



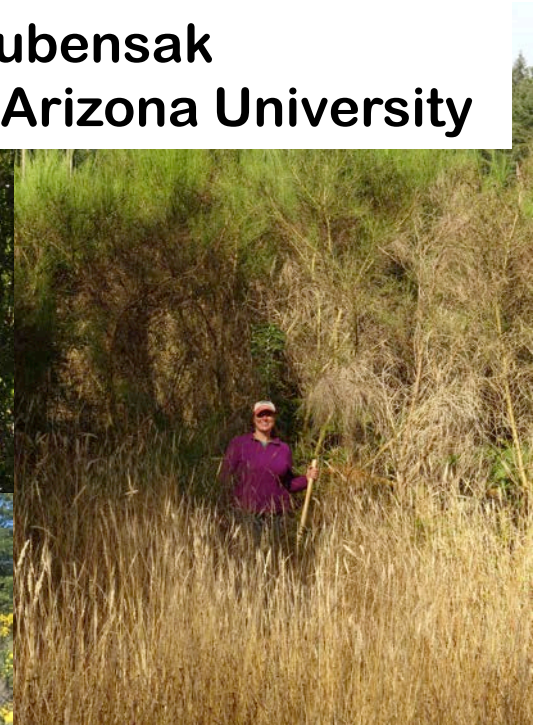
Development and persistence of soil legacy effects of Scotch broom and implications for reforestation

Sara Grove

Ecology & Evolutionary Biology

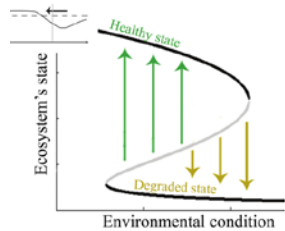
UC Santa Cruz

Karen Haubensak
Northern Arizona University



Ingrid Parker
University of California, Santa Cruz





Alternative stable states

Persistence following invader removal

Development over time following invasion

Plant-soil feedbacks

Temporal dynamics of soil legacies

Invasion Ecology



Applied Ecology



Scarifying

Control
Timing
Early v. late life stages



Forest Edge Effects
Soil Inoculations
Native Plant Genotypes
Herbicide
Brushcutting

Restoration following broom removal

Allelopathy

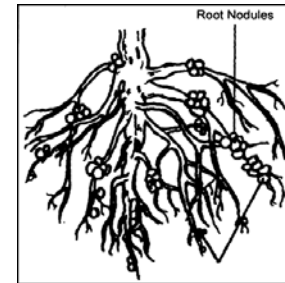
Nitrogen enrichment

Secondary invasions

Phosphorus depletion

Rhizobia limitation

Direct effects on native plants



Indirect pathway via mycorrhizal fungi

Species specific response to allelochemical

Mycorrhizal mutualism disruption

Role of "rare" mycorrhizal species

Does the composition of ectomycorrhizal fungal communities matter?

Is broom limited by mycorrhizae

Plant-fungal interactions



Impacts on abiotic and biotic soil properties

Nitrogen enrichment



Mycorrhizal fungi



How do soil impacts change with invasion age?

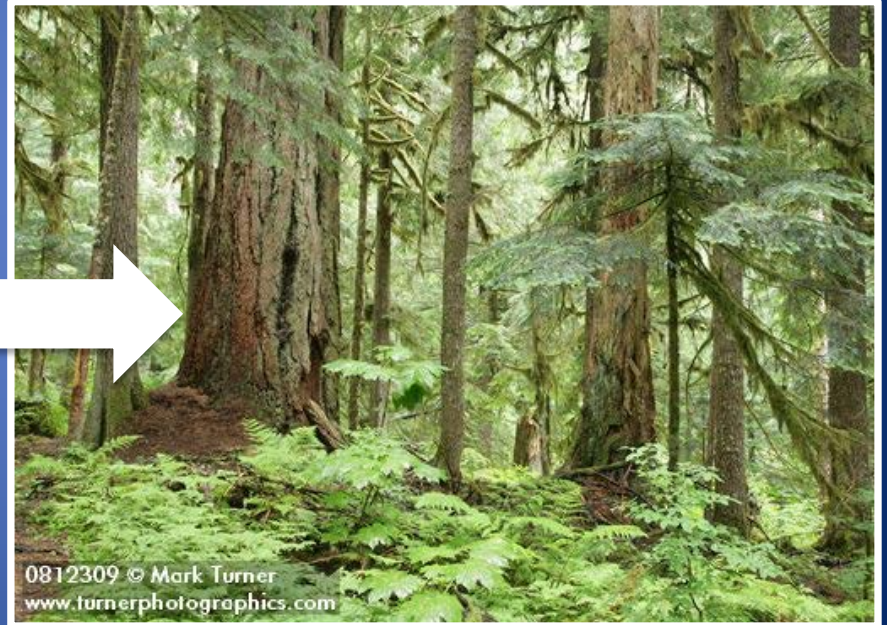


Greenhouse & Field Experiments

How long do the legacy effects of Scotch broom persist after it has been removed?

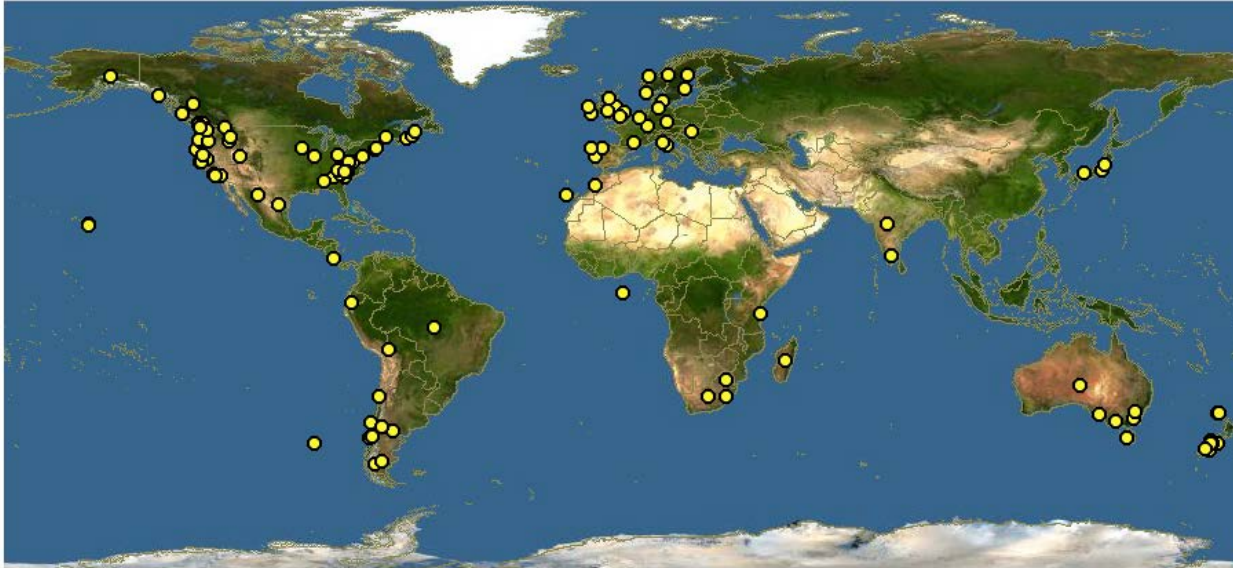


Reforestation following broom removal



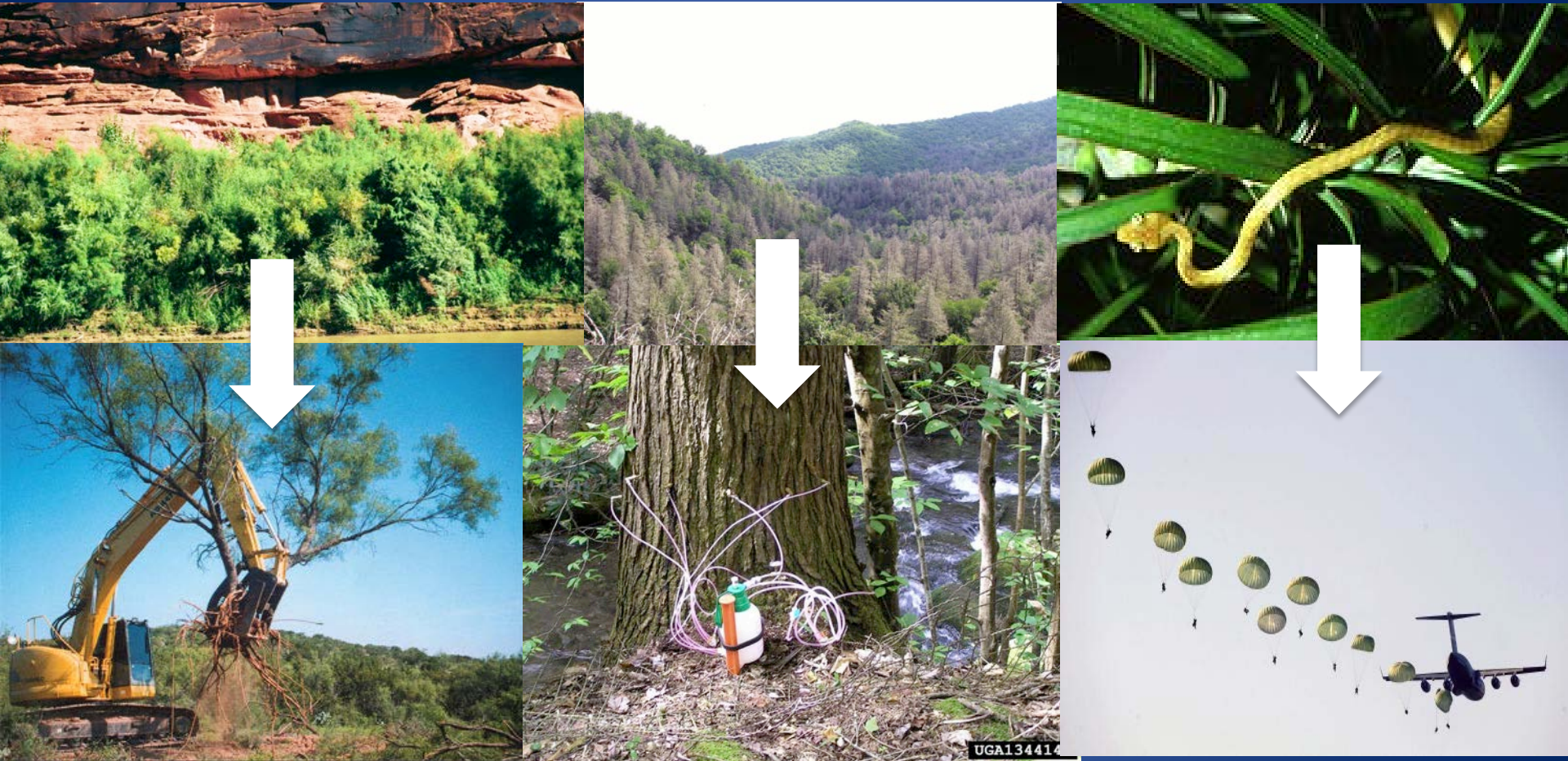
Scotch broom (*Cytisus scoparius*)

a globally problematic invasive plant



- Native to western Europe
- Introduced 200 + years ago
- Fixes nitrogen
- Excludes native vegetation
- Notoriously difficult to control
- Seeds persist for 80+ years

Invasive species impacts and control



It is generally assumed that when you remove an invasive species the impacts go away with it

Legacy Effects following invasive species removal

Legacy Effects:

- Species loss
- Nutrient cycling
- Microbial communities
- Positive feedbacks that reinforce invasion
- Do not have a sense of how common they are
- Useful for prioritizing management



Invasive Plant Science and Management 2012 5:117–124

Gone but Not Forgotten? Invasive Plants' Legacies on Community and Ecosystem Properties

Jeffrey D. Corbin and Carla M. D'Antonio*

LETTER

doi:10.1038/nature12798

Self-reinforcing impacts of plant invasions change over time

Stephanie G. Yelenik^{1†} & Carla M. D'Antonio¹

Oecologia (2013) 172:915–924
DOI 10.1007/s00442-012-2543-1

ECOSYSTEM ECOLOGY - ORIGINAL RESEARCH

Ecosystem legacy of the introduced N₂-fixing tree *Robinia pseudoacacia* in a coastal forest

Betsy Von Holle • Christopher Neill •
Erin F. Largay • Katherine A. Budreski •
Barbara Ozimec • Sara A. Clark • Krista Lee

Biol Invasions (2015) 17:2621–2631
DOI 10.1007/s10530-015-0900-9



ORIGINAL PAPER

Persistence of a soil legacy following removal of a nitrogen-fixing invader

Sara Grove • Ingrid M. Parker •
Karen A. Haubensak

Can invasions result in alternative stable states?



Scotch broom invasion following deforestation



Typical Doug-fir survival is $>80\%$

In broom invaded sites survival can be less $<10\%$

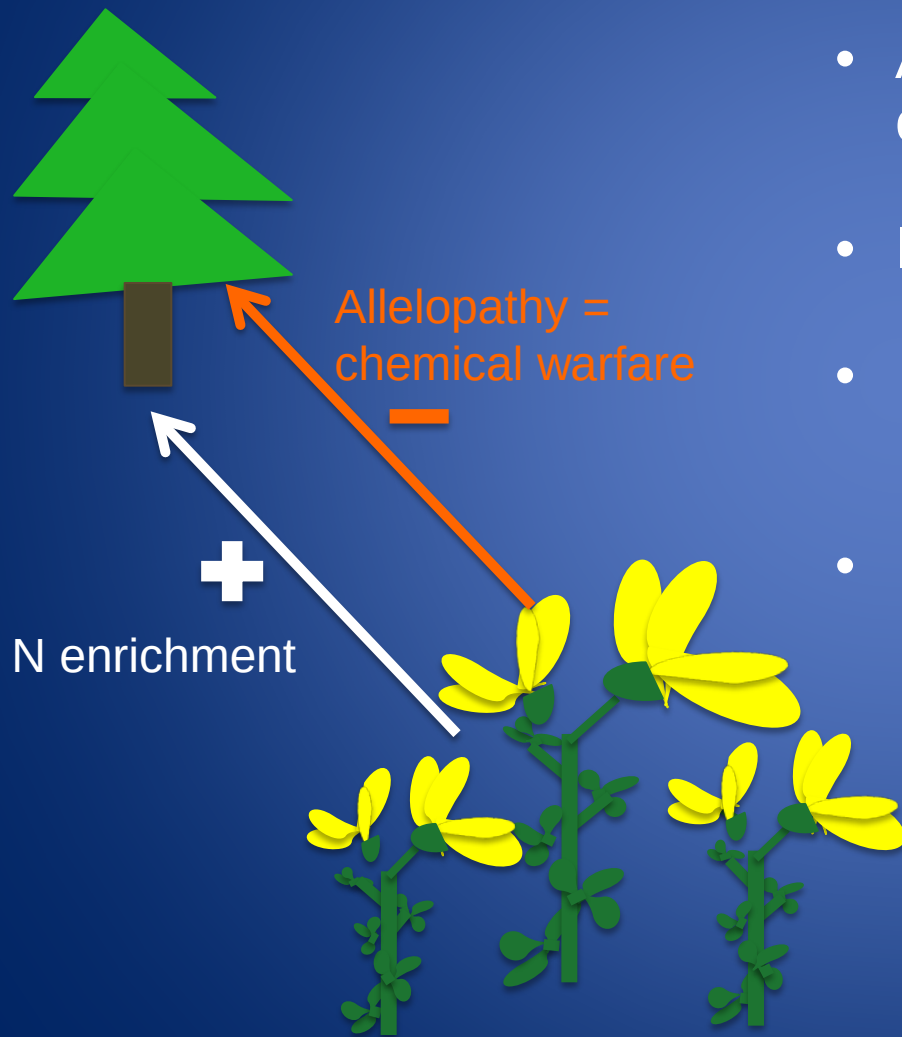
Broom has been removed, NOT direct competition killing Doug-fir



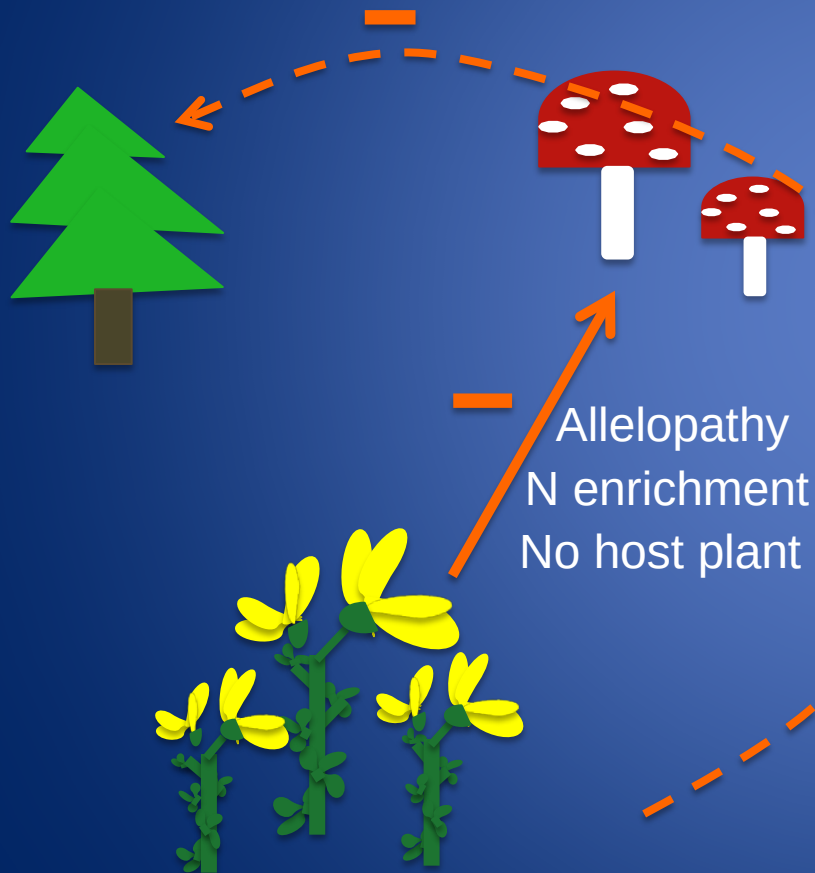
Potential pathways for soil legacy effects

Sparteine:

- Alkaloid secondary defense compound
- In leaf and stem tissues
- Protects against herbivores and pathogens
- Know virtually nothing about how it accumulates or persists in the soil



Impact of broom invasion: Loss of the ectomycorrhizal mutualism?



