Dynamic Global Vegetation Models

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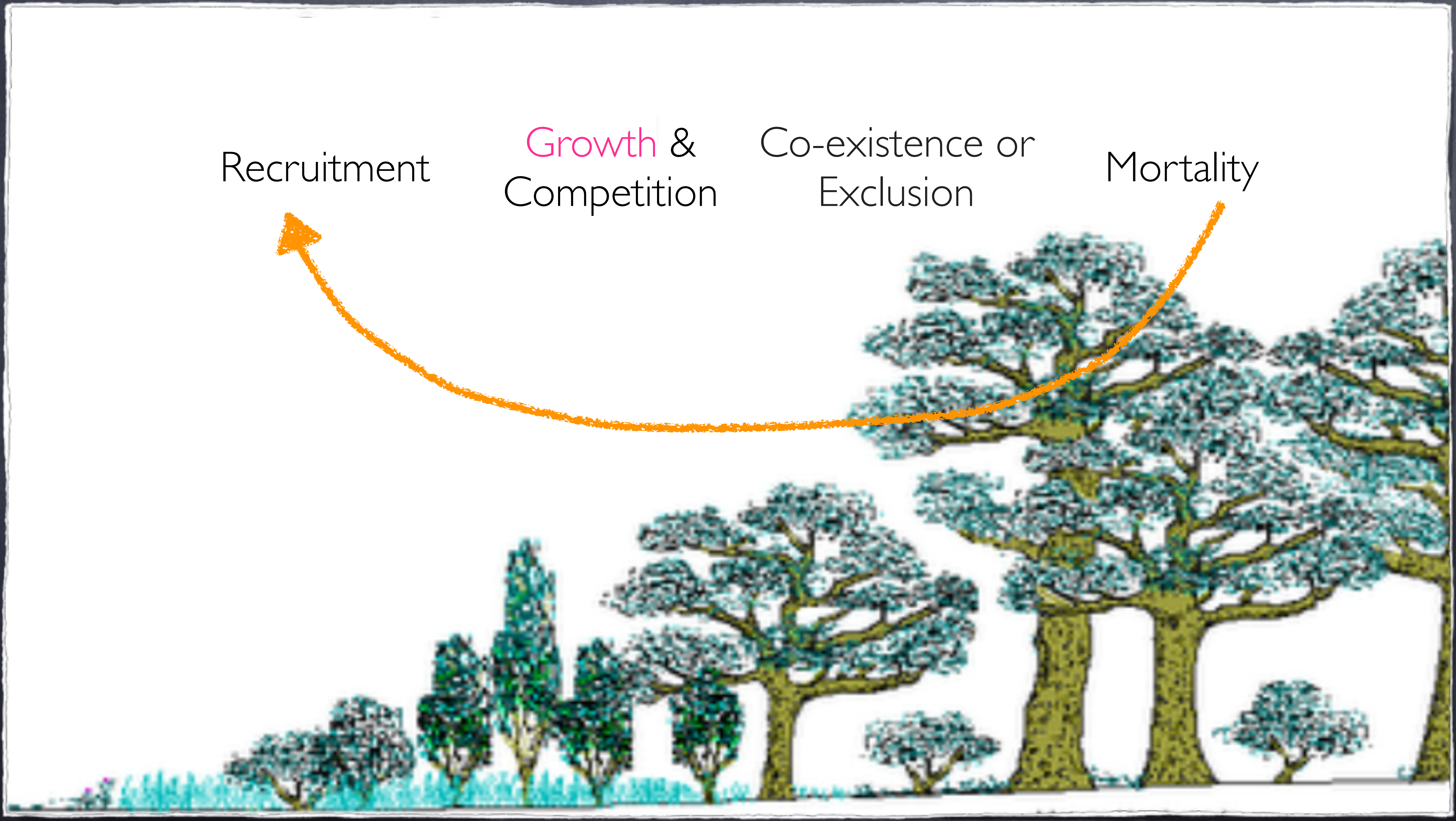
What is the 'D' in DGVM?

- Recruitment
- Assimilation
- Growth
- Competition
- Mortality & Disturbance
- Decomposition

→ Movement of vegetation in space predicted by model

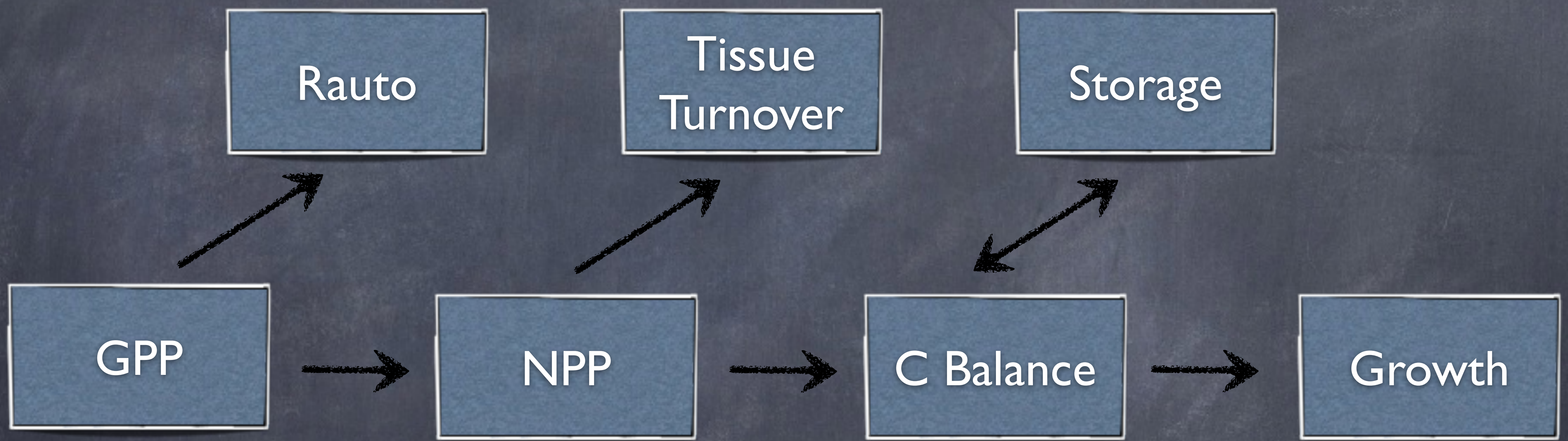
How do ecological systems organize the diversity of plant life?



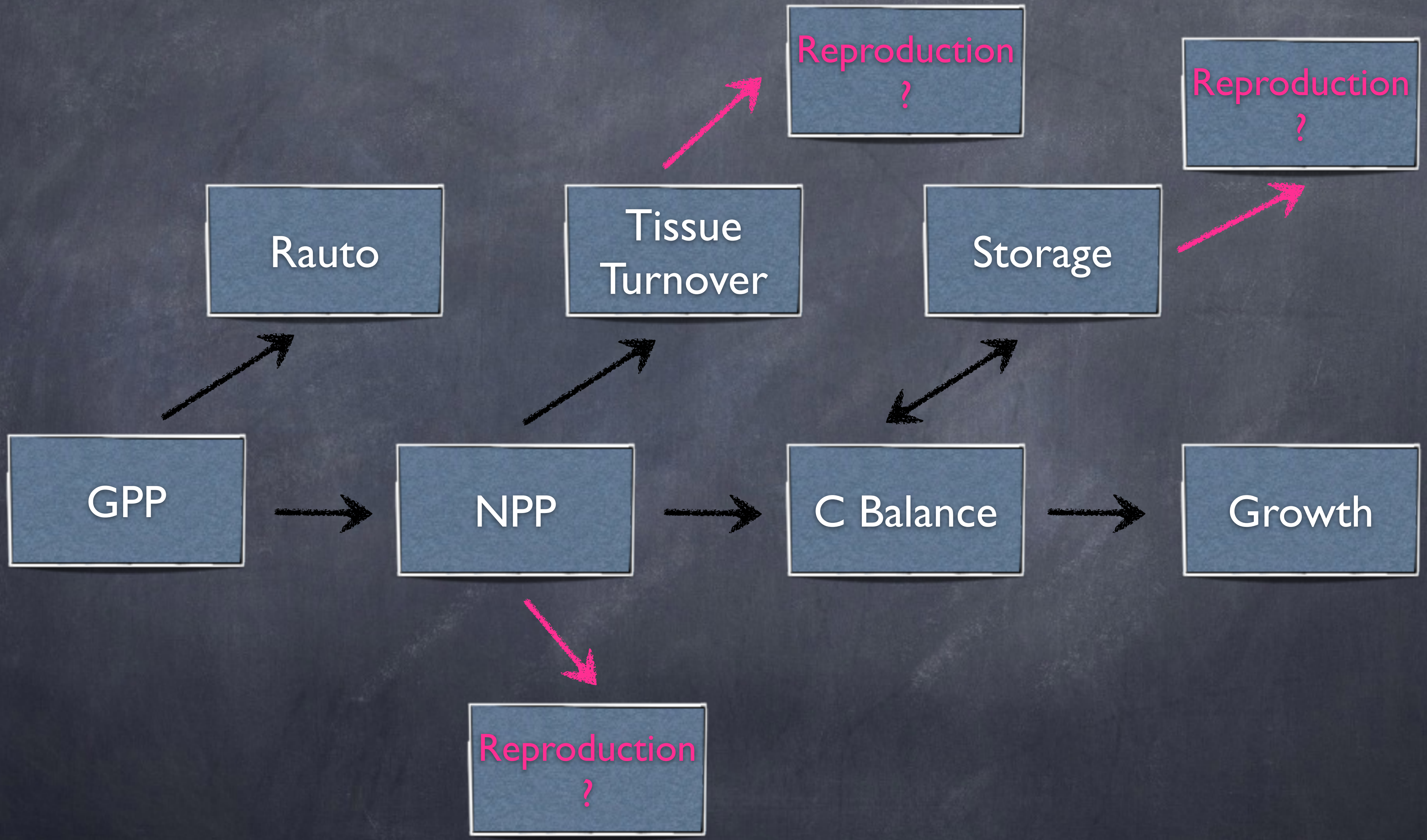
n.b This is for a light-limited system!

Recruitment

Reproductive Allocation



Reproductive Allocation



Recruitment: Bioclimatic Envelopes
(conditions needed for establishment)

