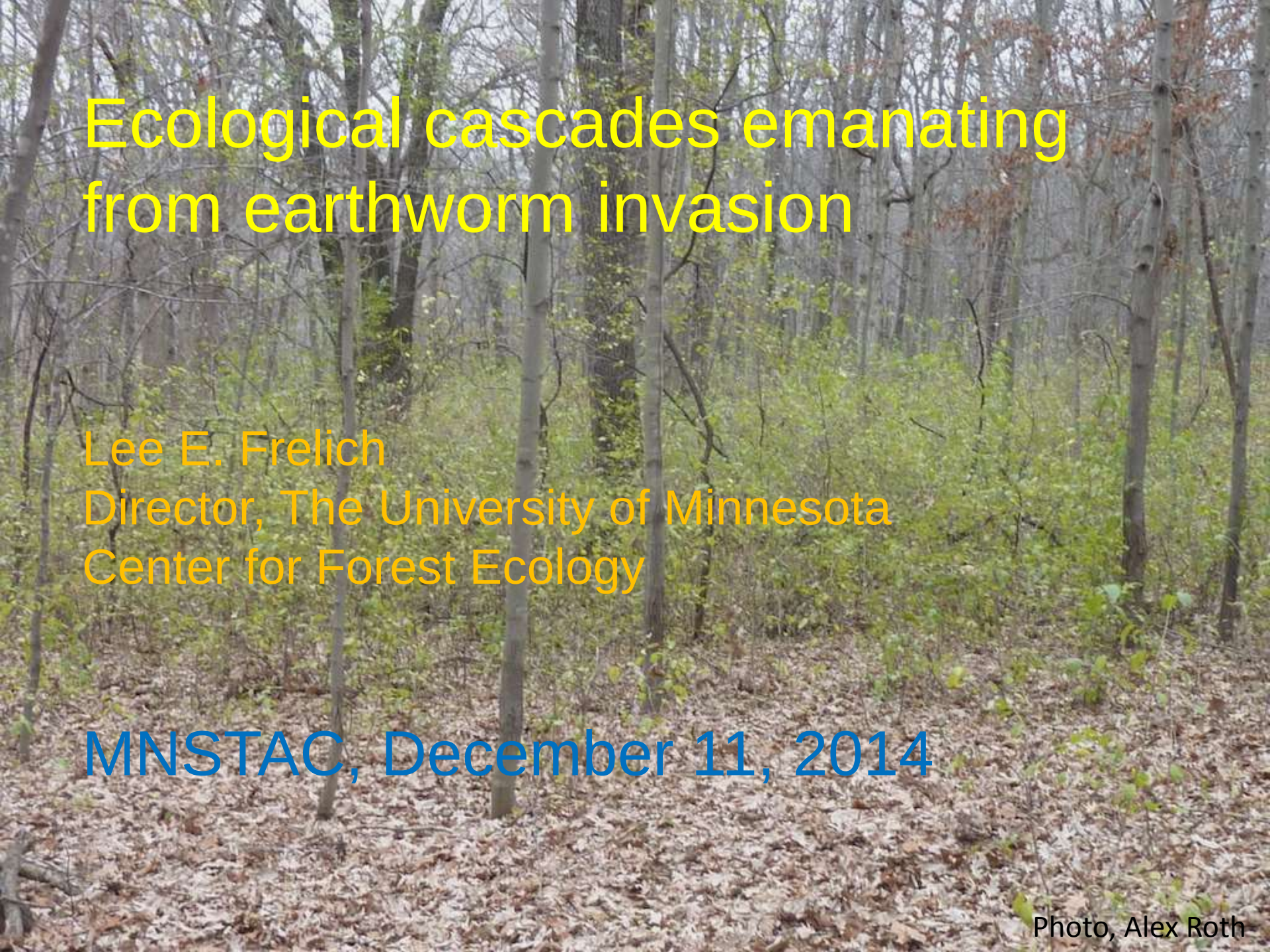


Ecological cascades emanating from earthworm invasion

Lee E. Frelich
Director, The University of Minnesota
Center for Forest Ecology

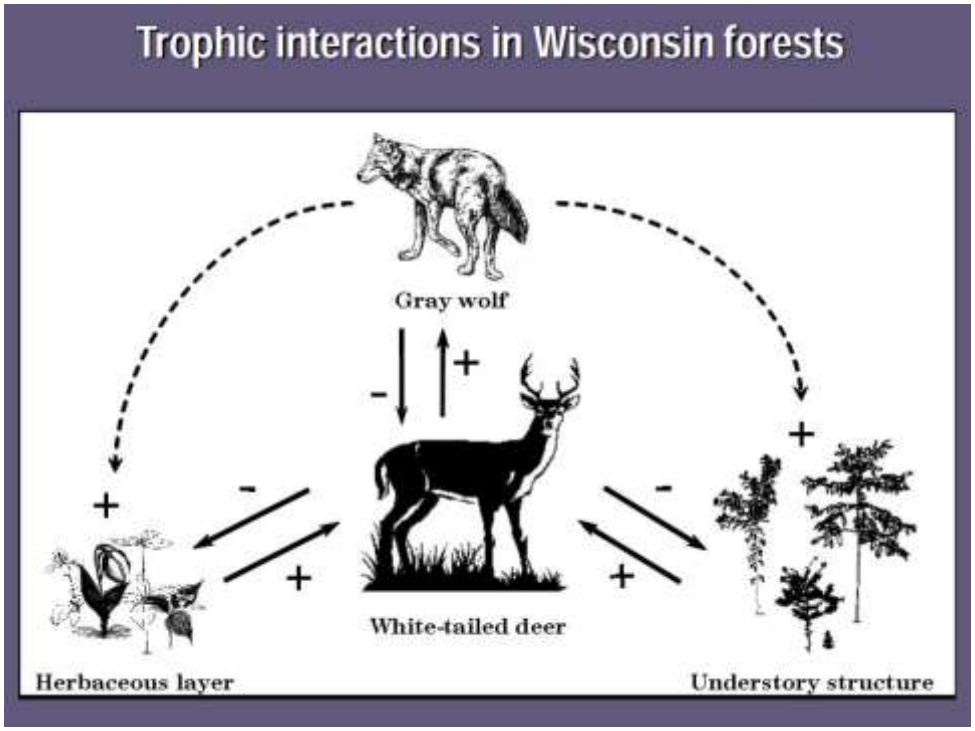
MNSTAC, December 11, 2014

Photo, Alex Roth

Earthworm invasion is a lens through which to view ecological theories on trophic cascades, ecological cascade effects, and biological invasion

- Trophic cascade: predator-prey (including herbivore) effects; top down or bottom up through predator or producer changes
- Ecological cascade effect: broader term for many types of changes that propagate through an ecosystem

Trophic cascades thought to be strong in aquatic systems and terrestrial systems with simple food webs

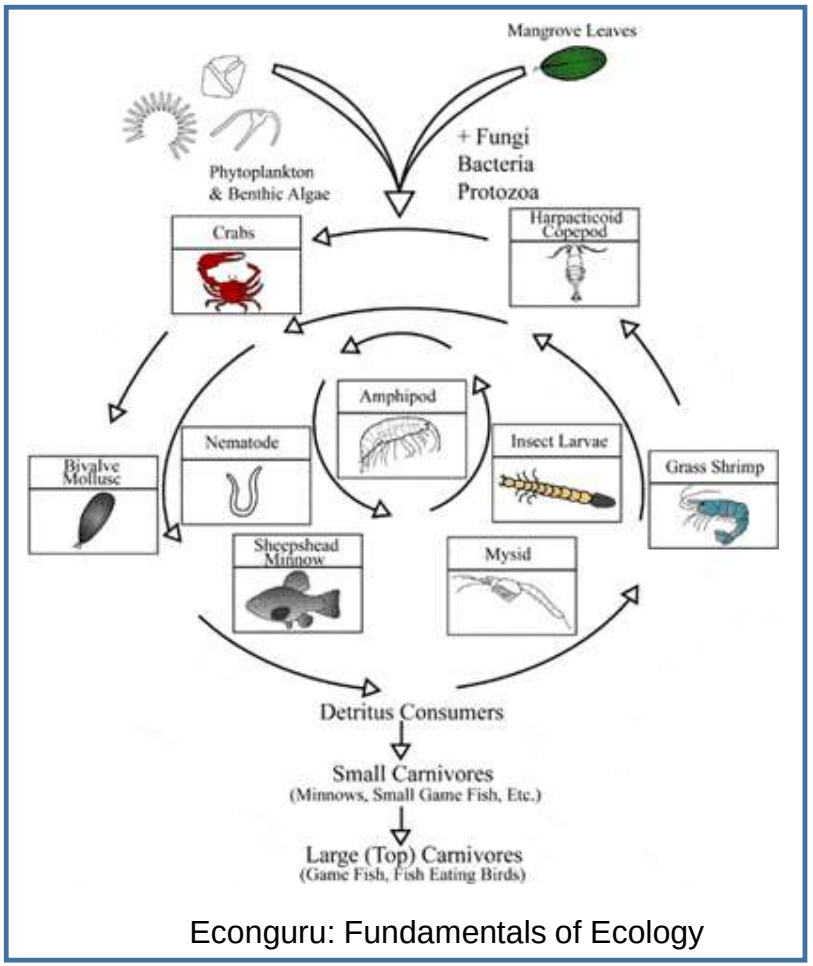


Callan, Nibbelink, Rooney, Wiedenhoeft, and Wydeven. 2013. *J. Ecol* 101: 837-845.

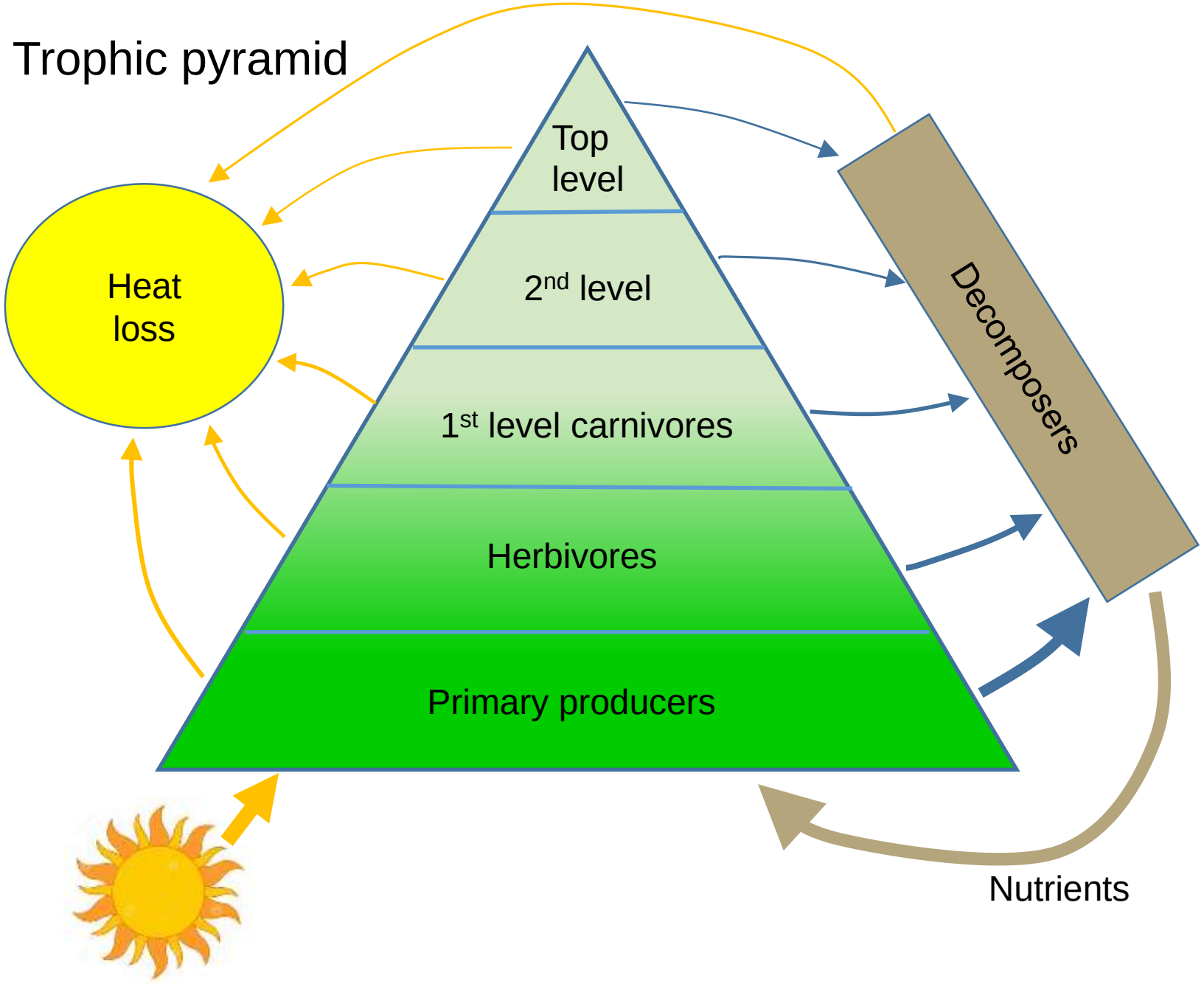
Trophic level—what does it mean for earthworms? Where are detritivores in most trophic pyramids?