- Increases soil surface area contact
- Increases access to nutrients and water
- Provides pathogen protection
- Increases drought tolerance
- Plants provide C (sugar/food) to fungi



Evidence of a soil legacy effect

findings from a greenhouse experiment



Soil Legacy Effects:



Trees grown in broom invaded soil were **SMALLER** than trees grown in uninvaded forest soil



Trees grown in broom invaded soil had **LESS** ectomycorrhizal colonization than trees grown in forest soil

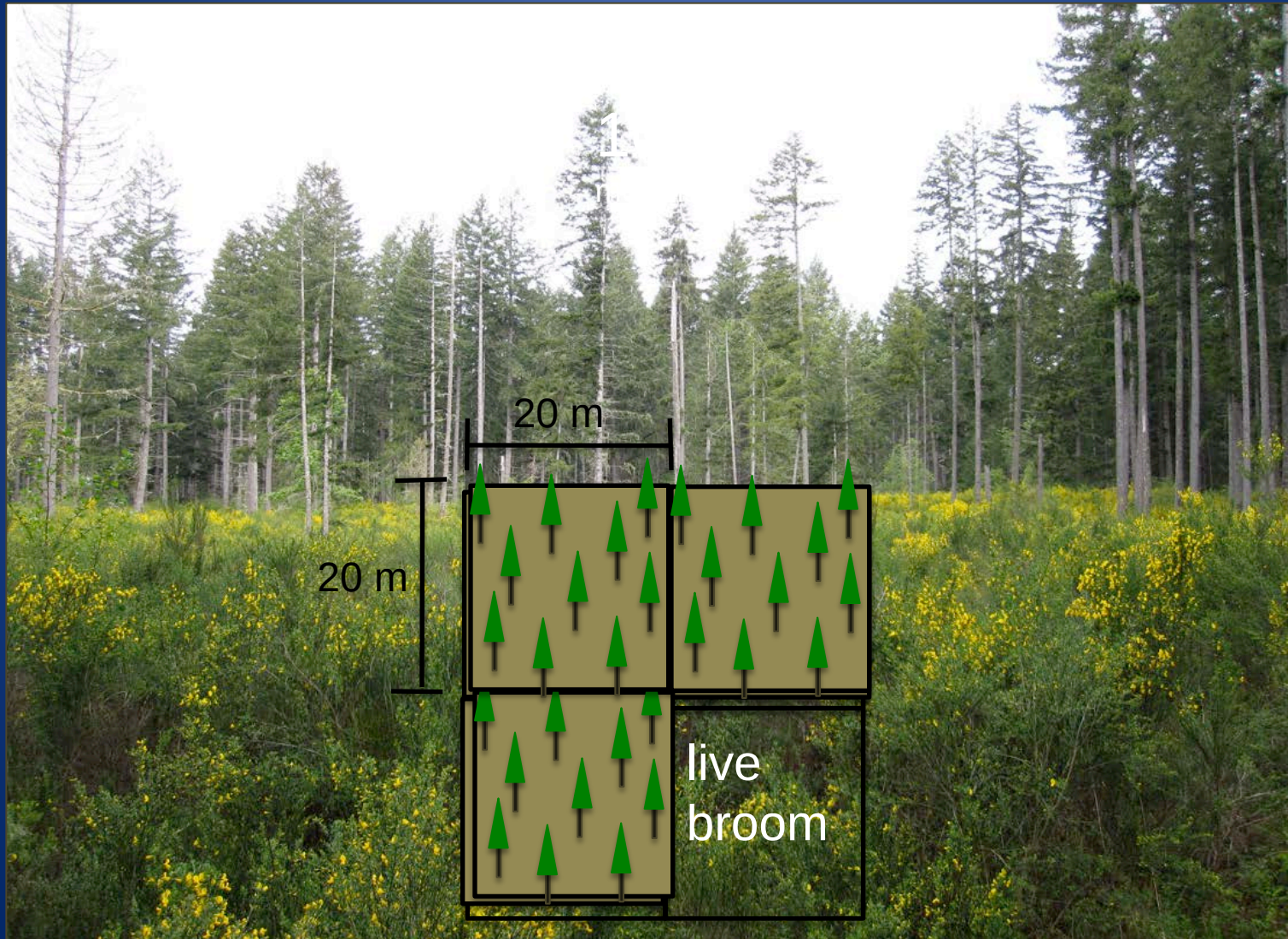


Adding Scotch broom mulch to forest soil **SUPPRESSED** tree growth and EMF

How long do the legacy effects of Scotch broom persist after it has been removed?



How long do the legacy effects of Scotch broom persist after its been removed?



How long does the nitrogen legacy effect persist after broom removal?



Soil cores
collected in field



Extracted
plant available N

Why worry about nitrogen enrichment ?

Douglas-fir forests are N limited



- Decrease abundance of ectomycorrhizal fungi

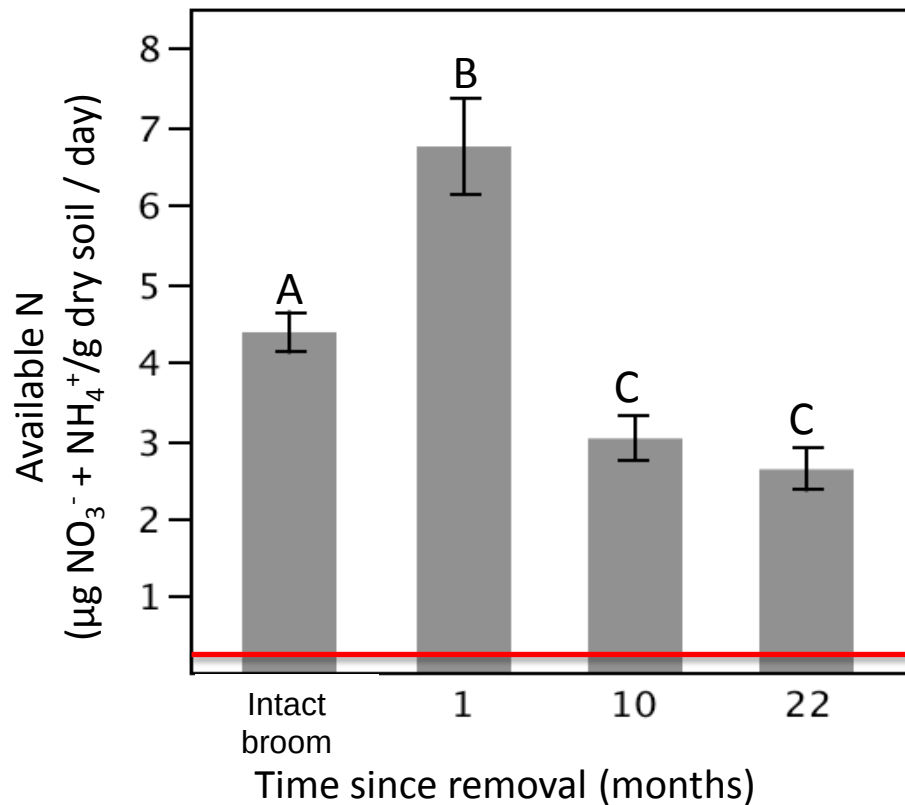


- Facilitate invasion by fast growing exotics that quickly utilize N



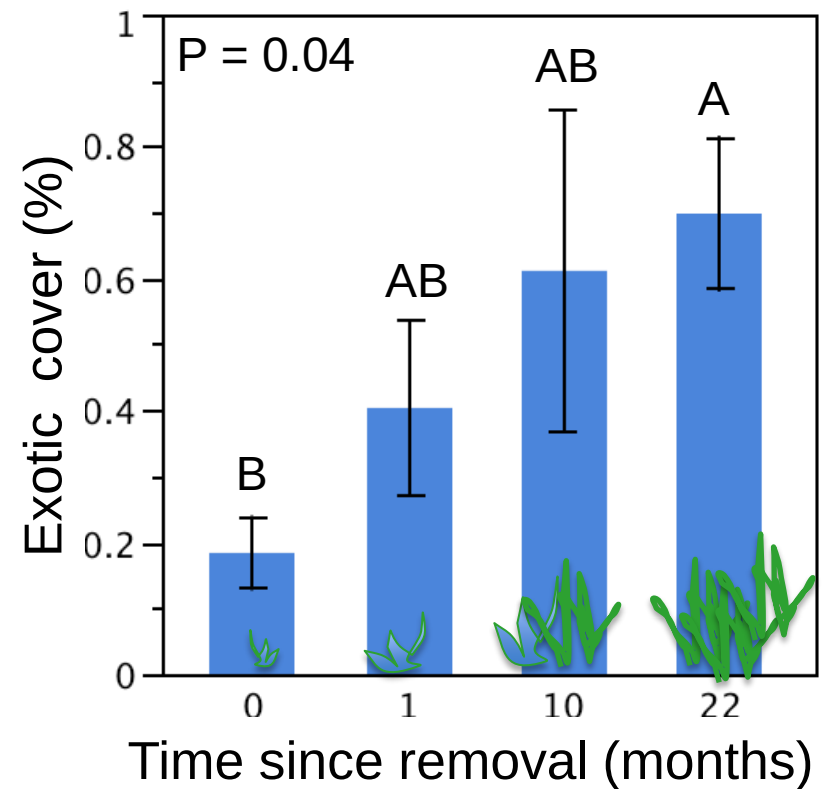
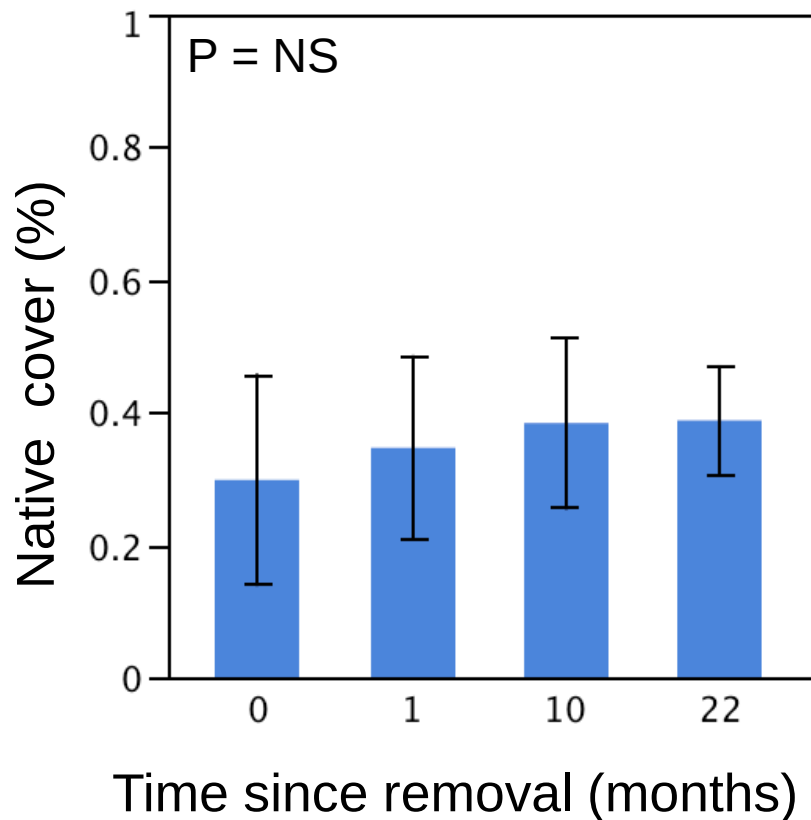
- Increase susceptibility to drought stress

How did N change following broom removal?

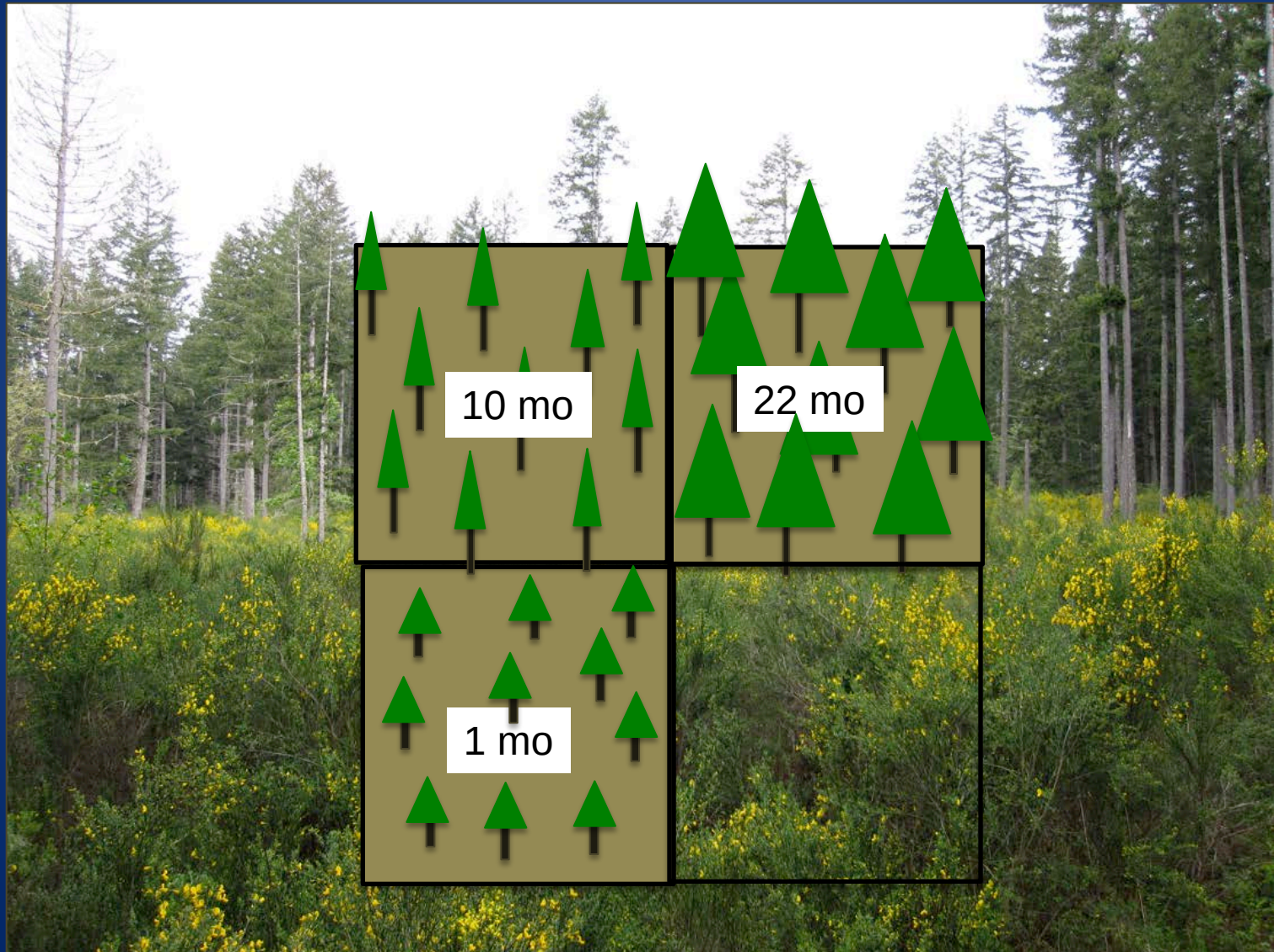


- An initial increase in N followed by a rapid drop at 10 months
- Rate of decline is either stabilizing or slowing.
- Elevated compared to uninvaded nearby forest soils (mean = 0.15 $\mu\text{g/g/day}$, SE = 0.04)

Exotic herbaceous species increased with time following broom removal



Expected soils to recover following removal, and trees to grow better where broom had been absent the longest

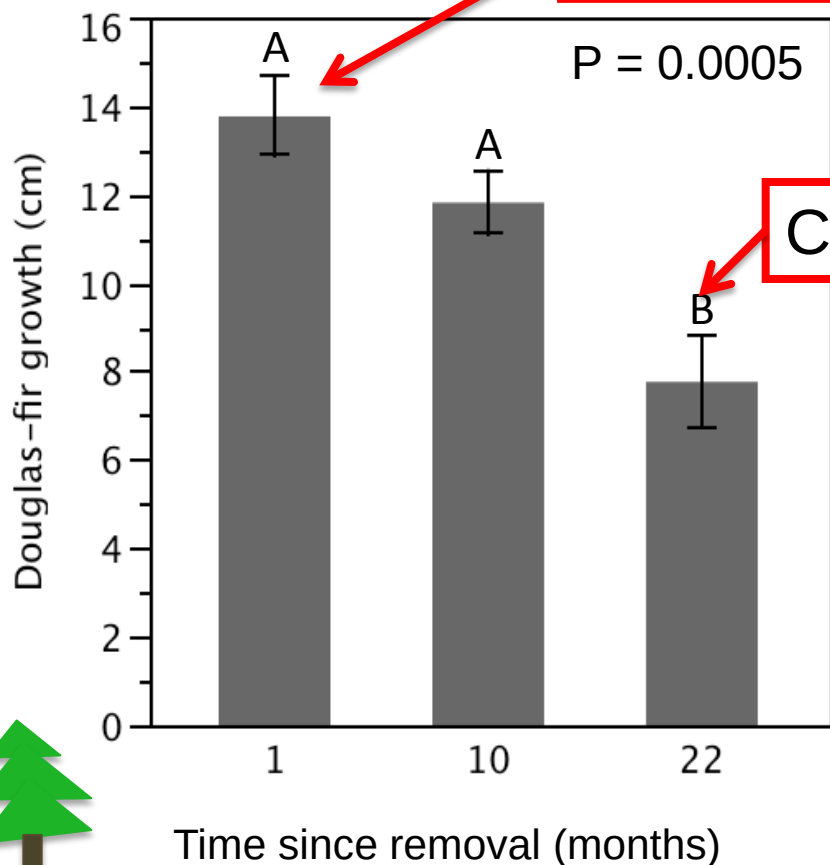




Doug-fir seedling growth



Elevated N?



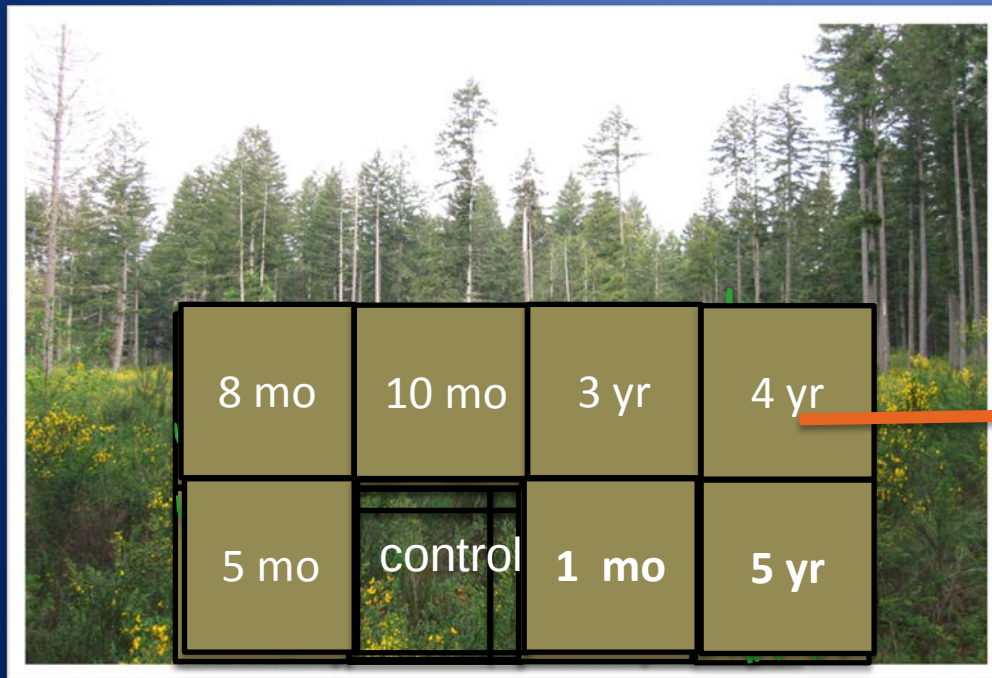
Competition with exotics?

