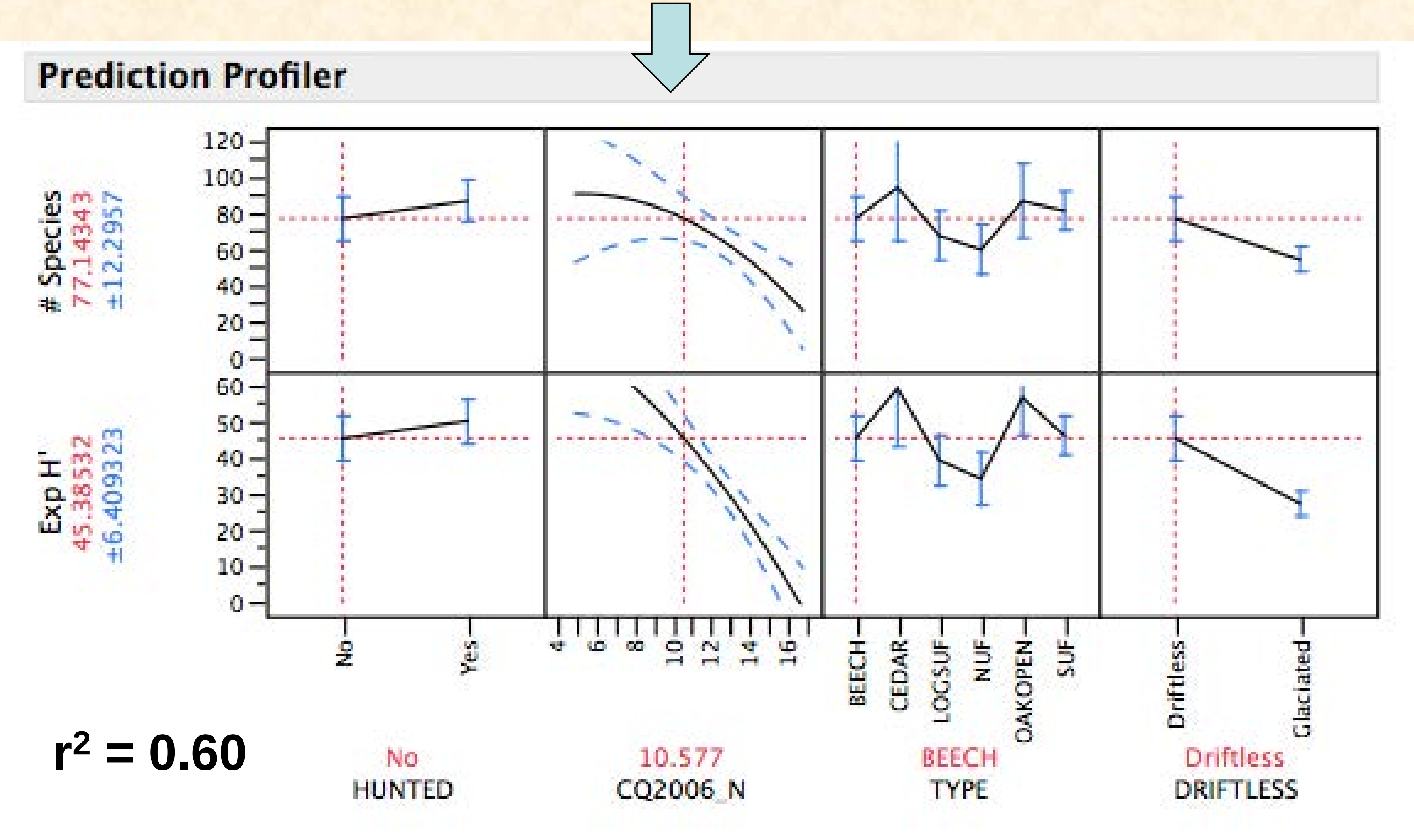
BIODIVERSITY REVIEW

Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework

Jane A. Catford[1]*, Roland Jansson[2] and Christer Nilsson[2]

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