Understanding Tree Mortality through Dendroecological Studies

Alison Macalady

Introduction to Dendrochronology

Oct. 12, 2010

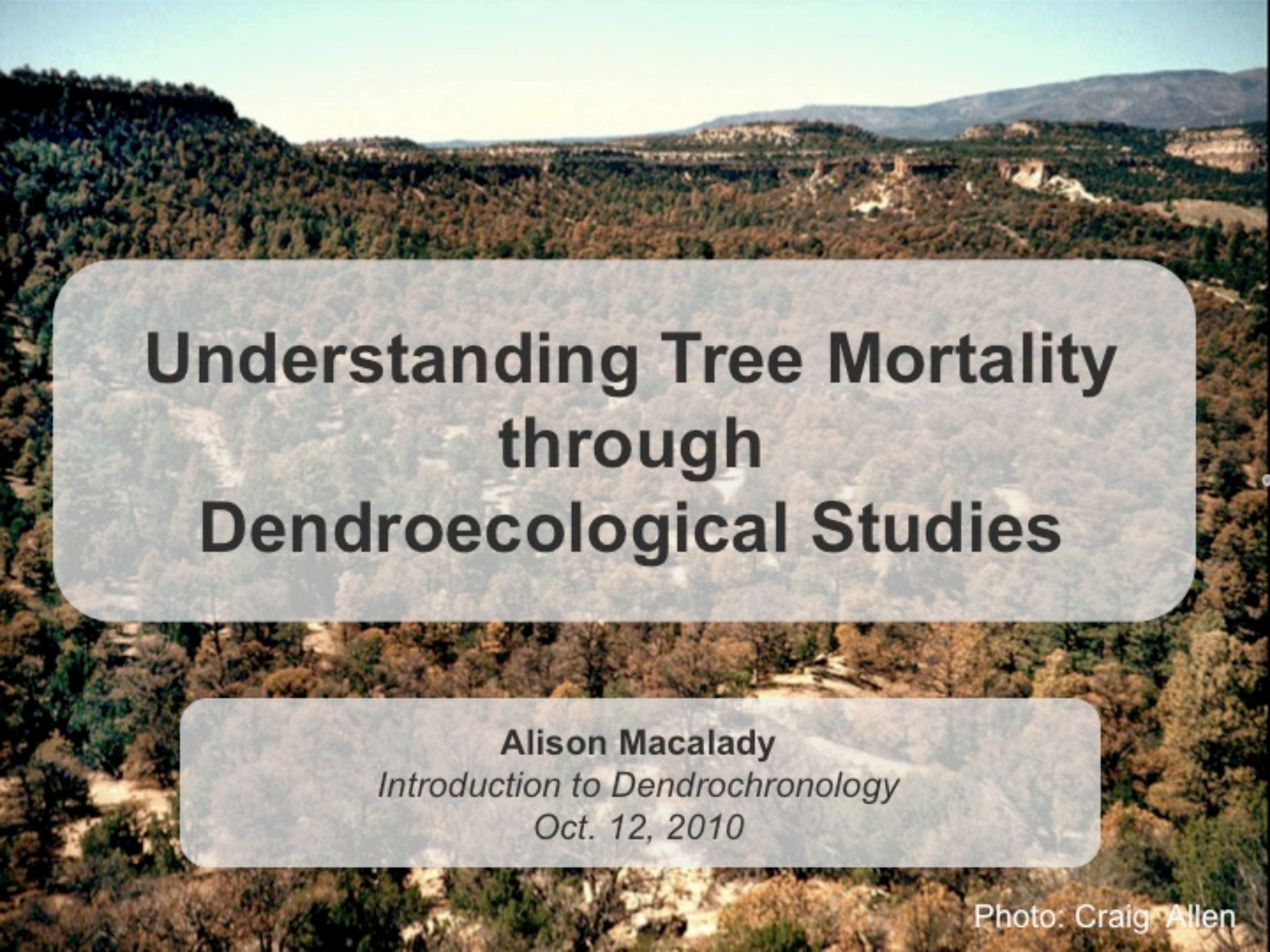


Photo: Craig Allen

Outline

- **Tree mortality – Why is it important?**

- **Why do some trees live and others die?**
  - Leading theories of tree mortality

- **Dendroecological approaches to studying tree mortality**

- **Some recent results from my research**

Tree Mortality – importance

Allen, Macalady et al. *FEM 2010*

Tree mortality due to drought and heat is widespread

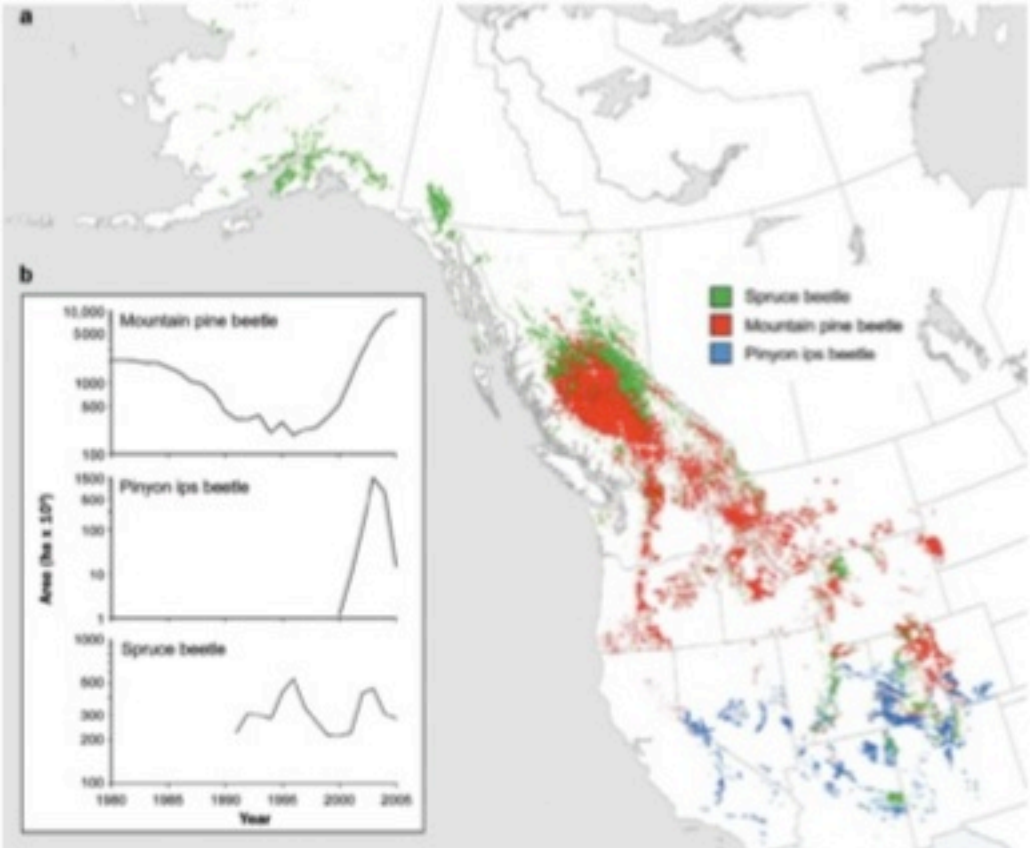
Slide credits: Slides 3:7 & 9 modified from slides by N. Mcdowell

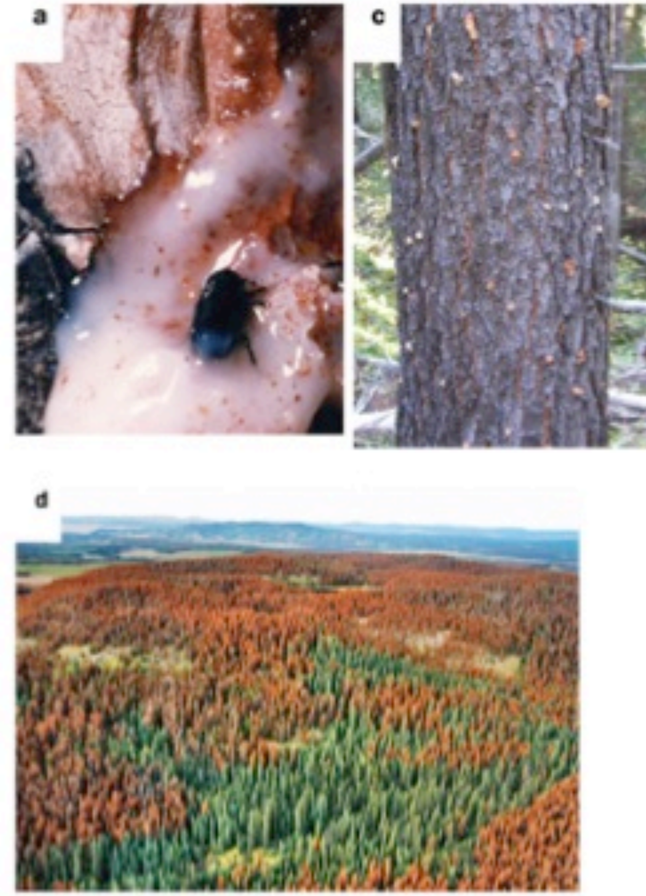
Distribution of documented, recent mortality due to drought and heat.

No global monitoring network exists.

Is it increasing?