What has been studied:

- So-called brown-field tropic cascades based on dung and its decomposers
- Falling detritus consumed at various depths and lake or ocean bottom



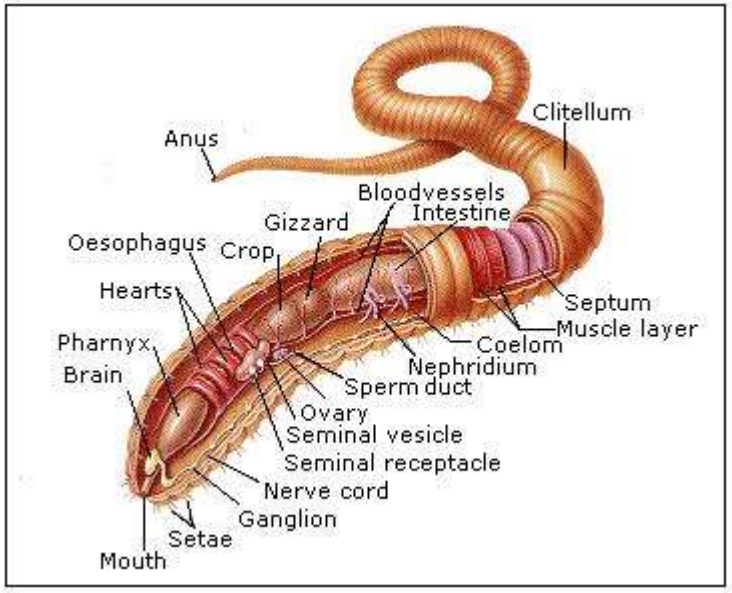
Econguru: Fundamentals of Ecology


Trophic pyramid
Heat loss
Top level
2nd level
1st level carnivores
Herbivores
Primary producers
Decomposers
Nutrients

Earthworms are:

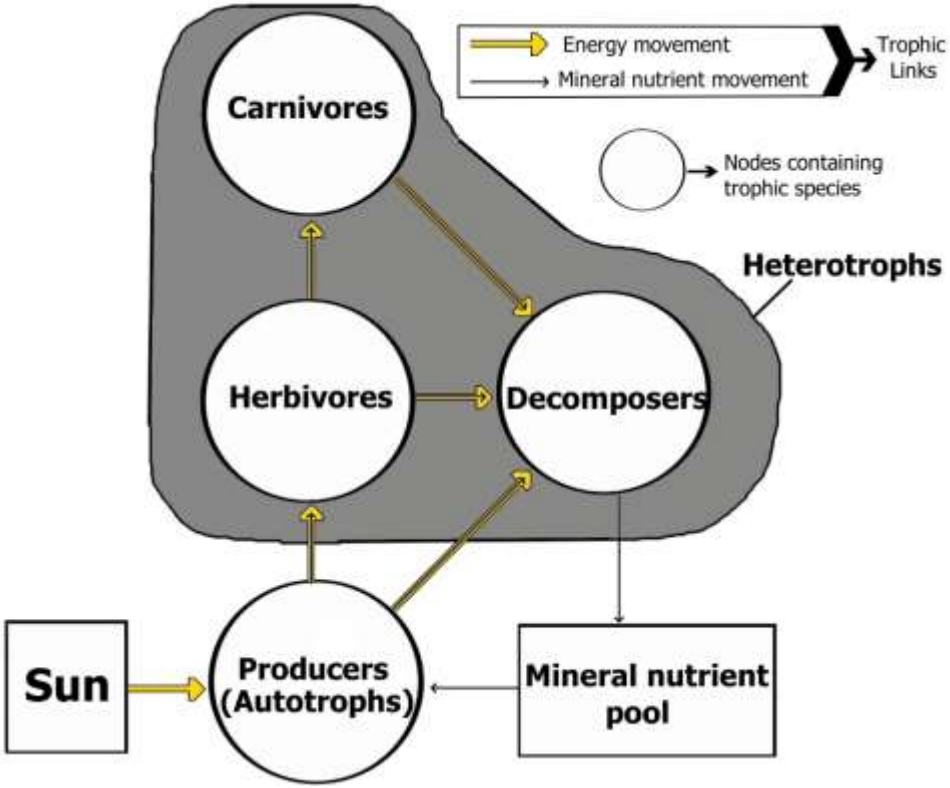
- Macrofauna decomposers
- Mobile hot spots for microbial decomposers within, as well as influencing other decomposers—microbial biomass and function

We commonly think about removing predators at top of the pyramid or changing growth of primary producers—but not so much about sideways entrance into the pyramid through a decomposer pathway



What happens when we step on the gas pedal that controls rate of decomposition?

Earthworms provide that experiment on a grand scale!



From Wikipedia

Earthworms are also engineers that alter energy flow, but also physical environment within the soil (density, temp, H_2O, nutrients)

Earthworms eat the habitats of other species

What trophic and ecological cascade effects will this combination of many types of change cause?

Earthworm functional groups

Epigeic: *Dendrobaena octaedra*

Anecic: *Lumbricus terrestris* (nightcrawler)

Epi-endogeic: *Lumbricus rubellus*

Endogeic: *Aporrectodea caliginosa*

Earthworm functional group—fundamental engineering effects

Epi-endogeic and epigeic (*L. rubellus, Dendrobaena, Dendrodrillus*)
Speed up litter decay—loss of litter habitat, loss of physical effects of litter, loss of water absorption capacity, insulation of soil temperatures

Endogeic—(*Aporrectodea rosea*, *caliginosa*, *longa*, *trapezoides*, *Allobophora chlorotica*, *Octolasion cynaeum,* O. octaedra); loss of litter, compact soil, integrate OM into thick black A horizon, leaching, soil mineralogy effects leading to effects on N, P, K, Ca, Mg availability

Anecic—*L. terrestris*. Eat fresh litter, maintain bare soil, predator on seedlings

Sampling earthworms in the field

Photos: Alex Roth

Five stages of invasion

Stage 1
Worm free

Stage 2
Epigeic only

Stage 3
Endogeic and epi-endogeic invade

Stage 4
Increasing Biomass and a few *L. terrestris*

Stage 5
High biomass,
L. terrestris dominated

Loss, Hueffmeier, Frelich, Host, Sjerven and Hale. 2013
Natural Areas Journal
33: 21-30

Stage 2, *Dendrobaena* only

Stage 3, + *Aporrectodea ssp.* and *L. rubellus*

Stage 5, + *L. terrestris*

2000

2010

Soil cores from the same location in 2000 and 2010…

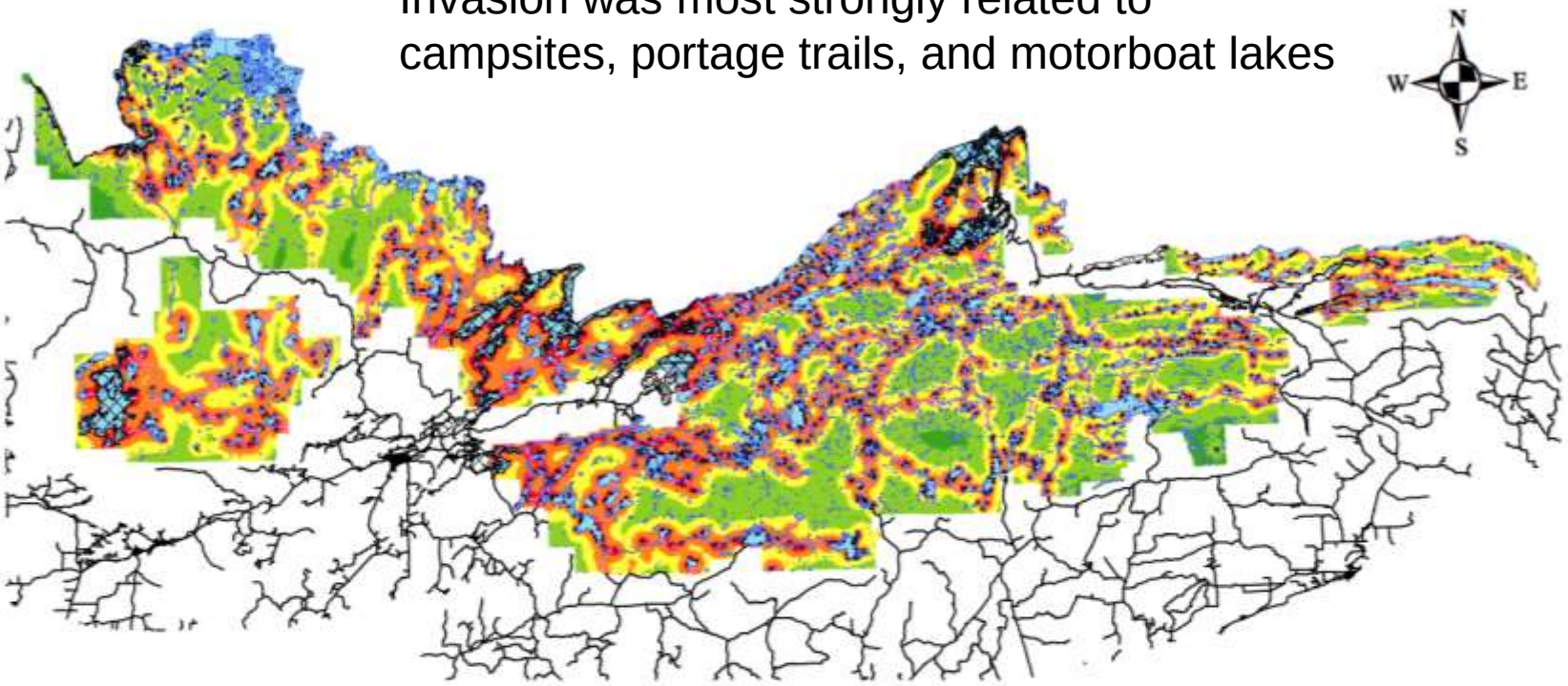
note color change and reduction in thickness of organic horizon

Photos: Dave Hansen and George Schlaghamersky

Base of balsam fir, stage 5 earthworm invasion, and European earthworms in the BWCAW. Photos: Doug Wallace, David Chaffin

Plant community and native species

Invasion was most strongly related to campsites, portage trails, and motorboat lakes



BWCAWOnlyCampsites
merged_rds_win_20k_BWCAW
PortageTrailsOnly
MotorLakes
BWCAWLakes
fullwpmap5