- Doug-fir grew larger in soils where broom was more recently removed
- After broom has been gone for ~2 years growth is suppressed



Ongoing soil legacies research:

- 1) Continuing to follow the nitrogen legacy over time following removal
- 2) Evaluating the relationship between N enrichment and secondary invaders
- 3) Testing role of secondary invaders in limiting tree success



How do soil impacts change with invasion age?



Greenhouse & Field Experiments

Chronosequence Field Exp. (space for time replacement)



Clearcuts ranged in age 5-45 years

9 clearcuts, 2-80 km apart

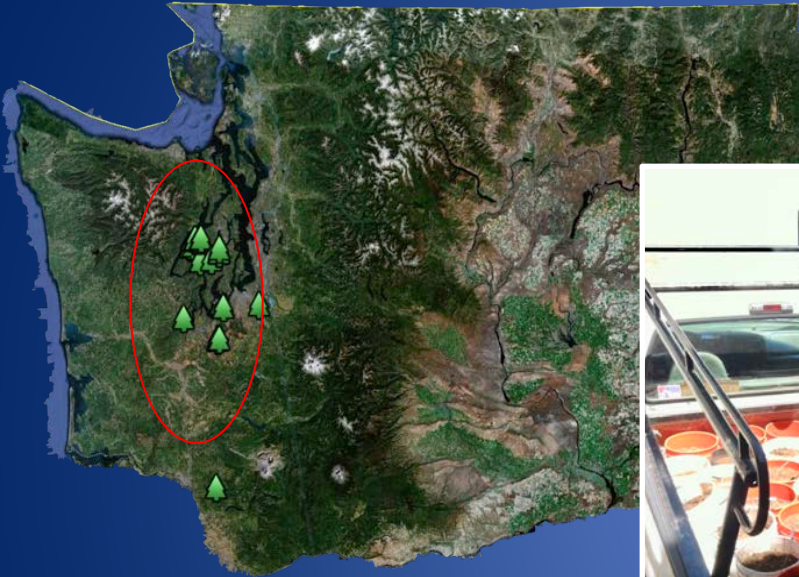
Invaded vs. uninvaded patches

Clearcut age=Invasion age

Cleared off aboveground biomass

Planted Doug-fir seedlings
(N=1600)

Chronosequence Greenhouse Exp.



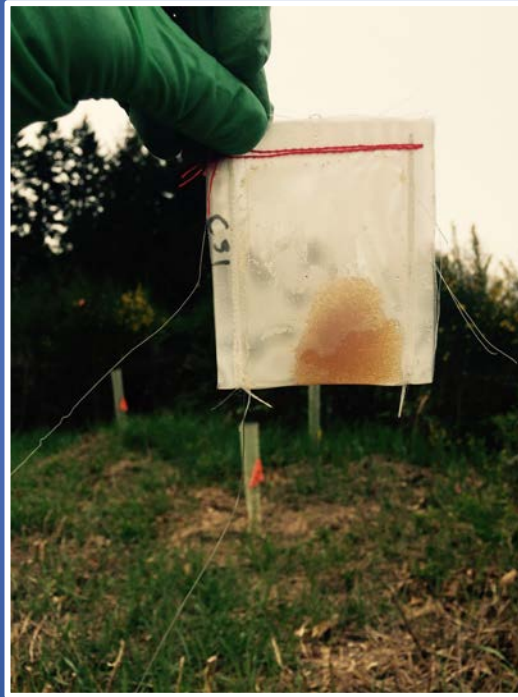
Collected soil
from invaded
and uninvaded
patches in 13
clearcuts in
western WA



Tree survival



Soil nutrients
(N & P)

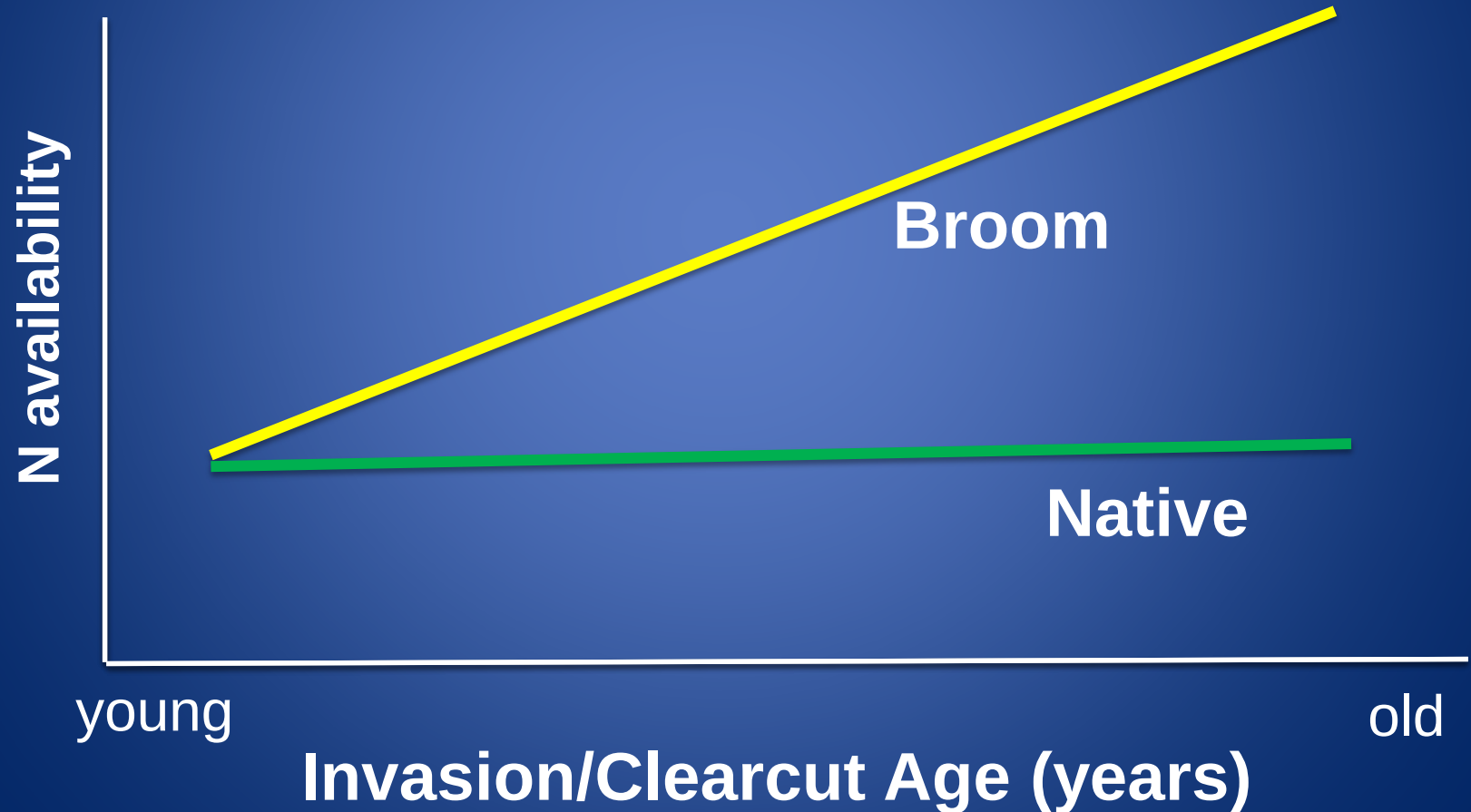


Mycorrhizal
colonization

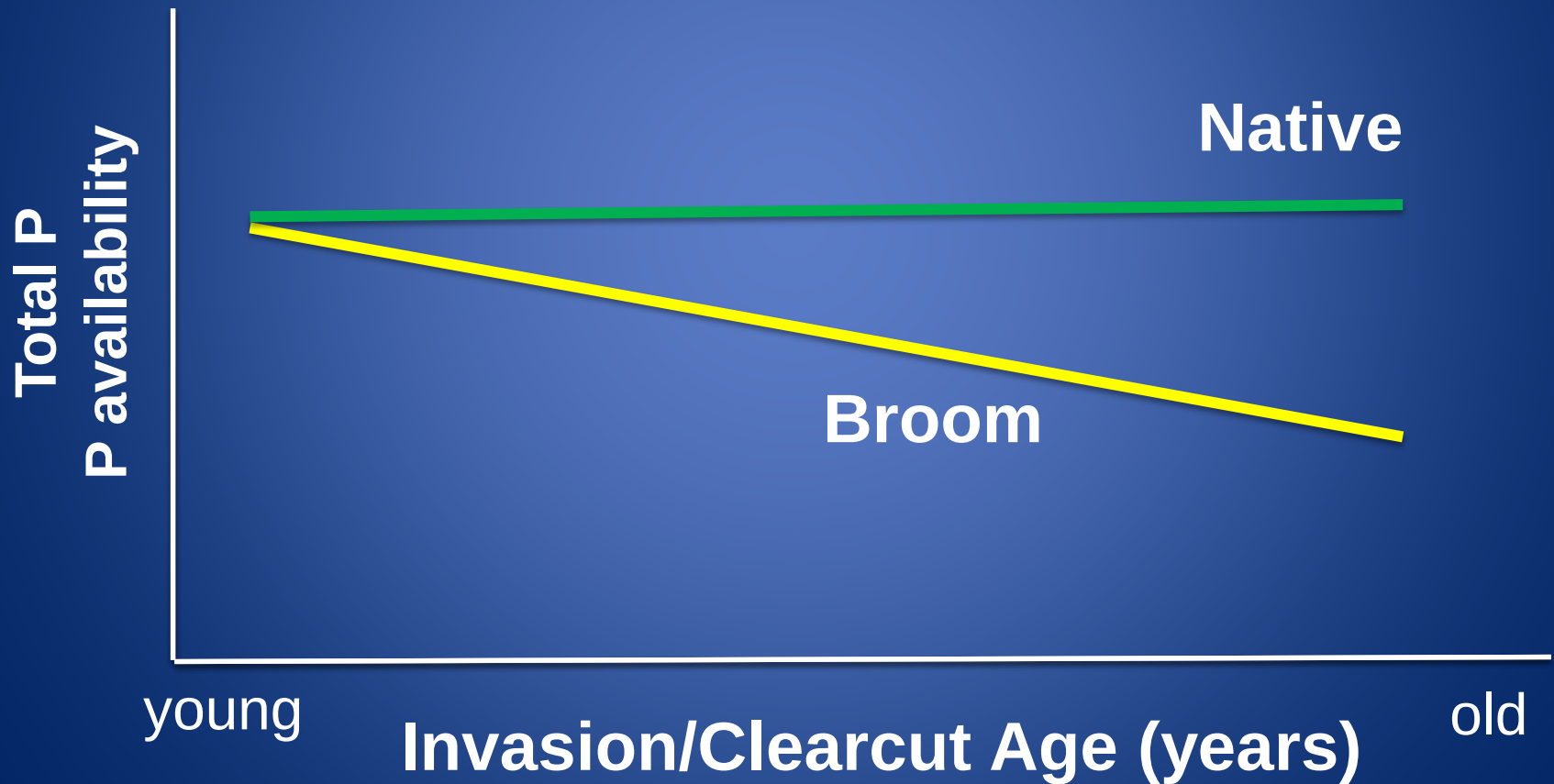


Field Experiment

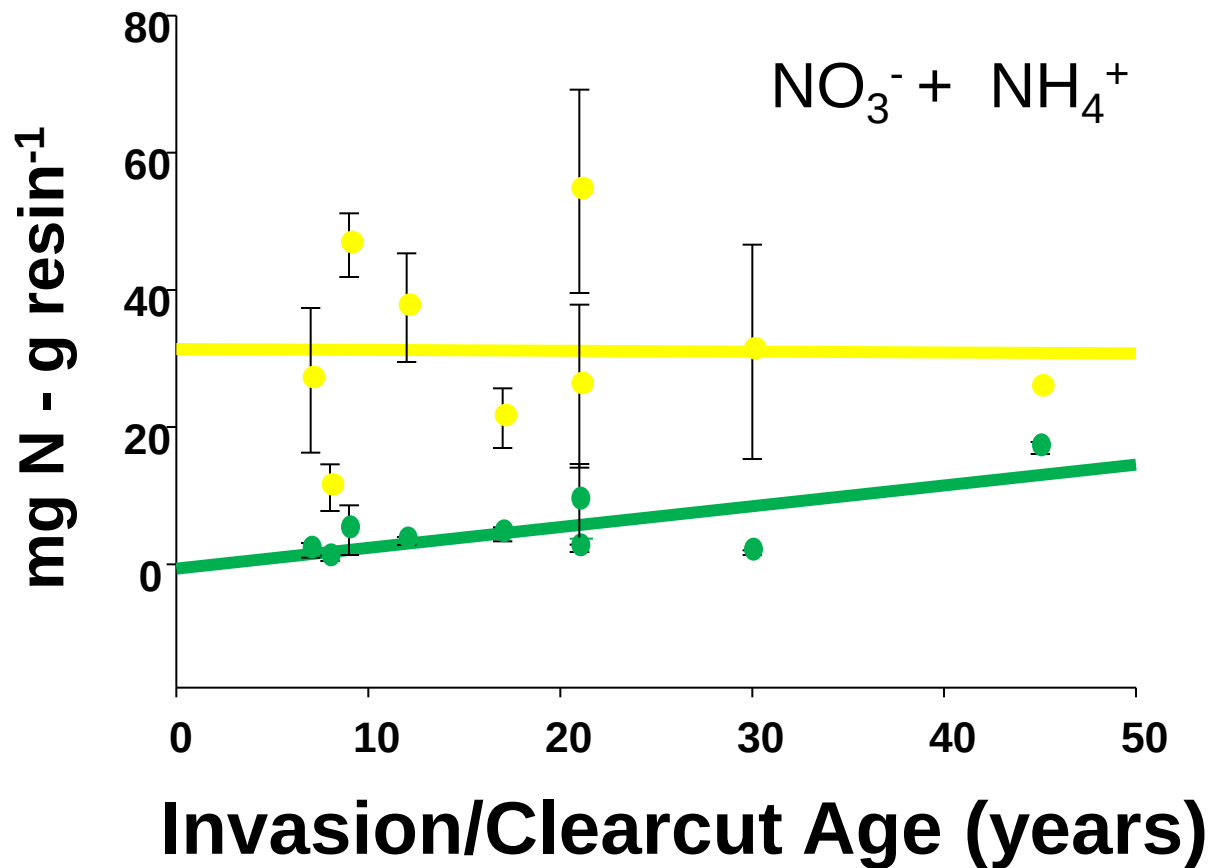
Predictions for Nitrogen Enrichment



Predictions for Phosphorus Depletion

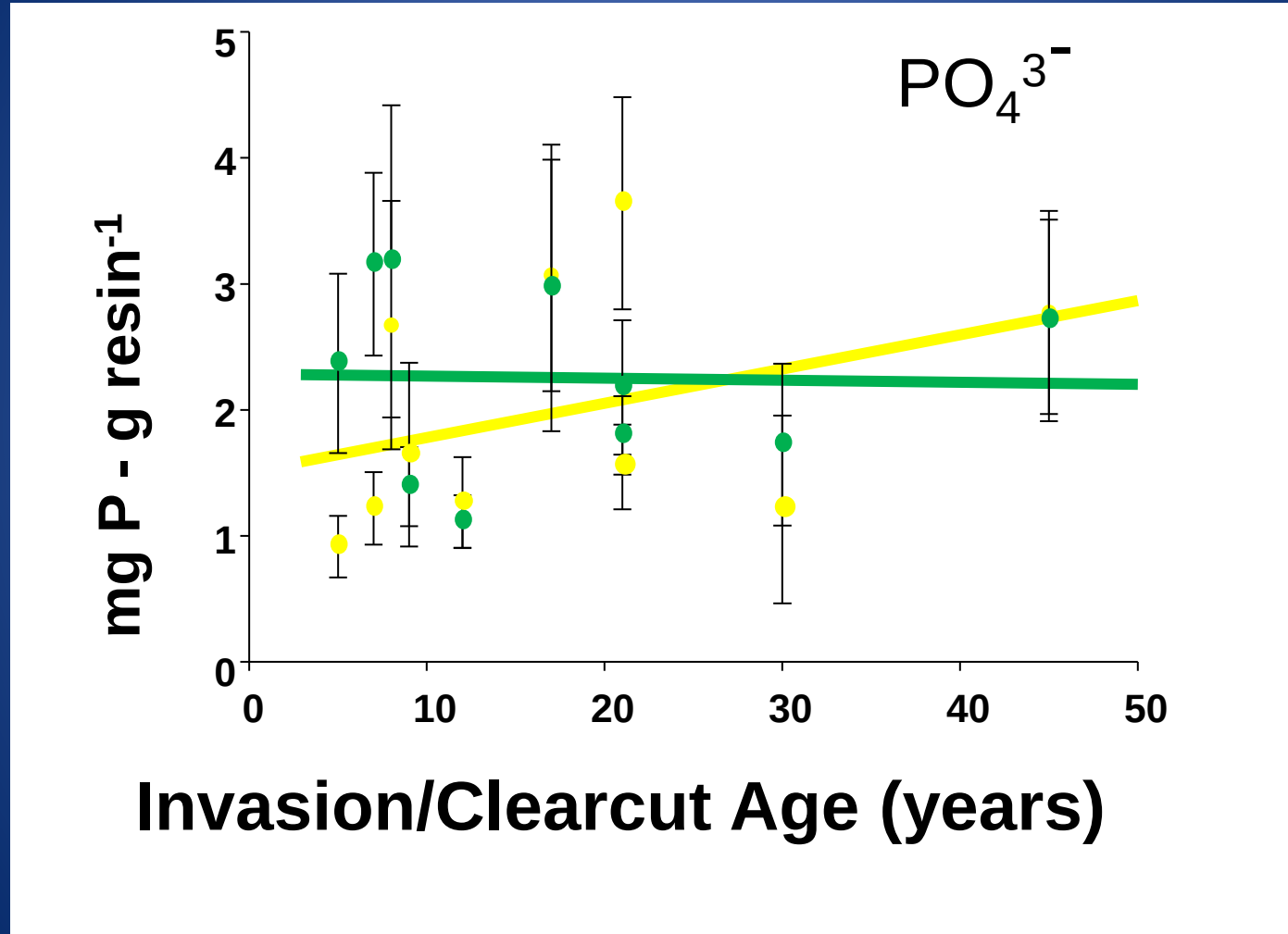


Nitrogen was higher in invaded soil
with no effect of invasion age



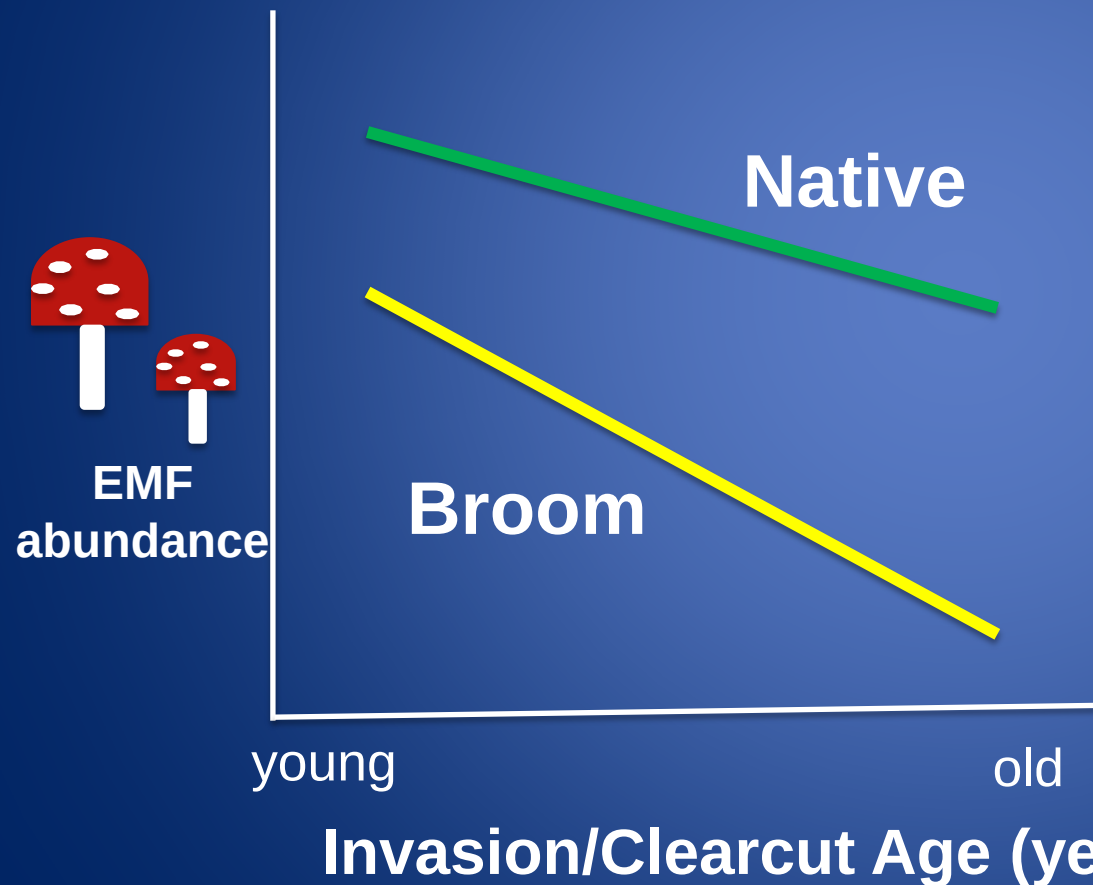
Field Exp.