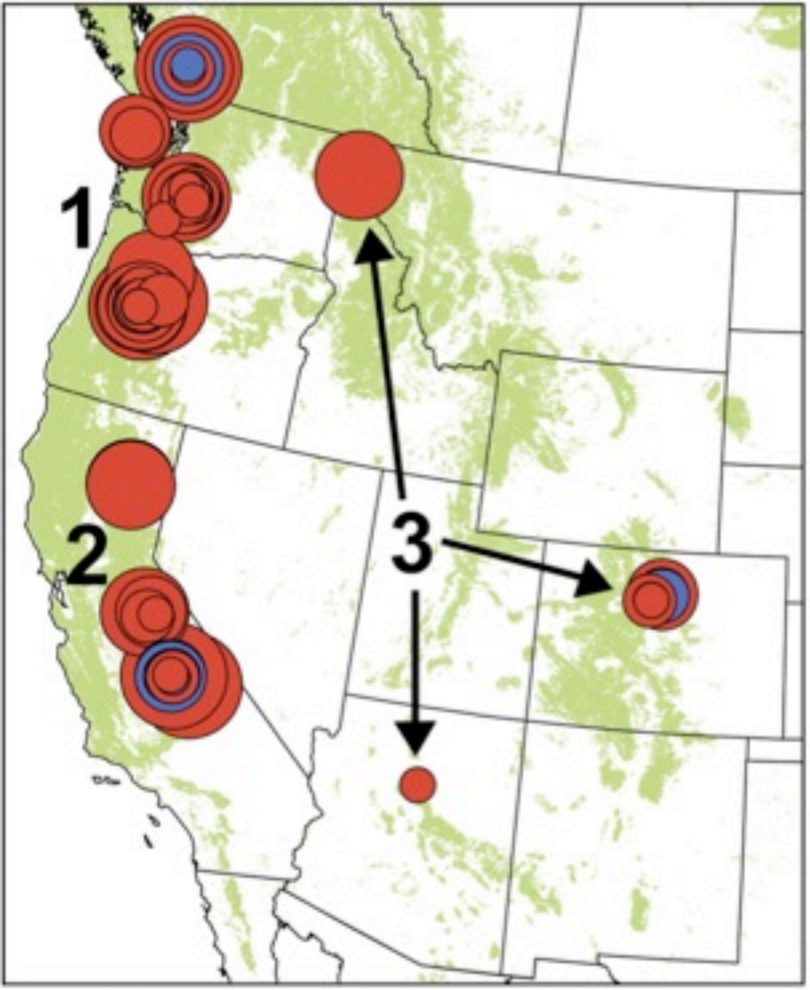
The western North American perspective



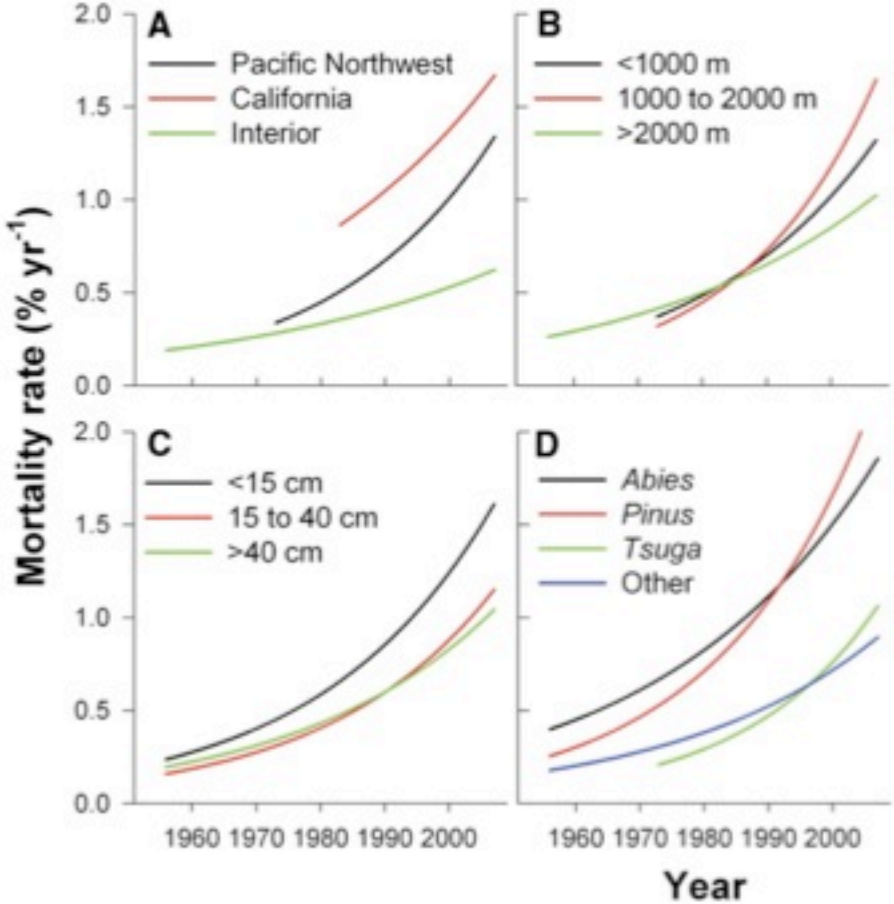


L – Areal assessment of recent mortality in N. America.
R – Bark beetle evidence on trees and across forested landscapes

Raffa et al. Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. *Bioscience 2008*



Red dots=increased mortality
Blue dots = decreased mortality



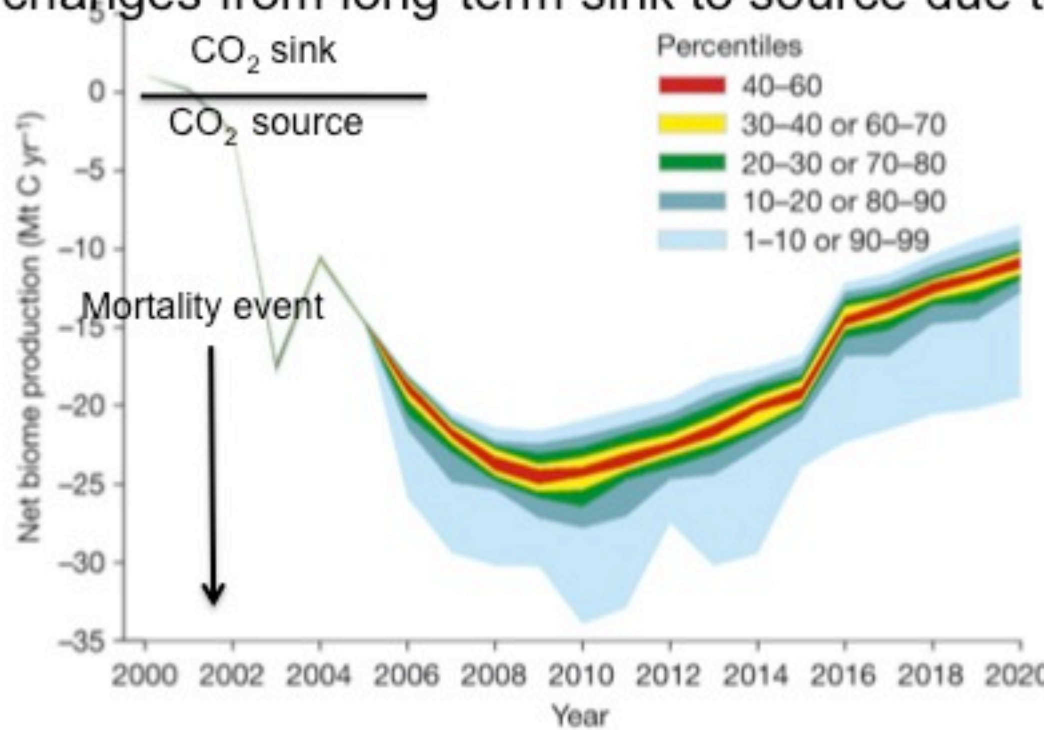
"Background" tree mortality rates increasing across the region; corresponds to increases in temperature.

Van Mantgem et al.
Widespread increase of tree mortality rates in the Western United States.
Science 2009

Why does tree mortality matter?

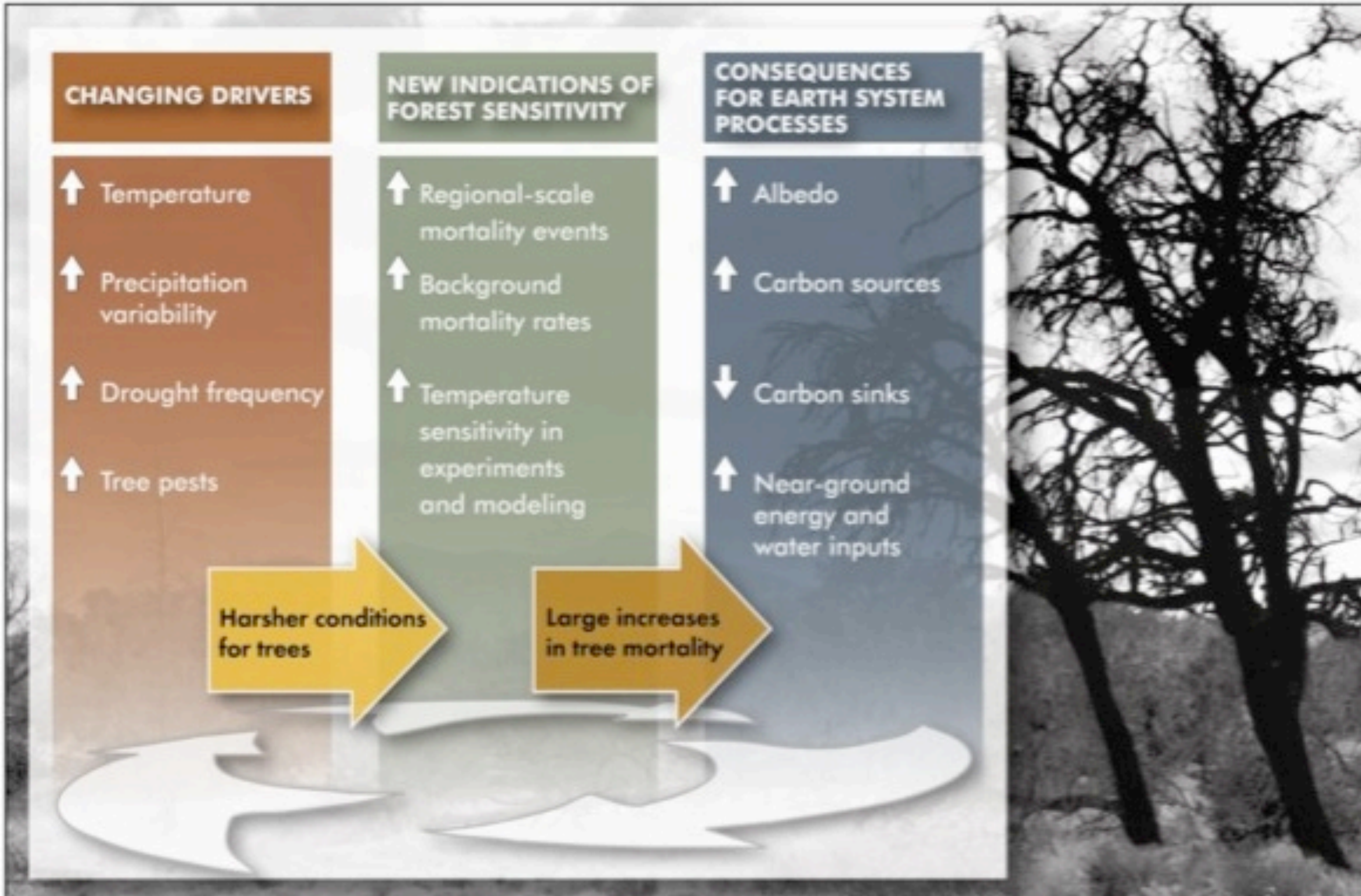
Abrupt changes in tree mortality rates can have major impacts on carbon budgets and climate policy

- MBP outbreak equivalent to 5 years of emissions from all of Canada's transportation sector.
- Amazon changes from long-term sink to source due to 2005 drought



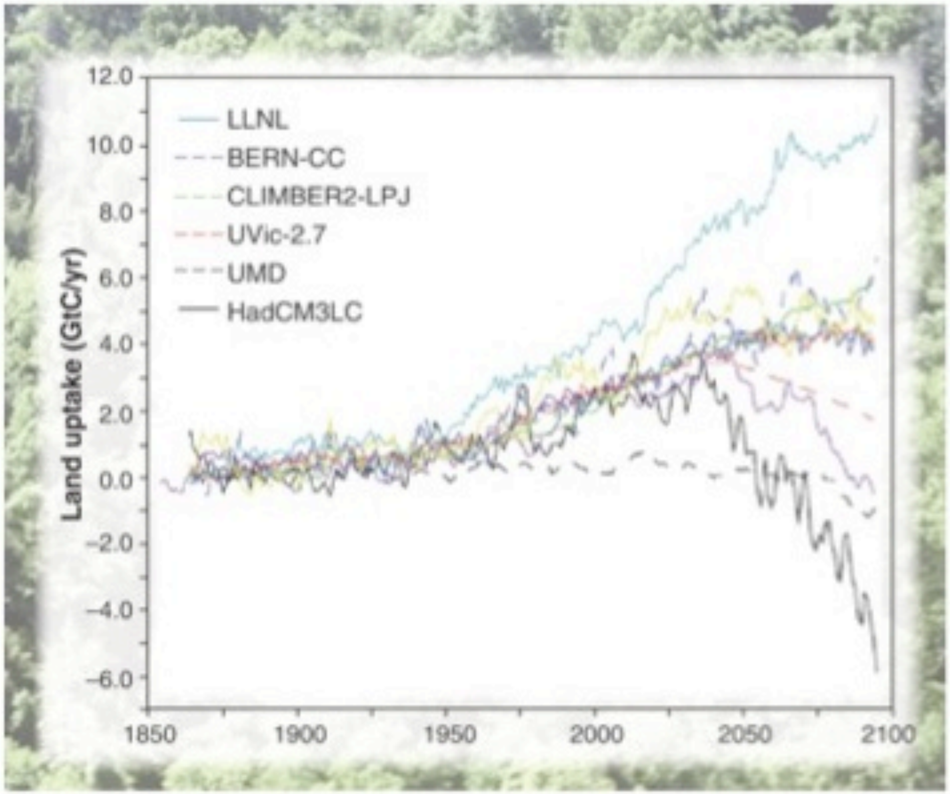
Kurz et al.: Mountain pine beetle and forest carbon feedback to climate change. *Nature 2008.*
Risks of natural disturbances makes future contribution of Canada's forests to the global carbon cycle uncertain. *PNAS 2008.*
Phillips et al. Drought Sensitivity of the Amazon Rainforest. *Science* 2009.