IERAT Rank
1
2
3
4
5

Extent And Pattern Of Invasion By Earthworms In The BWCAW

0 15 30 60 Kilometers

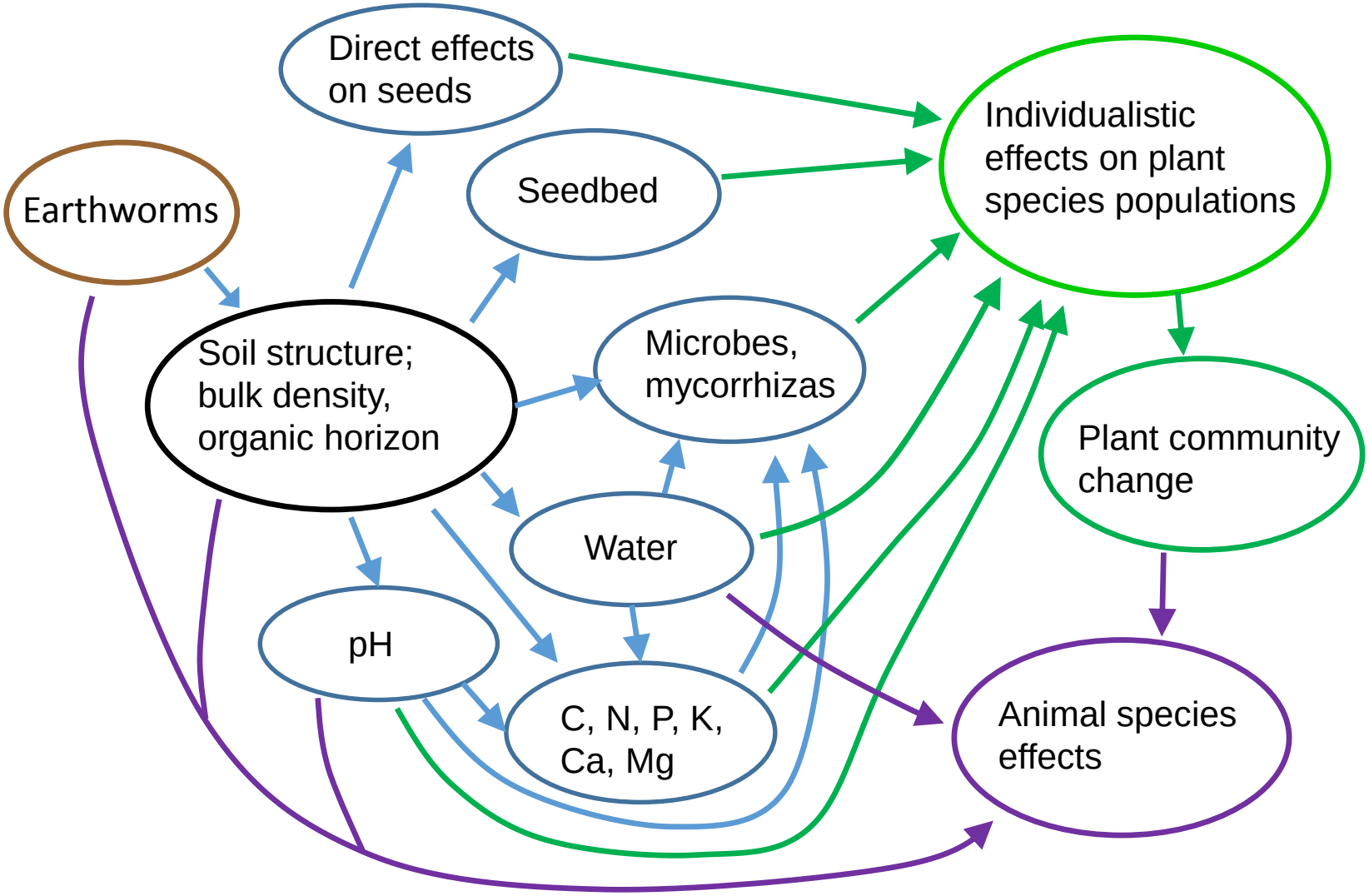
Map by David Chaffin

How earthworm invasion affects the environment

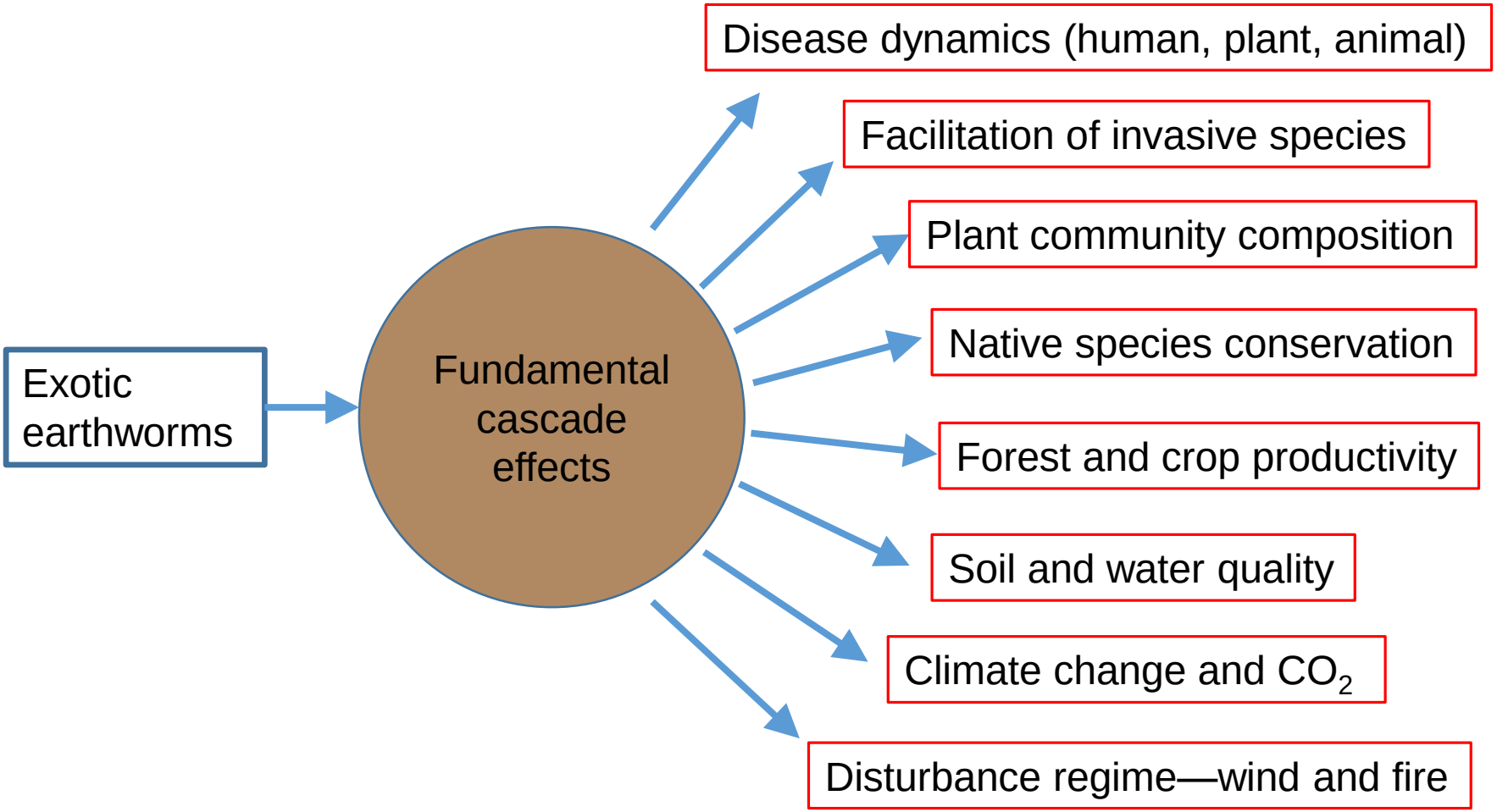
Micro cascades—small-scale ecosystem processes that are related to fundamental engineering effects, e.g. loss of O horizon, soil BD, water, temperature and nutrient cycles

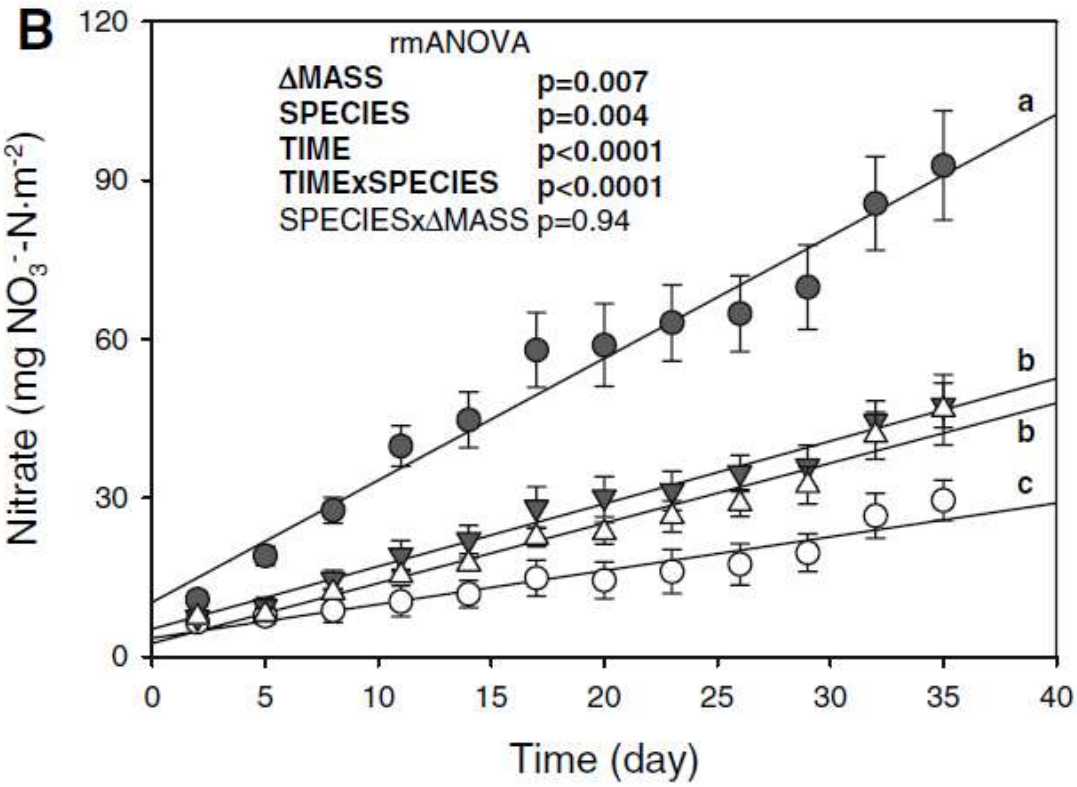
Macro cascades—extended ecological cascade effects and trophic changes of concern to human society at large spatial extents

The complex of micro cascades leading to fundamental effects on soils (blue arrows), and secondary/tertiary effects on plants (green arrows), and animals (purple arrows)



Earthworm macro-cascade effects of concern to human society





Nitrate leaching rates in riparian forest, northern WI

- *A. caliginosa*
- *L. terrestris*
- *L. rubellus*
- none

Oecologia (2008) 158:499–510
DOI 10.1007/s00442-008-1149-0

ECOSYSTEM ECOLOGY - ORIGINAL PAPER

Non-native earthworms in riparian soils increase nitrogen flux into adjacent aquatic ecosystems

David M. Costello · Gary A. Lamberti

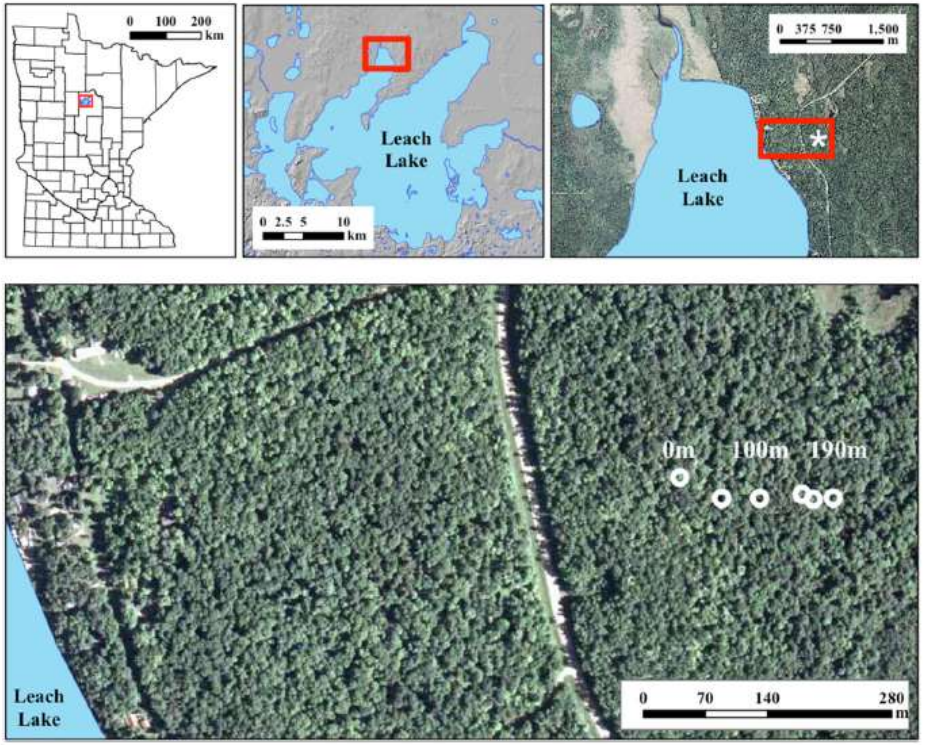
Soil and water quality

Ecosystems
DOI: 10.1007/s10021-014-9814-0

ECOSYSTEMS

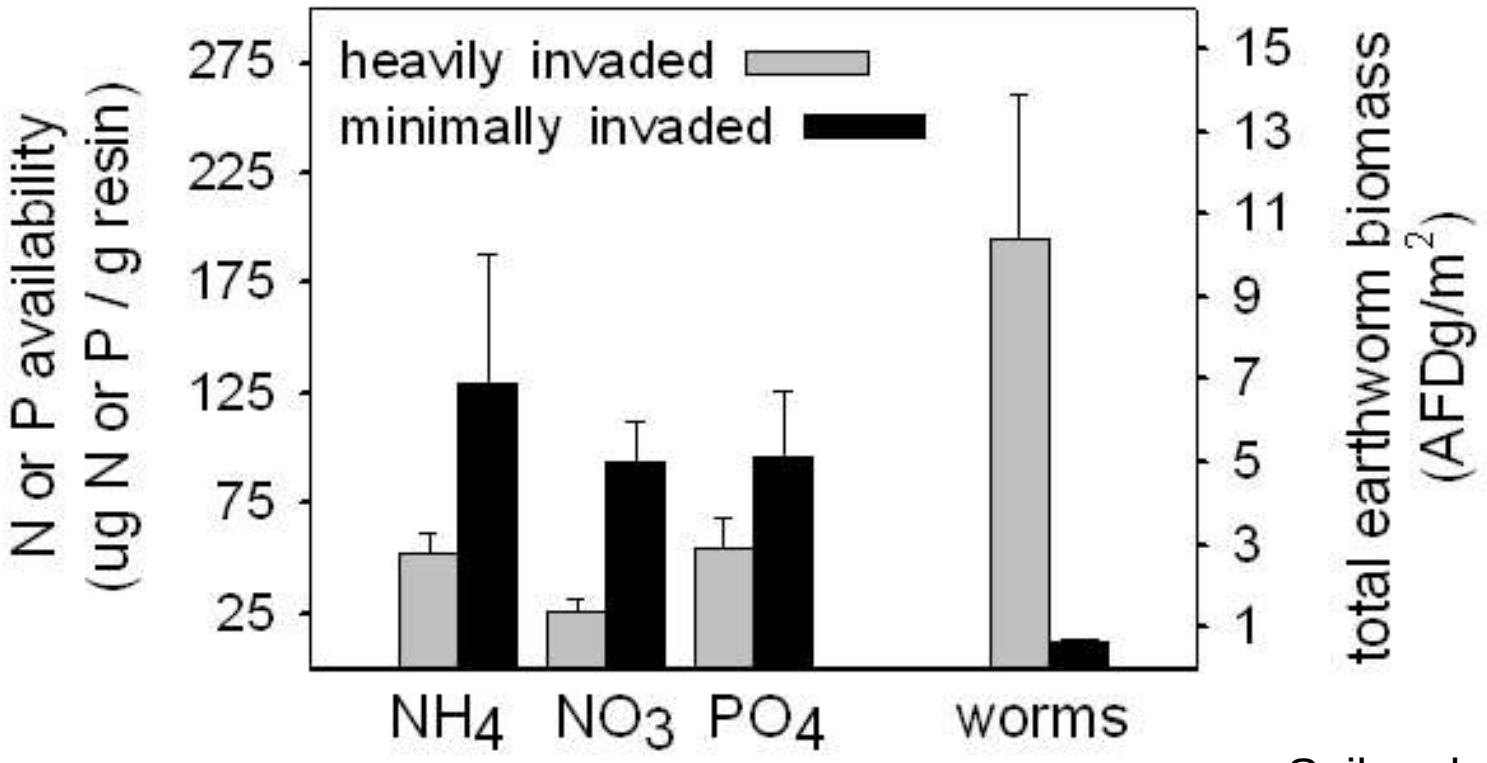
Invasive Earthworms Deplete Key Soil Inorganic Nutrients (Ca, Mg, K, and P) in a Northern Hardwood Forest