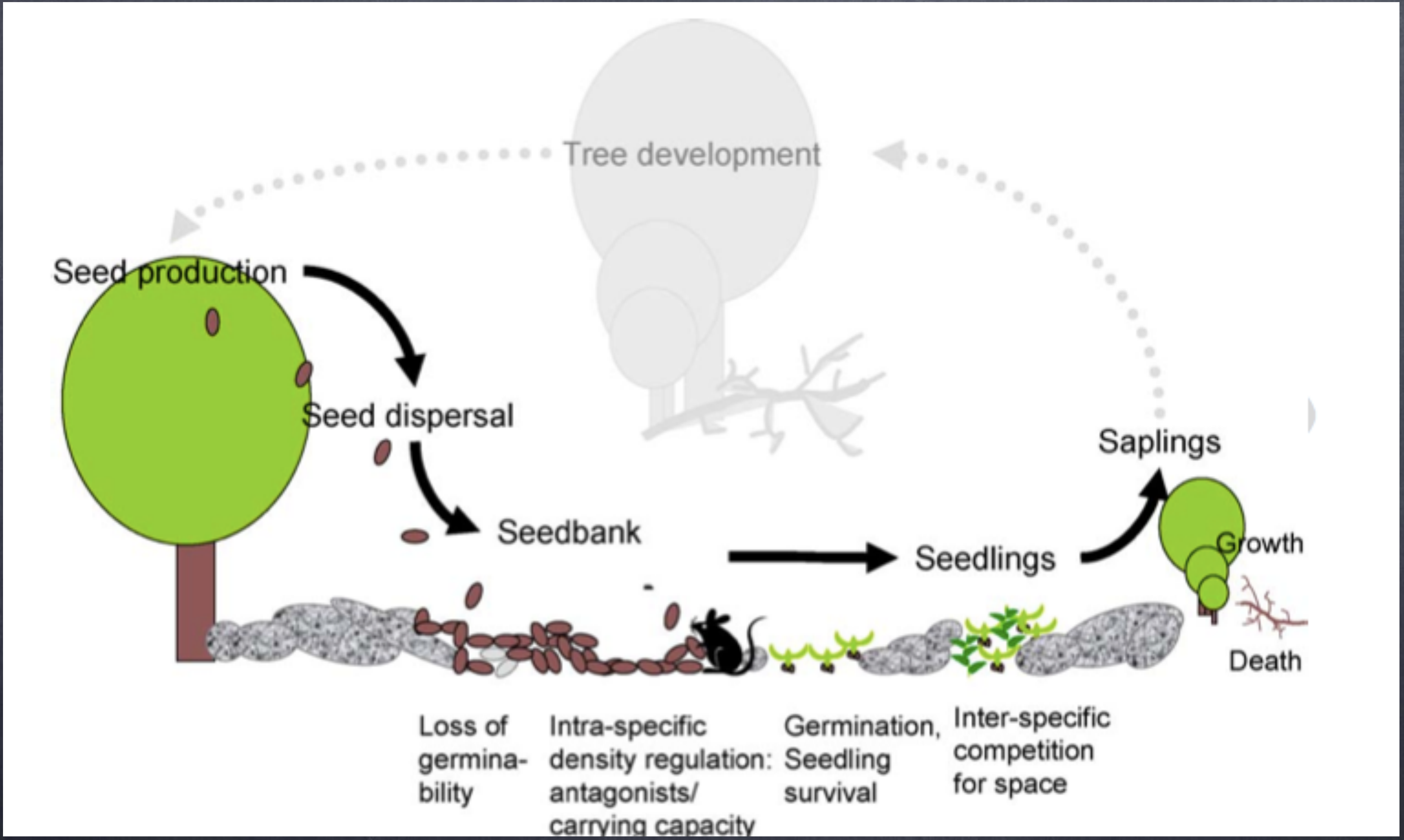
Table 2 PFT Bioclimatic limits: $T_{c,min}$ = minimum coldest-month temperature for survival; $T_{c,max}$ = maximum coldest-month temperature for establishment; GDD_{min} = minimum degree-day sum (5 °C base) for establishment; $T_{w-c,min}$ = minimum warmest minus coldest month temperature range

PFT	$T_{c,min}$ (°C)	$T_{c,max}$ (°C)	GDD_{min} (°C)	$T_{w-c,min}$ (°C)
Tropical broad-leaved evergreen	15.5	–	–	–
Tropical broad-leaved raingreen	15.5	–	–	–
Temperate needle-leaved evergreen	−2.0	22.0	900	–
Temperate broad-leaved evergreen	3.0	18.8	1200	–
Temperate broad-leaved summergreen	−17.0	15.5	1200	–
Boreal needle-leaved evergreen	−32.5	−2.0	600	–
Boreal needle-leaved summergreen	–	−2.0	350	43
Boreal broad-leaved summergreen	–	−2.0	350	–
Temperate herbaceous (TeH)	–	15.5	–	–
Tropical herbaceous (TrH)	15.5	–	–	–

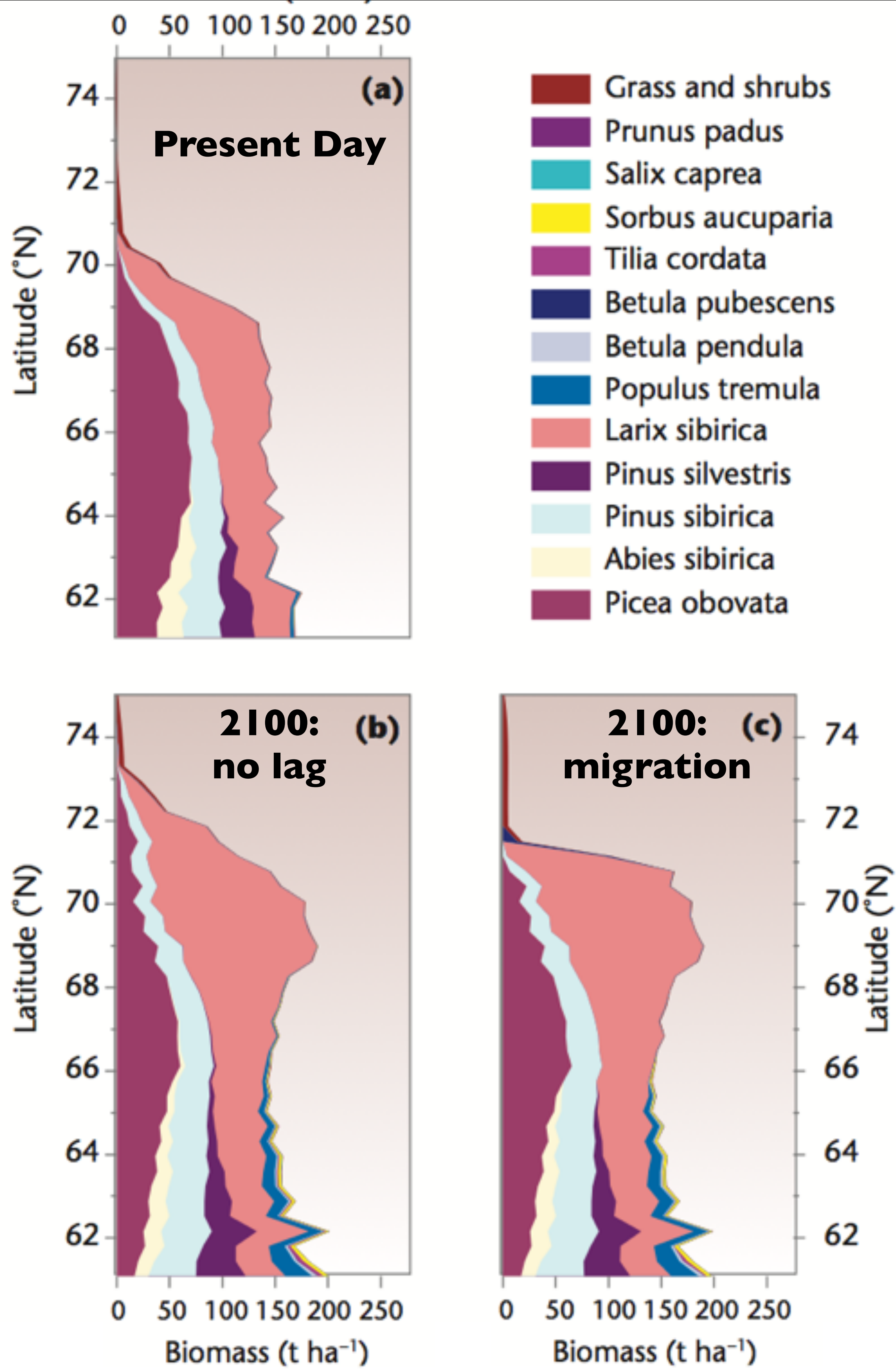
The standard assumption is that all seeds are everywhere

Sitch et al. 2003 (The LPJ model & CLM-Dynamic Vegetation Model)

Recruitment: Migration in TREEMIG



Lischke et al. 2009



- Implementing migration-induced lags in vegetation establishment has large impacts on biomass of expanding ecosystems
- n.b. this is not standard in DGVMs

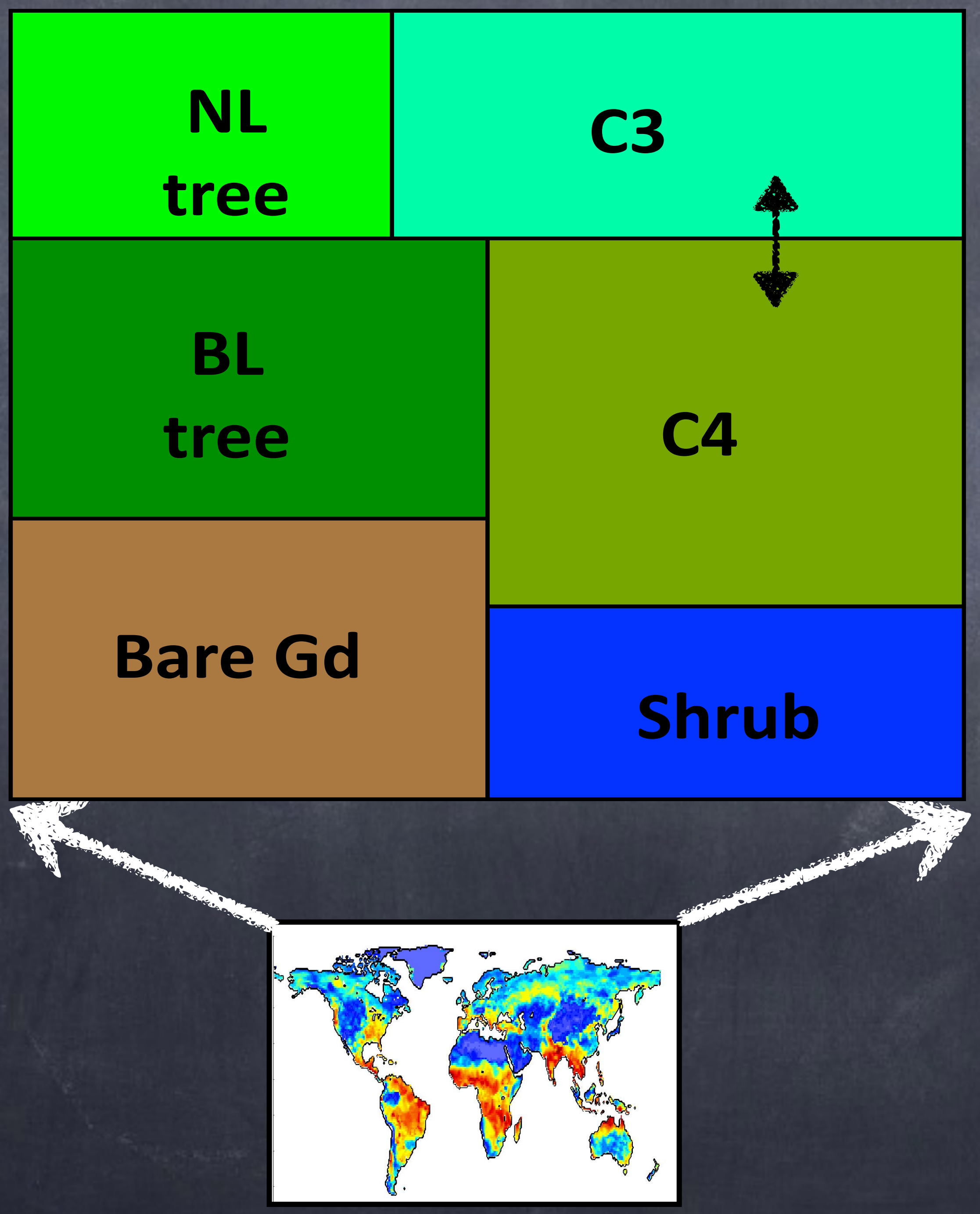
Epstein, Yu, Kaplan & Lischke 2007

Competition

'Area-based' Models

(e.g. CLM, TRIFFID, LPJ, IBIS - models used in IPCC assessments)