Not just an issue for carbon stocks and flows…



Adams, Macalady et al. Climate-Induced Tree Mortality: Earth System Consequences *EOS 2010*

Dynamic Global Vegetation Models (DGVMs) differ dramatically in their predictions of C uptake on land



Friedlingstein et al. Climate-carbon cycle feedback analyses: Results from the C4MIP model intercomparison. *JClim 2006.*

Purves and Pacala, Predictive models of fores dynamics. *Science* 2008

- Poor representation of tree mortality and its relationship to climate is part of the problem.
- Solutions? **improve mechanistic understanding, define empirical relationships, validate with better observations**

Tree mortality mechanisms

Mortality

slow | fast

Fungi

Drought

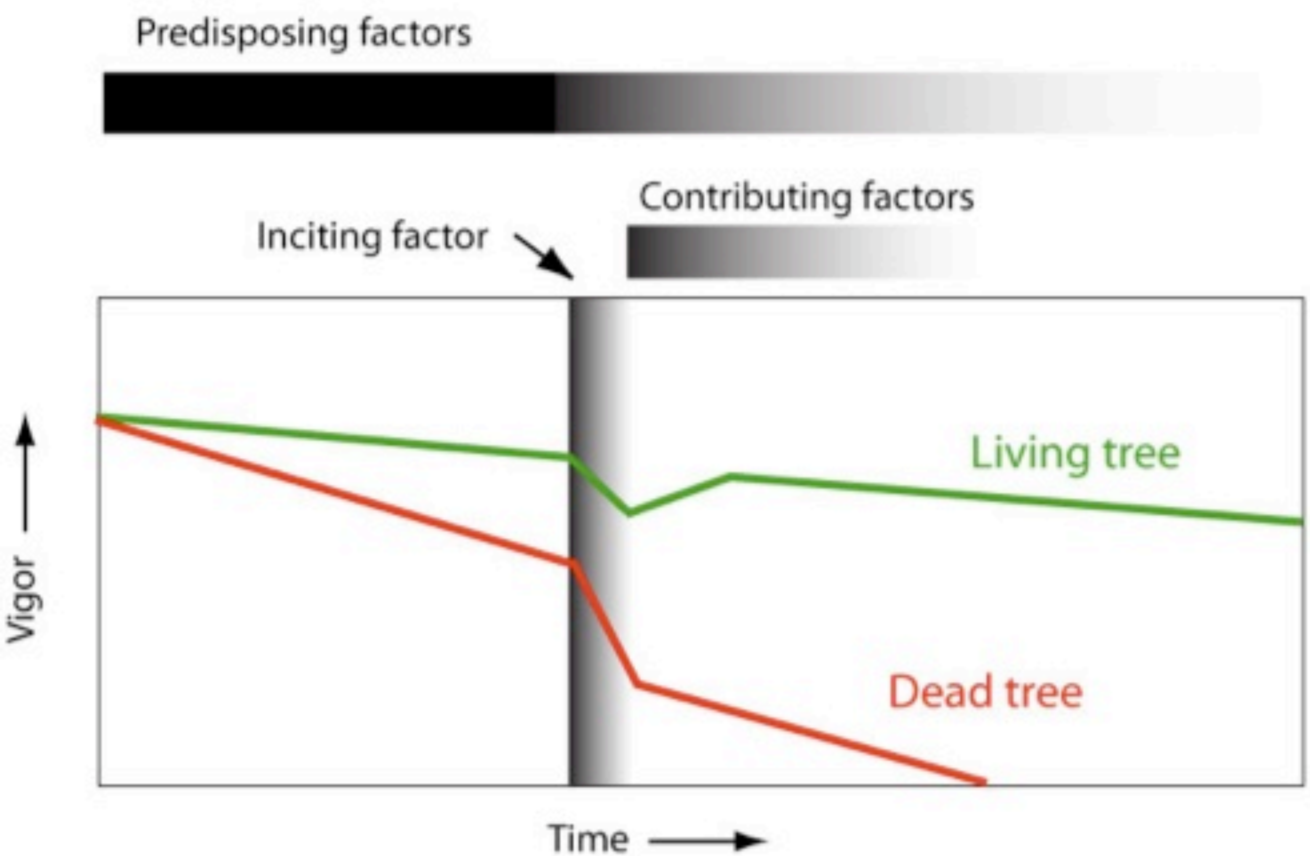
Fire

Wind

Slide credit: Harald Bugmann

Mechanisms of tree mortality

Decline-disease theory



Manion (1981), *Tree disease concepts*

Biotic and abiotic factors act over different timescales to cause tree decline and death.

Predisposing factors:
Competition, air pollution, position on the landscape. All increase susceptibility to inciting factors

Inciting factors:
Climate (drought), defoliation by insects

Contributing factors:
Secondary pathogens and insects, climate

Mechanisms of tree mortality

What are the underlying physiological mechanism(s) of mortality under drought?

A Few Hypotheses:

Hydraulic failure: irreversible desiccation

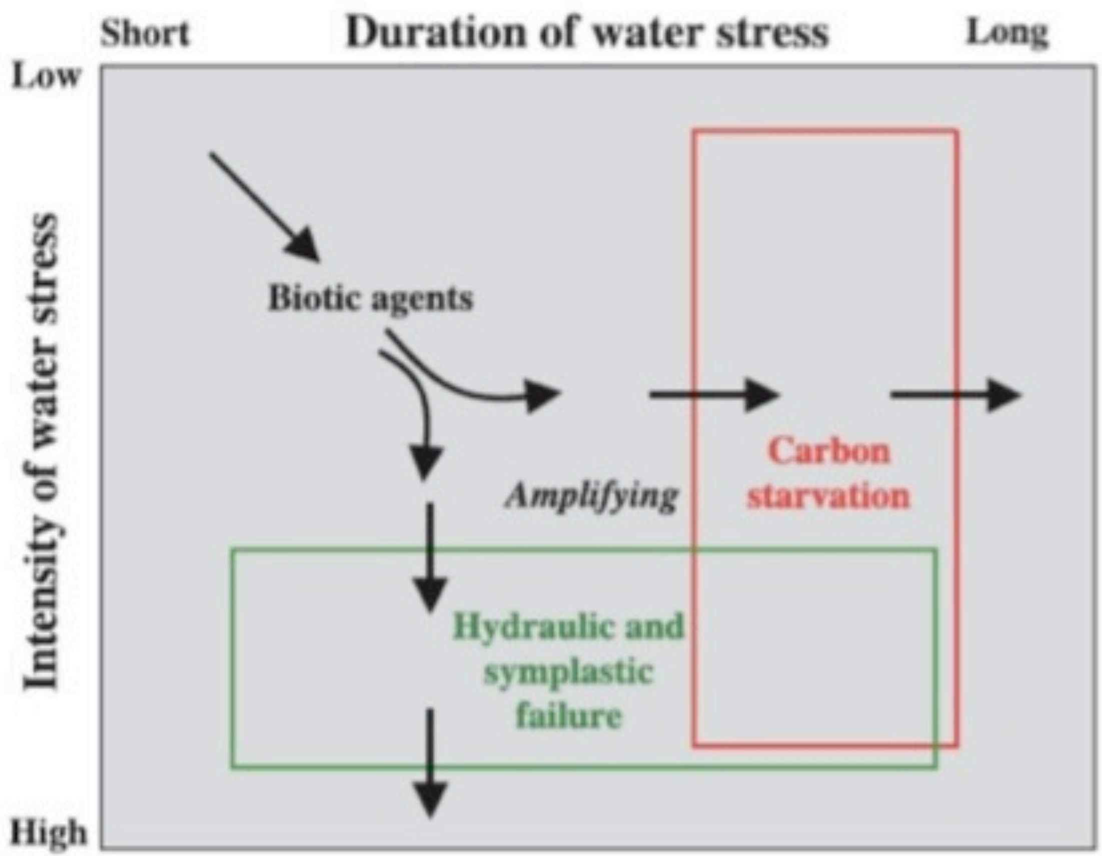
Carbon starvation: C demand exceeds supply (photosynthesis and carbohydrate storage)

Pathogen overwhelming: insects overcome defenses through sheer number of attacks, exhausting all defenses.

McDowell et al. 2008, Raffa et al. 2008, Sala 2009, Leuzinger et al. 2009
Based on lots of work including Manion 1987, Waring 1987, Ogle et al. 2000 and many others

Slide credit: N. McDowell

Mechanisms of tree mortality



McDowell et al. (2008), *New Phyto*

Dendrochronology and tree mortality

Why is dendrochronology a useful method for studying tree mortality?

- Refining Manion's framework
  - Understanding timescales and thresholds of mortality through investigating tree growth histories
- Modeling mortality risk based on prior growth
- Determining inciting/causal agents through comparison of growth histories and abiotic/biotic stressors
- Testing physiological mechanisms

Refining Manion's framework

Tree growth as a proxy for tree vigor

Tree rings are excellent integrators of biotic and abiotic influences on tree vigor (Fritts 1976; Waring and Pitman 1985; Kozlowski et al. 1991; Schweingruber 1996).

Why? Stem growth is a relatively low priority for resource allocation, so growth should be a very sensitive indicator of stress as felt by the tree.

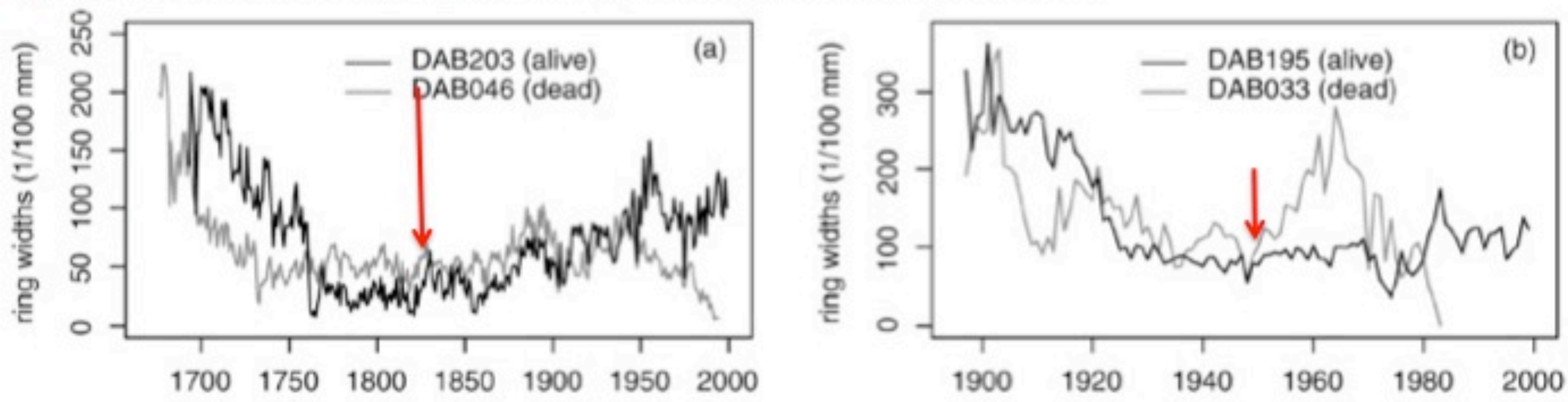
Low growth is commonly observed in dying trees (Manion 1981; Kozlowski et al. 1991; Pedersen 1998a, many others)

Is this the end of a simple story (e.g. the lower the growth rate, the greater the likelihood of death)? NOT REALLY!

Characteristics of dying trees

Some trees with chronically low growth survive for long periods and then recover …

Fig. 4. Comparisons of two sampled pairs of a living tree and a dead tree from the Davos site.

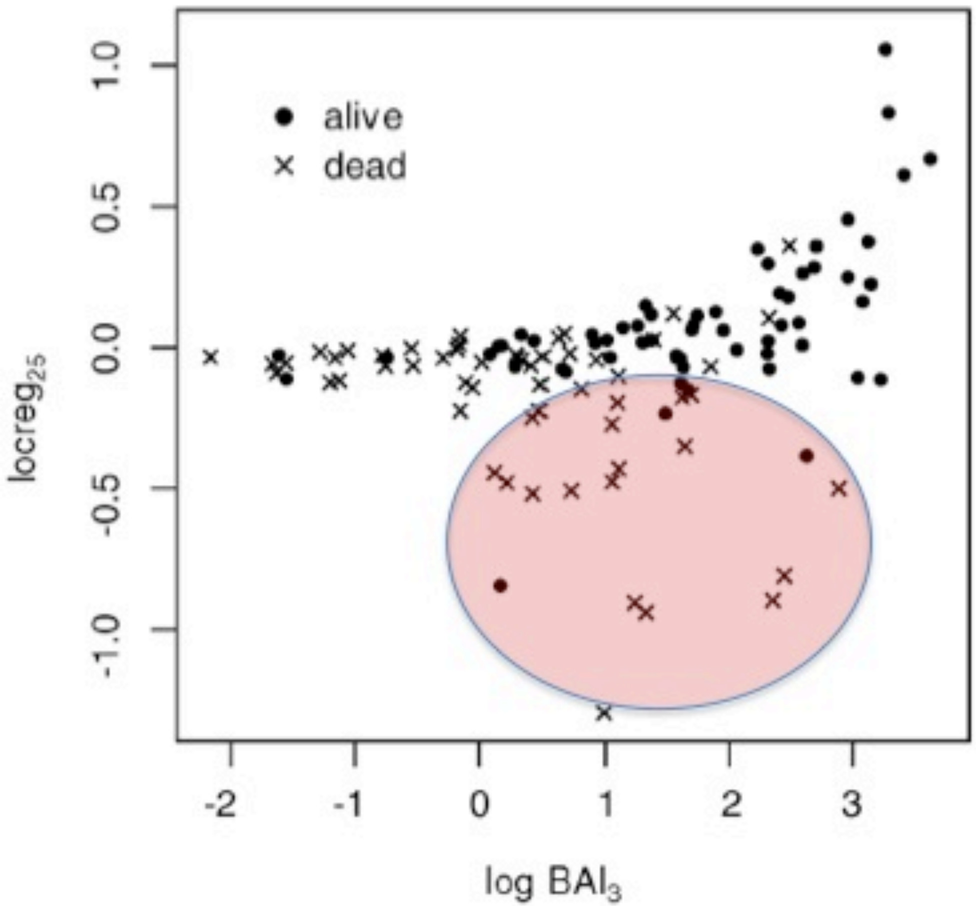


Norway Spruce (*P. abies*), Swiss Alps

Bigler & Bugmann. Growth-dependent tree mortality models based on tree rings. 2003 *CJFR*

Characteristics of dying trees

Growth trend also turns out to be very important…



Some live trees have very low growth (log BAI_3), but do not have negative growth trends ($locreg_{25}$)

Bigler & Bugmann. Growth-dependent tree mortality models based on tree rings. 2003 *CJFR*

Characteristics of dying trees

And so is growth variability….