No effect of invasion or invasion age on phosphorus depletion



Field Exp.

Predictions for ectomycorrhizal abundance

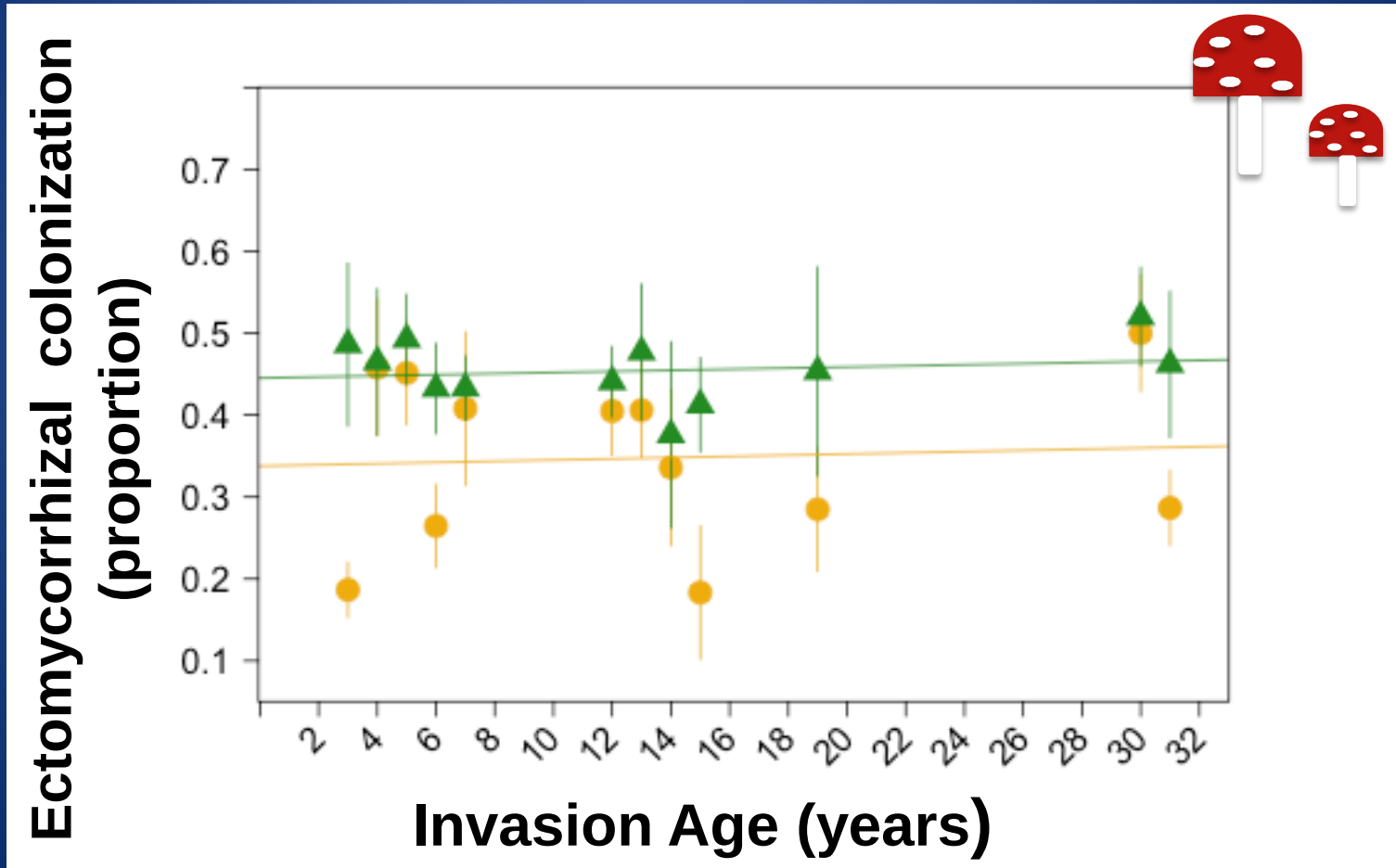


1) Decline with time following clearcut (no host plants)

2) Invaded soil would have less EMF than uninvaded

3) EMF decline would be faster in invaded soils

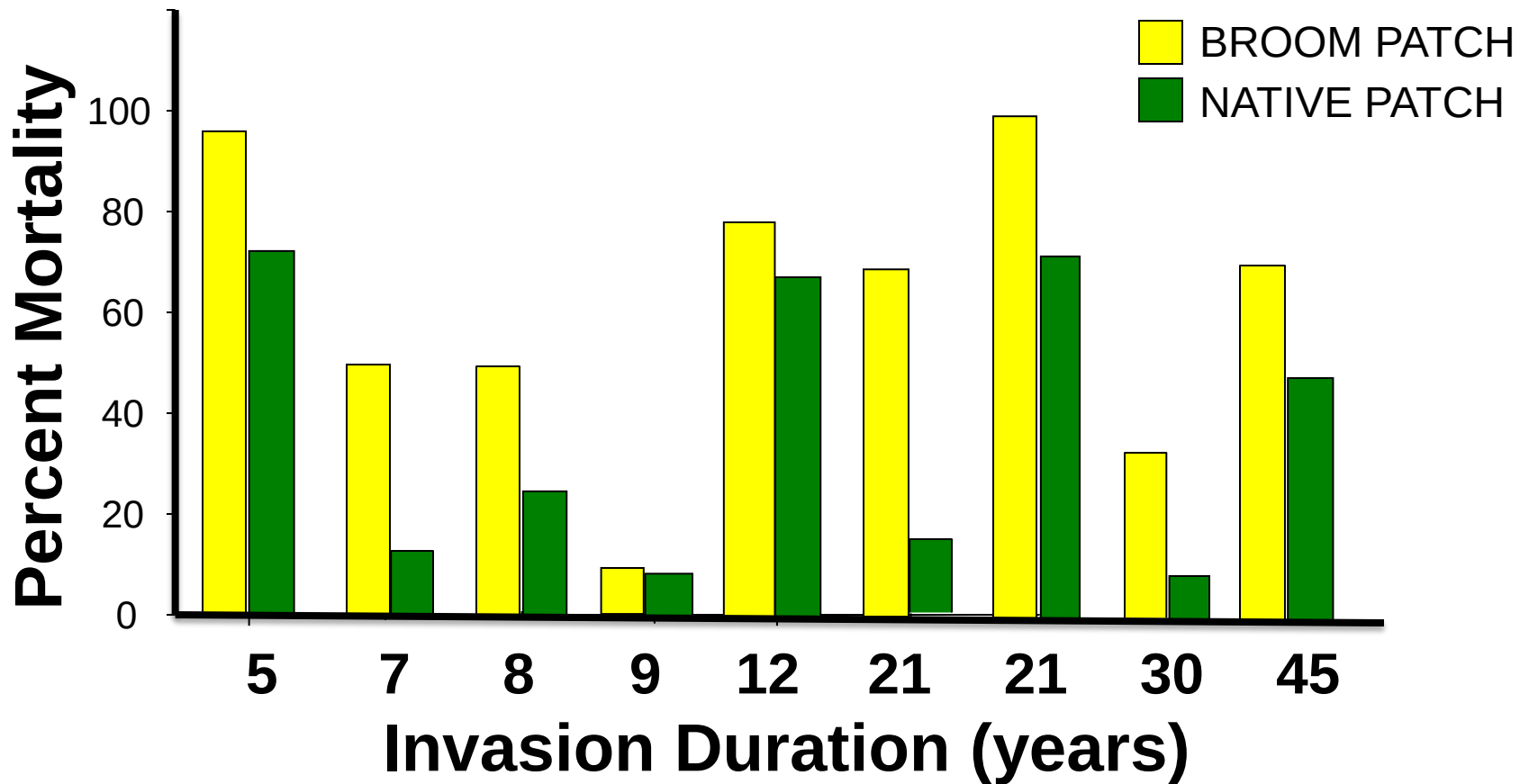
EMF colonization is less in broom invaded soil with no effect of invasion age



Data from greenhouse exp.

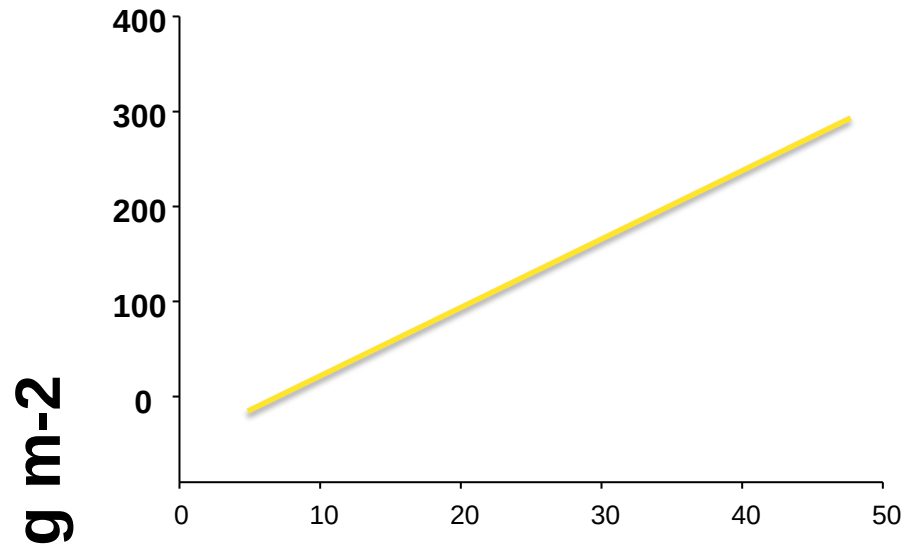
Grove et al. 2017

Doug-fir mortality is higher in invaded patches with no effect of invasion age

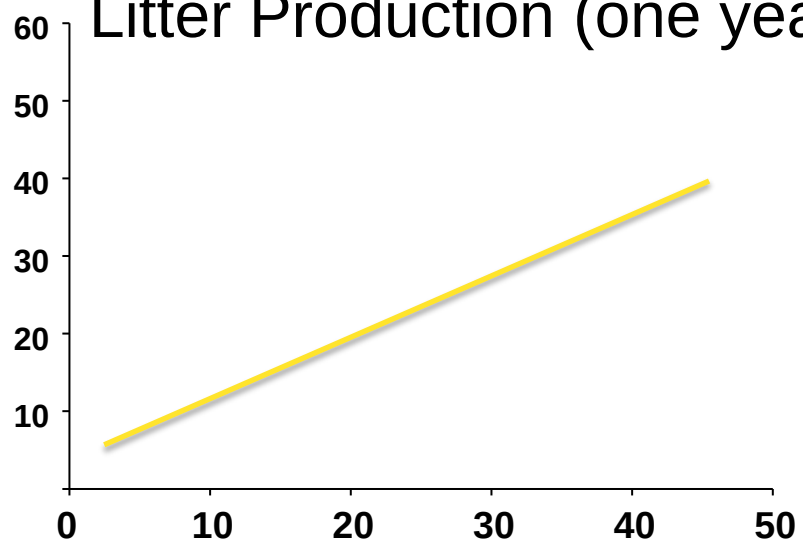


Field Exp.

Broom Aboveground Biomass



Litter Production (one year)



Invasion Duration (years)