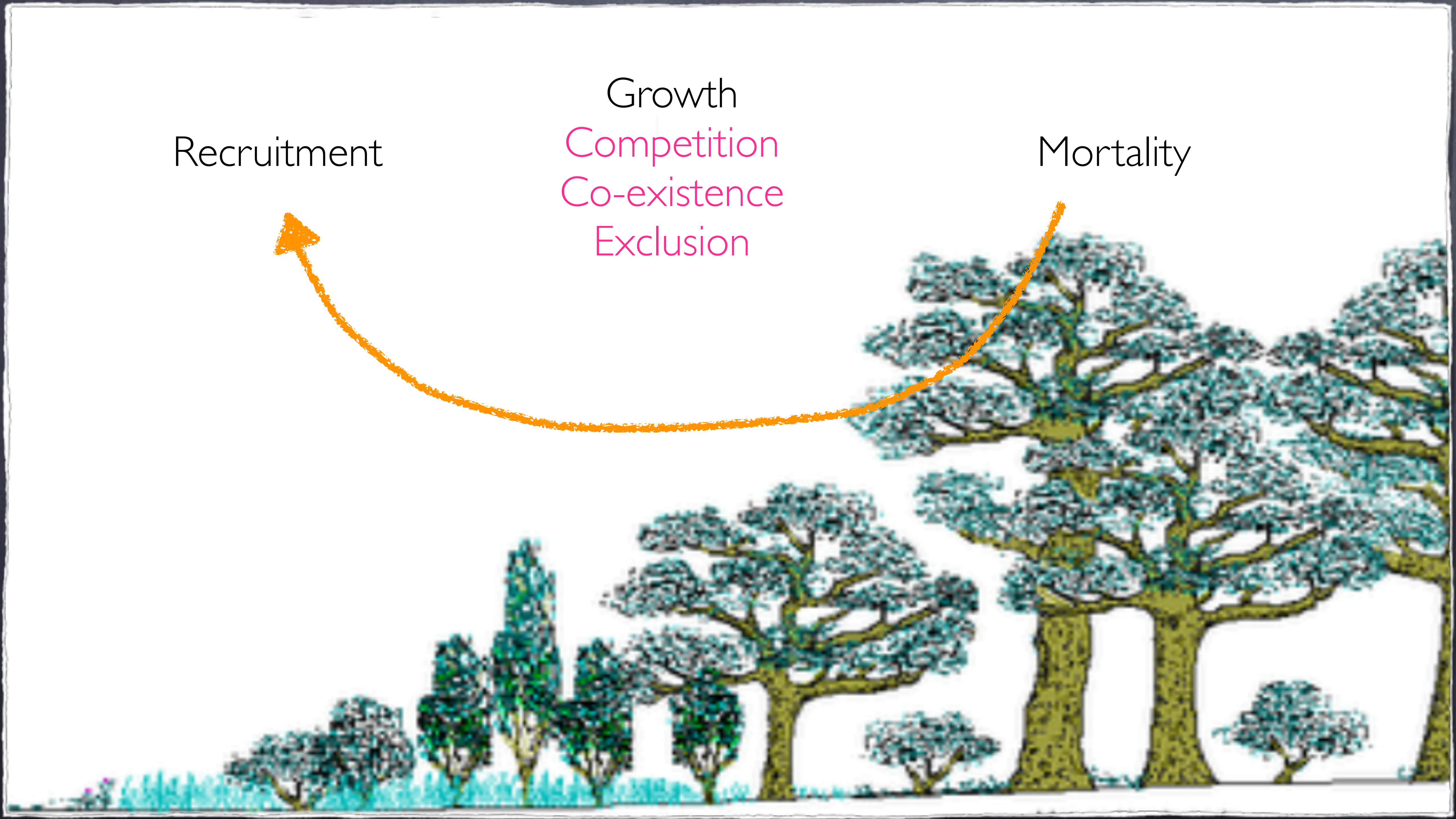
- Cell divided into plant type 'tiles'
- 1 'average tree' per plant type
- No competition for light
- Expansion via relative growth rates



- Deterministic
- Computationally efficient
- Widely used in climate simulations

“Climate models don’t represent competition realistically”
(most living plant ecologists)

How do ecological systems organize the diversity of plant life?

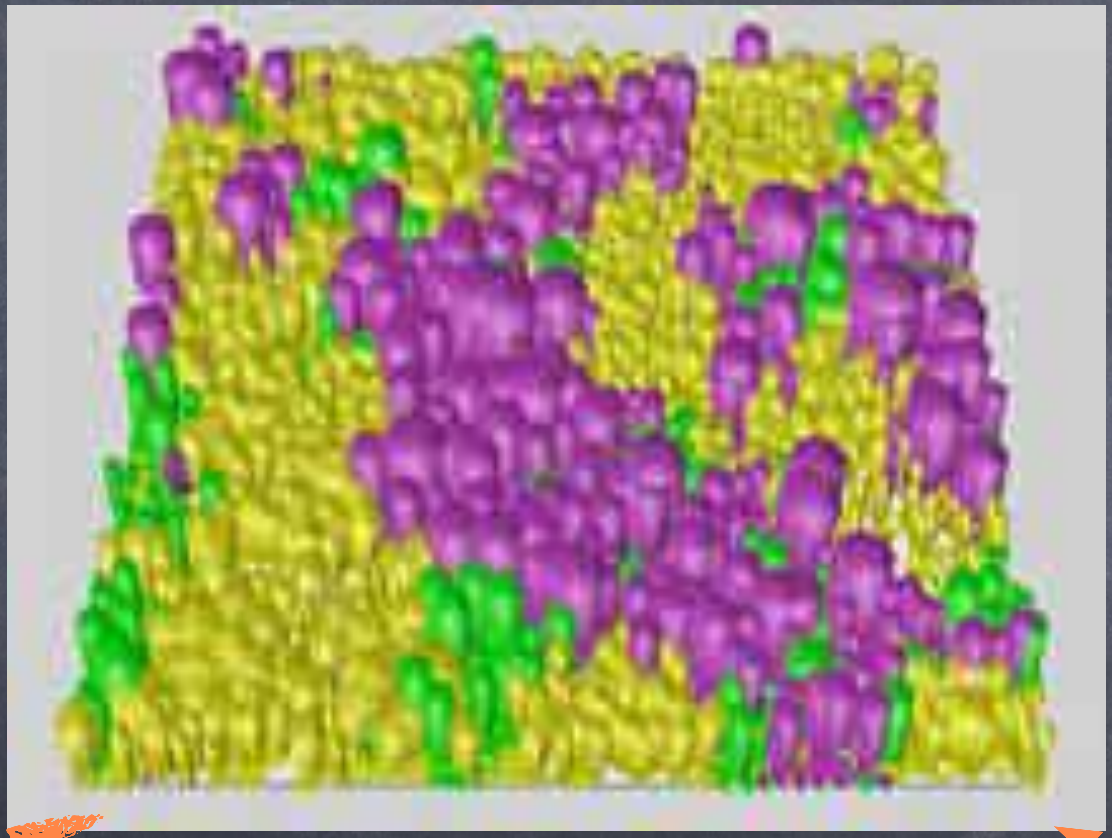


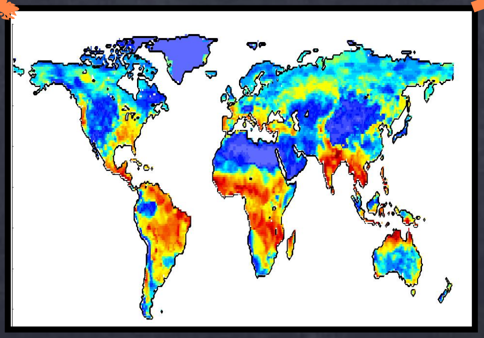
- Modeling competition for light requires that we have different plant functional types in the same vertical profile…

Individual-Based Models

(e.g. SORTIE, LPJ-GUESS, SEIB, aDGVM)

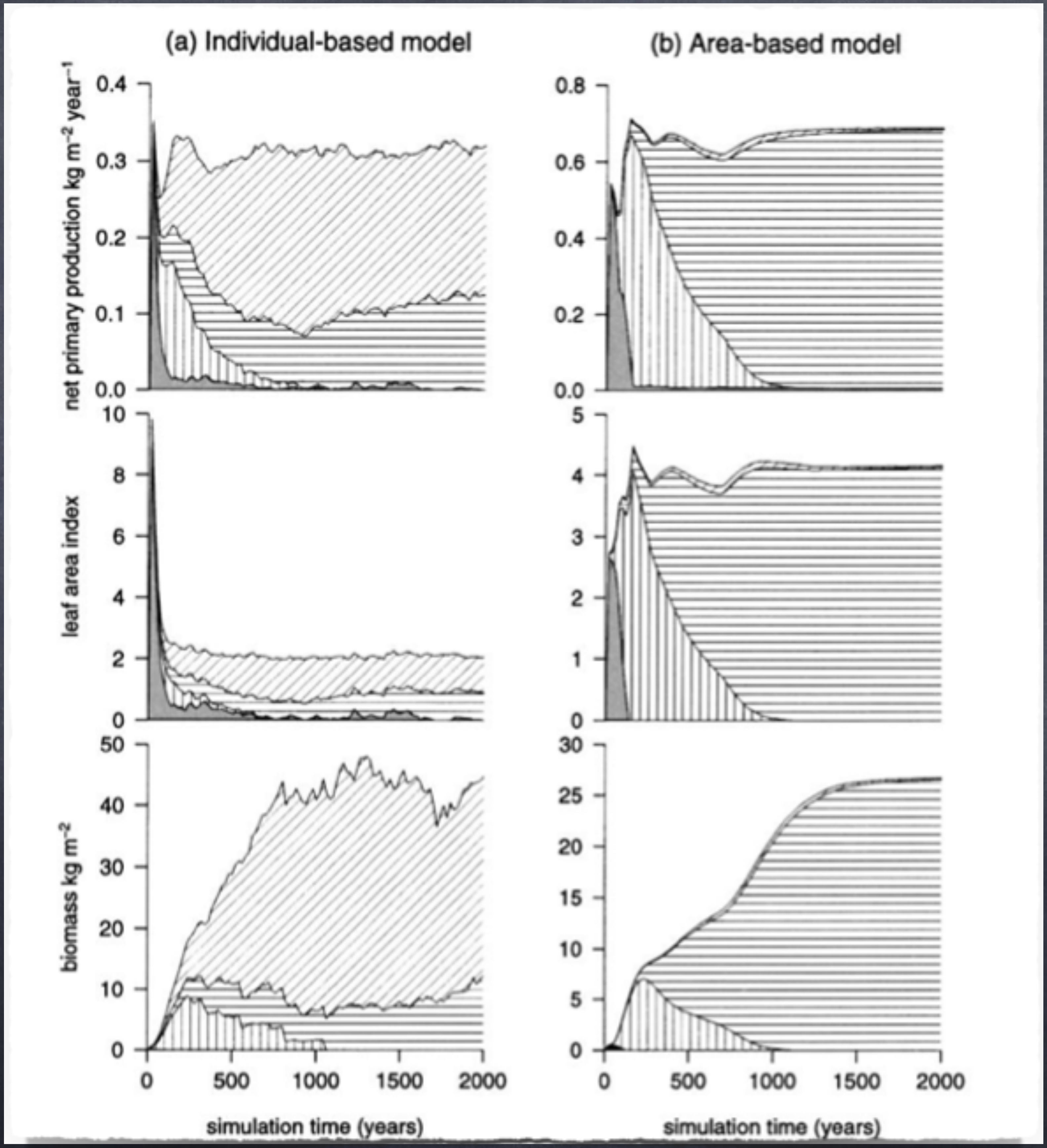
- Individual Based
- 3D light environment
- Simulates: recruitment competition disturbance





- Stochastic demographics
- Computationally intensive
- Ensemble approach required

Co-existence in LPJ vs LPJ-GUESS (Smith et al. 2001)



Ecosystem Demography Model (ED)