Parameter	Dead pinyon§	Live pinyon
Lifetime growth rate (mm/yr)‡	0.98 ± 0.036 (80)	1.00 ± 0.034 (78)
Variance in mean lifetime ring-width index	0.23 ± 0.018 (45)	0.18 ± 0.015 (45)*
Recent 10-yr growth rate (mm/yr)	0.85 ± 0.053 (45)	1.07 ± 0.062 (45)*
Tree age of sampled trees (yr)	96.7 ± 4.73 (80)	97.9 ± 5.56 (78)
Variance in mean ring-width index prior to 1980	0.18 ± 0.016 (45)	0.17 ± 0.017 (45)
Variance in mean 1980–1995 ring-width index	0.29 ± 0.051 (45)	0.20 ± 0.028 (45)*

Table 4 *Nothofagus dombeyi* adults performance that reflects ability to survive drought. Significant differences based on Mann–Whitney *U*-test ($P \leq 0.05$) are shown in bold

Variables	Dead adults Mean ± SD	Live adults Mean ± SD	*P*
Tree age (year)	84.95 ± 15.58	81.35 ± 19.46	0.6591
Lifetime radial growth (mm year^{-1})	2.04 ± 0.53	2.54 ± 0.80	0.0303
Recent 1988–97 radial growth (mm year^{-1})	1.24 ± 0.67	2.27 ± 0.97	**0.0013**
Recent 1973–97 radial growth (mm year^{-1})	1.54 ± 0.61	2.59 ± 0.91	**0.0004**
Sensitivity in mean lifetime ring-width index	0.28 ± 0.04	0.26 ± 0.06	0.1184
Sensitivity in mean 1988–97 ring-width index	0.33 ± 0.08	0.25 ± 0.06	**0.0038**
Sensitivity in mean 1973–97 ring-width index	0.29 ± 0.06	0.23 ± 0.05	**0.0048**
N° radii	38	36	

Ogle et al. Tree-Ring Variation in Pinyon Predicts Likelihood of Death following Severe Drought. 2000 *Ecology* ; Suarez et al. Factors predisposing episodic drought-induced tree mortality in Nothofagus… *2004* J. Ecology

Characteristics of dying trees

So slow-growing, highly sensitive trees should most likely to die during drought or other stressful events?
Not always…

Longevity under Adversity in Conifers[1]

Edmund Schulman

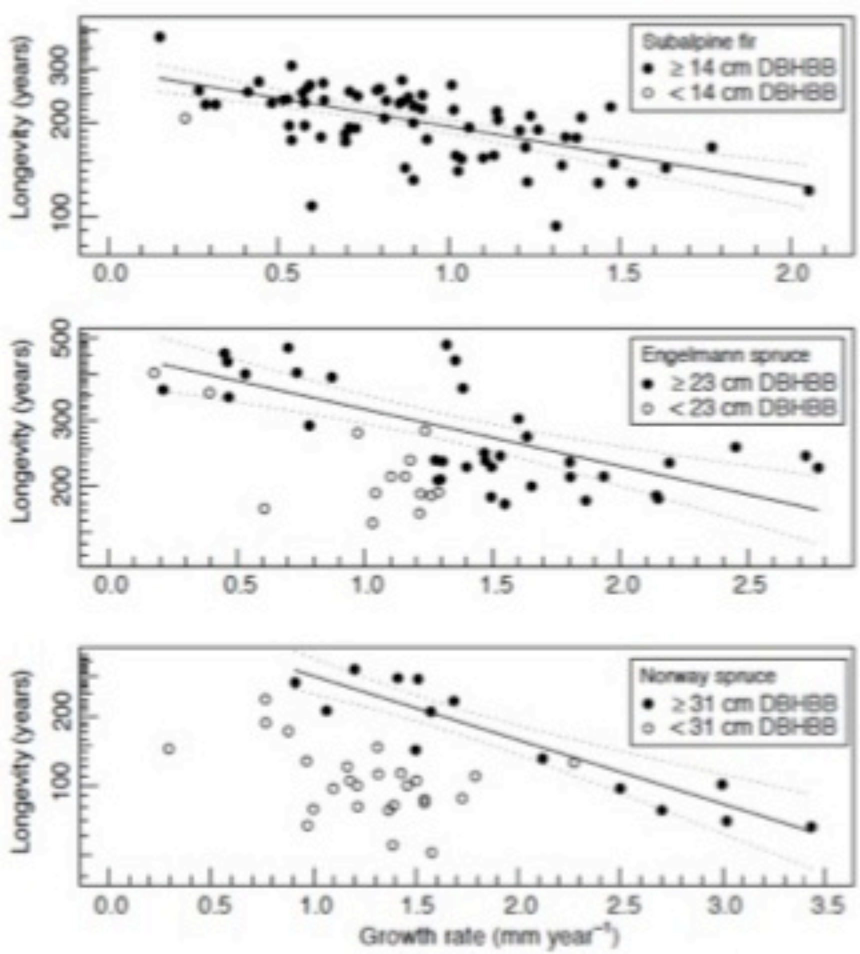
Division of Geological Sciences, California Institute of Technology,[2] Pasadena

On marginal sites in semiarid regions of the western United States, trees of several coniferous species have been found that far exceed the generally accepted maximum ages for these species. The annual stem growth of such trees is extremely small (*1*); nevertheless, the width of the annual rings in many of these trees is particularly sensitive to the varying rainfall from year to year (*2*). This remarkable combination of longevity and sensitivity makes it possible to derive tree-ring indices of past year-by-year rainfall that are more reliable than indices based on the much younger

It has long been observed that the oldest trees occupy the most stressful sites, and are slow growing…

Schulman. Science 1954.

Characteristics of dying trees



Bigler and Veblen. Increased early growth rates decrease longevities of conifers in subalpine forests. *Okios* 2009.

Average growth rates over first 50 yrs influences longevity in subalpine conifers.

Why?

1. Lower metabolic requirements?
2. Larger allocation to defensive structures?
3. Better wood resistance to decay and pathogens?
4. Genetic vs. environmental drivers?

Global warming implications?

Characteristics of dying trees

Summary

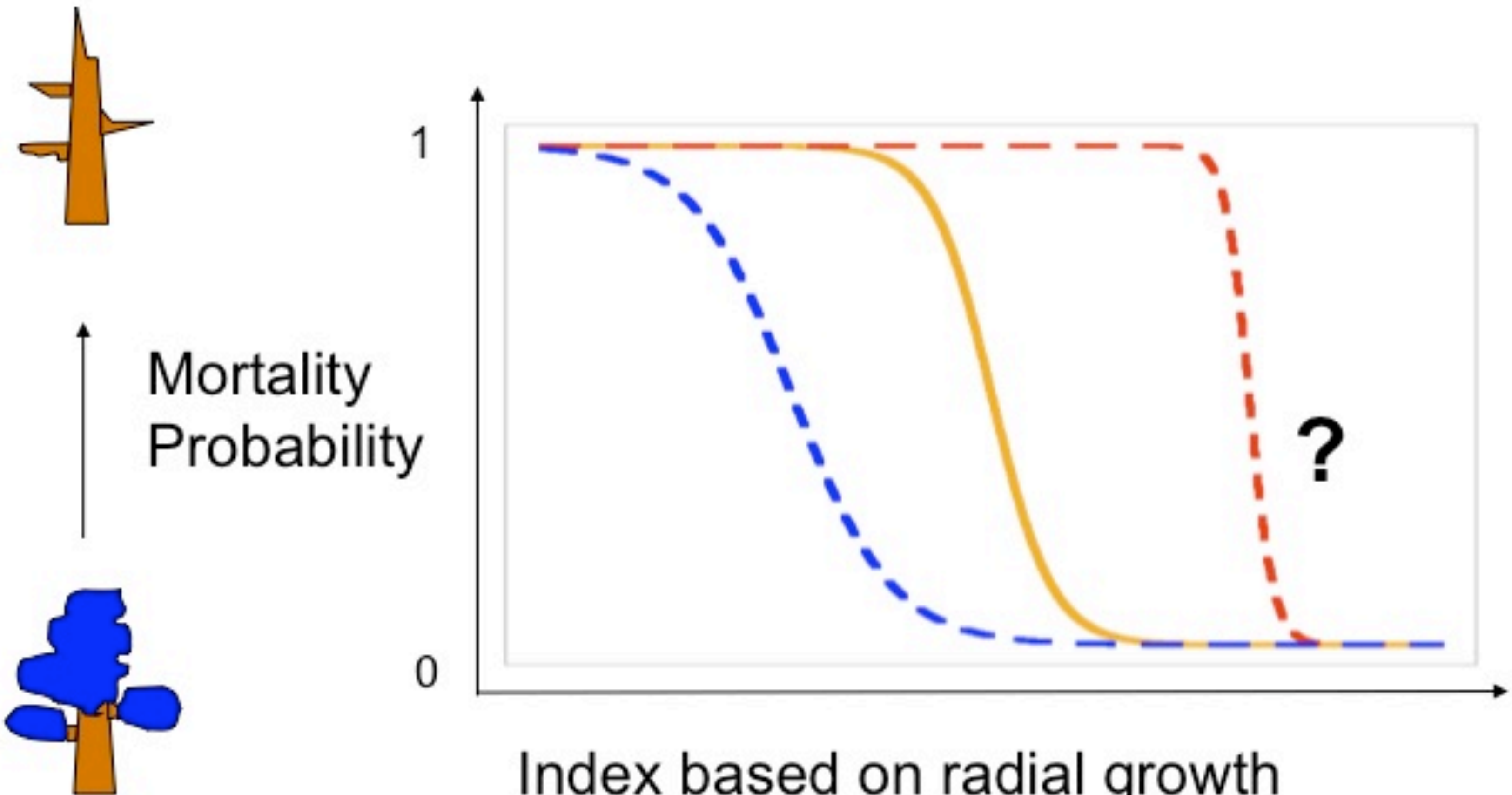
Low growth only sometimes a good indication of impending tree death; multiple indices reflecting different timescales of response are needed to accurately reflect mortality risk and mortality processes.

Growth trends and abrupt declines are key for discriminating between dying and healthy trees.

Growth variability and sensitivity to climate are also important.