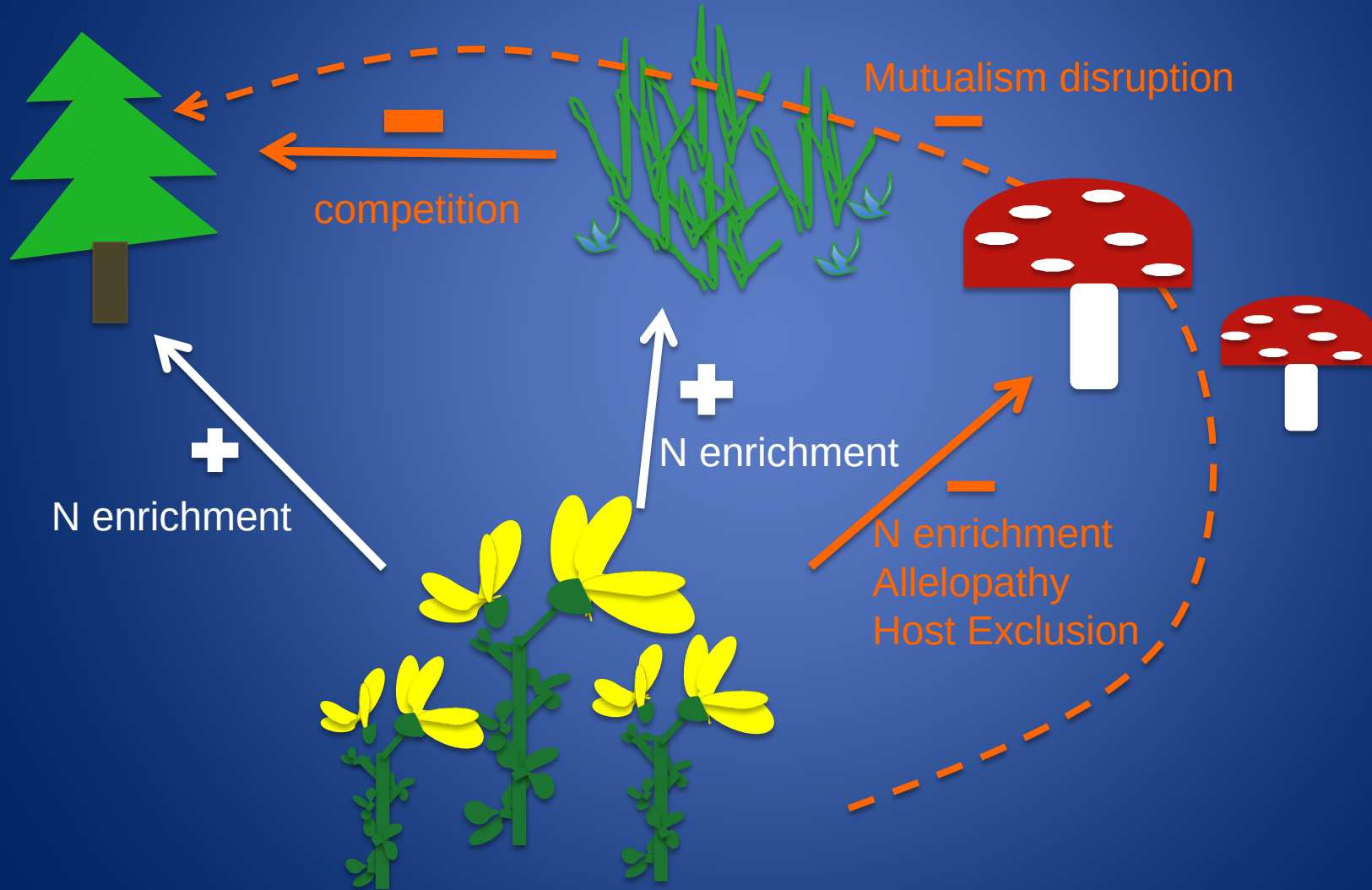
Differences in management

- Fire
- Repeated removals

Differences in soils

- Rockiness
- Organic matter content
- Texture

Scotch broom imparts positive and negative soil legacies

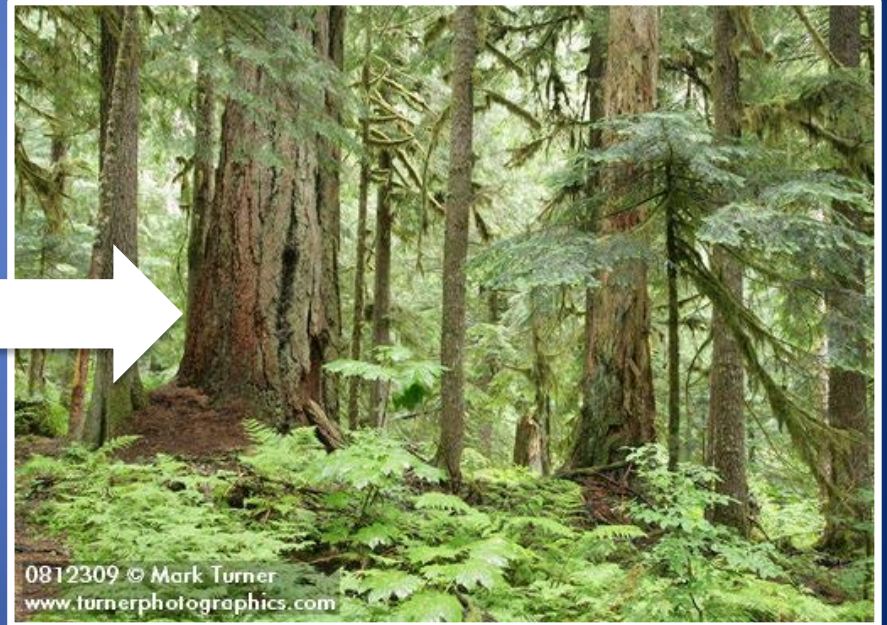


Temporal dynamics following invasion

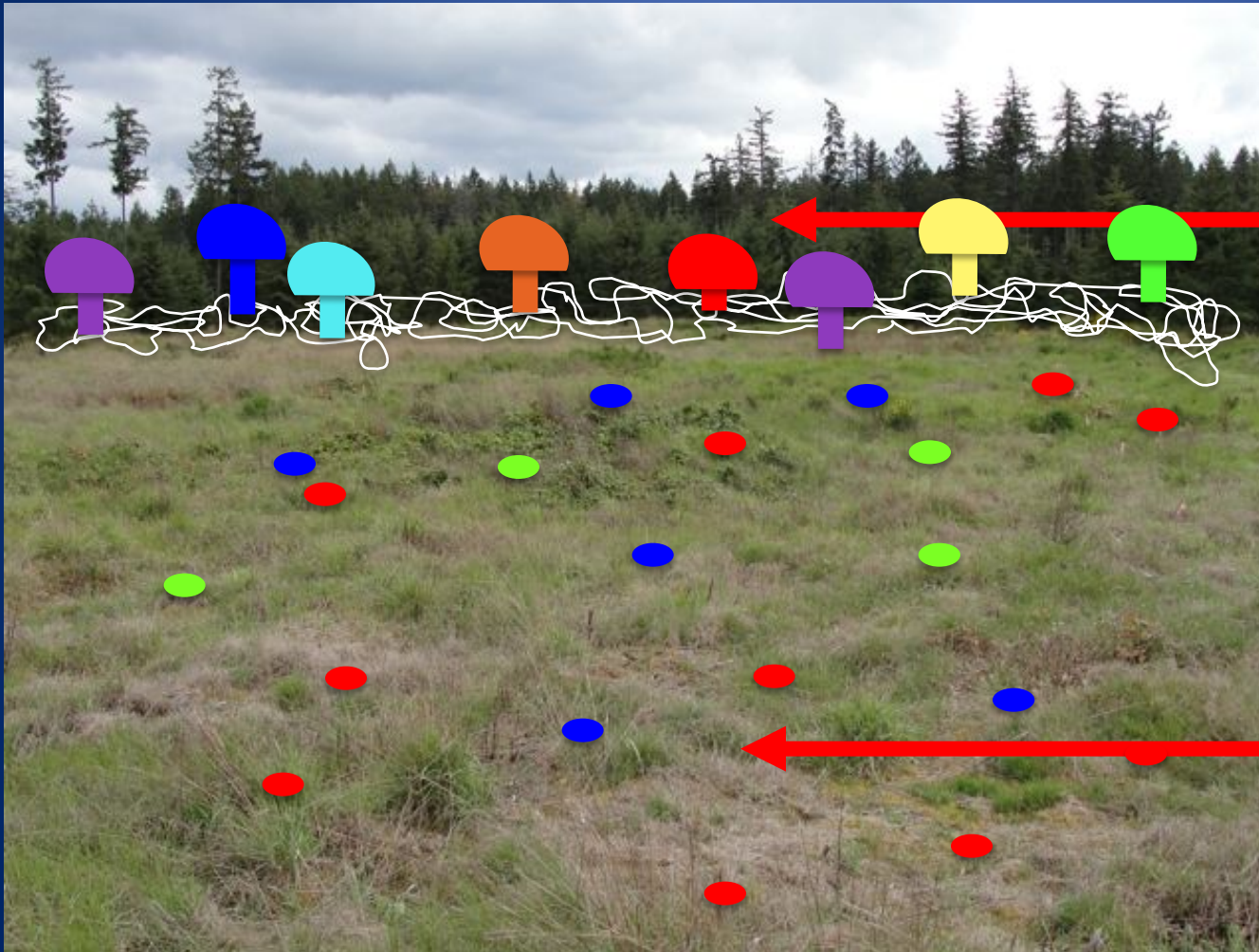
CONCLUSIONS

- Scotch broom changes nutrient pools and EMF abundance and these **impacts persist** following invader removal
- These persistent effects may **limit reforestation success**
- Remove broom before it establishes because the impacts it has on ecosystems **may not be (easily) reversible**
- Invasion age was not a driver of the variation in invasion impacts, for either soil nutrients, mycorrhizal abundance, or Douglas-fir survival.

Reforestation following broom removal



Can planting near to forest edges or transplanting forest soil into the invaded clearcuts increase mycorrhizal colonization and seedling establishment?



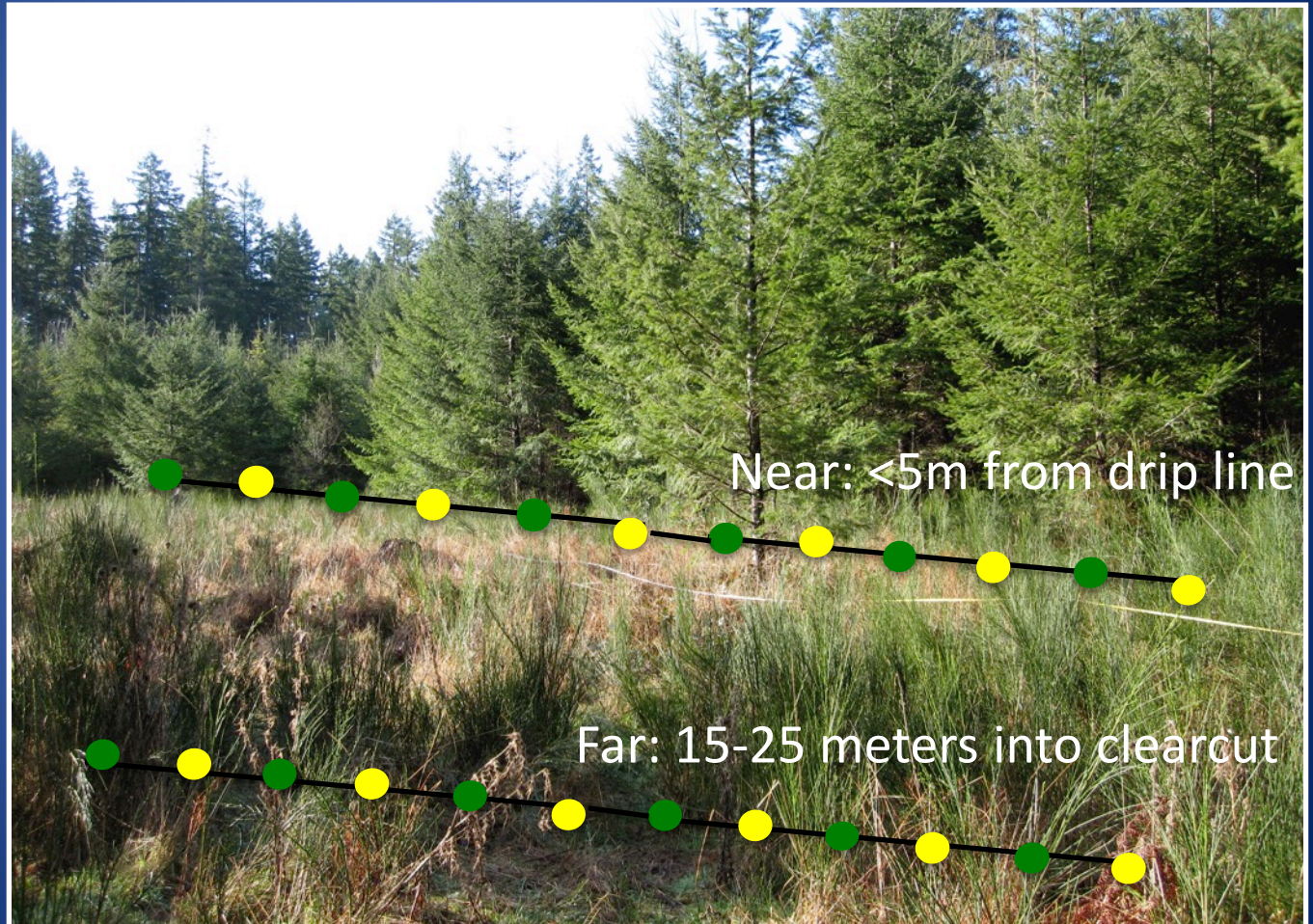
Why did these trees make it,

When nothing survived out here?

Collected and transplanted soils from invaded clearcuts & adjacent forests



Planted trees into broom-invaded or forest soil near to and far from forest edges



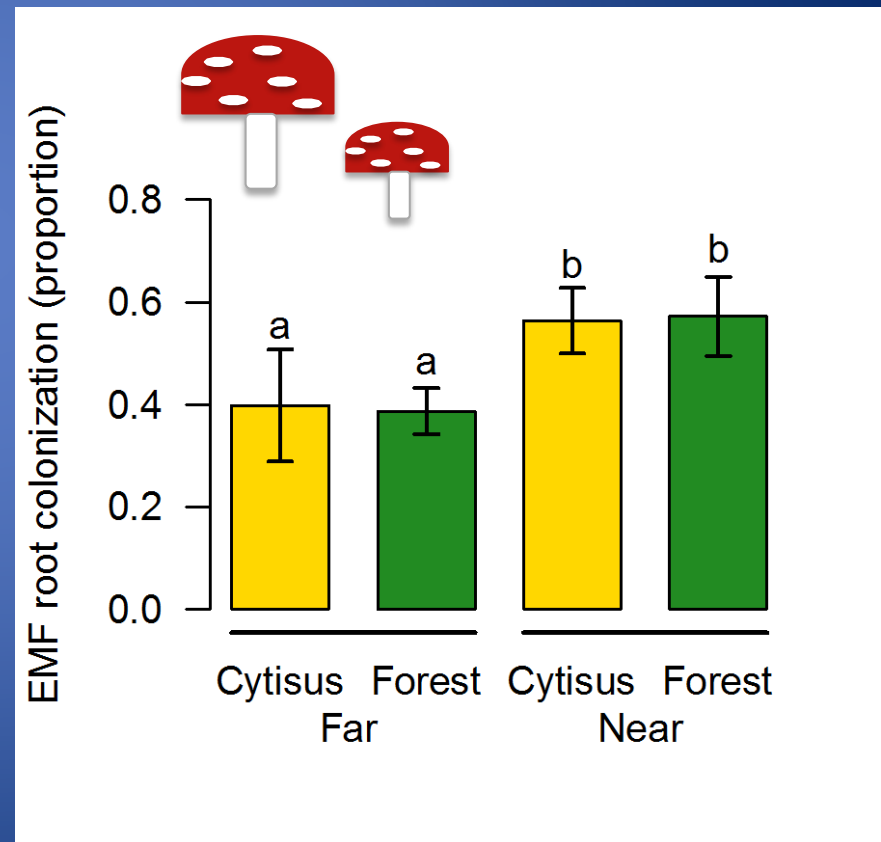
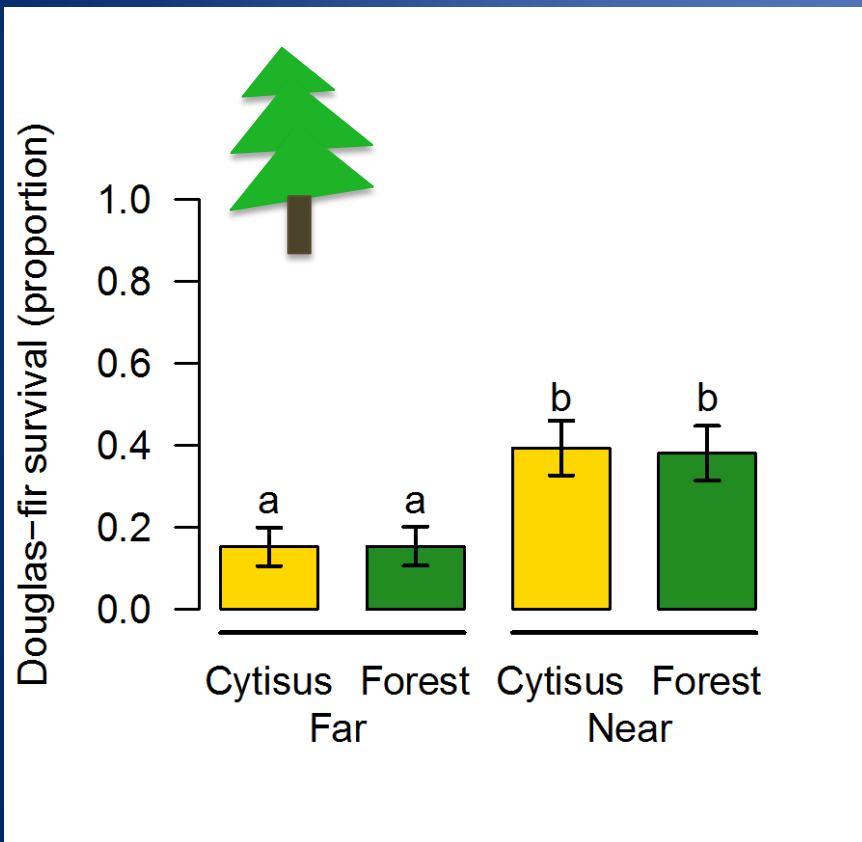
N = 1000 trees

Measured:

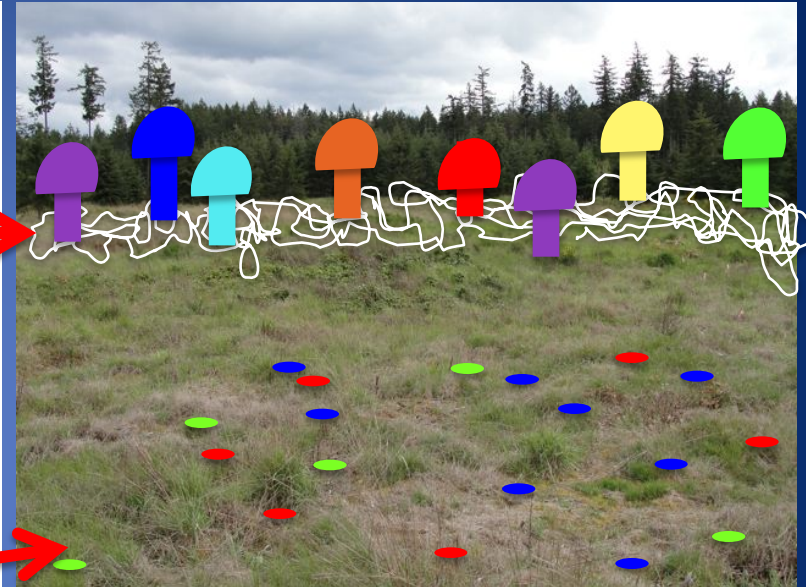
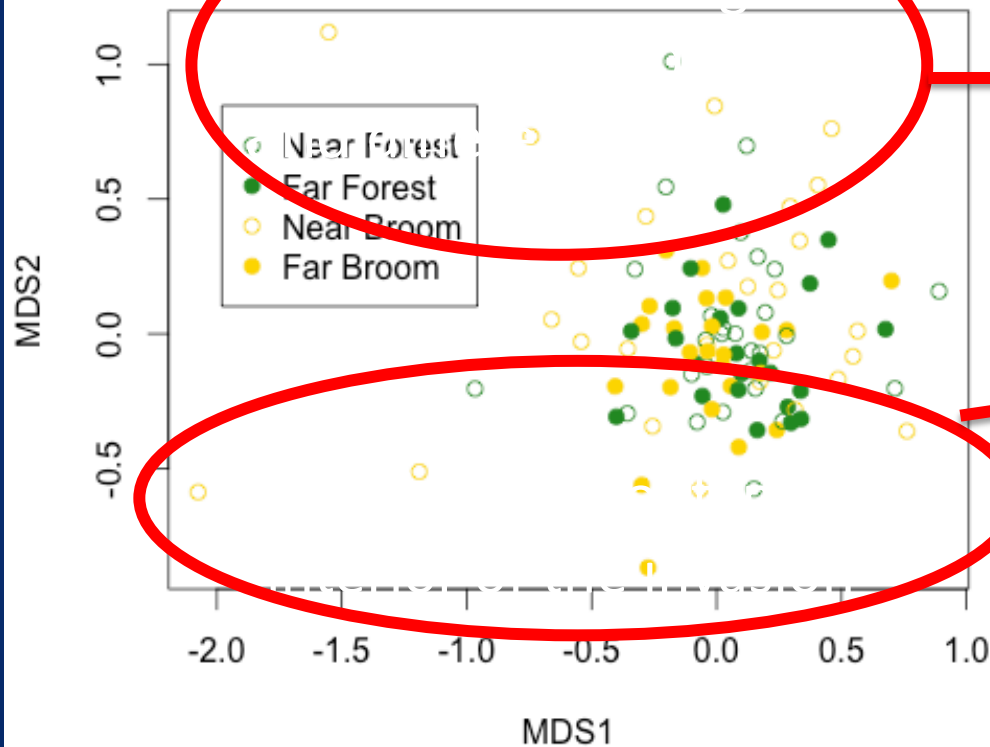
- Abundance and diversity of mycorrhizal fungi
- Douglas-fir survival & growth



EMF abundance and Doug-fir survival were greater near forest edges, but were not improved by forest soil inoculation



Communities by proximity to edge and soil type

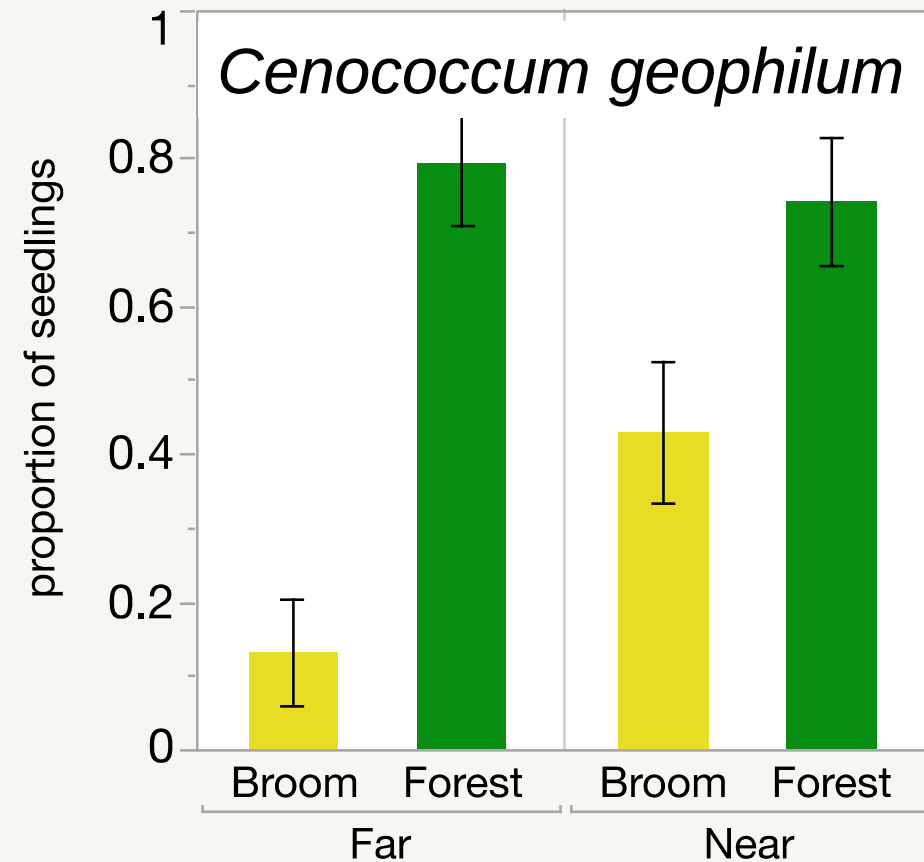


Permanova Term	P value
Edge Proximity	0.005 **
Soil	0.04 *
Edge Proximity x Soil	0.28