Kit Resner,[1] Kyungsoo Yoo,[1]* Stephen D. Sebestyen,[2] Anthony Aufdenkampe,[3] Cindy Hale,[4] Amy Lyttle,[1] and Alex Blum[5]



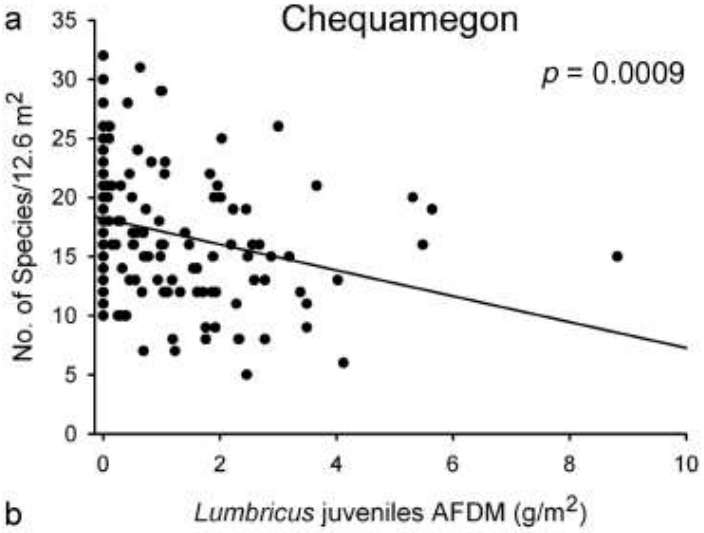
Soil and water quality

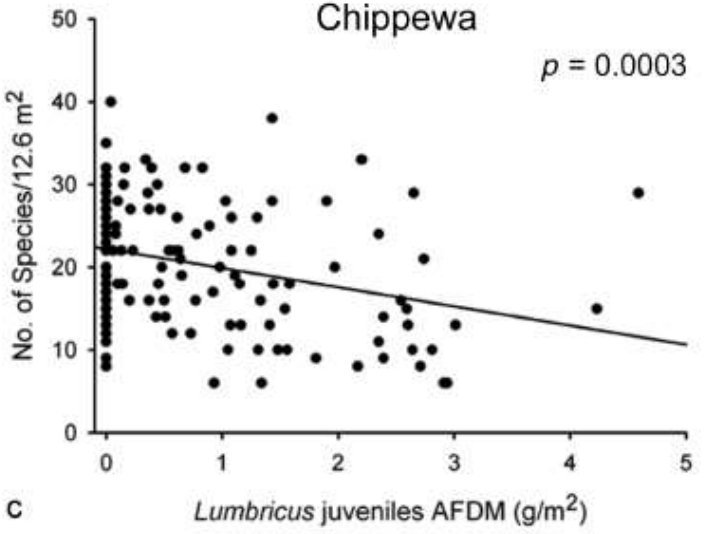
Availability of N and P is reduced, and bulk density INCREASED when earthworms invade forest soils. (Hale, Frelich, Reich and Pastor, *Ecosystems*, 2005)



Negative impacts on native plant species richness

(Holdsworth, Frelich and Reich, *Conservation Biology*, 2007)





Plant community and native species

Effects on seeds

- Burial
- Decrease viability (small seeds if ingested)
- Change fungal environment (orchids, mycorrhizae, sugar maple)
- Change seedbed structure to favor small seeded species

Example:

Goodyera pubescens—McCormick et al 2008, Seeds cast into lower soil layers, some no longer viable, and *Tulasnella* fungus needed for symbiotic relationship negatively impacted by lack of O horizon

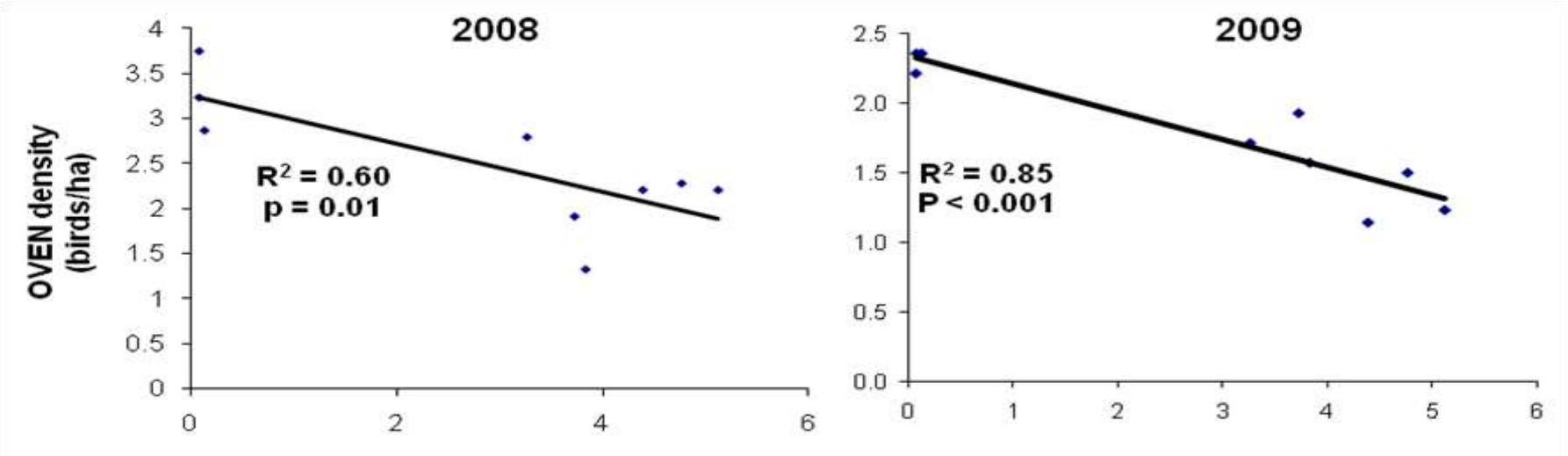
Plant community and native species

Botrychium mormo affected by earthworm invasion

L. rubellus was associated with extirpation of the plant for a survey of 28 sites on Chippewa NF, MN.
Gundale 2002, Conservation Biology 16: 1555-1561

Plant community and native species

Negative relationship between Ovenbird nest density on study sites in the Chequamegon National Forest, WI.



Conservation Biology

Contributed Paper

Reduced Density and Nest Survival of Ground-Nesting Songbirds Relative to Earthworm Invasions in Northern Hardwood Forests

SCOTT R. LOSS* AND ROBERT B. BLAIR†

*Conservation Biology Graduate Program, University of Minnesota, 1980 Folwell Avenue, St. Paul, MN 55108, U.S.A., email lossx004@umn.edu

Plant community and native species

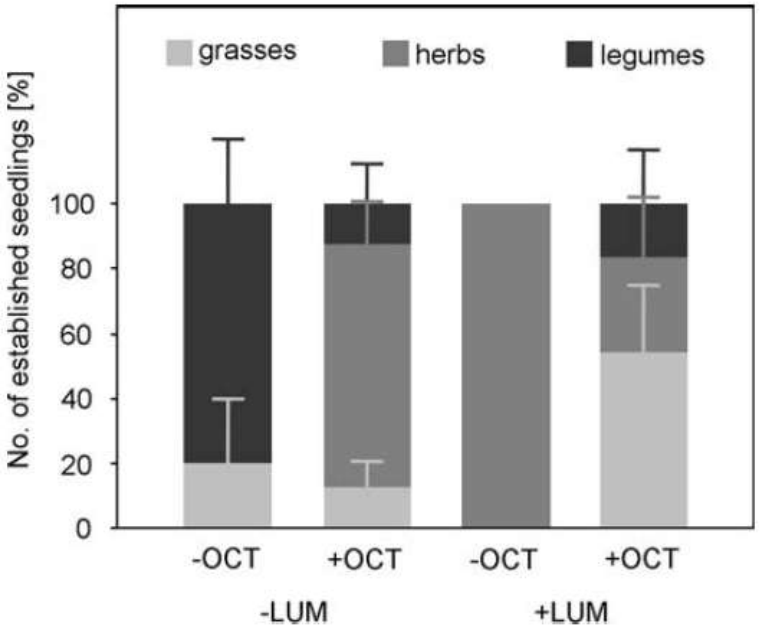
Ecosystems (2009) 12: 1008–1016
DOI: 10.1007/s10021-009-9275-z

ECOSYSTEMS

Exotic Ecosystem Engineers Change the Emergence of Plants from the Seed Bank of a Deciduous Forest

Nico Eisenhauer,[1,4]* Daniela Straube,[1] Edward A. Johnson,[2,3] Dennis Parkinson,[2] and Stefan Scheu[1,4]

Seed emergence experiment: With endogeic and anecic earthworms both present graminoids are favored

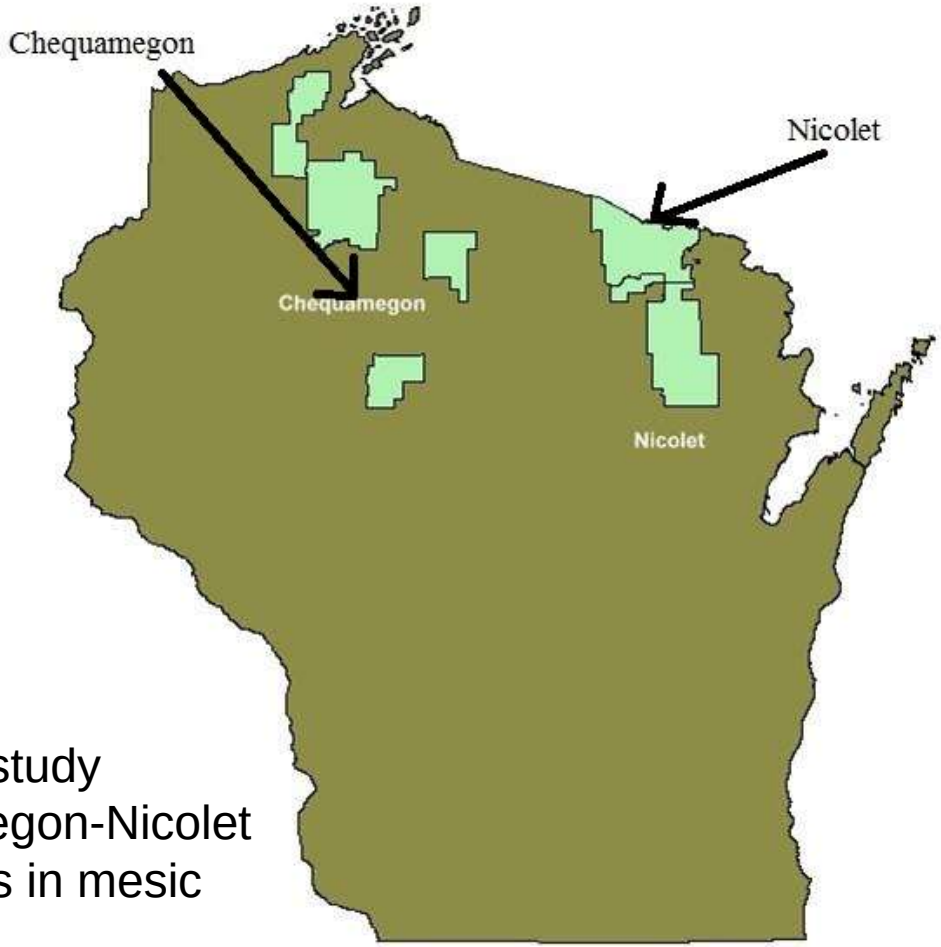


Plant community and native species

Wild ginger— *Asarum canadense*, root system exposed by earthworm invasion

Photo: Nick Fisichelli

Study Area



Paul Ojanen study on Chequamegon-Nicolet NF—106 sites in mesic maple forest.