Trees with low early growth rates tend to have greater longevity

Growth-mortality models



Slide credit: H. Bugmann

Growth-mortality models

Best mortality indices can be objectively selected when using logistic regression

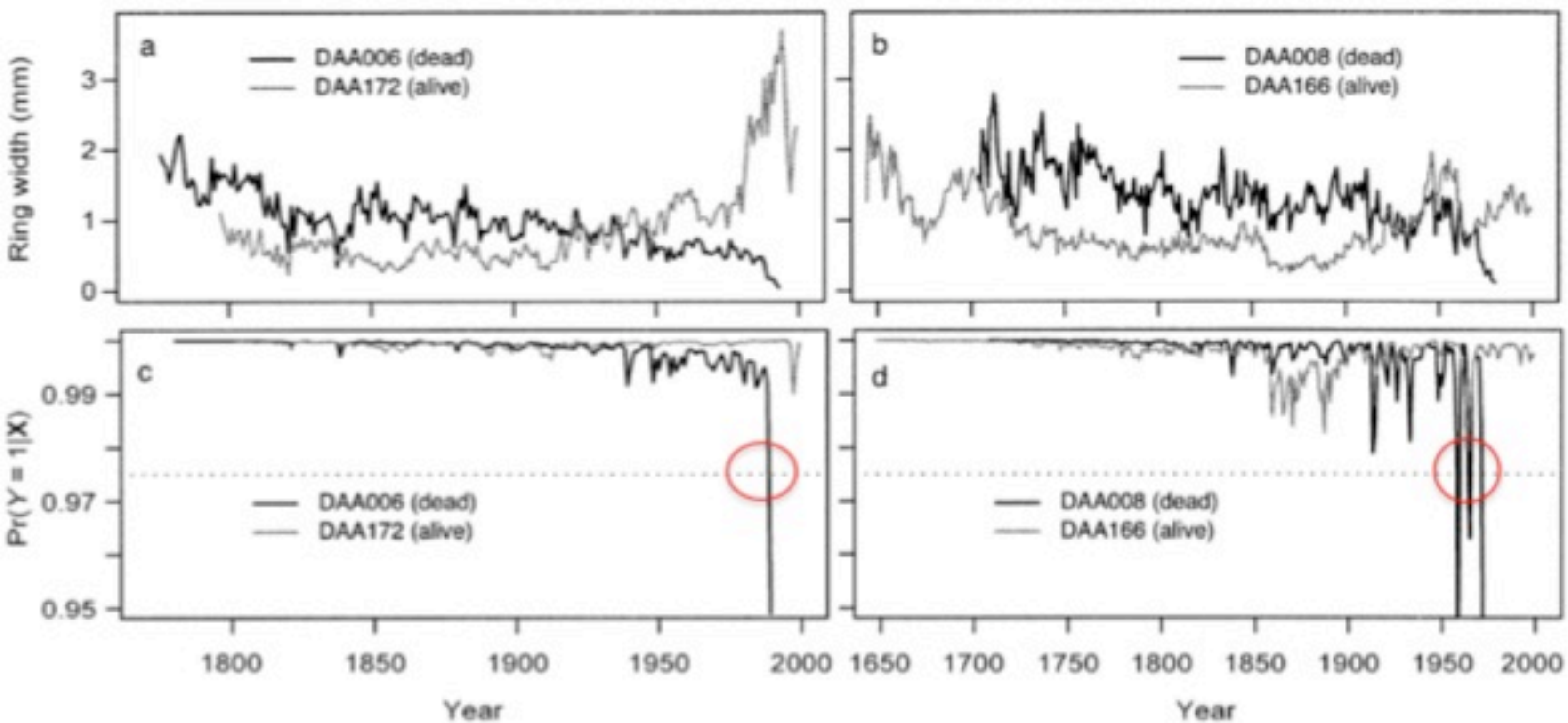
Misclassification rate for various models in Swiss Norway Spruce.

	log BAI_3	log BAI_5	log BAI_7
$locreg_5$	21.58	21.53	22.67
$locreg_{10}$	21.82	22.75	22.13
$locreg_{15}$	23.77	24.99	26.36
$locreg_{20}$	21.48	23.06	24.19
$locreg_{25}$	20.58*	21.84	21.49
$locreg_{30}$	21.55	22.46	22.88
$locreg_{35}$	22.59	24.16	24.9
$locreg_{40}$	22.47	24.44	25.56

Bigler & Bugmann. Growth-dependent tree mortality models based on tree rings. 2003 *CJFR*

Growth-mortality models

Annual survival probability can also be modeled through time for individual trees….

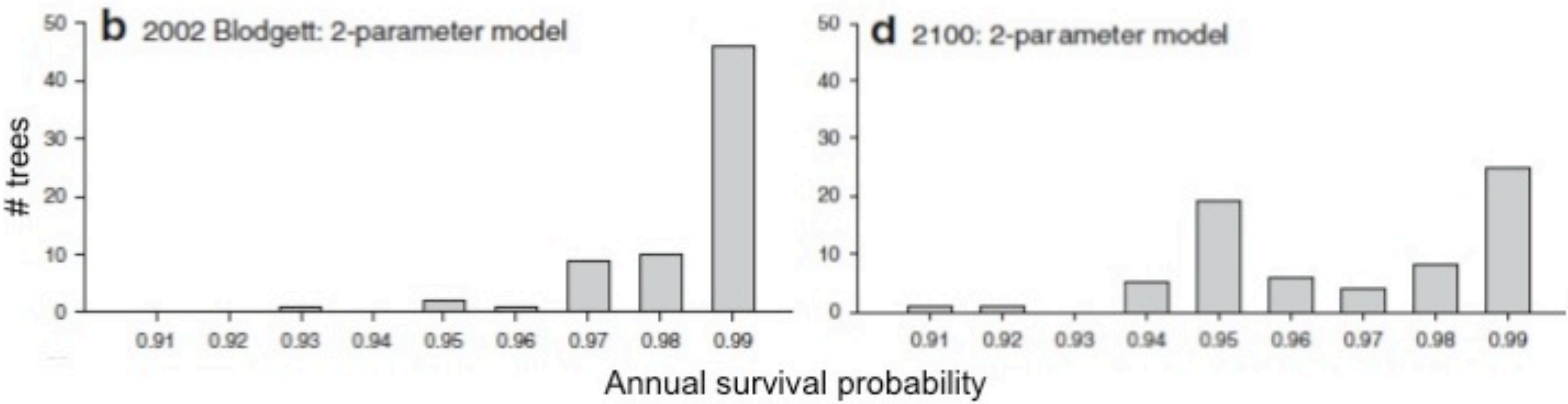


Performance for Swiss Norway Spruce: CCR ≈ 80% (D), >85% (L)

Bigler & Bugmann. Prediciting the timing of tree death using dendrochronological data, *Ecol Applications 2004*

Growth-mortality models

When parameterized on populations of trees, these models can be used to predict changes in growth-related tree mortality under different climate change scenarios…

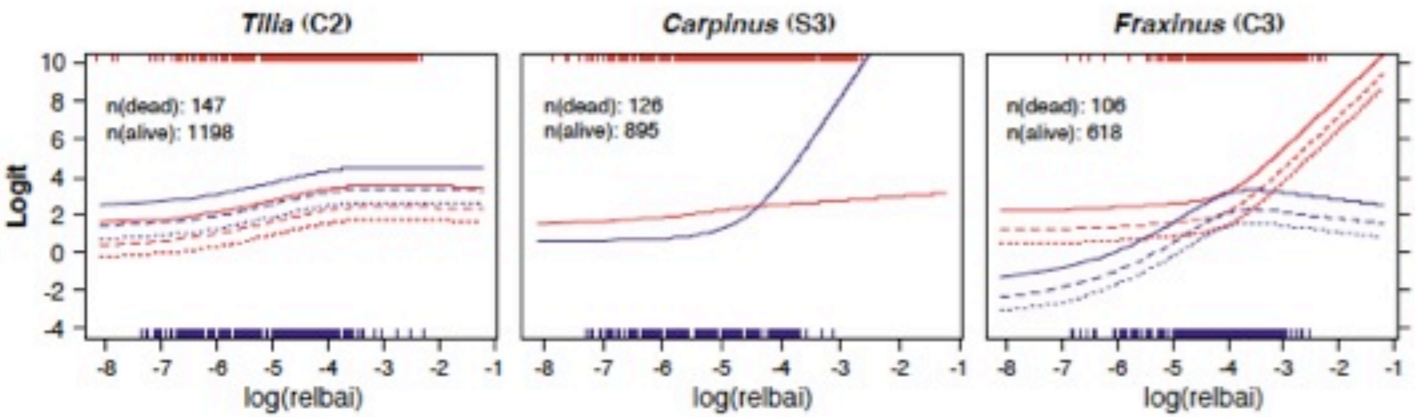


As of 2100, projected climate change shifts mortality probabilities only slightly for white fir in CA

Battles et al. **Climate change impacts on forest growth and tree mortality…**Climatic Change *2008*

Growth-mortality models

Problems: growth-mortality relationships may vary considerably by site (and by species).



Log of the ratio of survival/mortality probabilities for given growth;

Higher logit = higher survival probability

red = Polish sites,
blue= Swiss sites

Some species show similar shape growth-mortality relationships through space (Basswood), while others are distinctly different (Hornbeam, Ash)

Wunder et al., *Ecol Applications 2004*

Growth-mortality models

Summary

Tree-ring-based mortality models often have higher performance than theoretical mortality functions based on size and/or only recent growth, and are thus an important tool for understanding and predicting tree mortality.

Models can be parameterized in different ways to predict how mortality risk might change through time for individuals and populations of trees.

There may not be a species or site-independent growth-mortality relationship, complicating model application (see Wunder et al. 2008 for more here…).

Many species remain to be studied…

Growth-mortality models

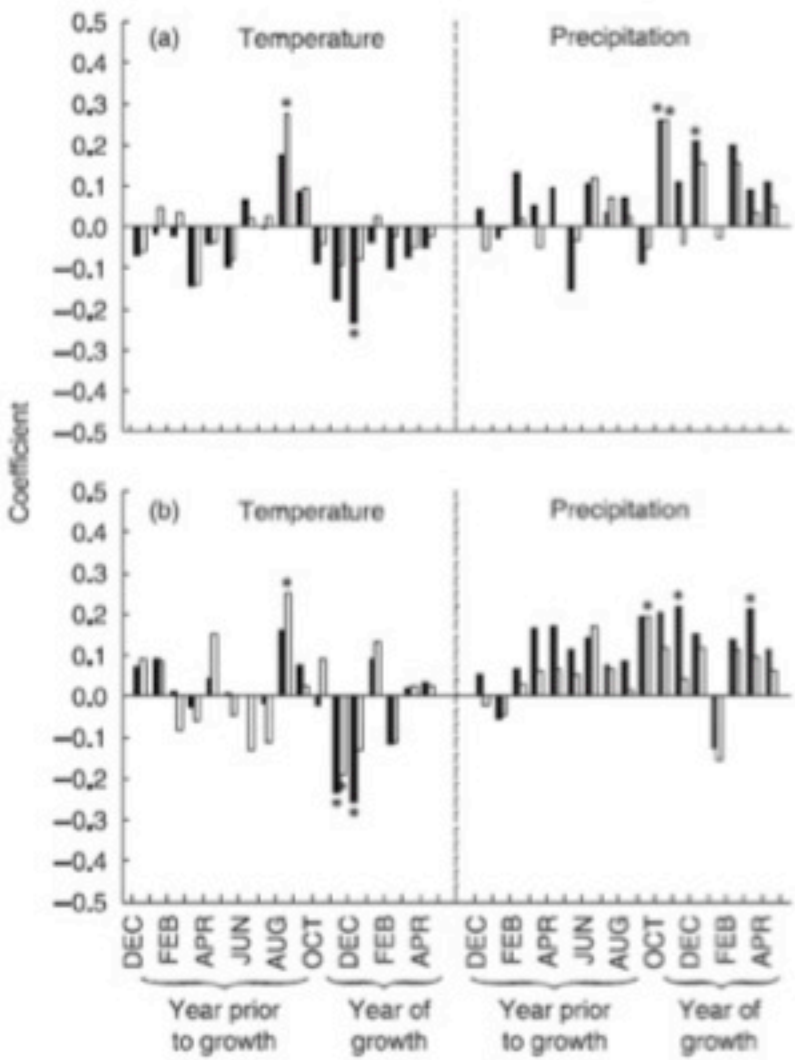
Interlude on methodological considerations….