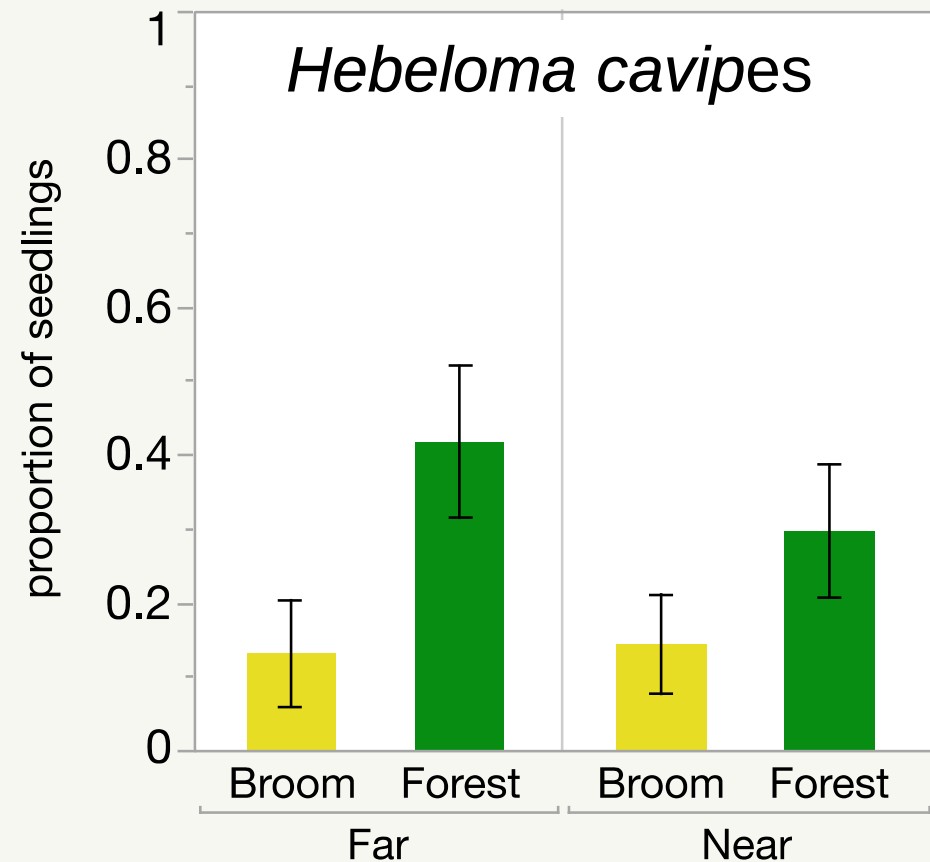
Only 2 dominant taxa responded to soil inoculation or proximity to edge

	% Douglas-fir seedlings colonized				
10 Most Abundant Taxa	Forest Near	Broom Near	Forest Far	Broom far	P value
<i>Wilcoxina mikolae</i>	84	82	83	91	NS
<i>Rhizopogon rogersii</i>	88	82	88	87	NS
<i>Tuber sp.</i>	76	71	71	61	NS
<i>Leucangium carthusianum</i>	60	61	50	56	NS
<i>Inocybe lilacina</i>	52	46	54	52	NS
<i>Tuber anniae</i>	52	39*	46	43	NS
<i>Tomentella coerulea</i>	44*	43	21*	39	NS
<i>Amanita sp.</i>	28*	25*	20*	30*	NS
<i>Hebeloma cavipes</i>	32*	14*	42	13*	0.002
<i>Tomentella sp.</i>	48*	42	42	35	NS
<i>Cenococcum geophilum</i>	80	43	79	13*	0.0001
<i>Inocybe sp.</i>	52	29	33*	30*	NS

Emerging as potentially important EMF species impacted by broom invasion

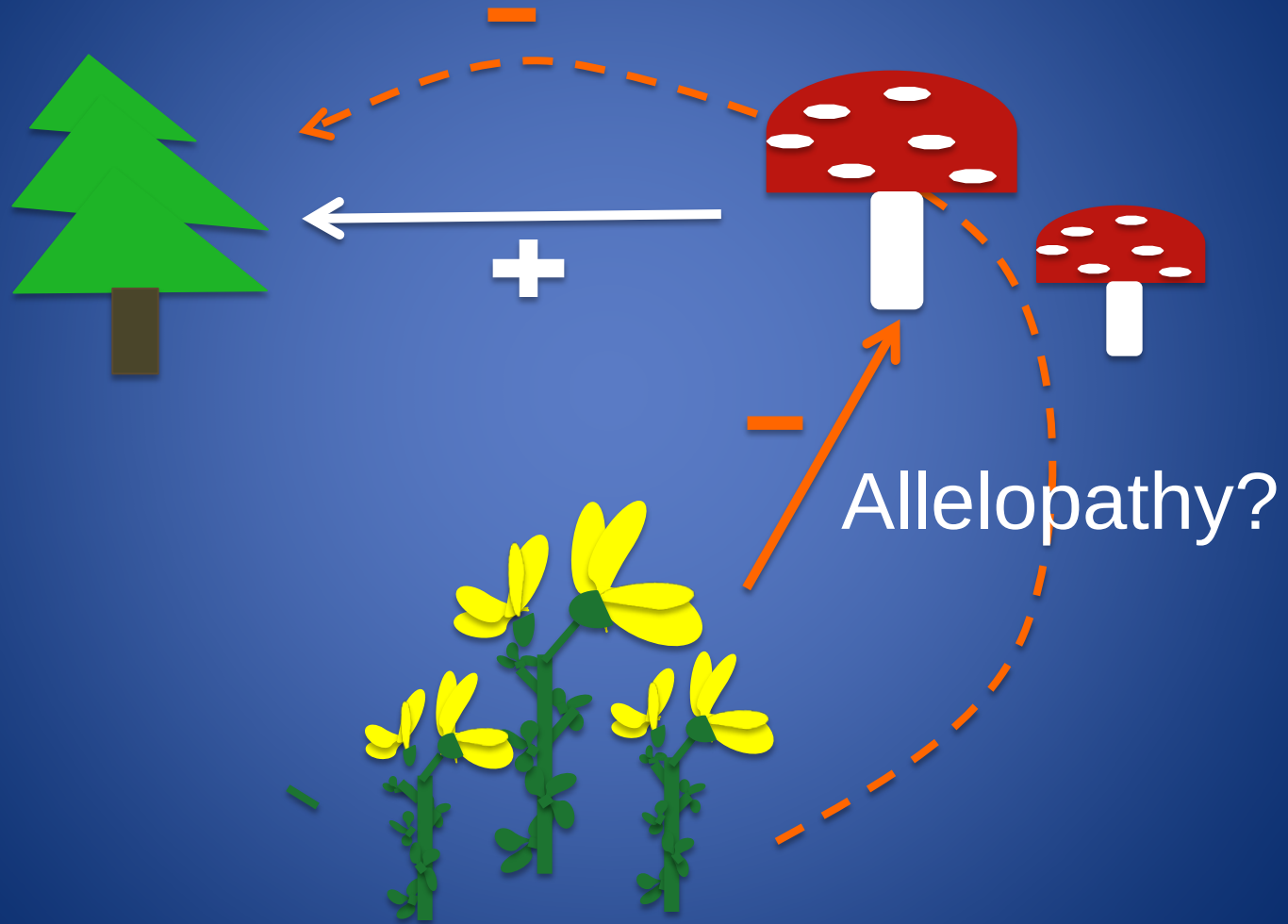


Proximity 0.16
Soil <.0001*
Proximity*Soil 0.05*

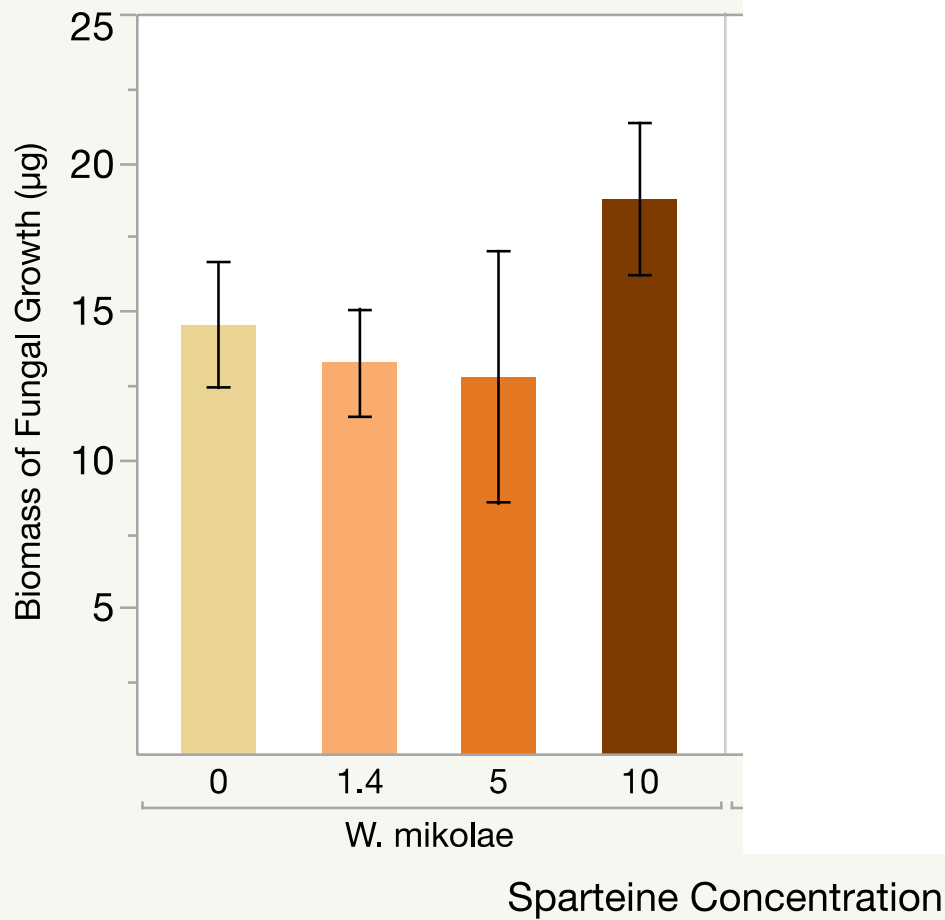


Proximity 0.34
Soil <.0001*
Proximity*Soil 0.28

Is allelopathy a mechanism for changes in the ectomycorrhizal community?

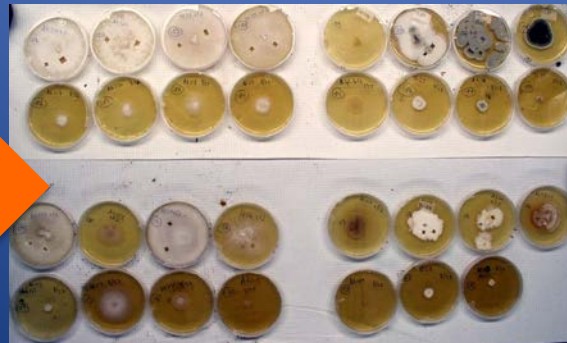
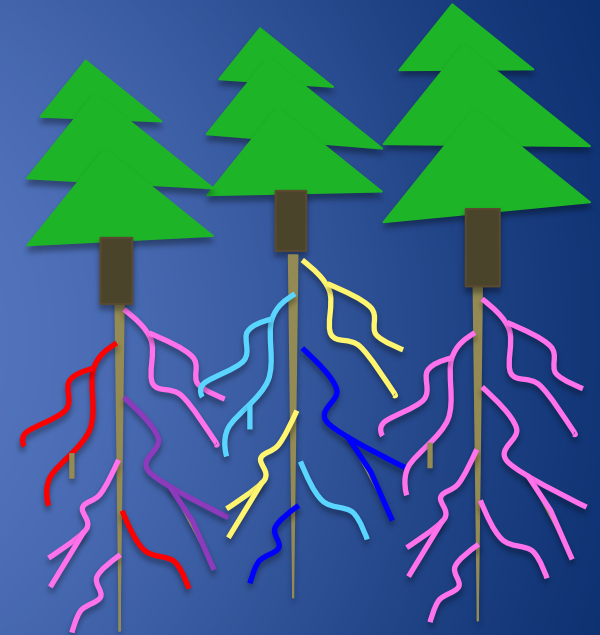


Sparteine effects on ectomycorrhizal fungi vary across species



Ongoing work: Does community composition of EMF matter?

- Inoculate Doug-fir seedlings with different species of EMF
- Plant into broom invaded areas
- Compare Douglas-fir performance



Acknowledgements

30+ UCSC undergrads – They do all the work!

Friends and family in WA – They help for free (in the rain!) just because they love us and support the cause

Sara Hammond at CNLM– Intellectual and moral support and providing AmeriCorps interns

Bill Taylor - WA-DNR Websters Forest Nursery

Steve Loy, Gary Schuyten, and Mark Wittenberg at **Green Diamond Resources**

Jeff Foster, Nancy Benson, and others at **Joint Base Lewis McChord**





Questions?



How to control it?

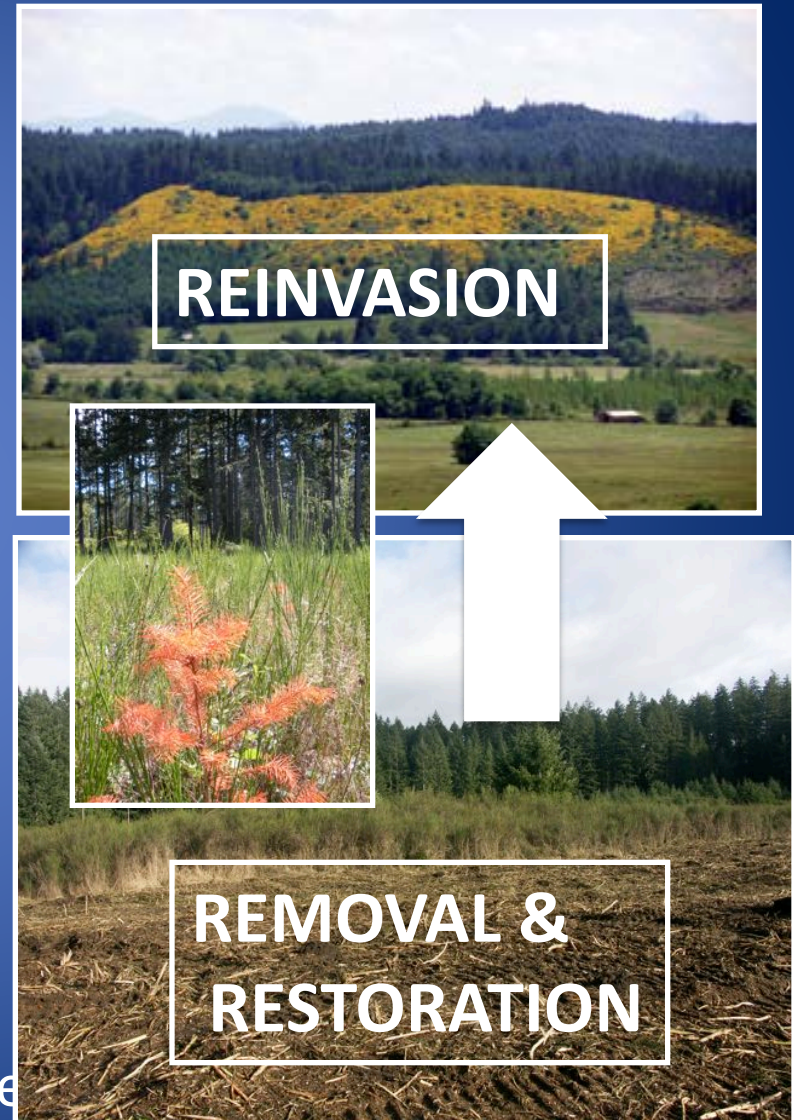


Ongoing Research Needs:

- The legacy effect pathways identified with our greenhouse experiments may not be capturing enough of the complexity in the system
- Future work: fungal community experiments, sparteine addition experiments, role of secondary invaders as competitors, longer legacy time horizon for soil recovery, does age of invasion affect effect size of soil impacts?