Moorcroft, Hurtt and Pacala. 2001

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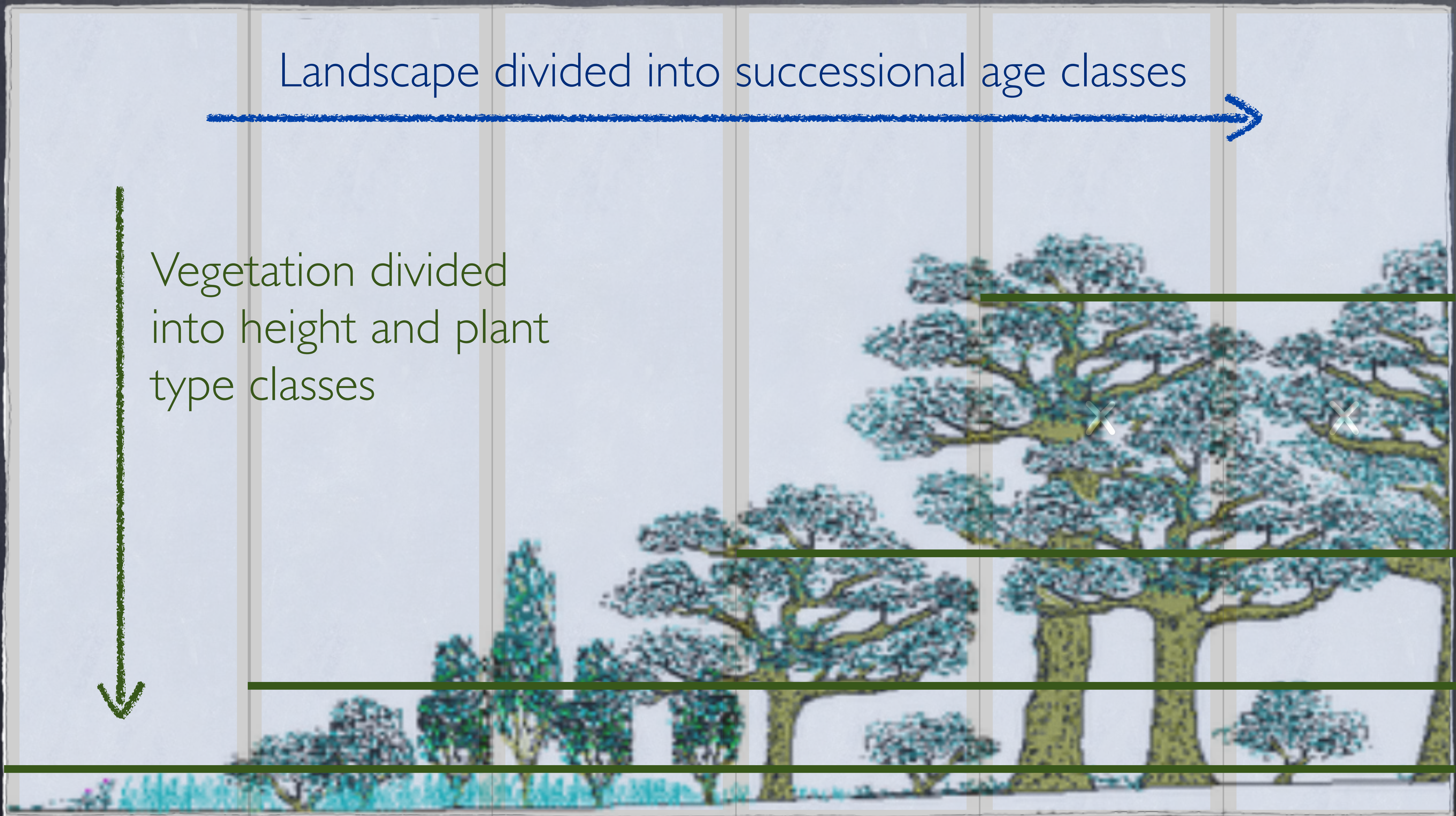
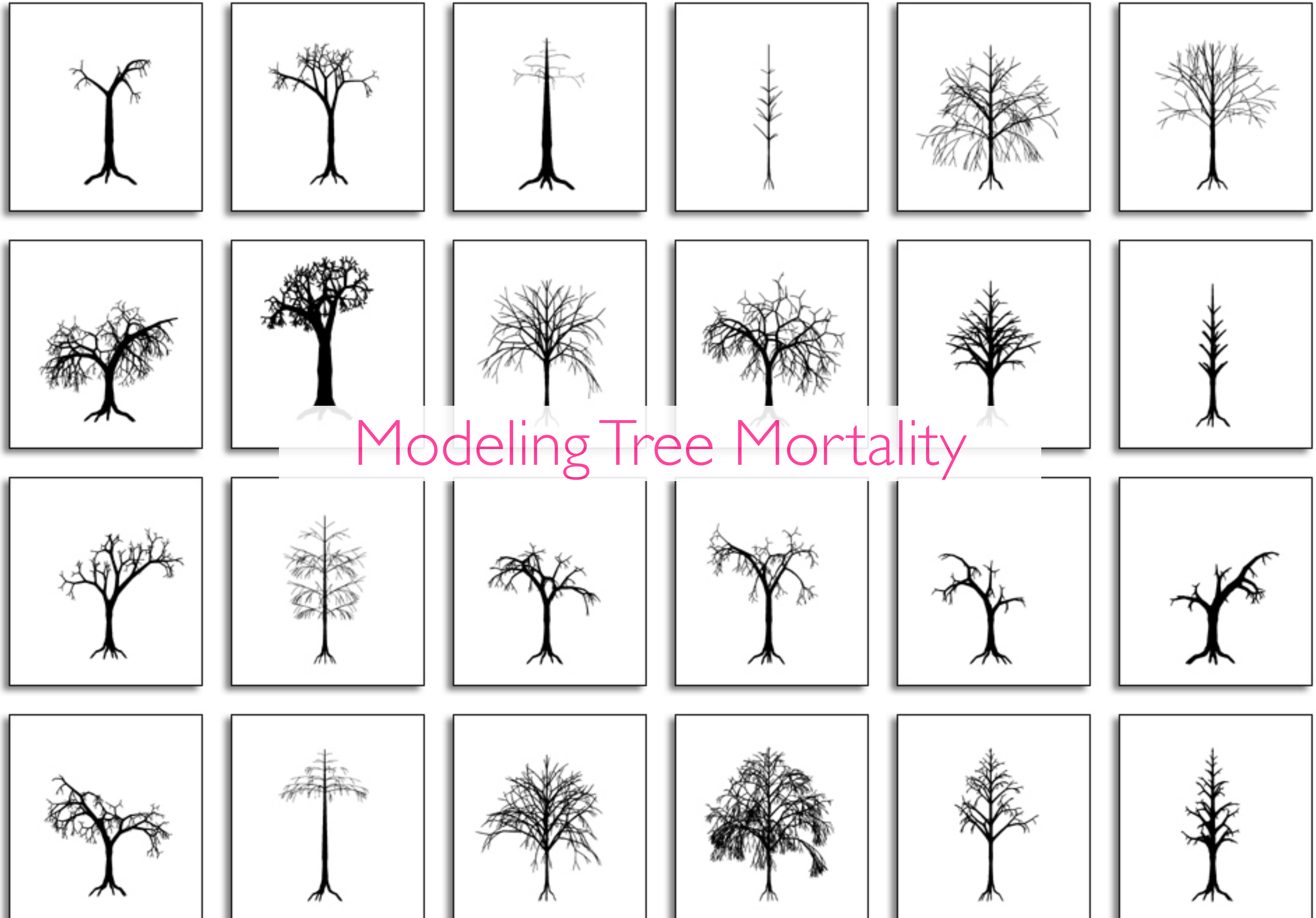
Moorcroft, Hurtt and Pacala. 2001



Benefits of ED approach to competition

- Computationally plausible simulations of ecological dynamics
- Represents vertical competition for light:
  - Representation of multiple niches & the possibility of plant co-existence
- Simulation of recovery from human and natural disturbance events.
- BUT - the extra ability to simulate ecological dynamics with a stochastic model is lost…

Modeling Tree Mortality



The status quo in DGVM world

The interdependence of mechanisms underlying climate-driven vegetation mortality

Nate G. McDowell[1], David J. Beerling[2], David D. Breshears[3], Rosie A. Fisher[4], Kenneth F. Raffa[5] and Mark Stitt[6]

[1] Los Alamos National Laboratory, Los Alamos, NM, USA
[2] Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK
[3] School of Natural Resources and the Environment, and Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA
[4] National Center for Atmospheric Research, Boulder, CO, USA
[5] Department of Entomology, University of Wisconsin, Madison WI, USA
[6] Max Planck Institute for Molecular Plant Physiology, Potsdam, Germany

Mortality algorithms are typically empirical, poorly tested, and based on proxies of plant health

CLM takes its mortality model from LPJ

Table I. Plant mortality algorithms from a selection of the most commonly used DGVMs, listed approximately in order of progressive increase in mechanistic detail, with example models cited in the references

Mortality algorithms	Description
Productivity dependence	No explicit concept of mortality; plant biomass reduced via declining productivity [88]
Background rate	Mortality is set at a constant, invariant rate (approximately 1–2% yr^{-1}). This does not allow climate to drive variation in mortality [89–91]. In [12,92], background mortality increases as wood density decreases relative to the community maximum
Climate tolerance	Death occurs if the 20-year average climate exceeds predefined monthly climatic tolerances [93–96]
Size threshold	Death occurs if trunk diameter > 1.0 m [96].
Age threshold	Death increases as stand age approaches the plant functional type-specific maximum [84]
Heat stress threshold	Mortality is a function of the number of days per year in which the average temperature exceeds a threshold temperature, and the number of degrees (°C) by which this threshold is exceeded [84,92–97]
Negative productivity	Death occurs if annual net productivity < 0.0 g [93–96]
Shading/competition	Mortality increases as a function of canopy cover [12,92–97]
Growth efficiency threshold	Mortality occurs when biomass increment per unit leaf area falls below a quantitative threshold that varies between models [86,93–96,98]
Carbon starvation	Mortality is a function of carbohydrate storage per unit leaf biomass [12]

What about more detailed forest models?

SORTIE-ND

Software for spatially-explicit simulation of forest dynamics

Mortality behaviors

The mortality behaviors cause tree death due to natural life cycle causes and competition. Tree death due to disturbance is covered by other behaviors.

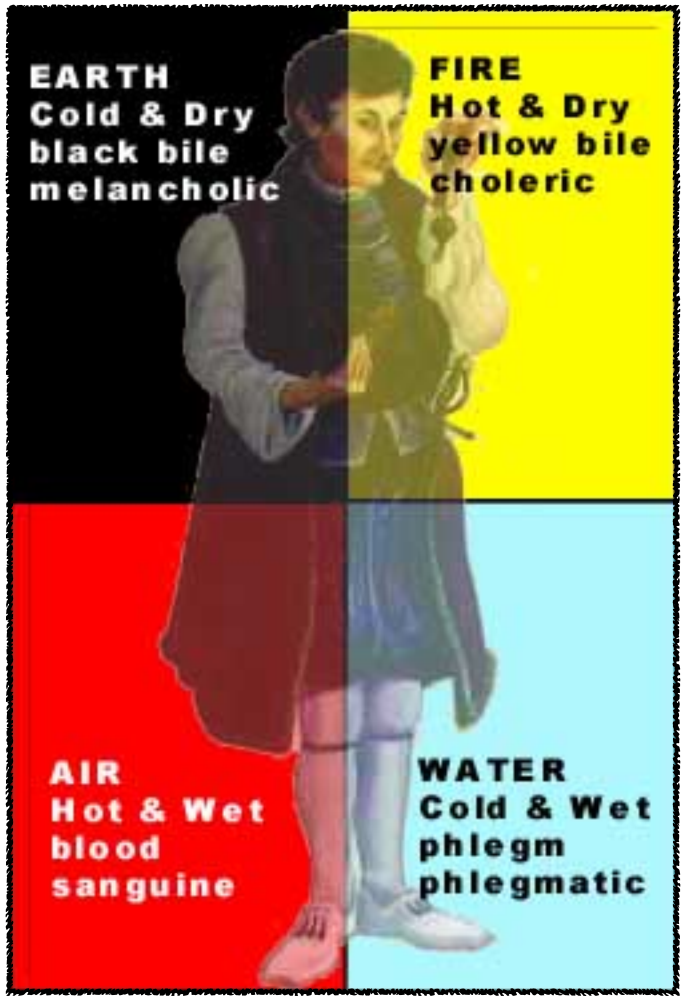
Mortality behaviors do not actually remove dead trees from memory. They set a flag which marks trees as dead. This is because some other behaviors, such as the Substrate group, have specific interest in dead trees. Dead trees are eventually removed from memory by the Dead tree remover behavior. You may notice this behavior in your behavior list. It is included automatically. It is important to include this behavior in your run to avoid incorrect results in behaviors that use dead trees and unacceptably slow model run times.