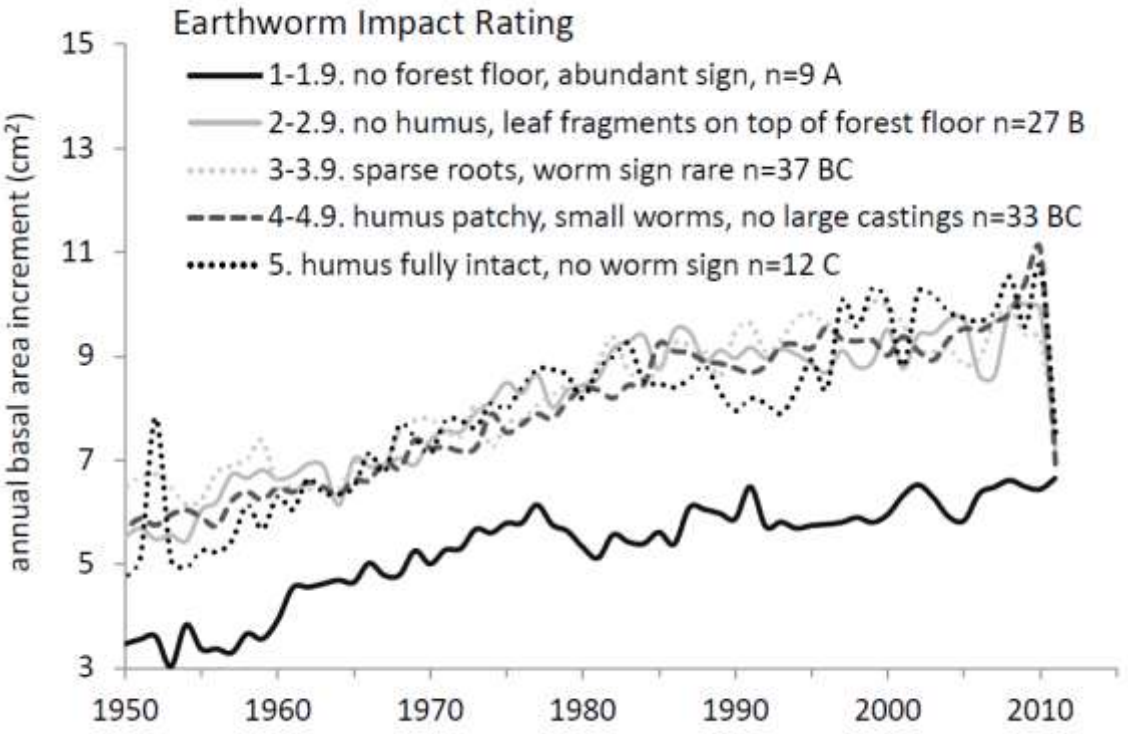
Multiple Response Permutation Procedure

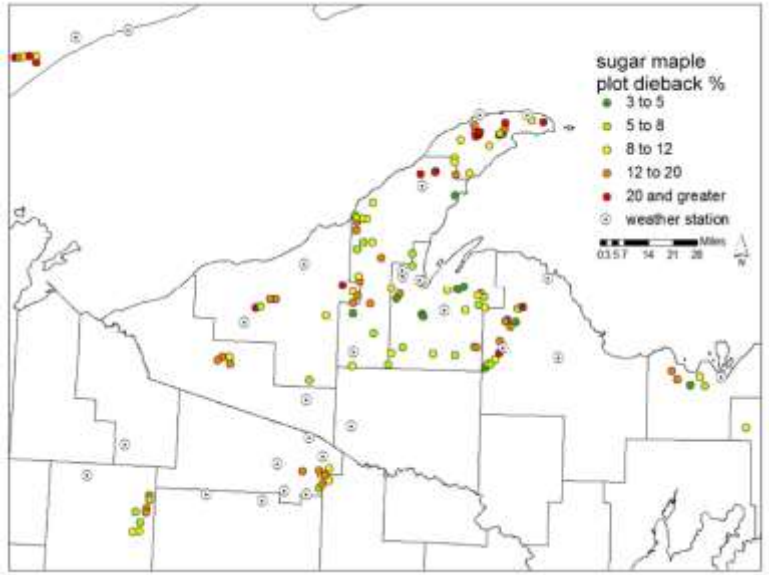
- A = 0.36175172: A value greater than .3 considered very high. McCune and Grace 2002.
- T = -22.995489
- Meaning: The two plant communities are highly separated in composition

Implications

- Seedling and sapling stages of current canopy species are reduced or sometimes nearly non-existent.

Figure 1.1. Sugar maple crown dieback in Keweenaw County, MI, 2009. Photo by Tara Bal





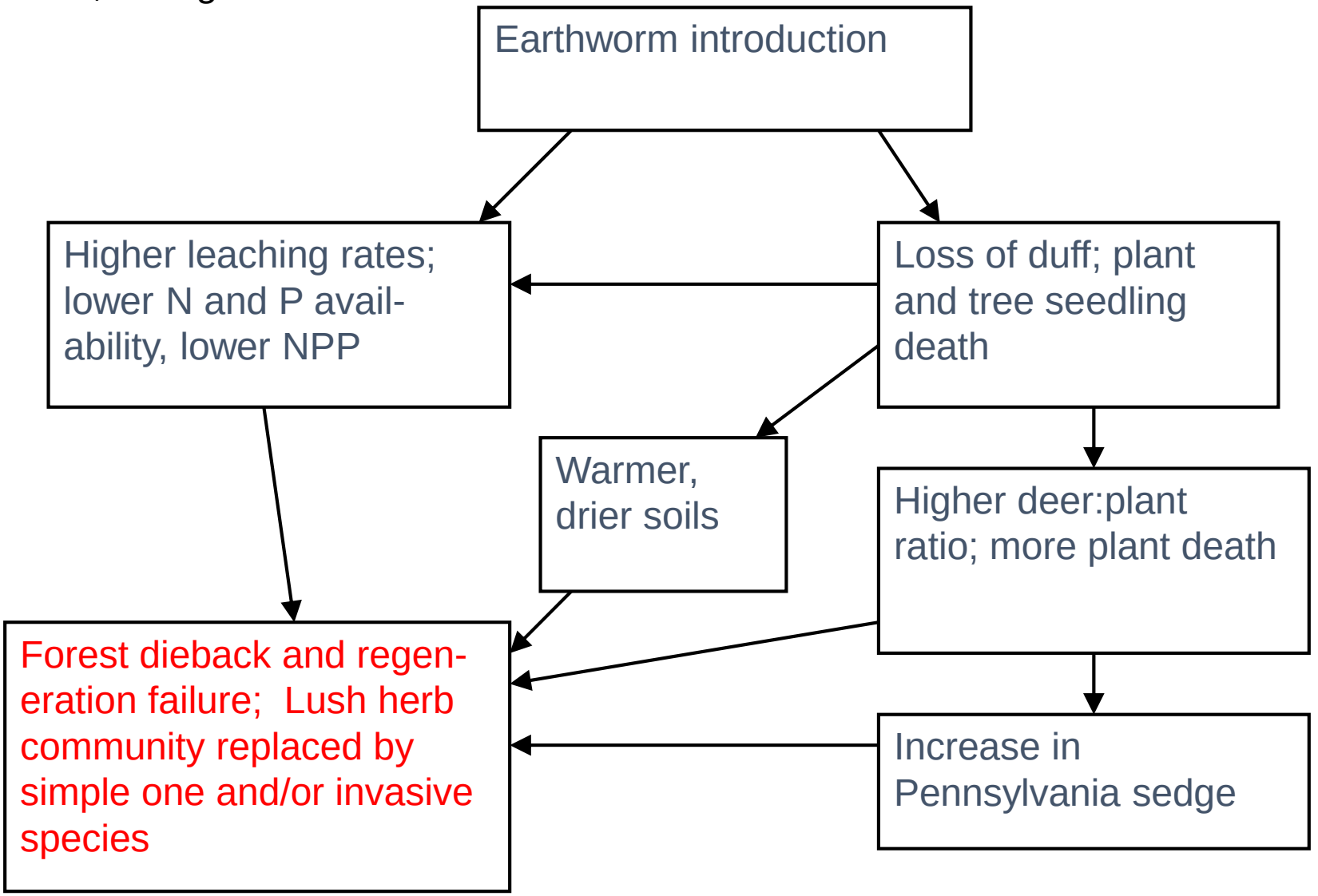
Earthworms were the most significant factor in sugar maple dieback in a study of 120 plots in MI, WI, and MN

Tara Bal, PhD Thesis, Michigan Tech, 2013

Forest and crop productivity

Forest Decline Syndrome caused by earthworm invasion

After Frelich, Hale, Scheu, Holdsworth, Heneghan, Bohlen and Reich, 2006, *Biological Invasions*



Facilitation of non-native plants in North America is huge, with good evidence from field and microcosm studies

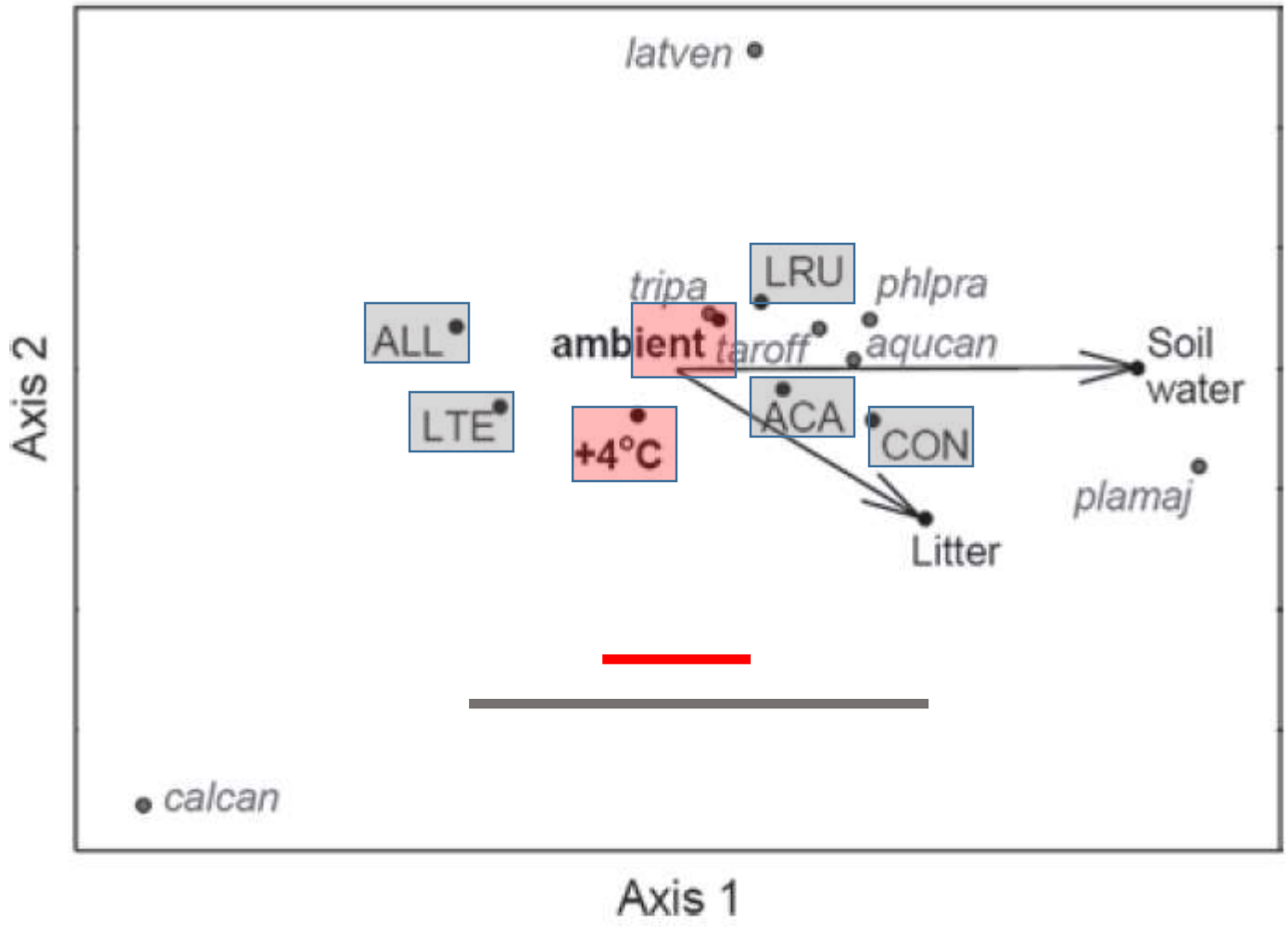
Interactive effects of global warming and 'global worming' on the initial establishment of native and exotic herbaceous plant species

Nico Eisenhauer, Nicholas A. Fisichelli, Lee E. Frelich and Peter B. Reich

N. Eisenhauer (nico.eisenhauer@web.de), N. A. Fisichelli, L. E. Frelich and P. B. Reich, Dept of Forest Resources, Univ. of Minnesota, 1530 Cleveland Avenue N., St. Paul, MN 55108, USA.