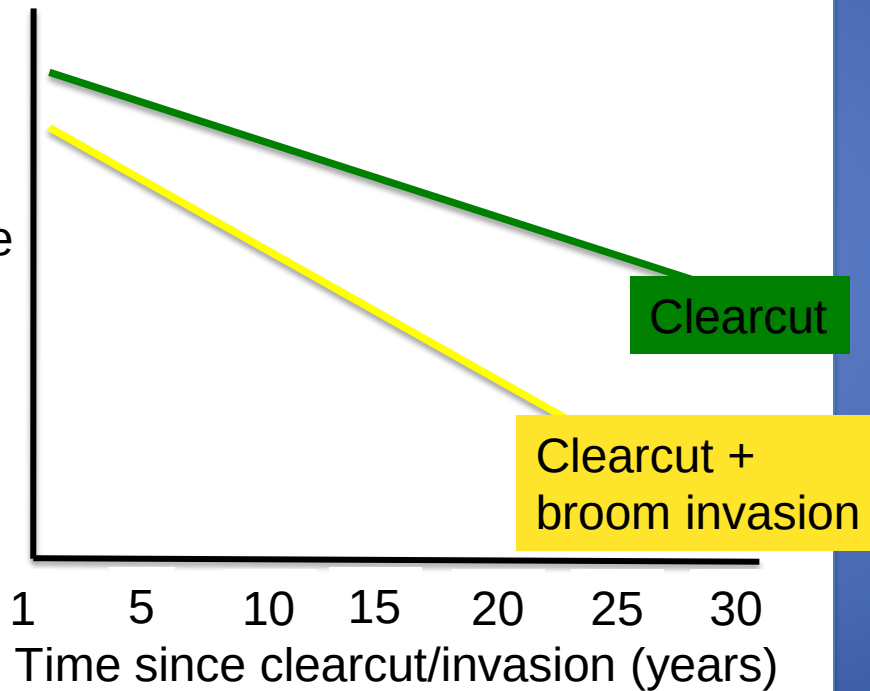
Invasions & Alternative Stable States

- Useful concept for prioritizing management
- All managers have way more populations than resources to manage them
- Difficult to measure alternative stable states
- -can look for signs of feedbacks that promote self reinforcement
- Assuming an invasion is irreversible could result in unnecessary abandonment of impacted areas and further degradation of natural resources



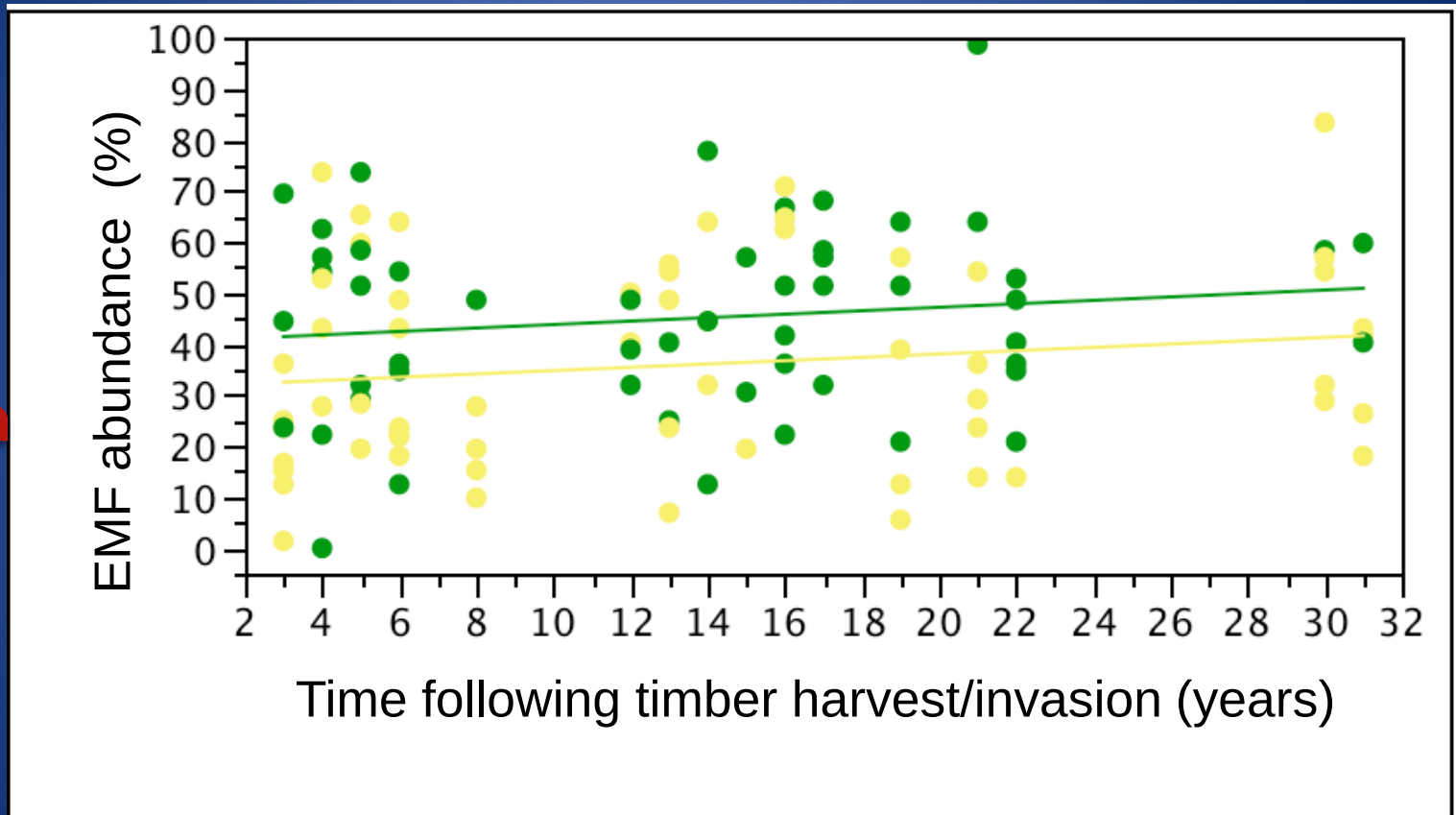
How does **Doug-fir** respond to time-since-invasion?

Expected results



- 1) negative effect of time following clearcut
- 2) Negative effect of invasion

EMF abundance decreases with invasion but is unaffected by time-since-invasion



ANCOVA

Invasion status

Time Since clearcut/invasion

Invasion status x Time since clearcut

P

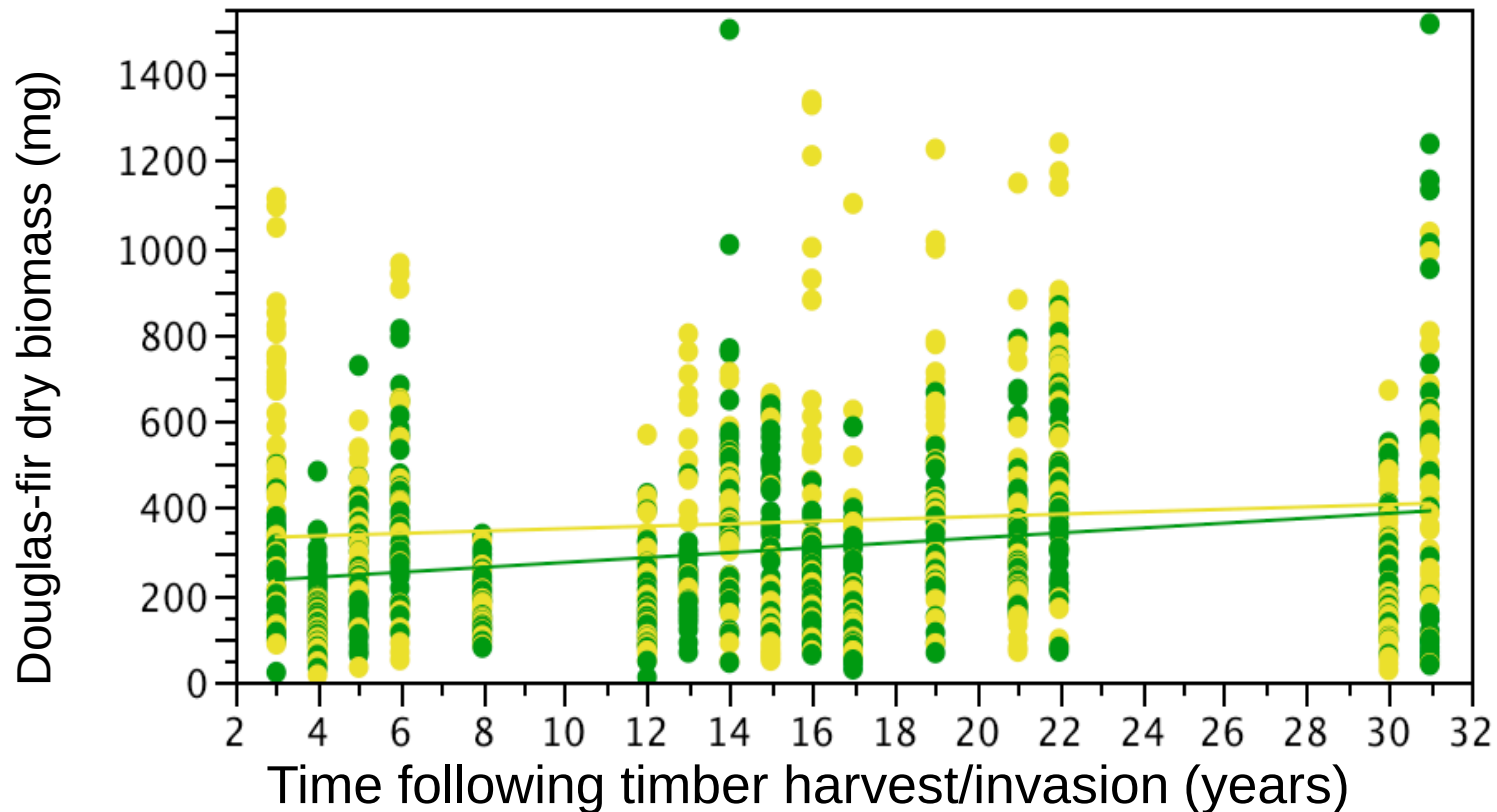
0.0002

NS

NS



Doug-fir growth increases with clearcut age AND with invasion



ANCOVA

P

Time Since Clearcut

0.0001*

Invasion Status

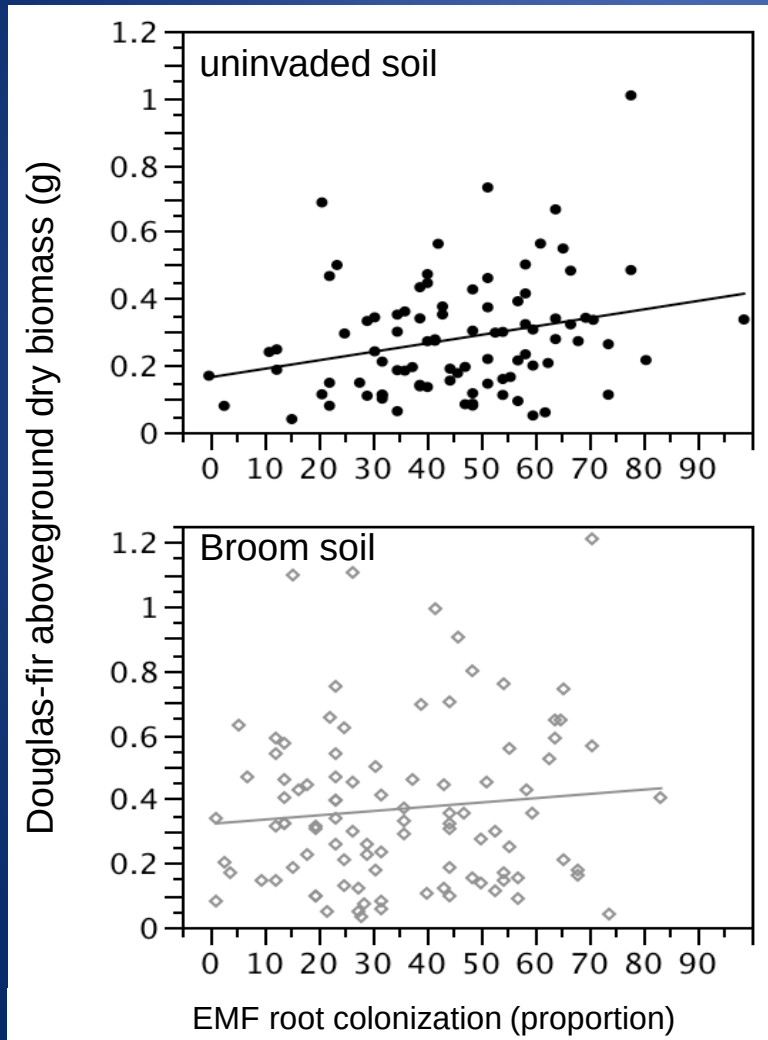
0.0001*

Time Since Clearcut x Invasion Status

0.09



Importance of EMF to Doug-fir growth is context dependant



- In uninvaded clearcut soils Doug-fir **grow more** as EMF abundance increases
- In broom invaded clearcut soils Doug-fir **do not benefit** from increased EMF abundance

Possible explanation:

Primary role of EMF is to provide N. When N readily available the mutualism loses value & and Doug-fir abandon the fungi

How do impacts of Scotch broom change with time?

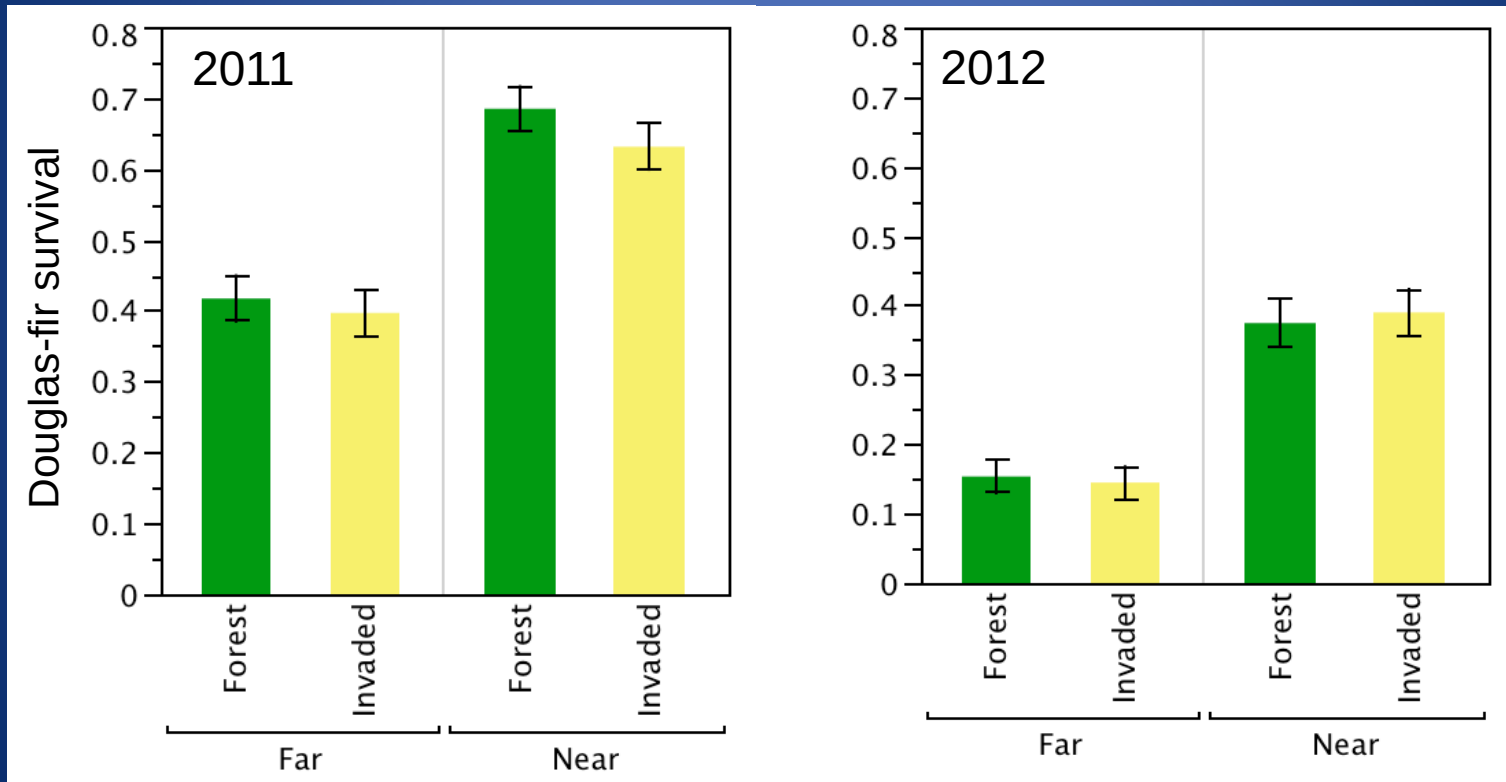
- Invasion does decrease the abundance of EMF
 - Effect occurs quickly
- EMF loss does not necessarily translate into decreased seedling growth
- Effects of invasion on Doug-fir are slightly positive with time-since-invasion
- Broom legacies can have positive effects on Douglas-fir
- It remains unclear when the net effect of broom legacies on Doug-fir is going to be positive or negative.

How can we mitigate the soil legacies of Scotch broom and improve reforestation success?





Edge Effects: Doug-fir survival

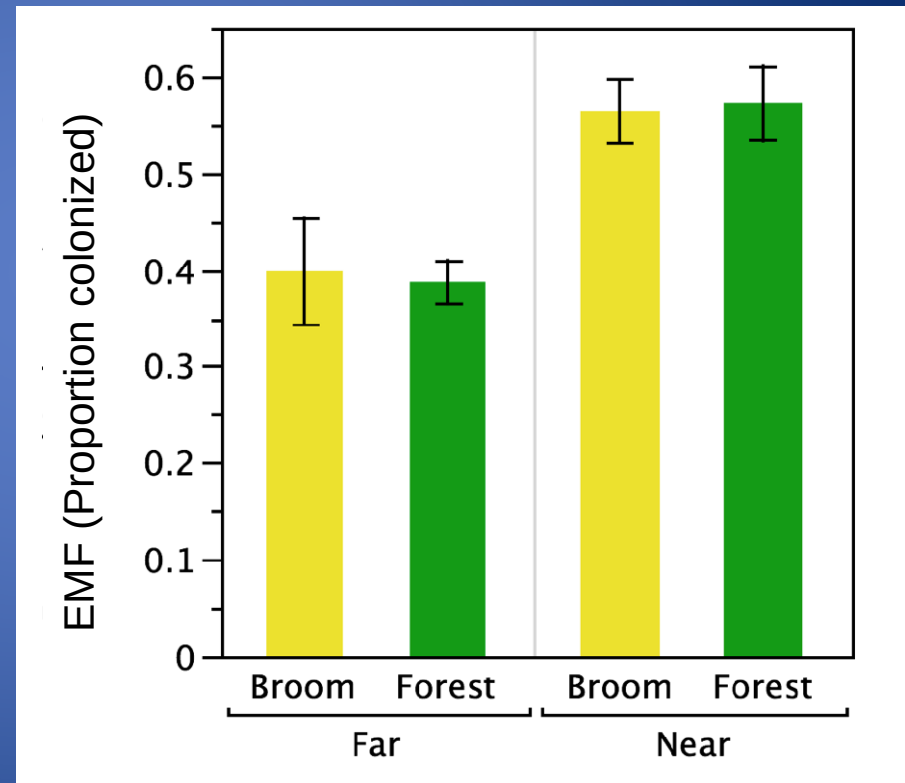
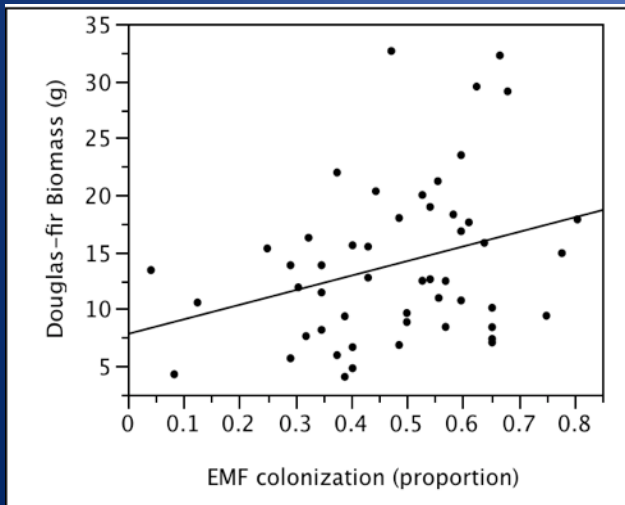