Behavior	Description
Aggregated Mortality	Kills trees randomly to match a predetermined mortality rate, clumping together the deaths in both time and space.
BC Mortality	Kills trees as a function of growth rate.
Browsed Stochastic Mortality	Simulates the effects of herbivory by allowing different background mortality rates for browsed and unbrowsed trees.
Competition Mortality	Kills trees as a function of growth. Uses the results of the NCI growth behavior.
Density Self-Thinning Mortality	Calculates the probability of mortality of an individual juvenile tree as a function of the density and mean diameter of the neighborhood trees.
Exponential Growth and Resource-Based Mortality	Calculates probability of mortality as a function of growth and some second resource.
GMF Mortality	Kills trees as a function of growth rate.
Gompertz Density Self Thinning	Calculates the probability of mortality of an individual tree as a function of the density of conspecific neighborhood trees.
Growth and Resource-Based Mortality	Calculates probability of survival as a function of growth and some second resource.
Height-GLI Weibull Mortality with Browse	Calculates the probability of mortality using a Weibull function of tree height and GLI (light level). It can also simulate the effects of herbivory by using different parameters for browsed and unbrowsed trees.
Insect Infestation Mortality	Causes mortality in trees that are infested with insects.
Logistic Bi-Level Mortality	Calculates the probability of survival according to a logistic equation, with the possibility of two sets of parameters for each species: one for high-light conditions and one for low-light conditions.
NCI Mortality	Uses multiple effects, including neighbor competitiveness, to calculate mortality rates.
Post Harvest Skidding Mortality	Simulates an increase in mortality after harvesting attributable to skidding damage or other effects.
Self Thinning	Uses a pseudo-density dependent function designed to increase the death rate in dense uniform-age stands.
Senescence	Provides for an uptick in mortality rates among large adult trees.
Stochastic Bi-Level Mortality - Storm Light	Applies a constant rate of mortality to trees, with different rates for high-light and low-light conditions. This works with the Storm Light behavior.
Stochastic Bi-Level Mortality - GLI	Applies a constant rate of mortality to trees, with different rates for high-light and low-light conditions. This works with the GLI behavior.
Stochastic Mortality	Produces background mortality by randomly choosing trees to die according to a specified rate.
Suppression Duration Mortality	Evaluates mortality as a function of tree age. This is particularly useful for simulating suppression in seedlings.
Temperature dependent neighborhood survival	Assesses tree survival as a function of mean annual temperature and neighbor adult basal area. For efficiency, it calculates survival rates for cells in a grid and assigns trees the survival probability of the grid cell in which they are found.
Weibull Climate Survival	Assesses tree survival as a function of climate and larger neighbor trees.
Weibull Snag Mortality	Controls snag fall according to a Weibull function of snag age.

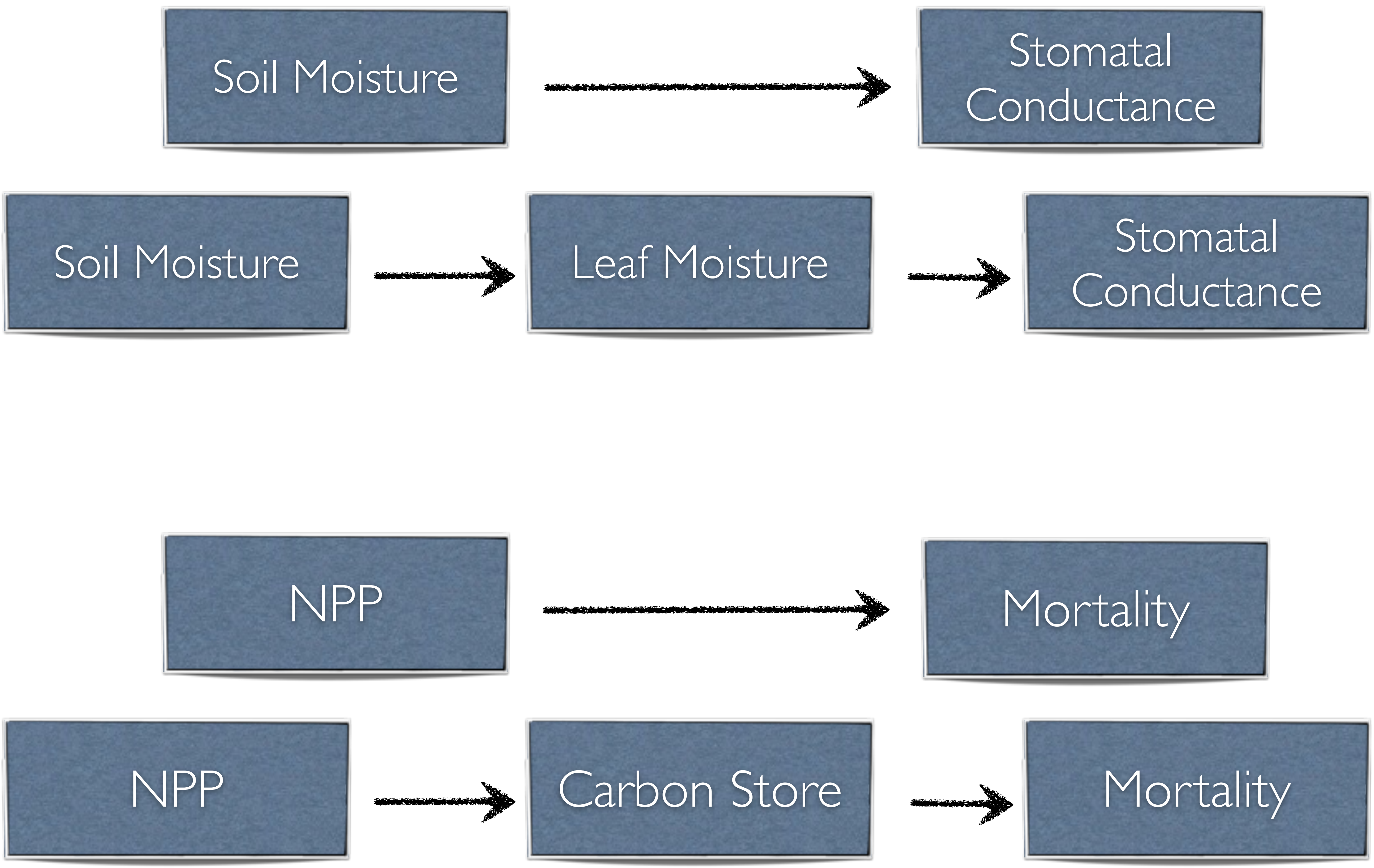
http://www.sortie-nd.org/help/manuals/help/data/mortality_behaviors

Can we do any better?

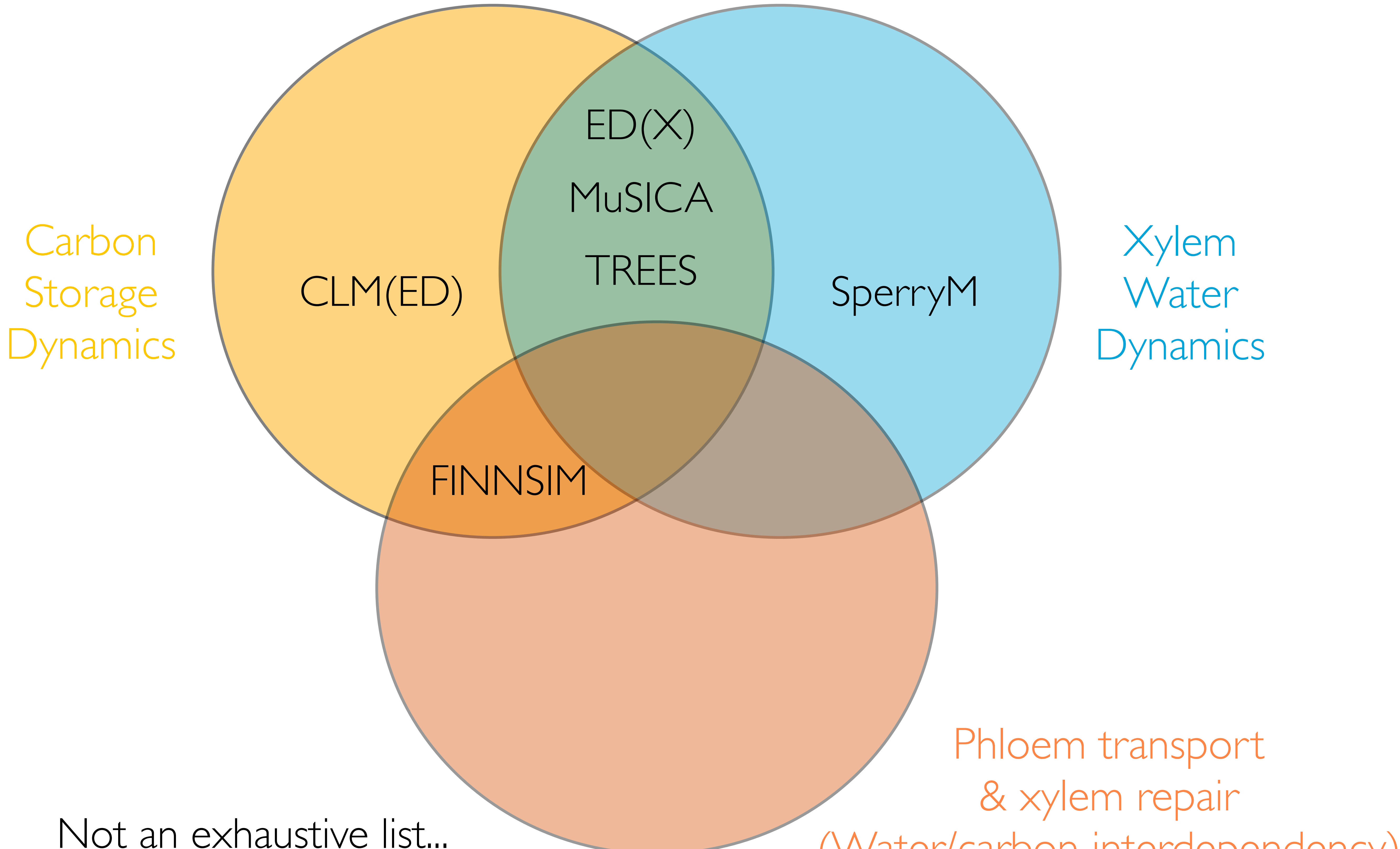
- Why makes plants die?
  - Carbon Budget Failure?
  - Hydraulic Failure?
  - Phloem Transport Failure?