Oikos 121: 1121-1133, 2012

NMDS ordination—effects of earthworms on plant community composition larger than that of 4 degree C temperature difference!

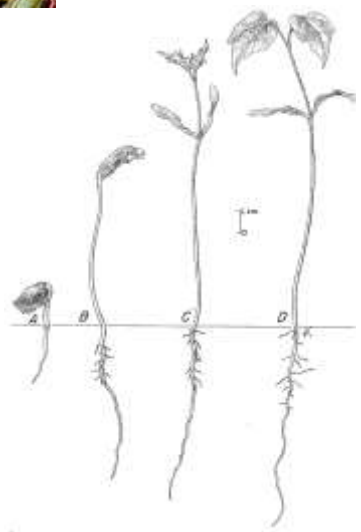


Invasive plants that may be facilitated by earthworm invasion:

Buckthorn (common and glossy)
Garlic mustard
Tatarian honeysuckle
Black swallowwort (*Cynanchum*)
Japanese barberry
Hemp nettle (*Galeopsis tetrahit*)
Veronica ssp.
Stiltgrass (*Microstegium*)

Sugar maple dominated forest-floor plant community buffeted from above and below ground

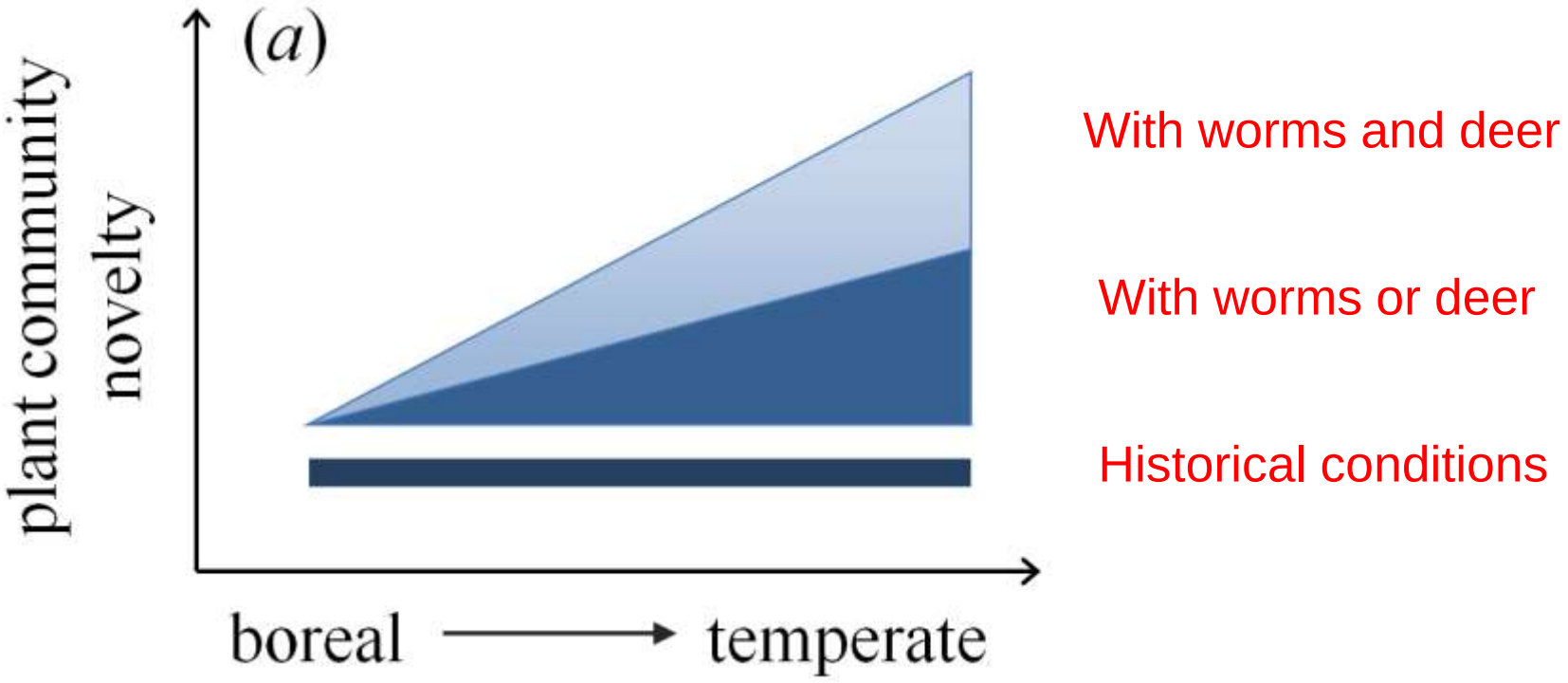
Stability of maple forests now questionable; Complex food web processes will accentuate effects of warming climate



Sugar maple

USDA-NRCS PLANTS Database
And USDA Forest Service

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



Transition from boreal to temperate forest with novel filters on composition

Figure from: Frelich, Peterson, Dovciak, Reich, Vucetich, and Eisenhauer. 2012. Phil. Trans. R. Soc. B. 367, 2955-2961

Sugar maple forests of the past

Photos: Bob Leverett (upper)
Pchgorman (lower)

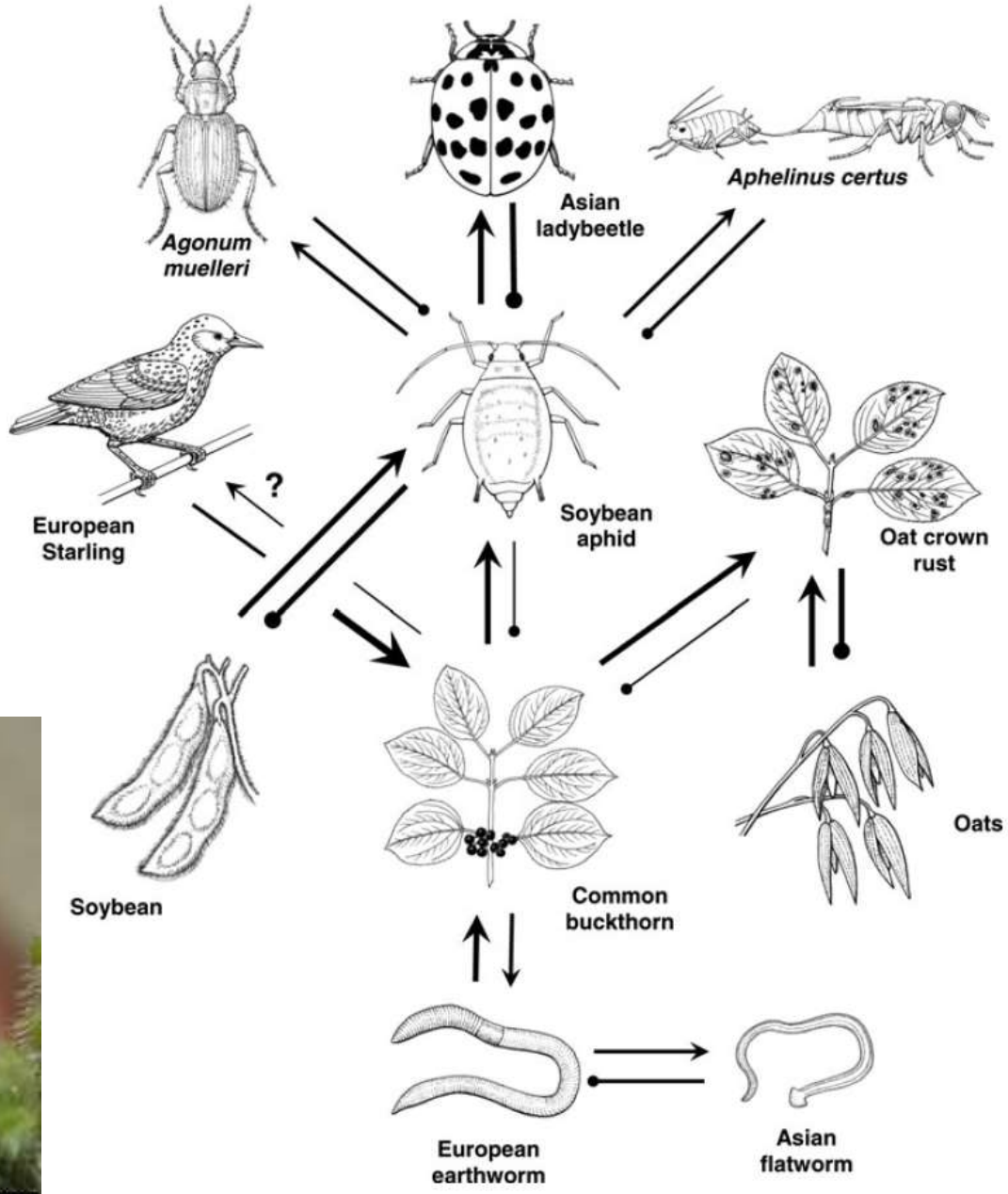
Future temperate forest with red maple and Pennsylvania sedge, or conversion to savanna

Photos: Paul Ojanen

A case study of invasional meltdown

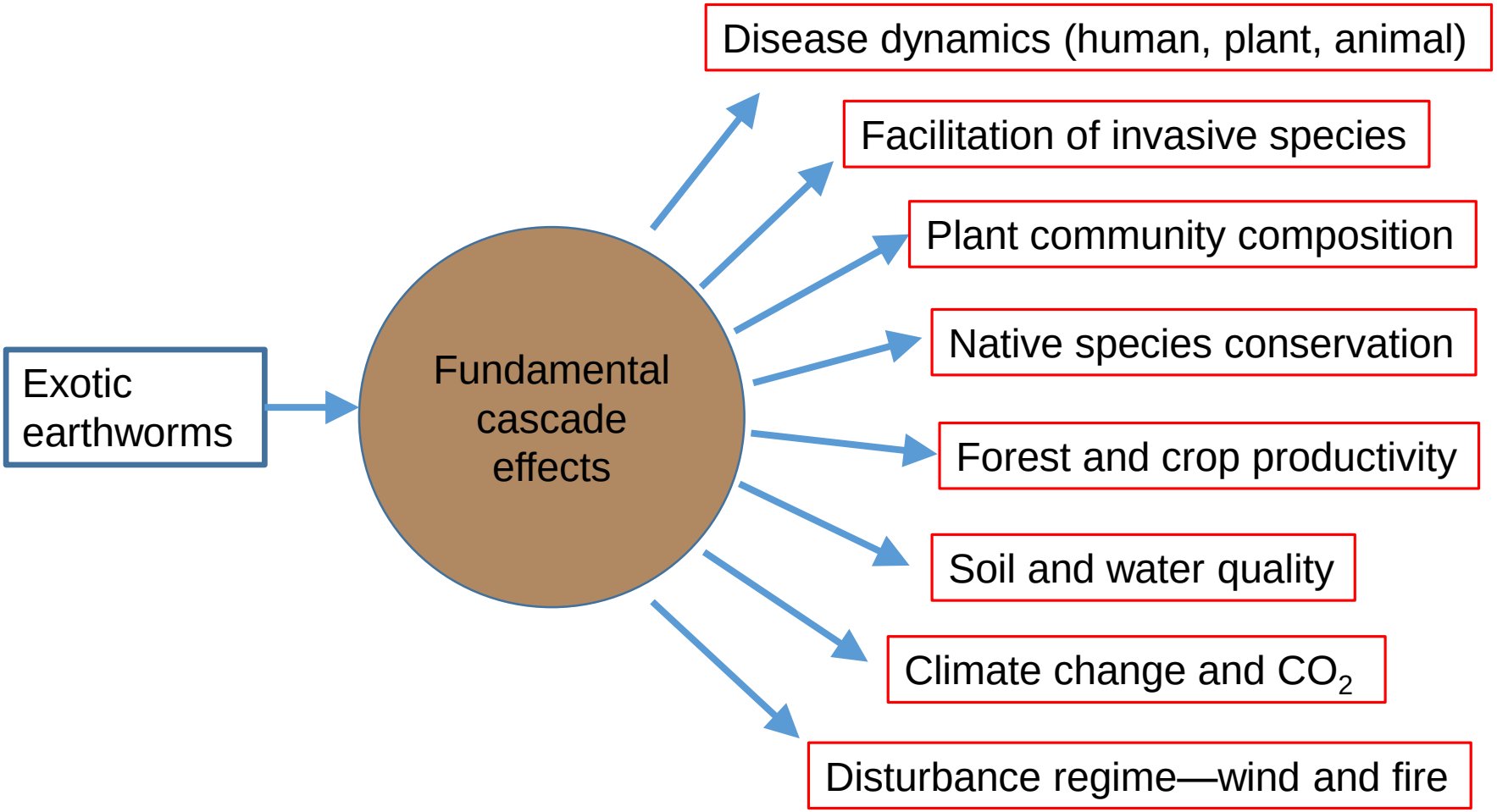
Heimpel, Frelich, Landis, Hopper, Hoelmer, Sezen, Asplen, and Wu, *Biological Invasions*, 2010