Cross-dating essential to understand timescales most important for mortality processes, and to test relationships between tree vigor and biotic and abiotic drivers

Many of the best models utilize raw (un-standardized) growth variables

- Why? (Absolute vs. relative vigor)
- Must be aware of age and size-effects on growth

Pinpointing casual agents



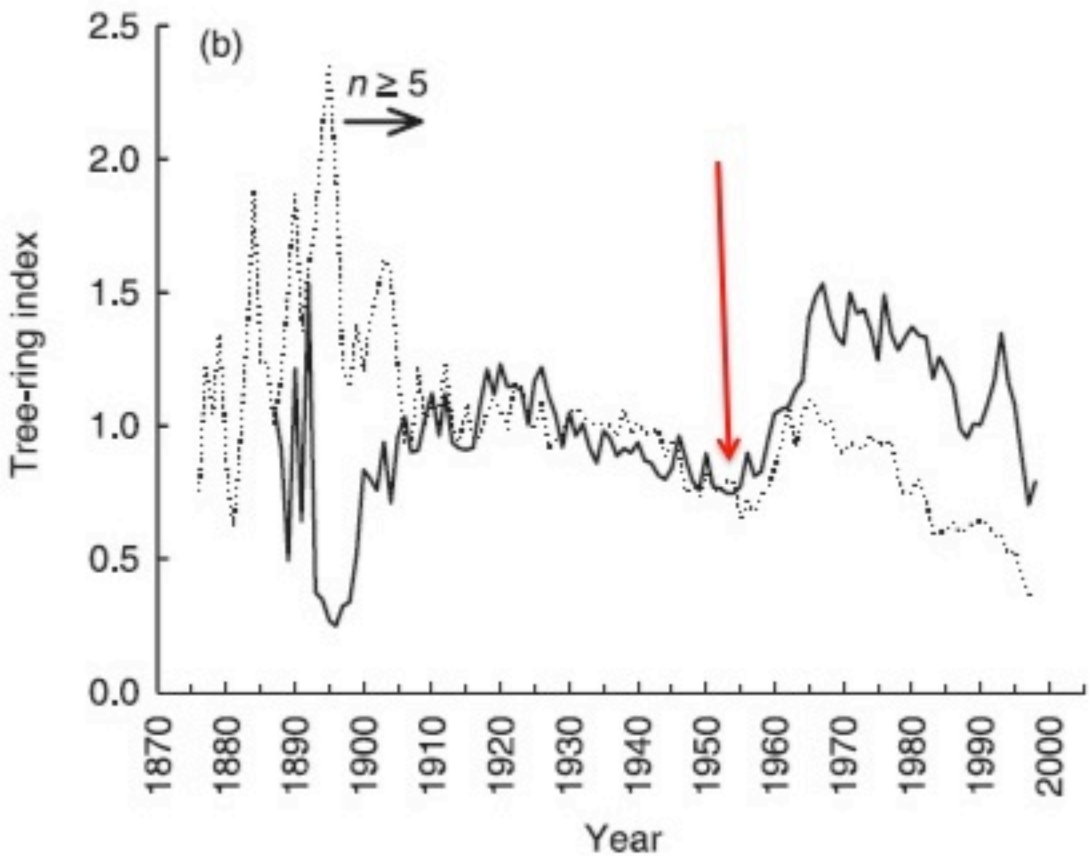
Increased growth variability may not mean increased climate sensitivity in trees predisposed to die

Correlation (open) and response function (closed) analysis reveals similar patterns between adult trees that lived (top) and died (bottom) after drought in Patagonia

What could be driving increased variability of dead trees, if not climate?

Suarez et al. Factors predisposing episodic drought-induced tree mortality in Nothofagus… *2004* J. Ecology

Pinpointing casual agents



Growth trajectories diverge at last previous drought.

Highlights the role of repeated droughts in predisposing trees to subsequent stress

Drought affects additive?

Global change implications?

Suarez et al. Factors predisposing episodic drought-induced tree mortality in Nothofagus… *2004* J. Ecology

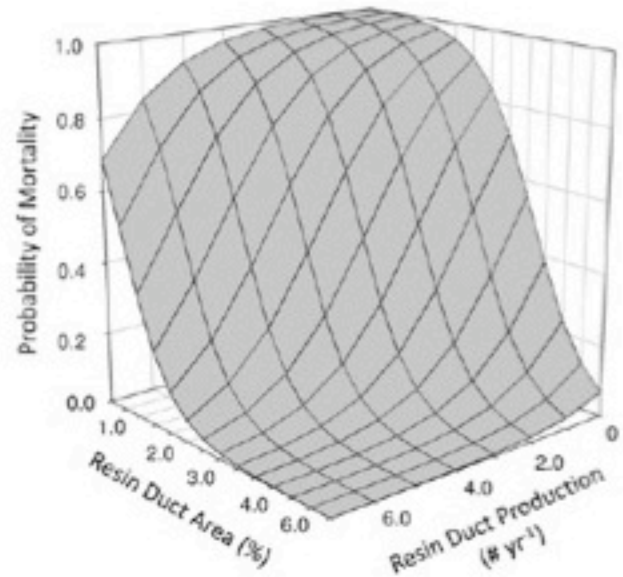
Physiological mechanisms

Sometimes, growth is not a good predictor of mortality.

Carbon allocation to defensive structures may be more important than overall tree carbon status where insect/pathogen pressure is high.

>80% CCR using resin duct indices to predict mortality in Ponderosa pine after drought-related bark beetle outbreak in AZ.

What drives differential allocation? Genetic predisposition?



Kane and Kolb. Importance of resin ducts in reducing Ponderosa pine mortality from bark beetle attack. *2010* Okios

A few take-home points

Tree-ring based studies of tree growth have provided support for the idea that whole tree carbon status, driven by chronic resource stress, is a major driver of tree mortality in a wide variety of situations.

Tree allocation of carbon (versus whole tree carbon status), may be more important in some cases (e.g. where pathogen/insect pressure is very high).

Tree mortality processes operate on both short and long timescales, complicating understanding and prediction of tree mortality. (Dendrochronological studies are KEY!)

Empirical studies of tree mortality using tree rings improve our understanding of the ecology of tree mortality, in addition to providing important observations against which to test models of forest dynamics under climate change.

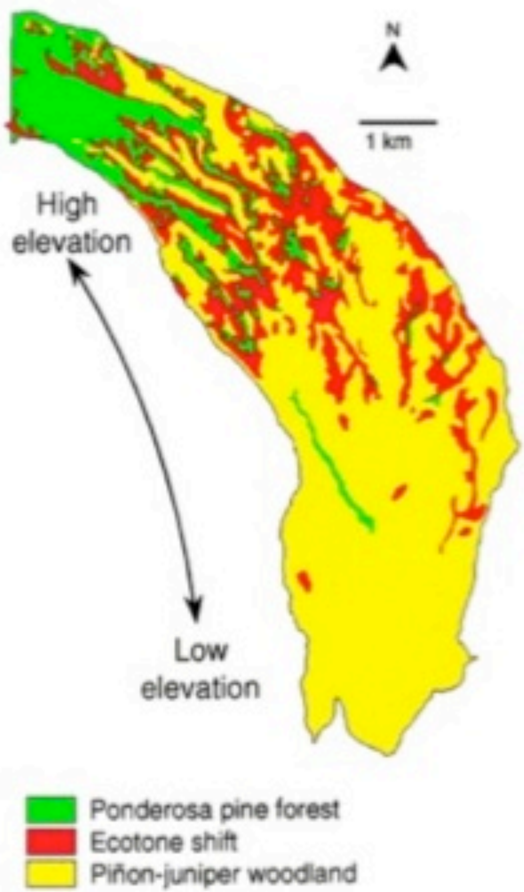
Results from my research

Photo: Craig Allen

Mortality in the 1950s and 2000s

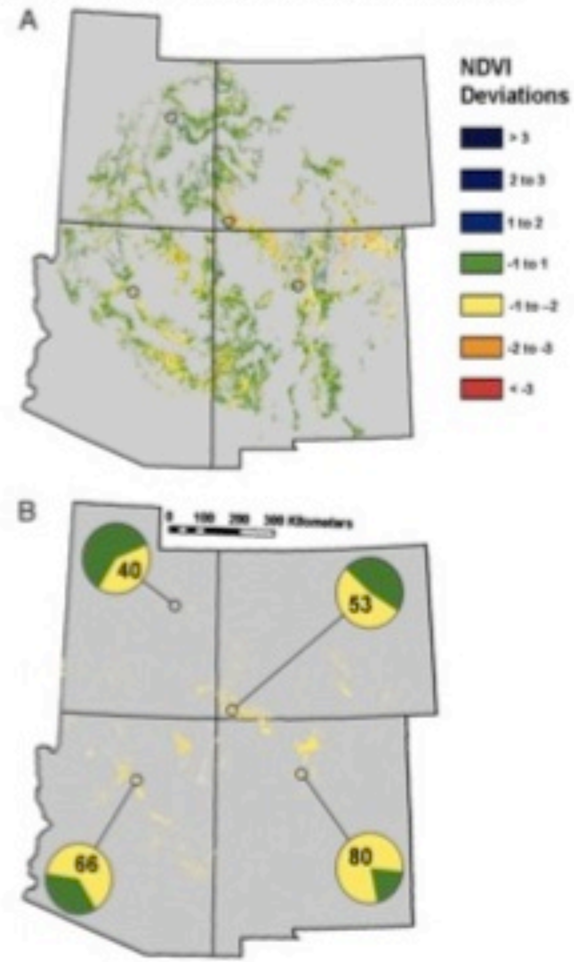
1950s

Allen and Breshears (1998), *PNAS*

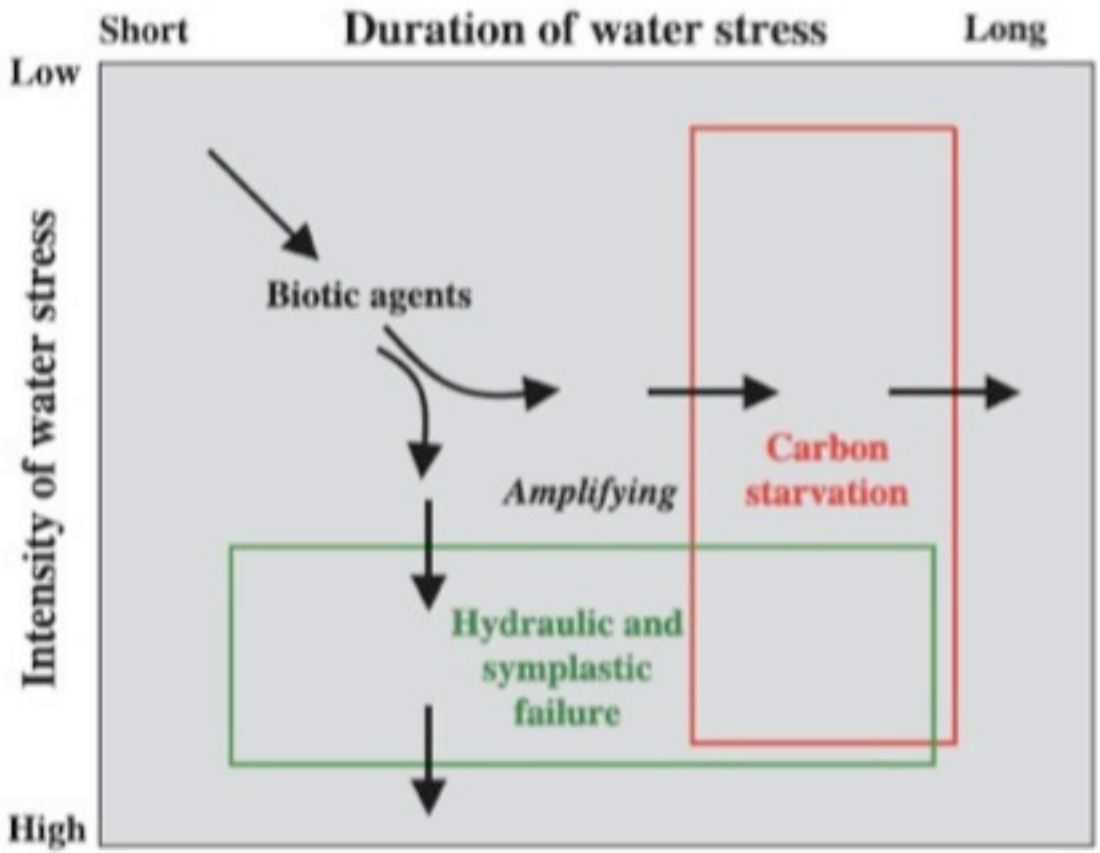


2000s

Breshears et al. (2005), *PNAS*



Mechanisms of tree mortality



McDowell et al. (2008), *New Phyto*

Research questions

Can the probability of piñon mortality under drought be accurately modeled using indices derived from diameter growth?