A conceptual revolution: Internalizing plant physiology models

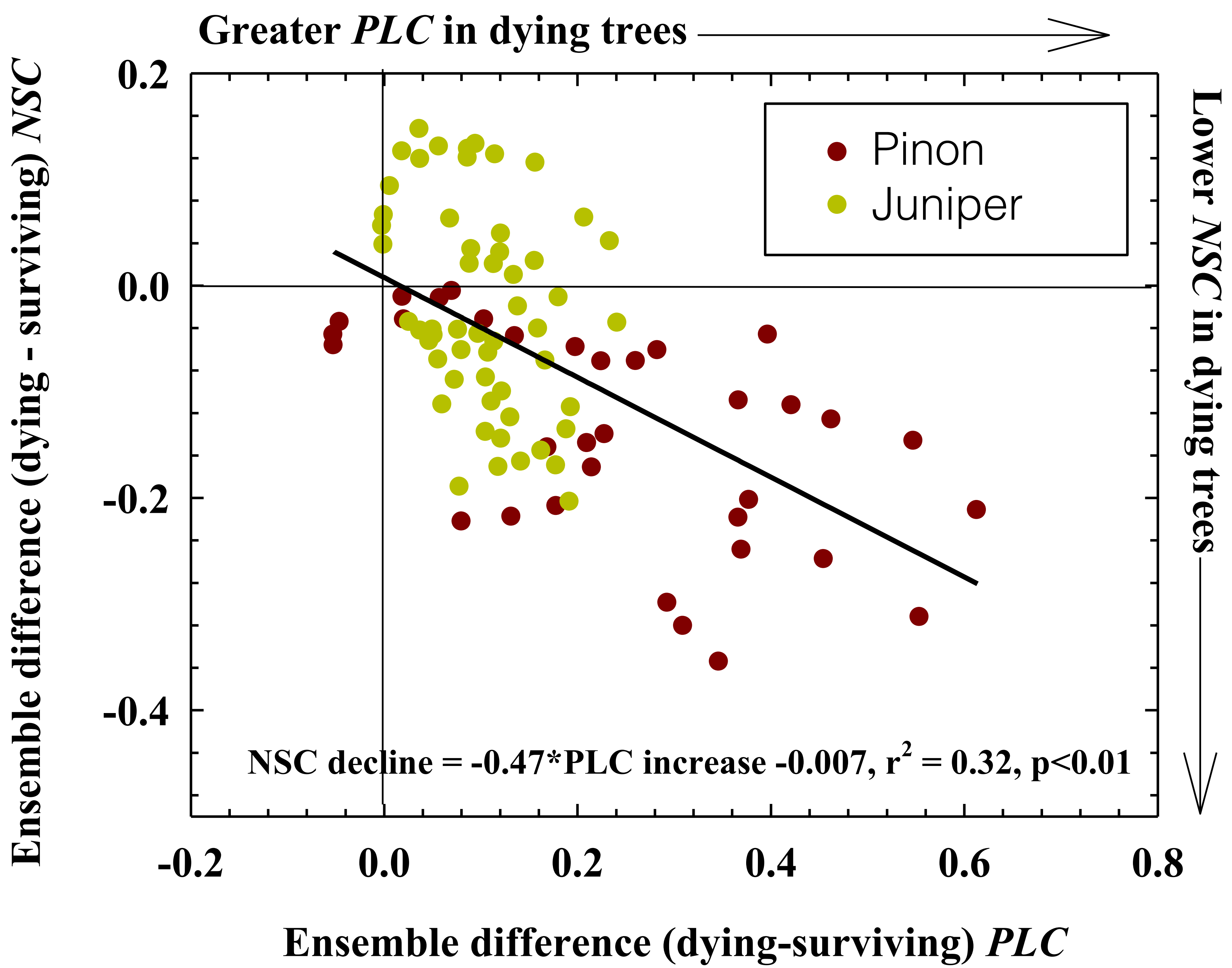


Recent developments in mortality models...



Not an exhaustive list...

Modeling drought mortality

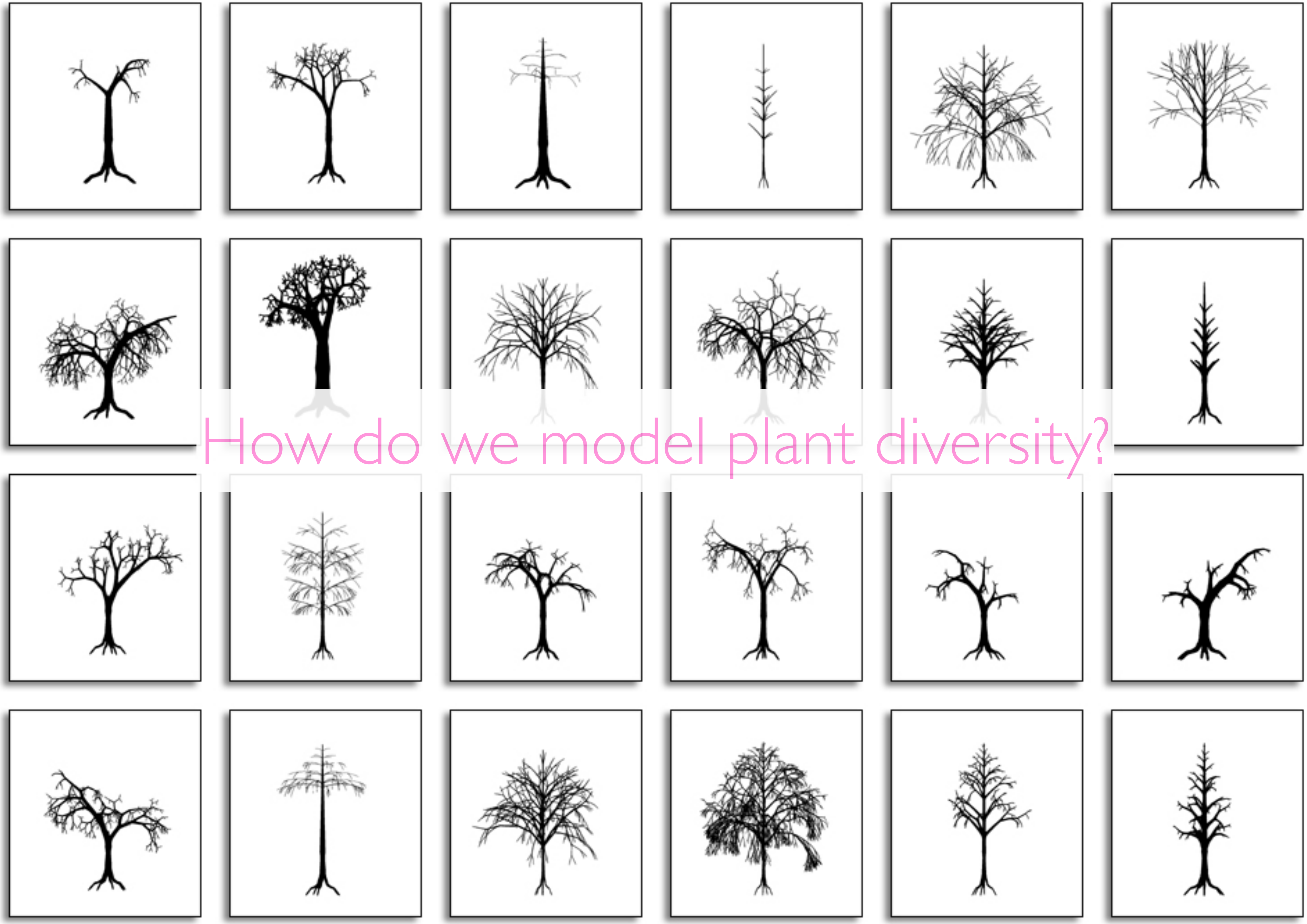


McDowell, Fisher, Xu, Domec, Holtta, Mackay, Sperry et al. New Phytologist (2014)

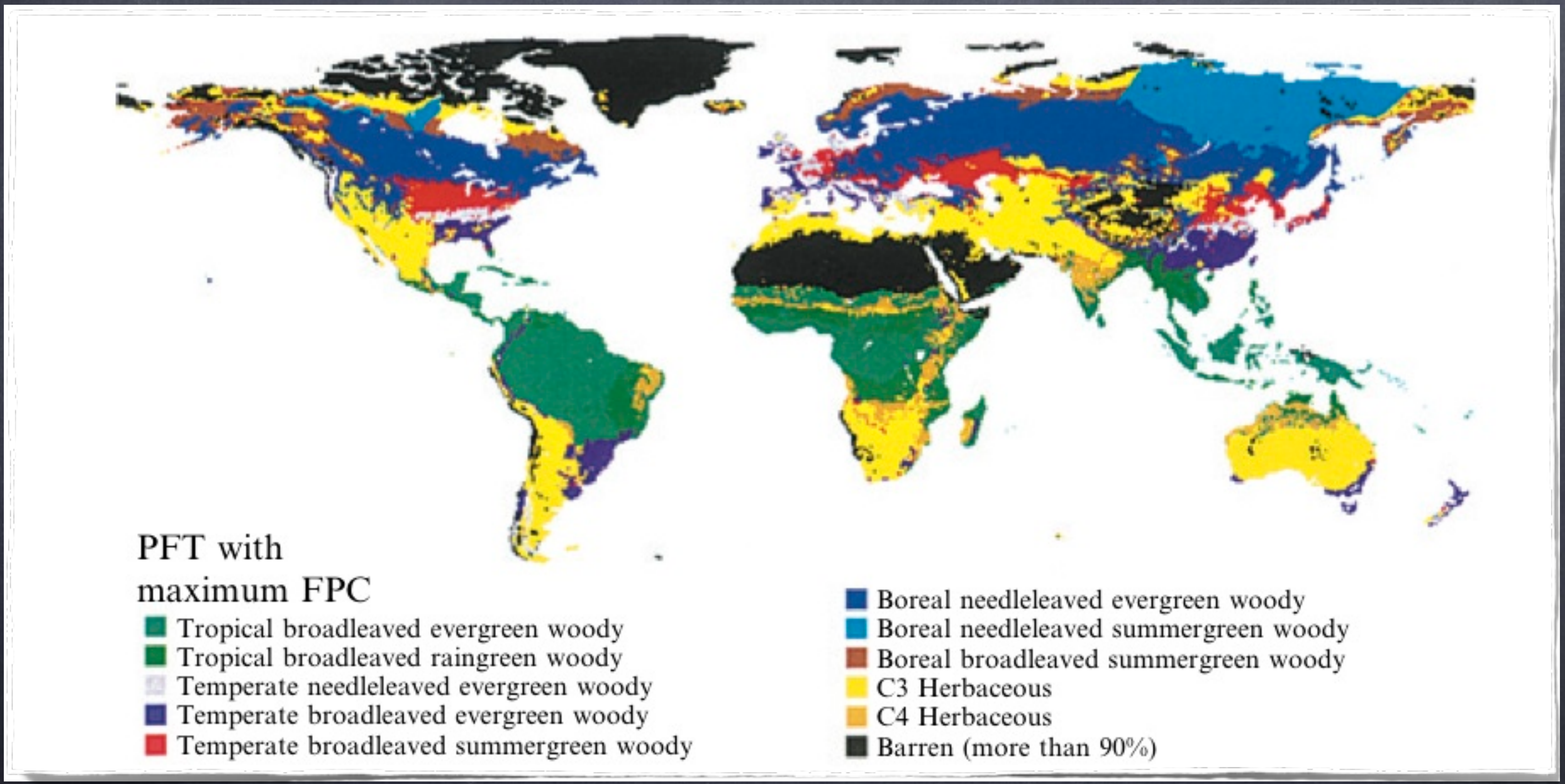
Why bother with the extra complication?

- Mortality models can be parameterized with real observations (carbon pool sizes, plant hydraulic properties, LWP obs, etc.)
- Some features (lags, relations to other plant traits) cannot be predicted from average productivity metrics (NPP/LAI).

How do we model plant diversity?



Plant Diversity in DGVMs



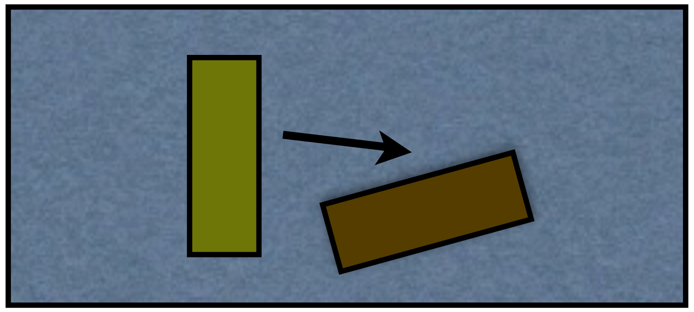
Sitch et al. 2003

Why dieback : aggregation of plant diversity?