Art Work by Julie Martinez

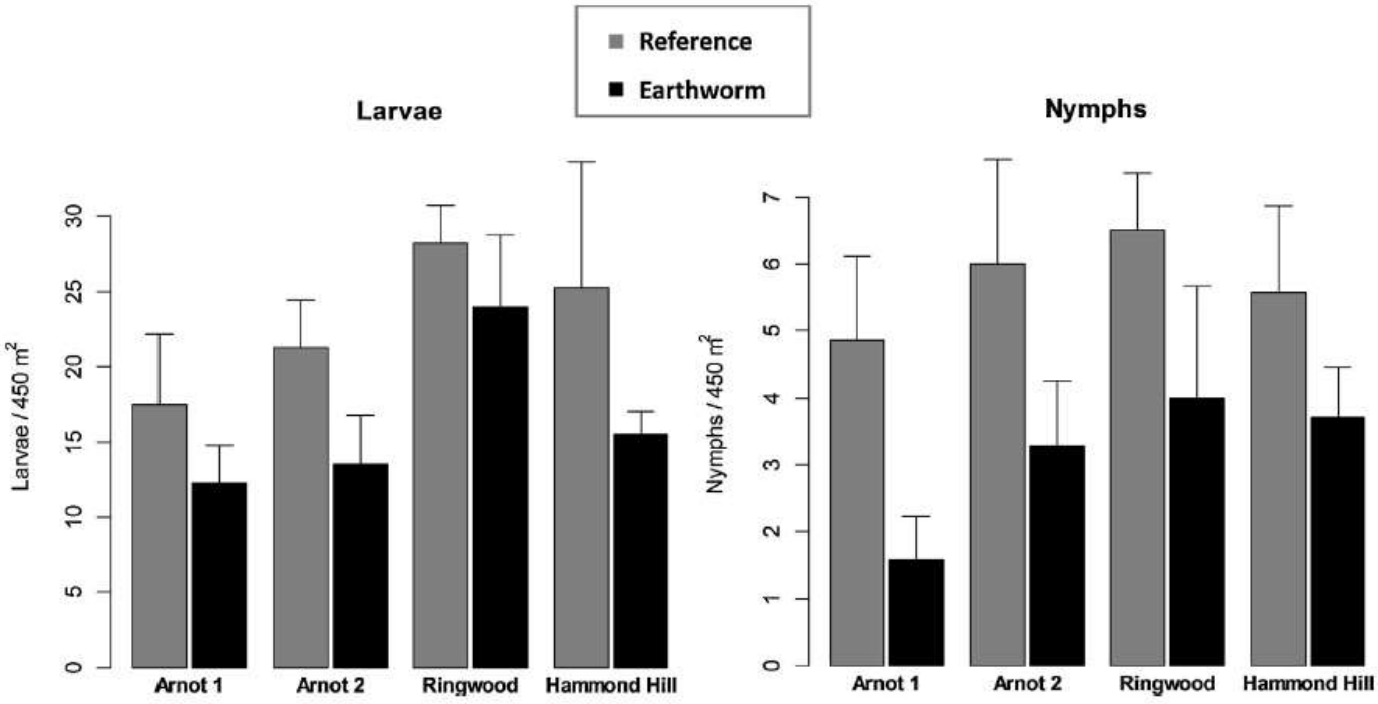


Forest and crop productivity

Earthworm macro-cascade effects of concern to human society



Negative impacts of earthworm invasion on *Ixodes scapularis* in central New York, due to changes in forest floor litter and moisture. Burtis, Fahey and Yavitt 2014. *Applied Soil Ecology*

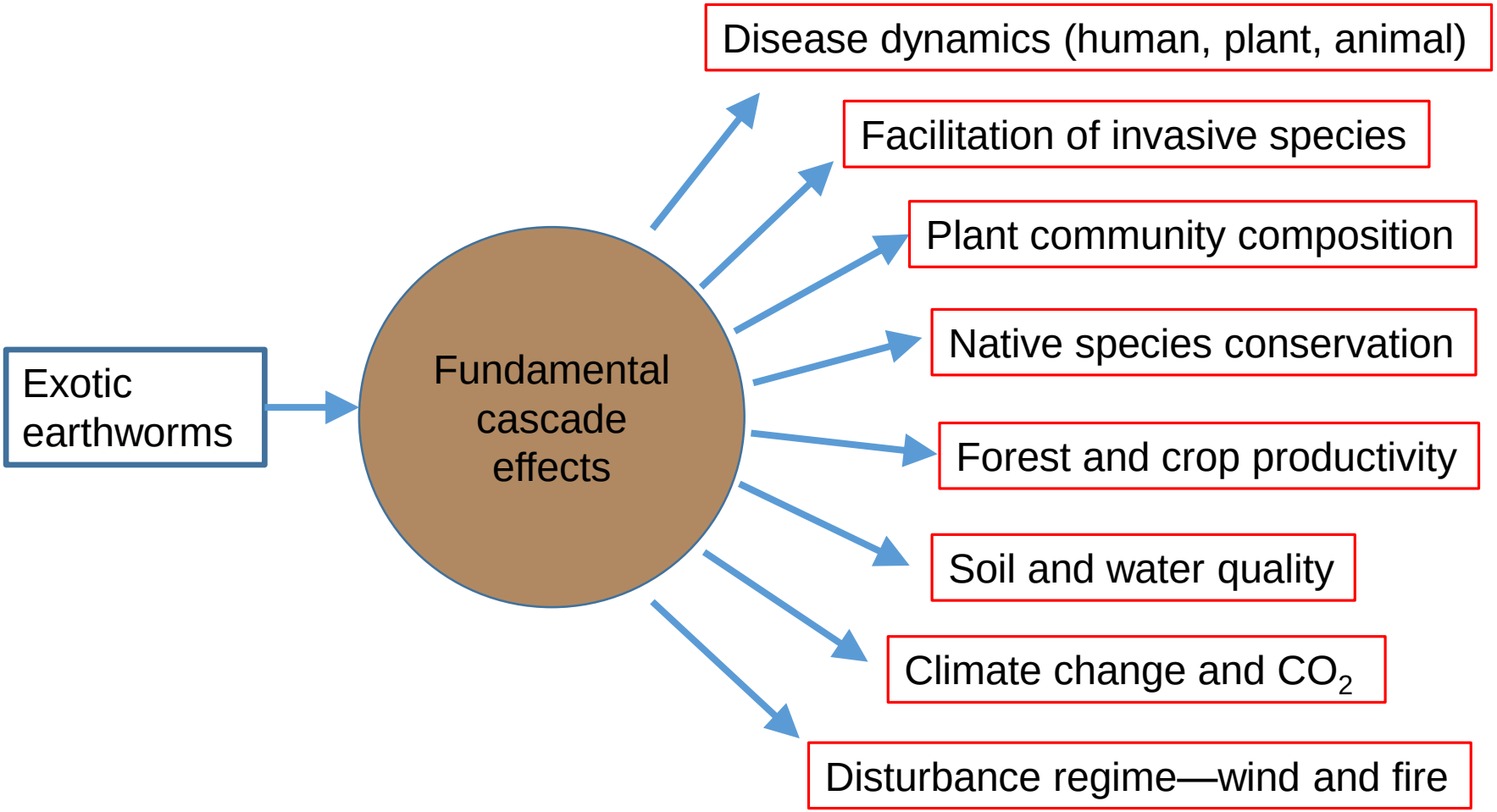


Disease dynamics

However, at later stages of invasion on certain sites, a graminoid lawn may form and favor ticks, and mice that carry ticks may also increase in abundance

Disease dynamics

Earthworm macro-cascade effects of concern to human society



Earthworm invasion and disturbance

- Fire—2-6 T less fuel per ha, and lower contiguity to carry fire once forest floor is gone
- Wind—thinner crowns of trees, smaller trees and higher bulk density of soil could increase tree stability

Figure 1.1. Sugar maple crown dieback in Keweenaw County, MI, 2009. Photo by Tara Bal

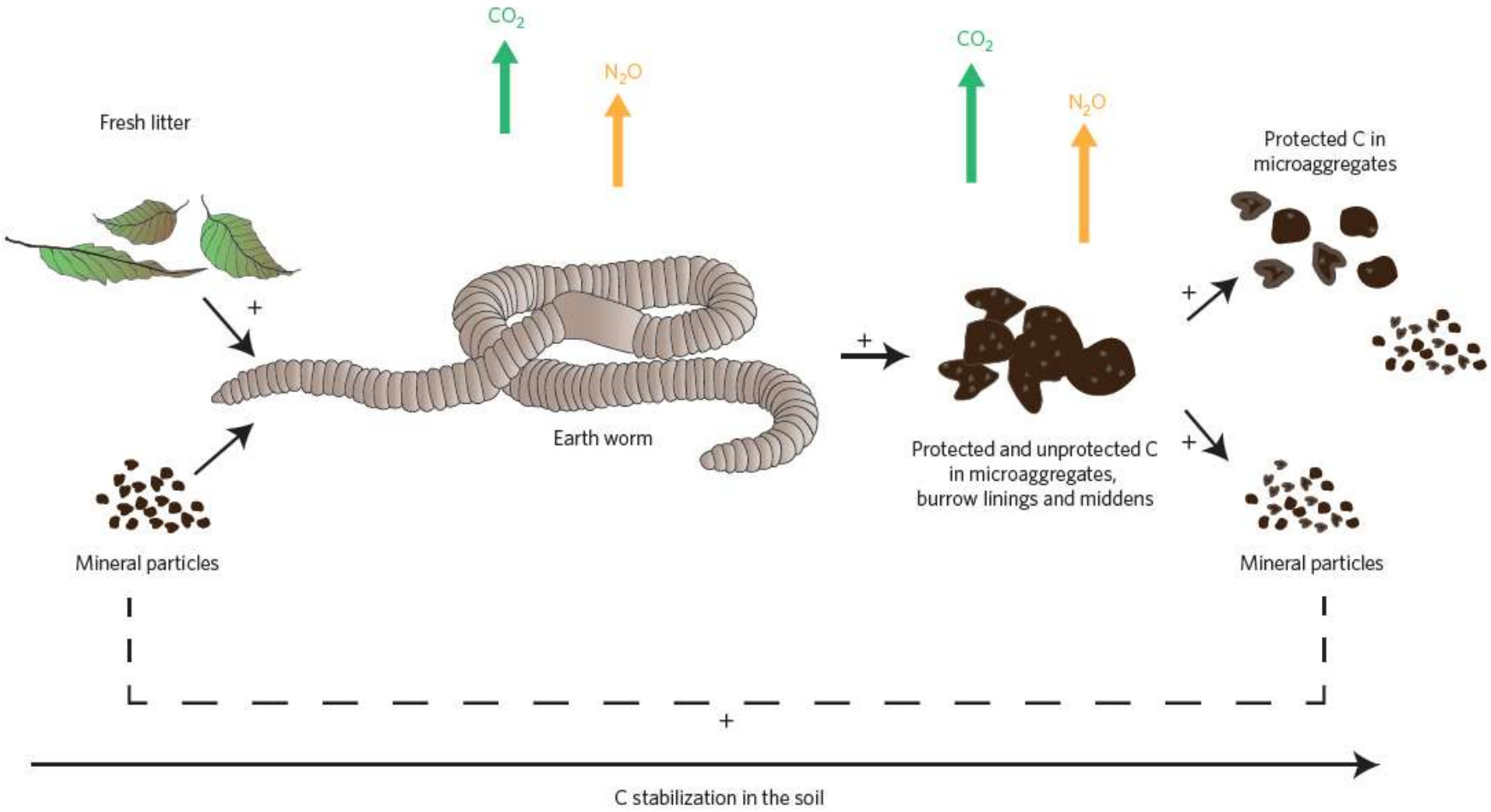
Climate change impacts include facilitating or working against certain plant species migrations, drought, and CO_2 effects

Temperate forest invasion in the BWCAW: Red oak in boreal forest understory (upper right); Red maple replacing black spruce and birch-spruce forest (Upper left and lower left, respectively). Photos: Lee Frelich, Dave Hansen

Red maple densities range from 62 to 384 per acre from east to west in the BWCAW

CO_2 impacts of earthworm invasions

From Lubbers et al. 2013, Nature Climate Change



nature COMMUNICATIONS

ARTICLE

Received 28 Apr 2013 | Accepted 9 Sep 2013 | Published 15 Oct 2013

DOI: 10.1038/ncomms3576

Earthworms facilitate carbon sequestration through unequal amplification of carbon stabilization compared with mineralization

Weixin Zhang[1], Paul F. Hendrix[2], Lauren E. Dame[2], Roger A. Burke[3], Jianping Wu[4], Deborah A. Neher[5], Jianxiong Li[6], Yuanhu Shao[1] & Shenglei Fu[1]

nature climate change

REVIEW ARTICLE

PUBLISHED ONLINE: 3 FEBRUARY 2013 | DOI: 10.1038/NCLIMATE1692

Greenhouse-gas emissions from soils increased by earthworms

Ingrid M. Lubbers[1]*, Kees Jan van Groenigen[2], Steven J. Fonte[3], Johan Six[4], Lijbert Brussaard[1] and Jan Willem van Groenigen[1]