Edge: $P < 0.0001$
Soil transplant: $P = 0.10$

Edge: $P < 0.0001$
Soil transplant: NS



Edge Effect: EMF abundance



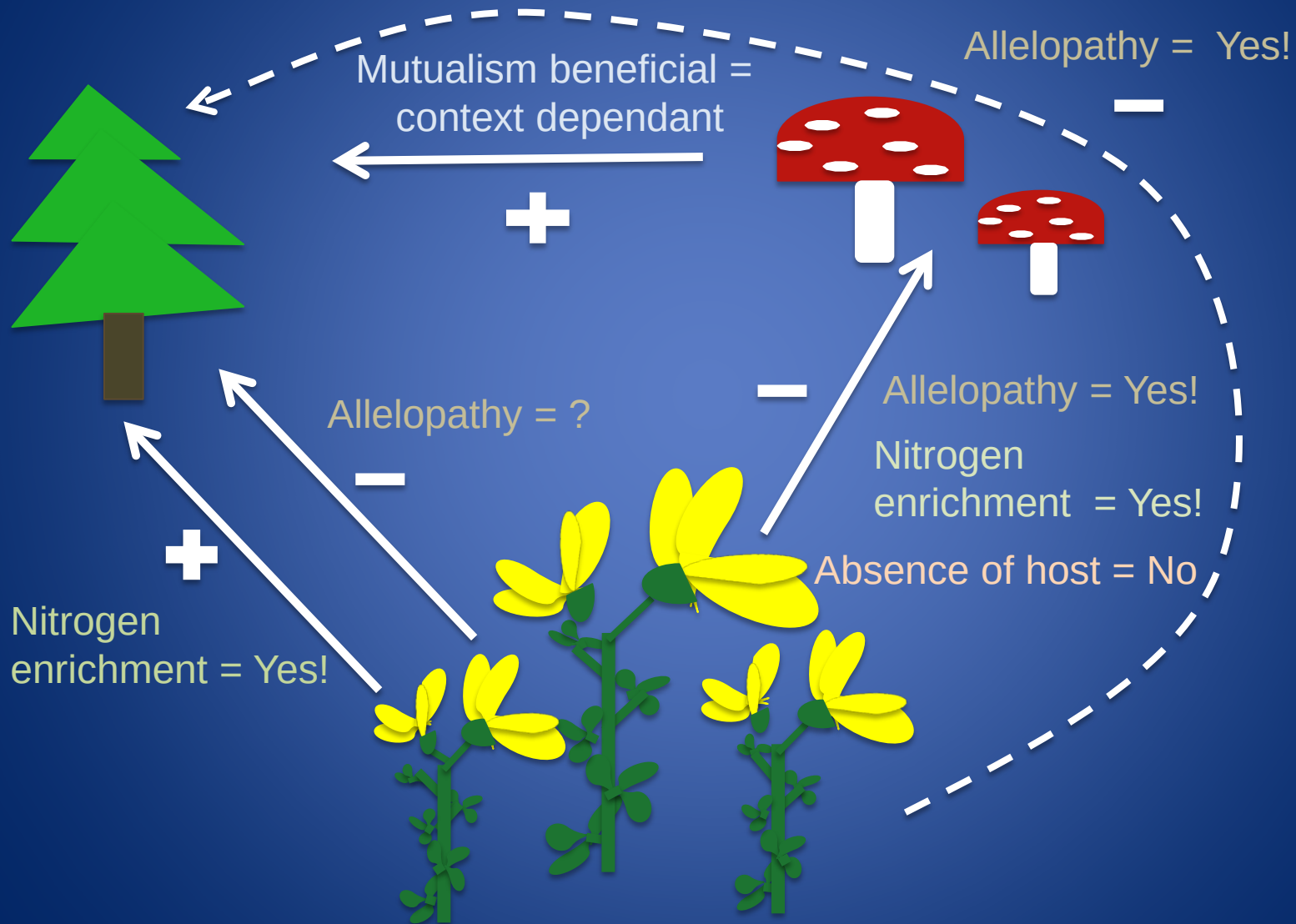
Proximity to edge: $P < 0.0001$
Soil transplant: NS

Management recommendations

- Replant near edges
- Don't bother transplanting soil
- Design timber harvest to maximize edges

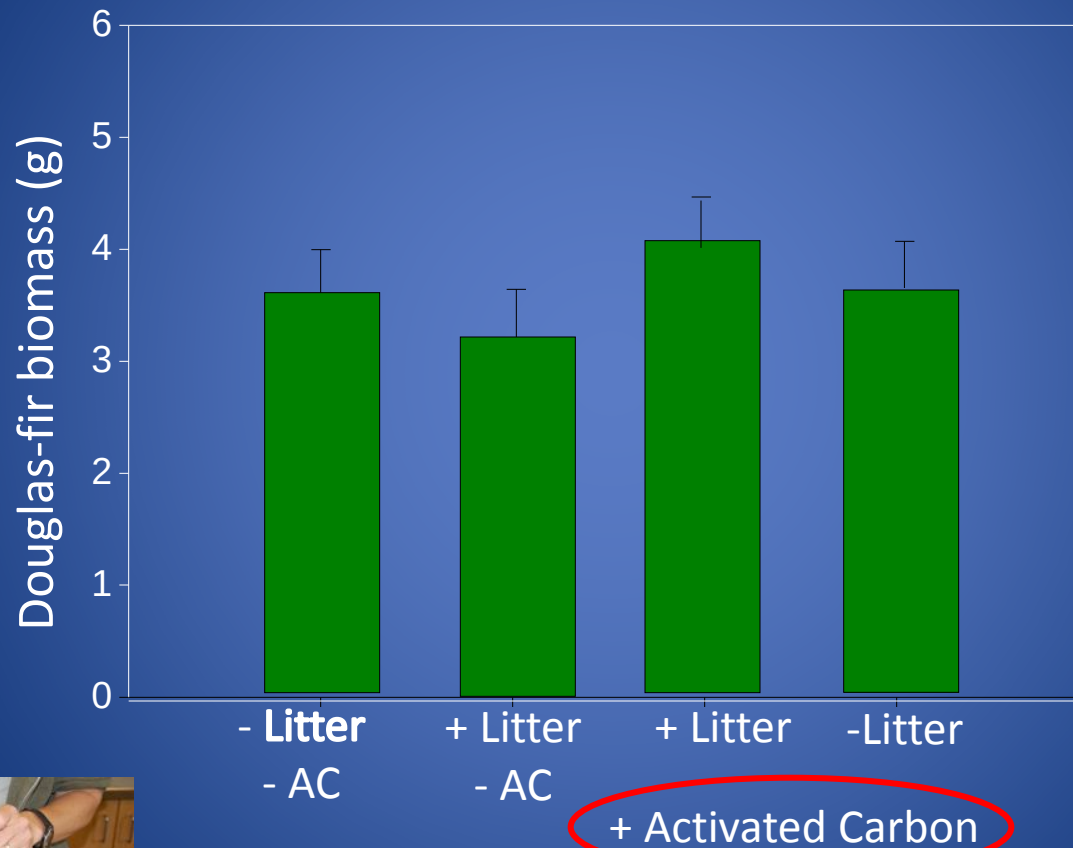


Direct and indirect pathways for soil legacy effects



Evidence for Allelopathy

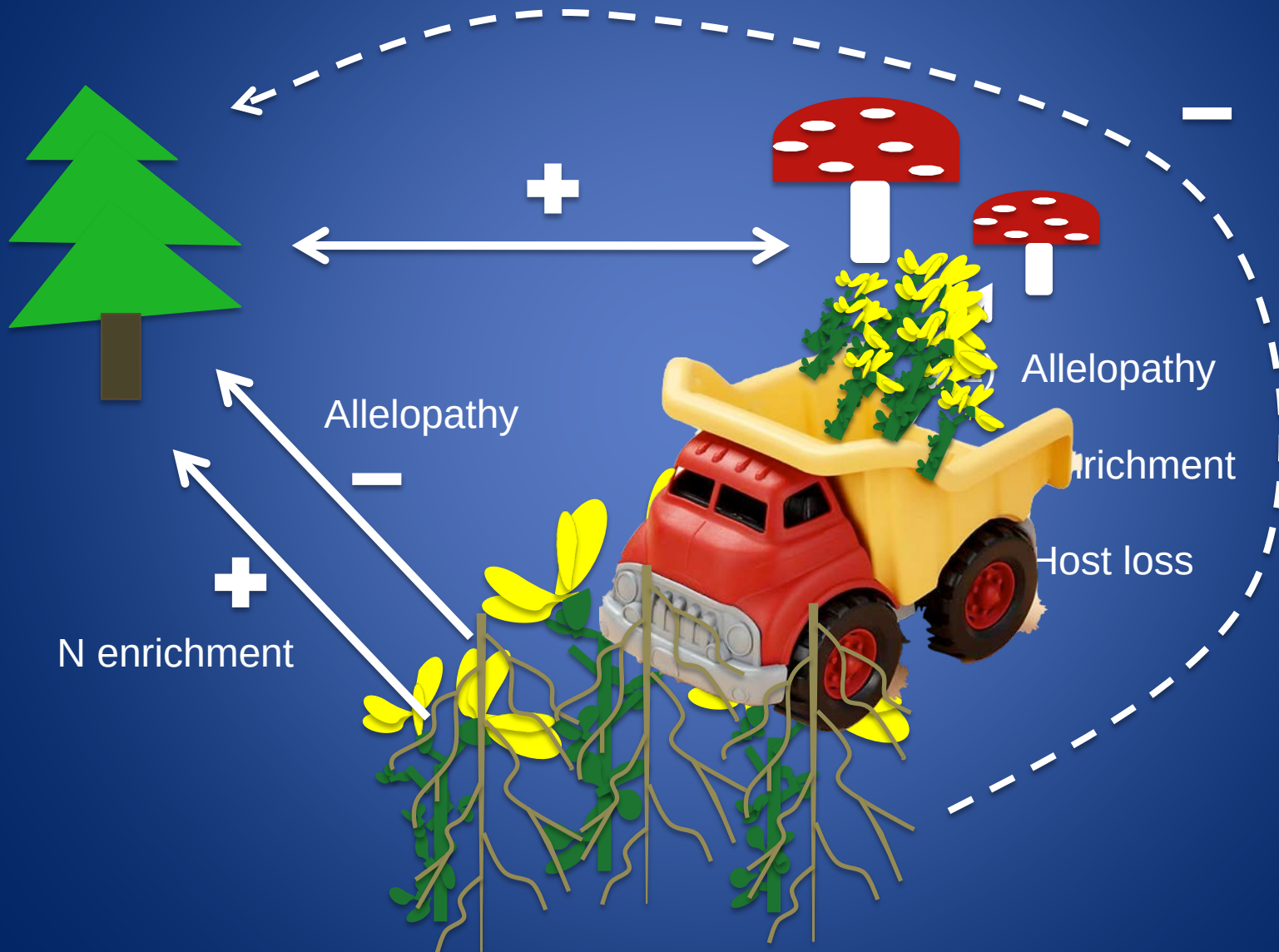
results from a broom mulch addition experiment



Forest soil



Potential pathways for soil legacy effects

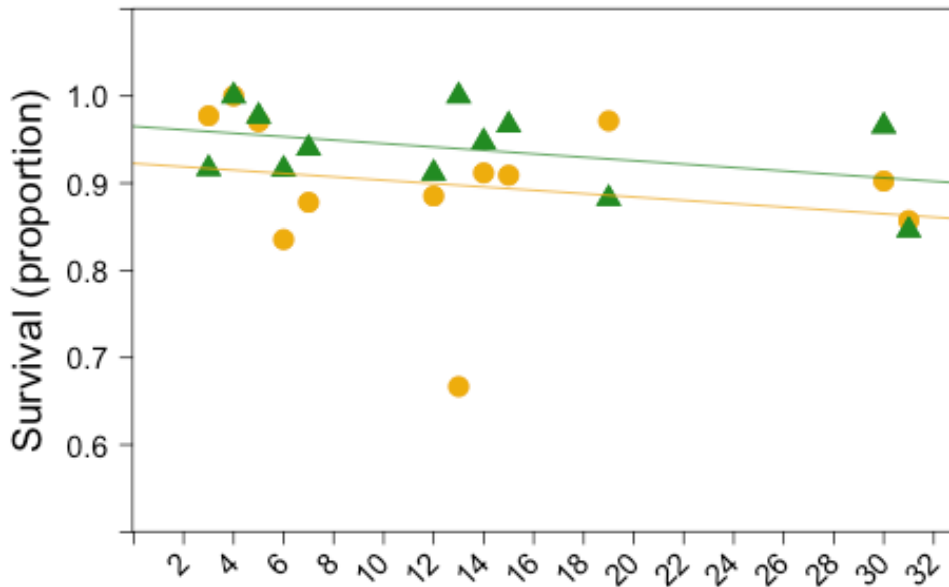
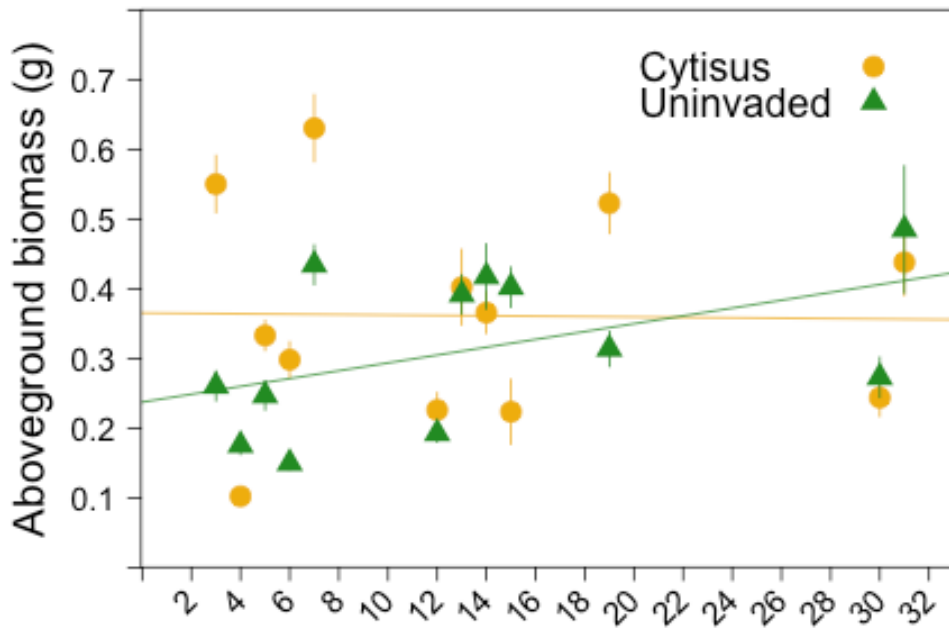


Dissertation questions

- Is there a legacy effect of Scotch broom that inhibits reforestation?
- What are the direct and indirect mechanisms?
- How long do the legacy effects persist following broom removal?
- Does impact increase with time-since-invasion?
- How can we mitigate the soil legacies of Scotch broom and improve reforestation success?

How to control it?





Doug-fir survived
and grew more in
uninvaded soil

Greenhouse Experiment

How do impacts of invasive species change with time?

Impacts could increase

- Abiotic changes may accumulate over time
- Invaders could acclimate over time to conditions in introduced range

Impacts could decrease

- Evolutionary and ecological responses to invaders can attenuate impacts
- Exception to the rule
 - Otherwise we wouldn't really worry about invasions

Invasive Tamarix



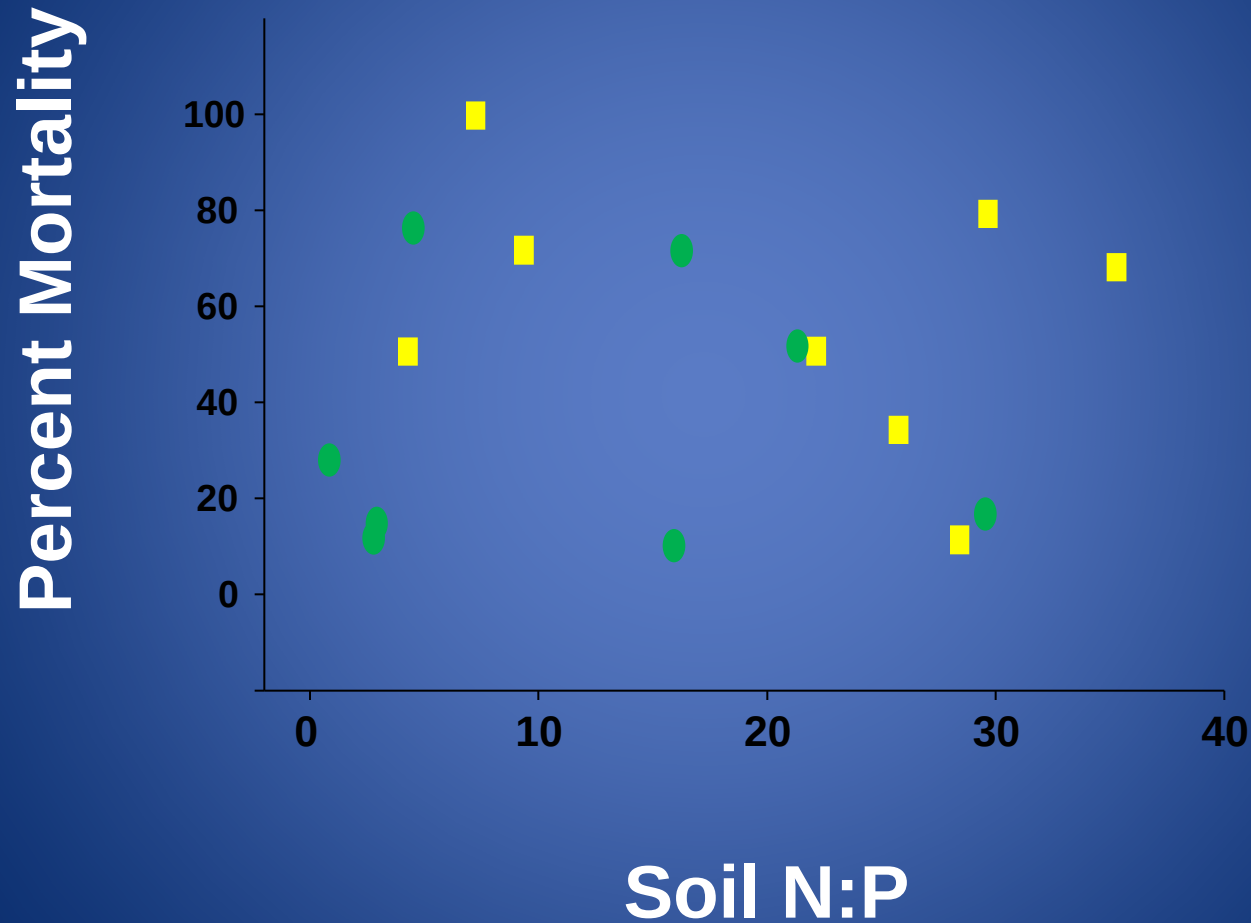
Invasive cane toad



Native snakes



Is DF mortality associated with soil nutrients?



1. Who do manage invasive species for?

- a) Federal agency
- b) State agency
- c) Local gov. agency (county, city, etc.)
- d) Non-profit
- e) Volunteer
- f) Private org. (consultant, etc.)

2. If not using herbicide to control invasive plants, why not?

- a) Human health
- b) Public pressure
- c) Infrastructure/capacity
- d) Cost
- e) Other

3) **Why do you chose to use herbicide?**

- a) Long term effects
- b) Not enough man power for other options
- c) Direct evidence that it is more effective
- d) Outside evidence that is more effective
- e) Cost effectiveness