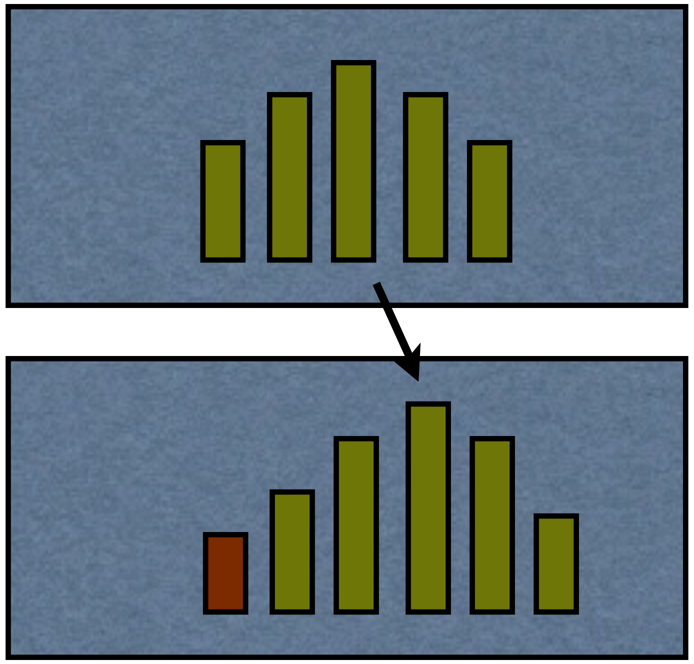
- There are only ~10 kinds of plant.
- Dieback events occur at the physiological thresholds of single plant types.
- Is it realistic that, e.g. all boreal trees, have the same physiological thresholds?

“There are not enough plant types in climate models”

(every living plant ecologist)

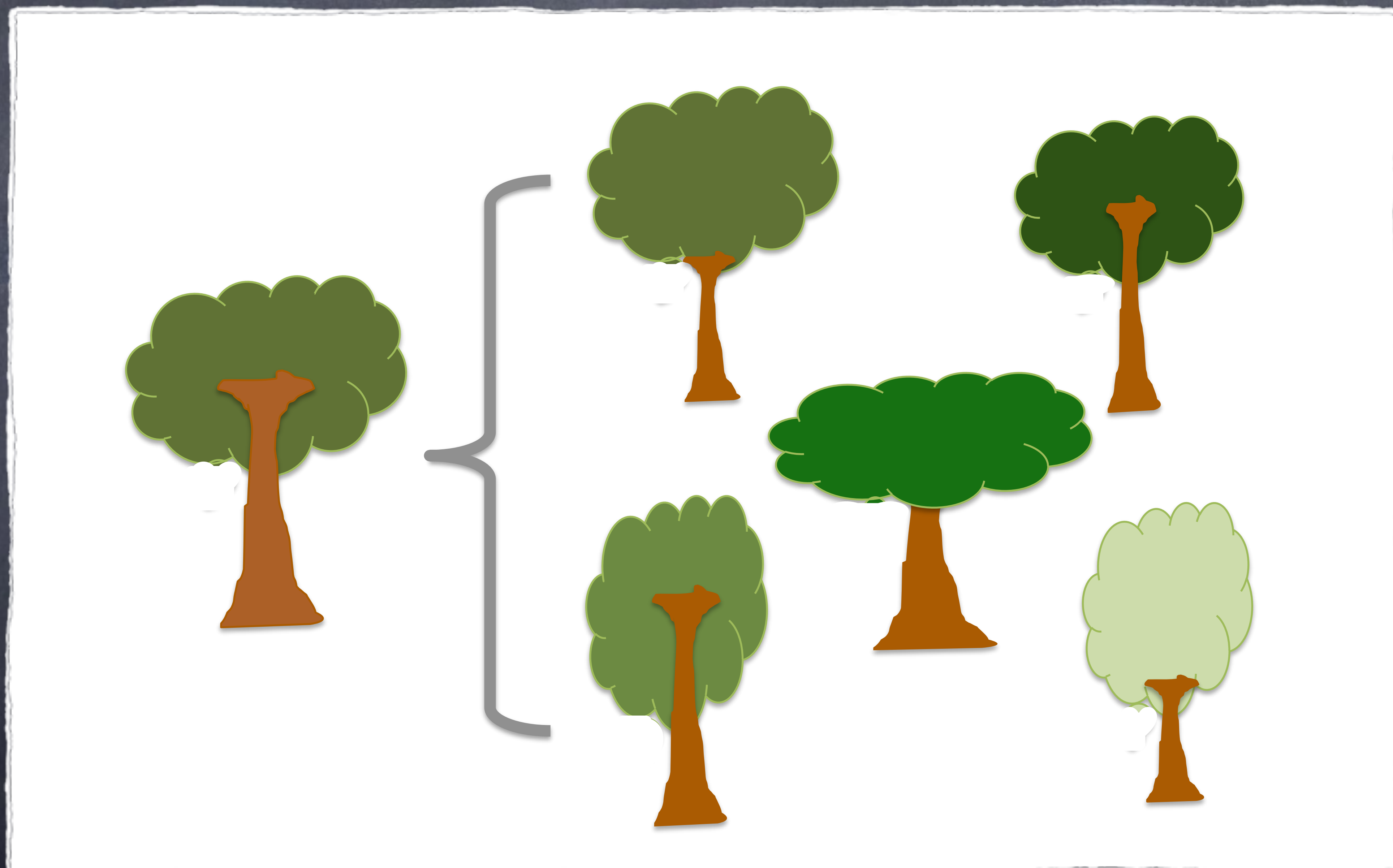


- Low (functional) diversity causes low resilience to change.



Improved resolution of plant functional types?

What do we want to represent?

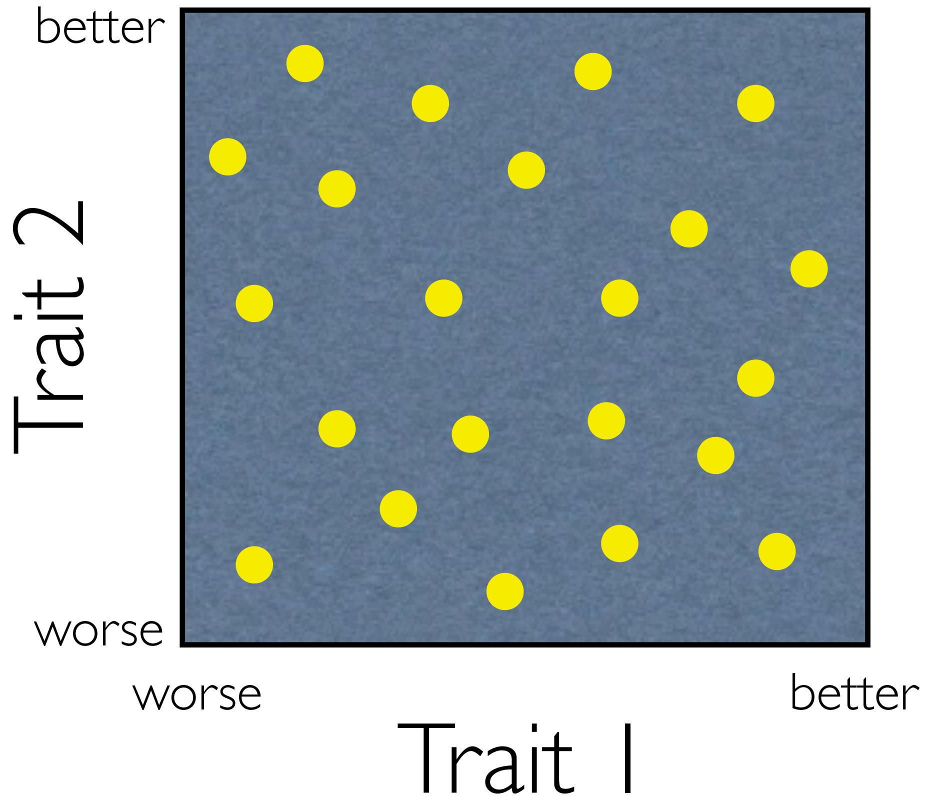


Plant Traits

- Functional properties of plants are called 'traits'
- Models define plant properties according to a set of trait values
    - wood density, leaf lifespan, photosynthetic capacity,
    - root depth, allometry, reflectance, nitrogen content, etc.
- Representing diversity involves increased sampling of trait space.
- This is made easier by 'trade-off's between plant traits.

Plant variation through multi-dimensional 'trait space'