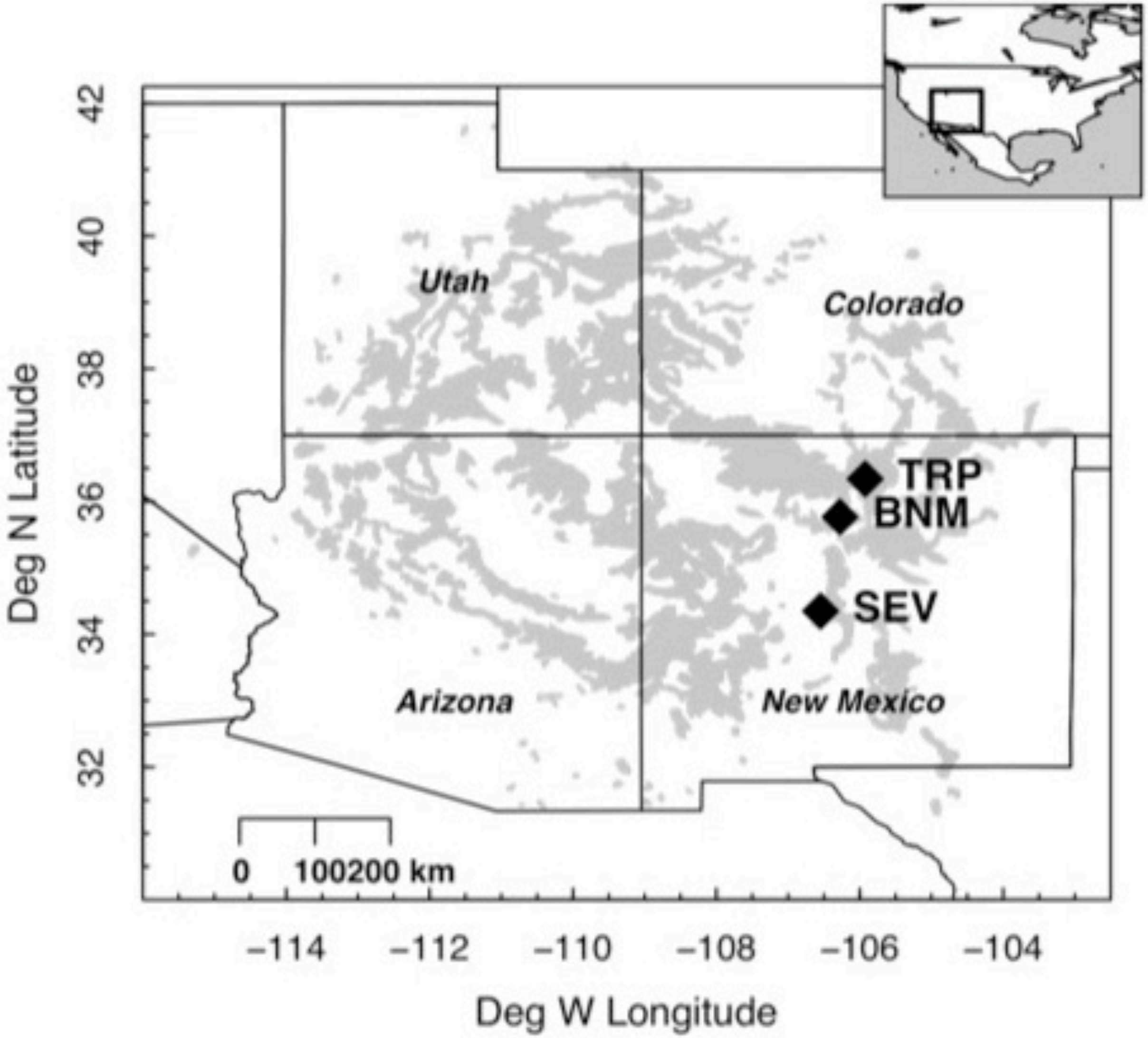
What do growth-mortality models reveal about the drivers of tree mortality through space and time?

Hypotheses

1) Successful growth-mortality modeling would support the "carbon starvation" mechanism of pinyon pine mortality under drought (McDowell et al. 2008)

2) In areas and at times when drought was extreme, or where strong insect/pathogen pressure occurs, there will be little relationship between growth and mortality probability.

Field sites



Utah
Colorado
Arizona
New Mexico
TRP
BNM
SEV
0
100200 km
42
40
38
36
34
32
Deg N Latitude
−114
−112
−110
−108
−106
−104
Deg W Longitude

Sampling design

Mortality wave	Site	Site Acroynm	Stand-level pinon mortality	*Target trees* n Alive	n Dead
1950's	***(LTRR archive, sampled in 1990s)***				
	Sevilleta National Wildlife Refuge, NM	SEV50	32-65%	32	22
	Bandelier National Monument, NM	BNM50	54-73%	28	28
2000's	***(Sampled in 2008-2009)***				
	Sevilleta National Wildlife Refuge, NM	SEV2000	20%	30	30
	Bandelier National Monument, NM	BNM2000	100%	0	28
	Carson National Forest, Tres Piedras, NM	TRP2000	64%	29	30
				119	**138**
			Total n=	***257***	

Field methods

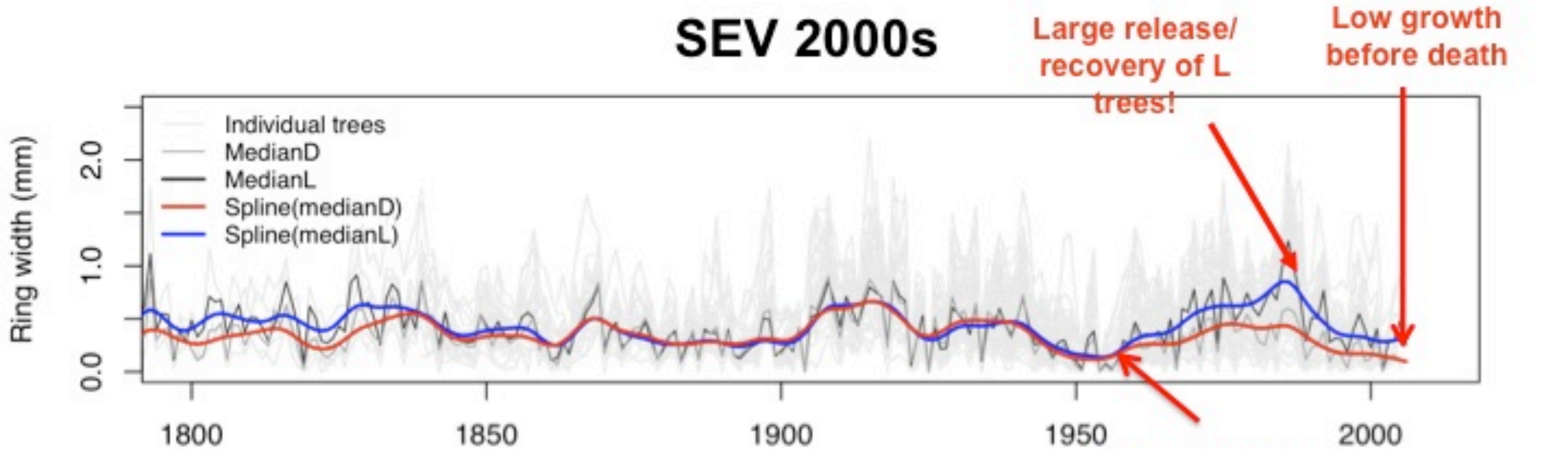
Matched-pairs case-control study, widespread in epidemiological research

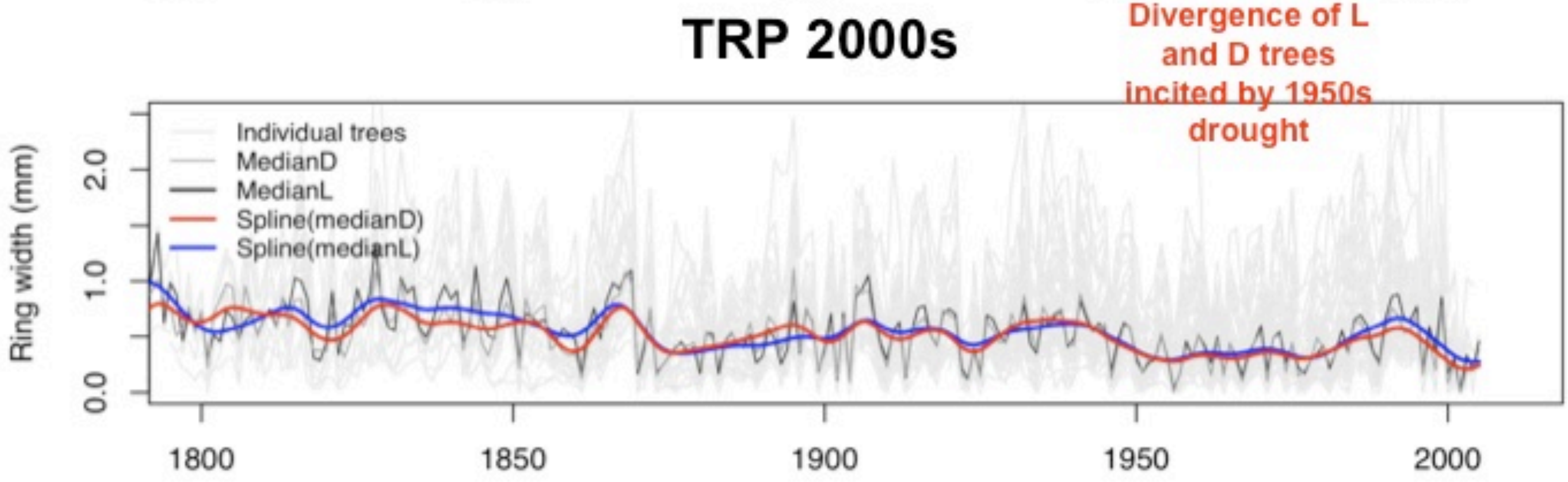
30 live/dead pairs
Adult trees only
(DBH >9 cm)

Neighborhoods quantified at SMD and CNF sites

LTRR archive mined for wood that died in the 1950's

Tree growth – typical patterns





Fitting mortality models: one site

Sevilleta, 1950s Model	AIC	Area under ROC curve	Dead trees correctly classified	Live trees correctly classified	Total trees correctly classified
Best recent growth					
log(bai10)	56.71	0.828	69.4%	78.3%	74.6%
bai7	57.16	0.826	62.3%	80.0%	72.7%
Best growth sensitivity					
ms bai50	42.51	0.886	78.0%	79.4%	78.7%
ms bai45	45.65	0.873	72.2%	76.8%	74.7%
Best growth trend					
gr bai30	60.11	0.620	49.3%	55.9%	52.6%
locreg bai55	61.28	0.601	36.9%	61.9%	49.3%

Internal validation: 60% fitting, 40% testing
500 simulations

Fitting mortality models: all sites

Site/period	Variable	AU ROC	CCR
SEV 1950s	mean sensitivity 50	0.89	78.7%
BNM 1950s	mean sensitivity 25	0.92	82.0%
SEV 2000s	recent growth 3	0.83	75.3%
BNM 2000s	–	–	–
TRP 2000s	growth difference 15	0.67	59.6%

Validating mortality models

	Calibration data [shown is CCR]		
Validation	**SEV 1950s**	**BNM 1950s**	**SEV 2000s**
SEV 1950s	–	73.1	77.4
BNM 1950s	77.4	–	60.0
SEV 2000s	55.9	61.7	–
BNM 2000s	31.6	16.7	14.3
TRP 2000s	53.4	55.9	52.5

What's going on?