Lubber's et al. meta analysis of earthworm mesocosm studies

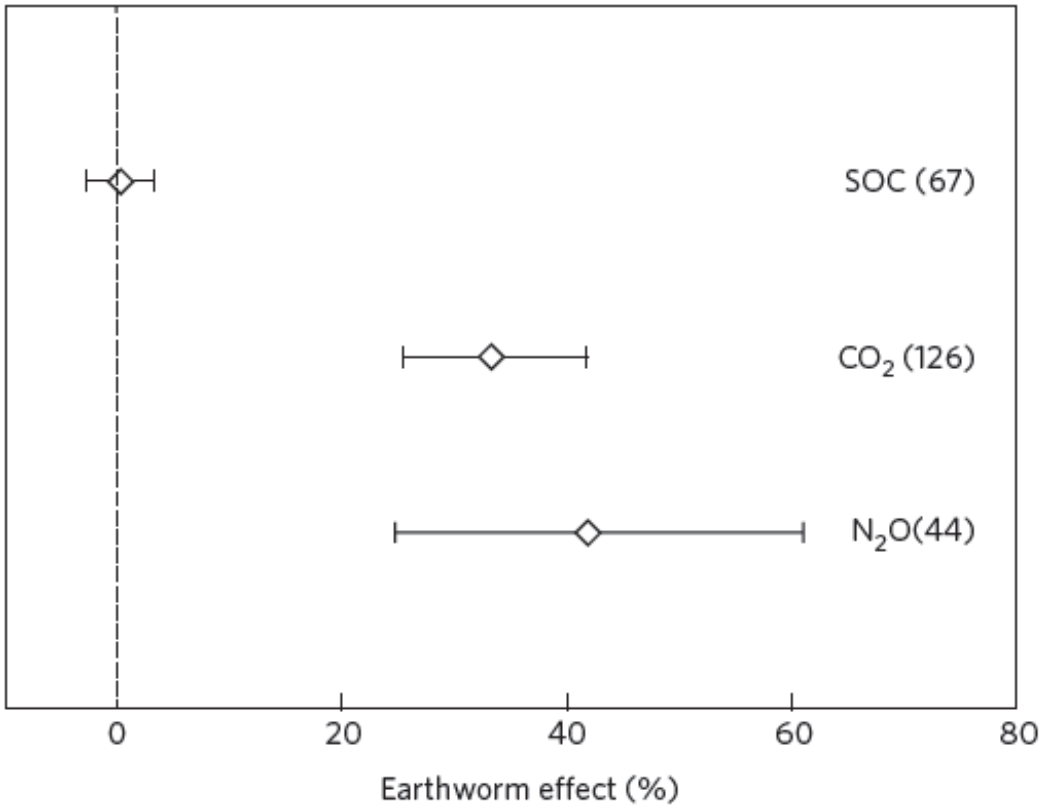
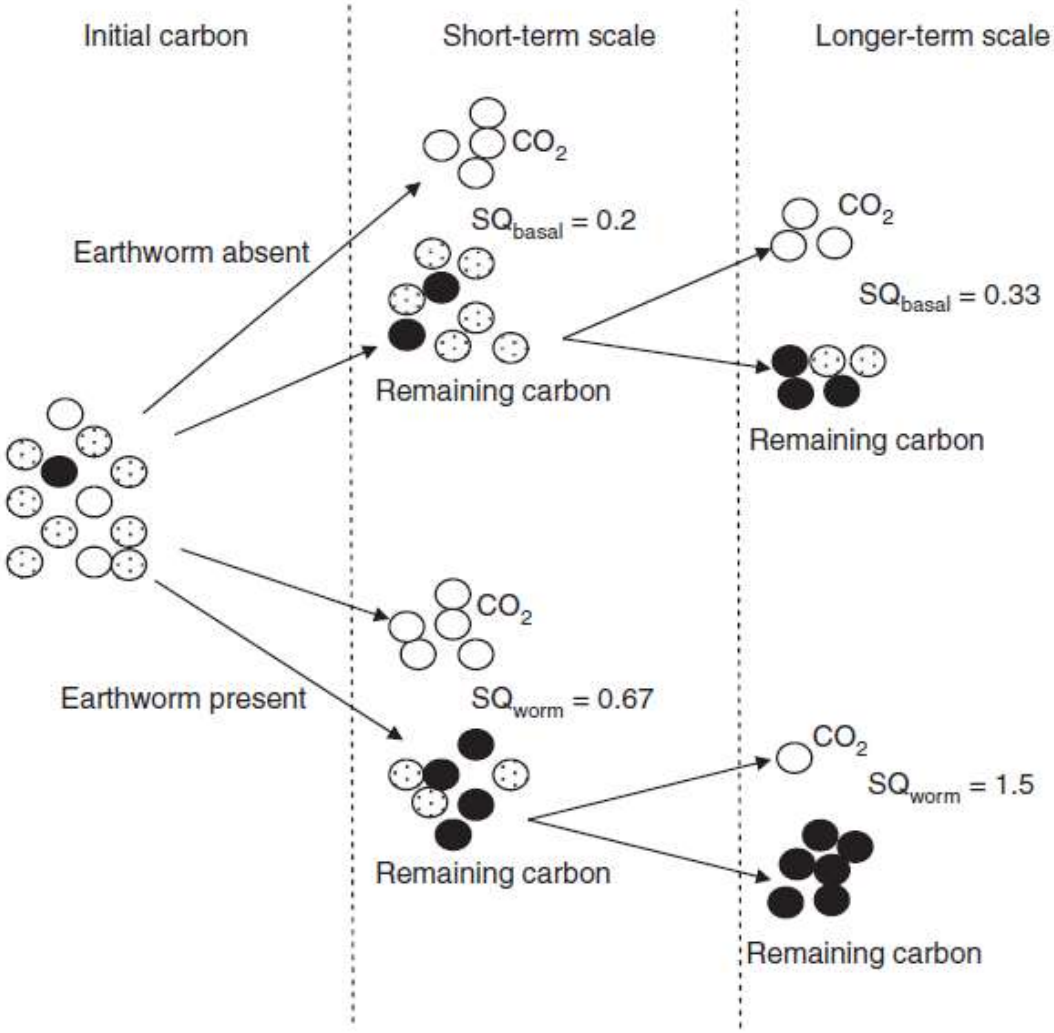
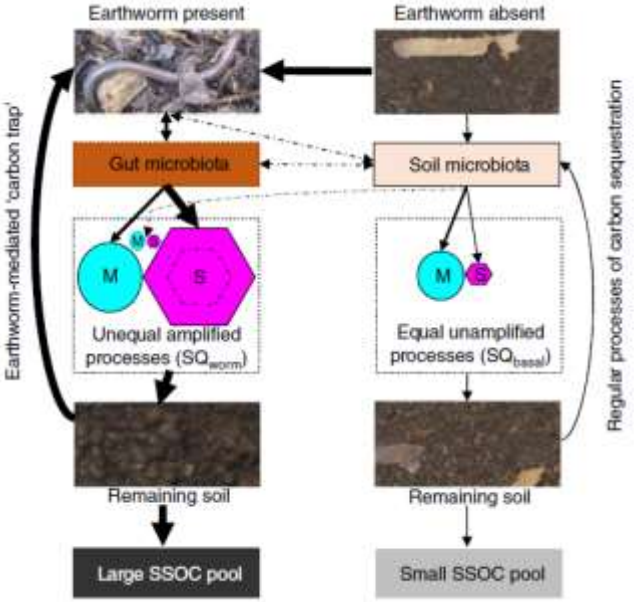


Figure 1 | Percentage effect of earthworm presence on N_2O and CO_2 emissions from soil and SOC. Effect sizes in all meta-analyses were weighted by the inverse of the pooled variance. Error bars denote the 95% confidence intervals. Numbers of observations are in parentheses.

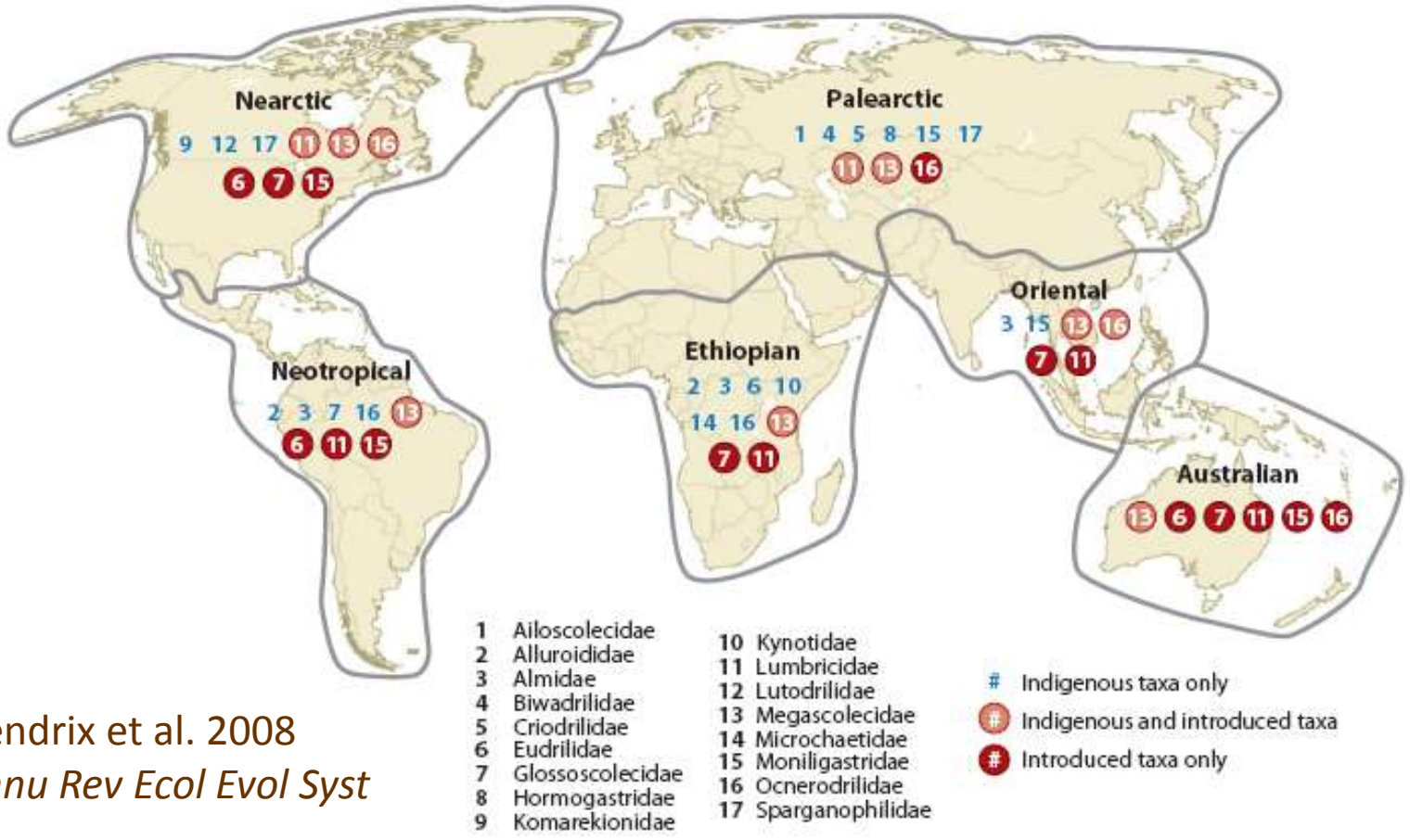
According to Zhang et al., the Lubbers et al. study looked at studies done over too short a time span to see the net long-term result of worms on CO_2





According to Frelich,

Lubbers et al. 2013 and Zhang et al. 2013 studies are both flawed—neither recognizes the large spatial extent of worm invasions consuming newly Invaded forest floors



Hendrix et al. 2008

Annu Rev Ecol Evol Syst

Figure 1

Global distribution of indigenous and introduced species within earthworm families in each biogeographic realm (modified from Reynolds 1994, with data from Gates 1982, Jamieson 1981, Omodeo 2000, Sims 1980).

Direct effects of earthworm invasion

- Removal of organic horizon
- Compaction of mineral soil
- Disturbance of soil

Indirect effects

- Alteration of seedbed conditions
- More runoff, drier soils
- Lower nutrient availability

Cascading effects on plant community

- Drought stress
- Changing growth rates and alteration of competitive relationships
- Mortality of plant populations
- Lower native plant species richness

Continued cascading effects

- Water quality
- Wildlife and insect habitat
- Facilitation of invasive plant species
- Plant animal interactions

Conclusions

Earthworms have large fundamental effects on physical environment of the soil (temperature, moisture, nutrient content, structure) which ultimately tug on a lot of links in the food web

Multi-species and multi-effect invasion with strong trophic and long ecological cascades that run 4-5 links and tend to branch

Natural area conservation—profound implications and we can't stop worms at this time, known control measures are damaging, e.g. coarse sand, chemicals, biocontrol not much explored

Acknowledgments:
Forest Ecology Lab group, Cindy Buschena, Peter Reich, Cindy Hale, Andy Holdsworth, Paul Ojanen, Alex Roth, Sascha Lodge, Nico Eisenhauer, many others.
Funding: Wood-Rill Foundation, Bruce and Ruth Dayton, Wally and Mary Lee Dayton, Jonathon Bishop, John and Charlotte Parish