High model accuracies associated with 1950's and SEV 2000's data reflect a chronic stress signal associated with mortality risk

- Best predictors reflect the resource status of the trees over different time periods.
- Supports chronic resource stress and carbon starvation as mechanisms of mortality

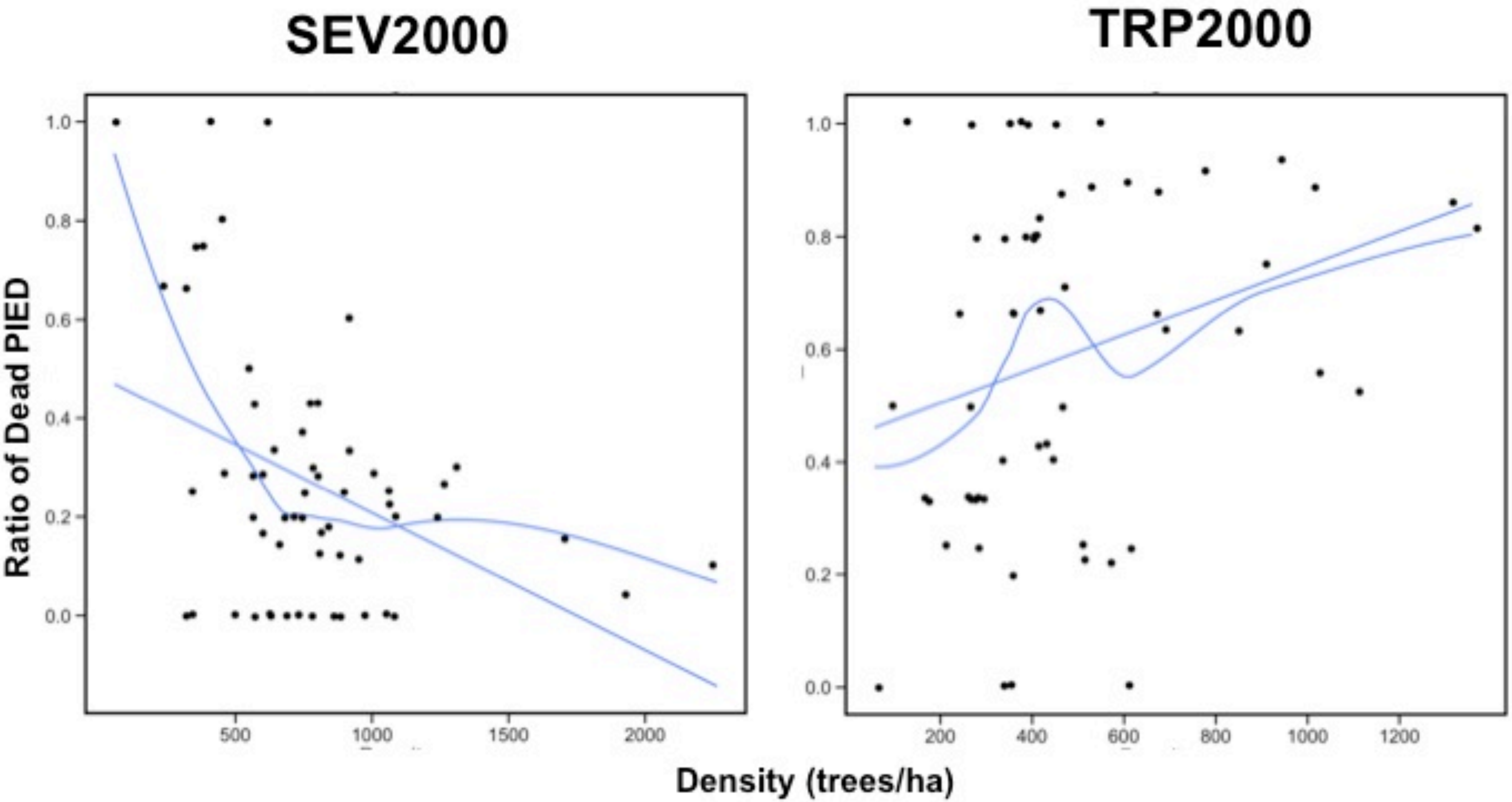
Lack of fit in 2000's models suggests other processes.

- Acute drought stress overwhelms even healthy trees?
- Increased temps drives accelerated bark beetle/fungi dynamics?
- Would carbon allocation to defensive compounds be a better proxy than overall tree vigor (Kane and Kolb 2010, Oikos)?

Spatial patterns of mortality

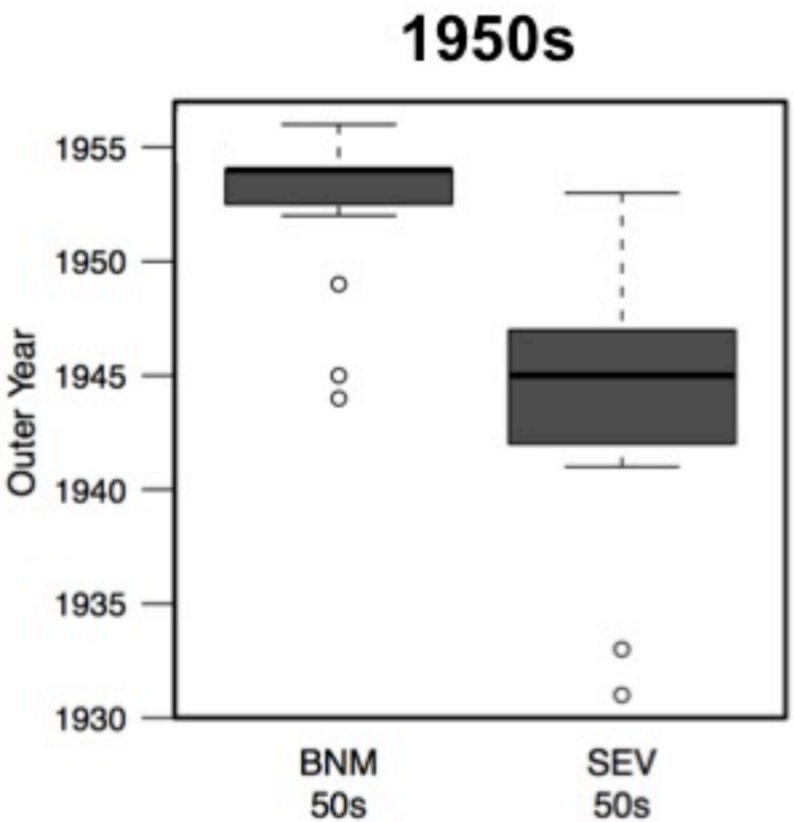
	SEV2000			TRP2000		
	L	D	*p-value*	L	D	*p-value*
Density (trees/ha)						
All	775.3	790.4	0.7895	454.7	511.2	0.1236
PIED	318.8	343.3	0.8293	**296.6**	**369.7**	**0.036**
JUMO	399.9	390.5	0.6608	101.5	84.9	0.4367
Dead PIED	54.7	60.4	0.6883	**171.7**	**279.2**	**0.0049**
Dead JUMO	11.3	13.2	0.7582	2.0	3.8	0.5907
Basal Area (m^2/ha)						
All	11.3	11.1	0.8201	7.6	9.9	0.2183
PIED	3.2	3.1	0.6735	5.0	7.1	0.2183
JUMO	8.2	8.0	0.6543	2.6	2.8	0.9817
Dead PIED	0.6	0.8	0.4427	**2.4**	**5.3**	**0.0051**
Dead JUMO	0.4	0.4	0.8011	0.3	0.0	0.6186

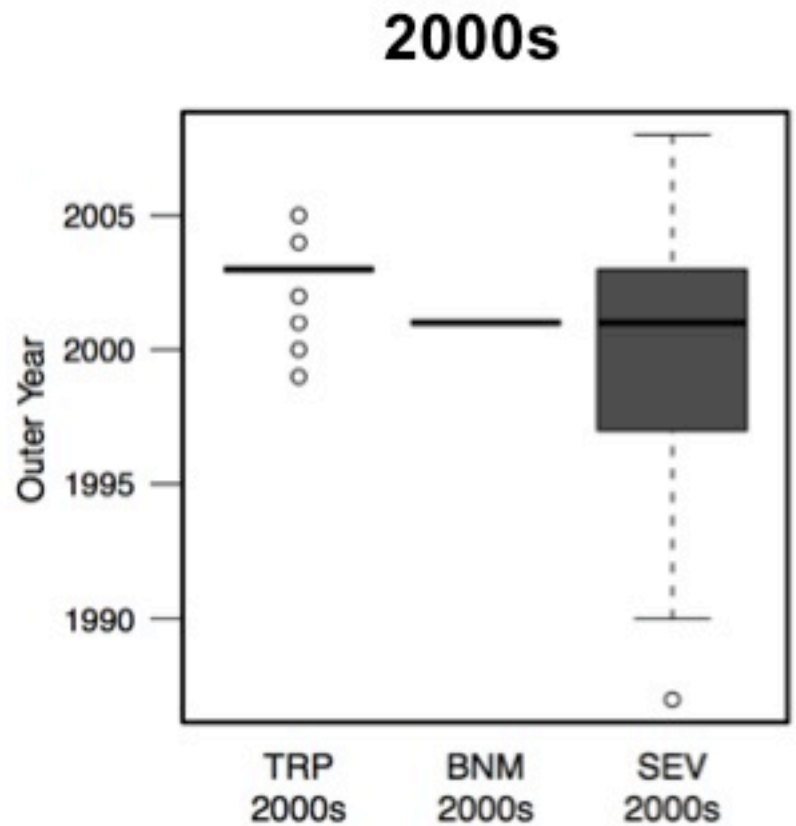
Spatial patterns of mortality



Site scale…

When did the trees die?





Conclusions

Results point to the influence of acute drought stress and/or bark beetle/fungi dynamics at northern sites in the 2000's, versus chronic resource stress in the South and during the 1950's

Difference in growth-mortality models highlight the potential as well as the challenges of predicting mortality under drought.

Next steps

Multiple-variable models to improve prediction accuracies and cross-validation

Model climate-growth responses to reveal drivers of ring width variability

Measure resin duct variation over time in order to assess whether allocation to defense predicts mortality where growth fails (M. Klay master's thesis)

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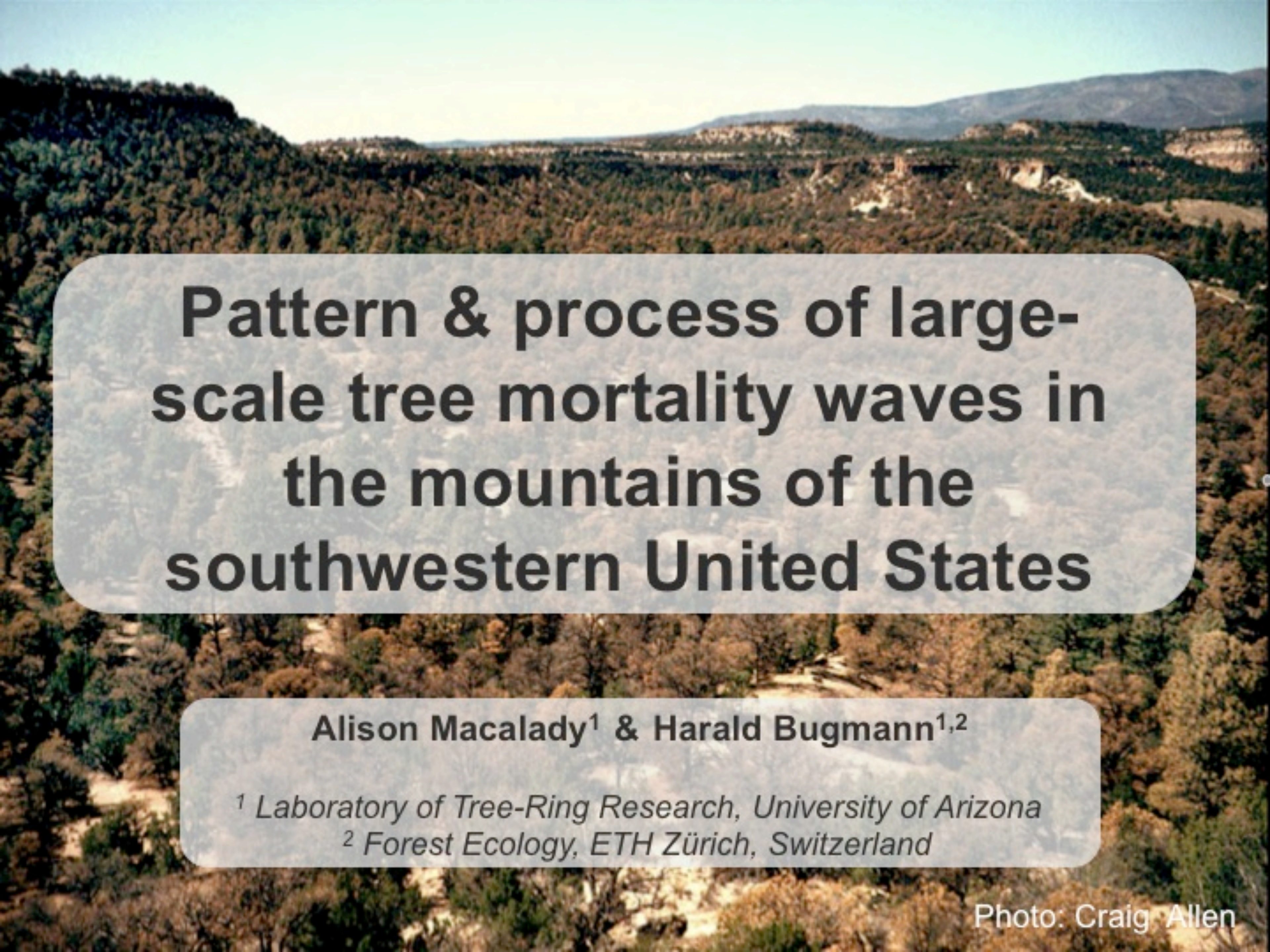
Pattern & process of large-scale tree mortality waves in the mountains of the southwestern United States
Alison Macalady[1] & Harald Bugmann[1,2]
[1] Laboratory of Tree-Ring Research, University of Arizona
[2] Forest Ecology, ETH Zürich, Switzerland
Photo: Craig Allen