ALL THEORETICAL PLANTS



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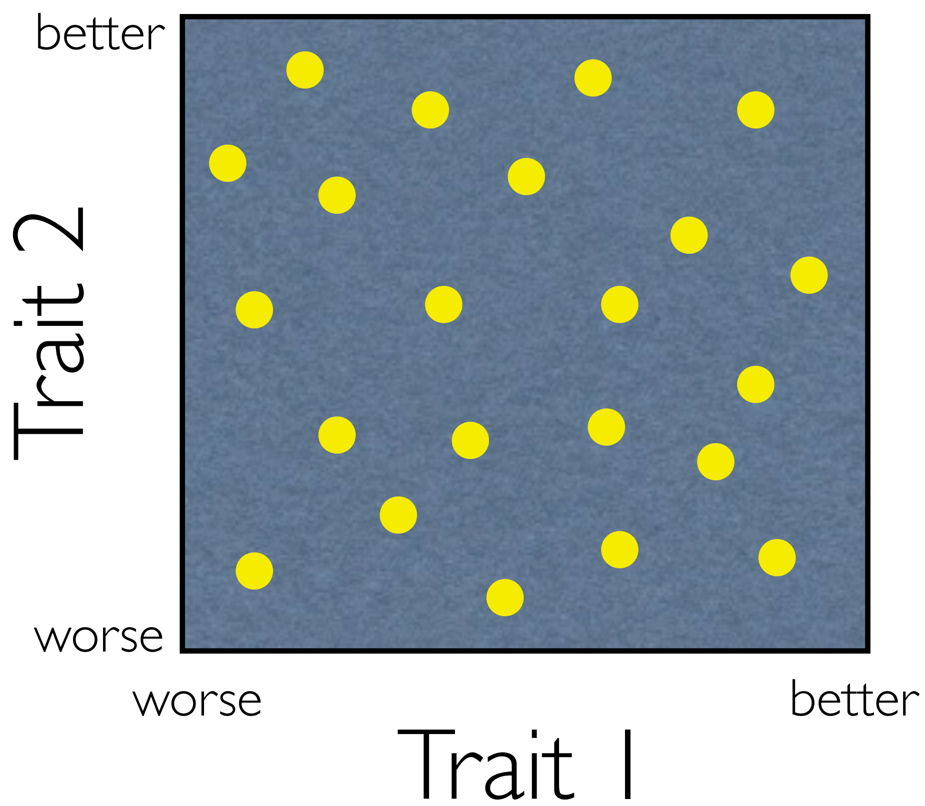
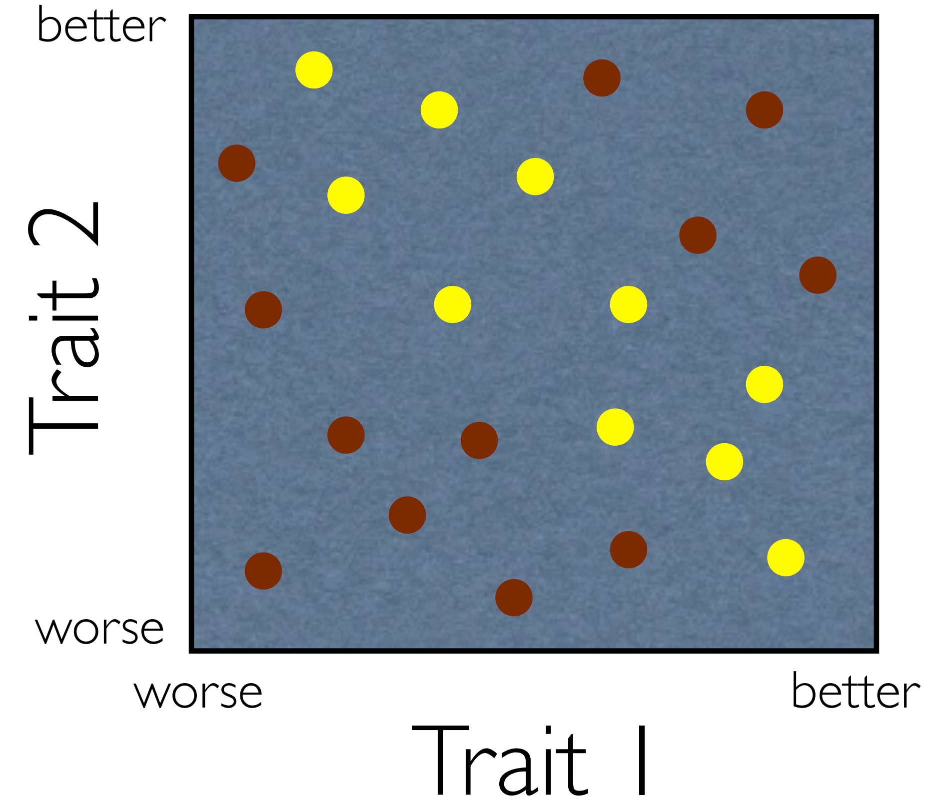
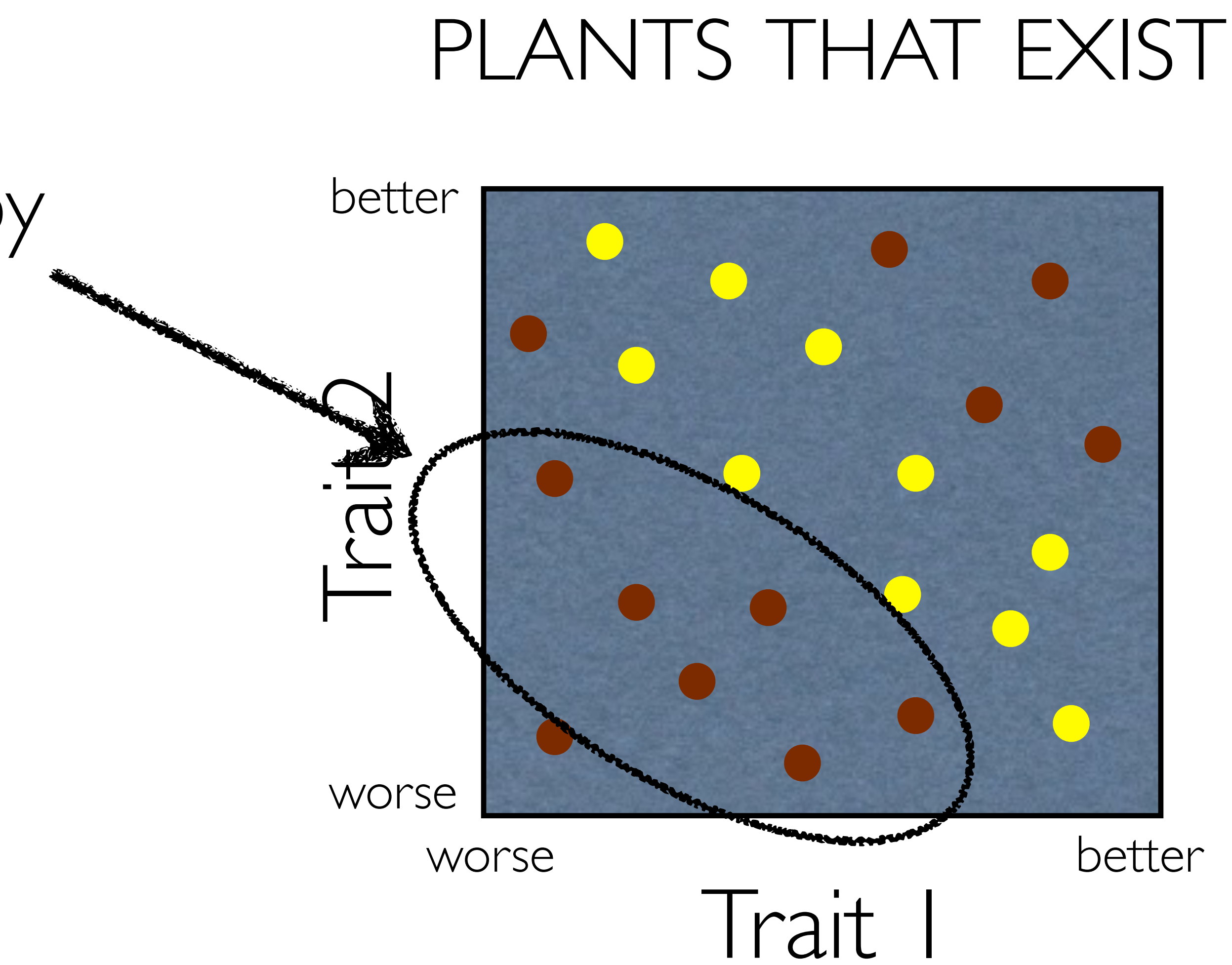


PLANTS THAT EXIST



Plant variation through multi-dimensional 'trait space'

These plants do not exist because they are eliminated by natural selection



Plant variation through multi-dimensional 'trait space'

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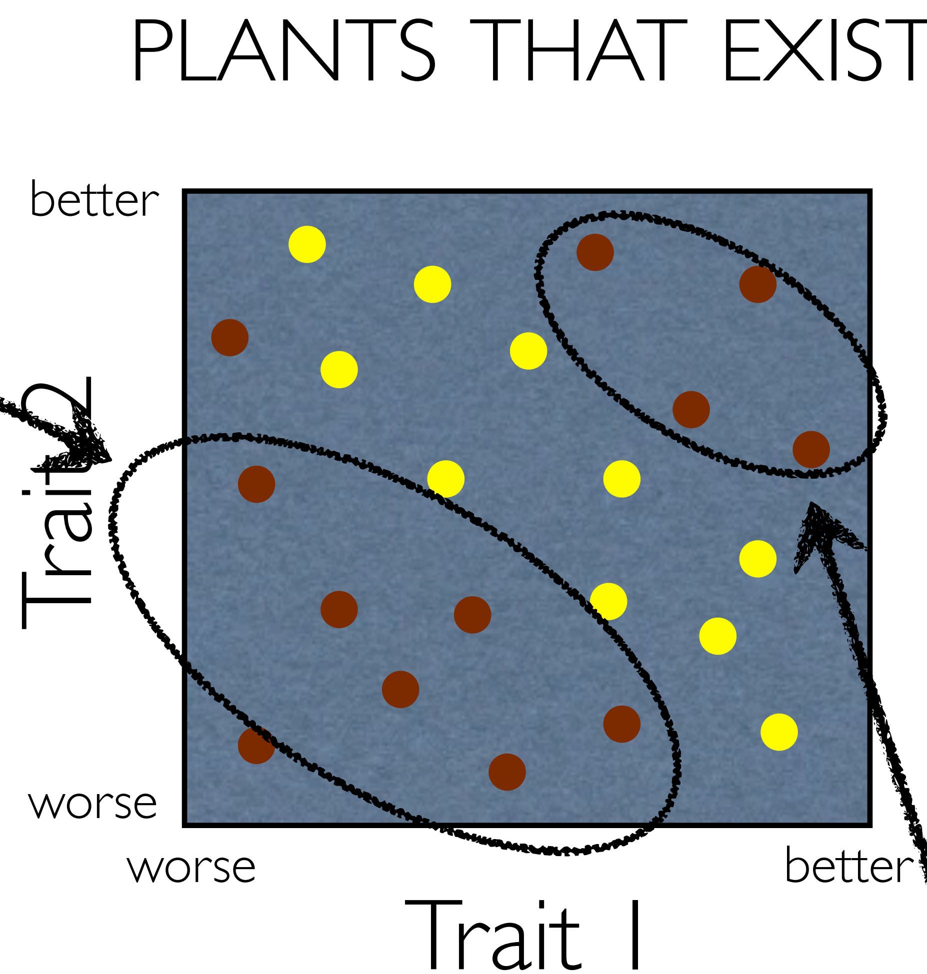
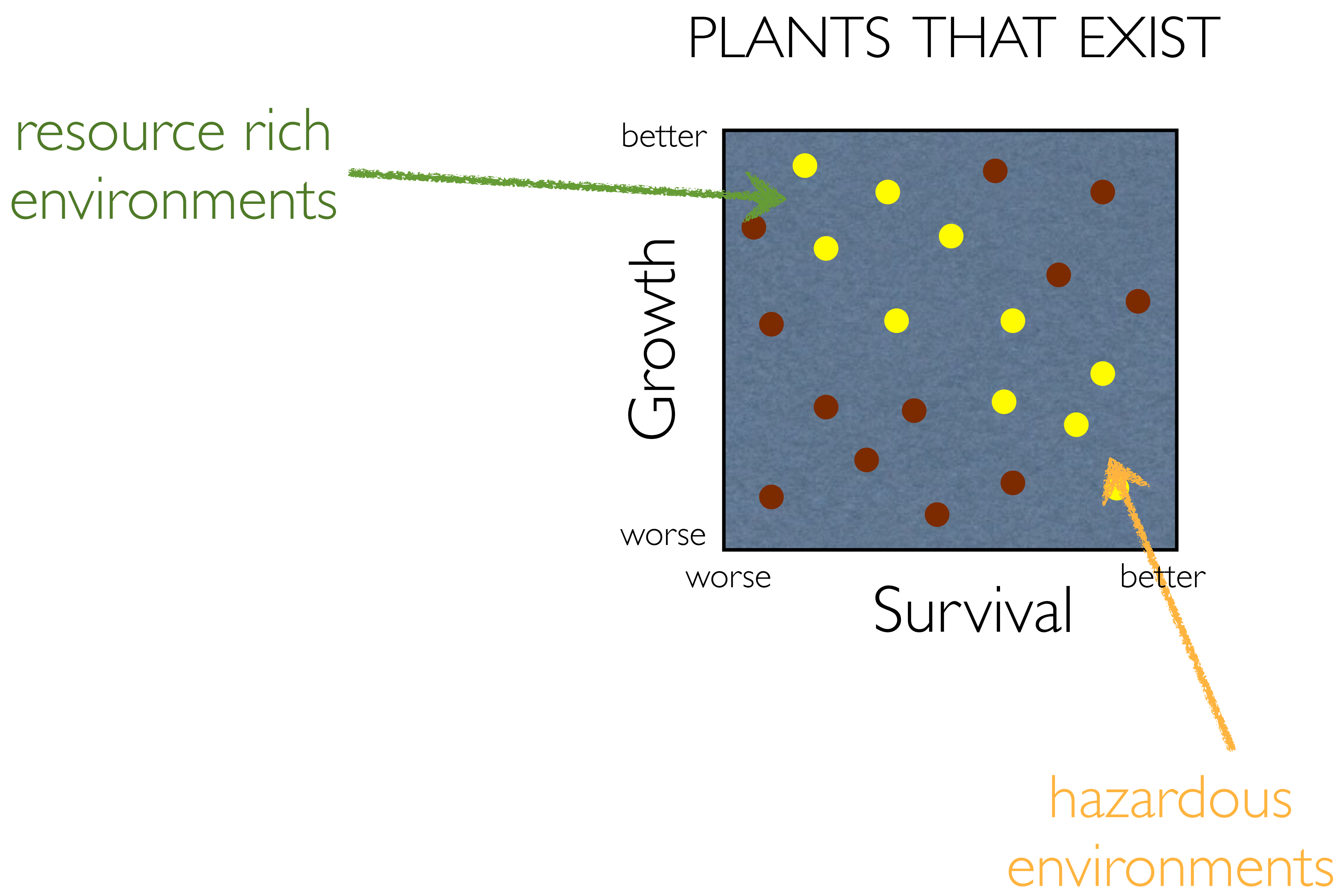
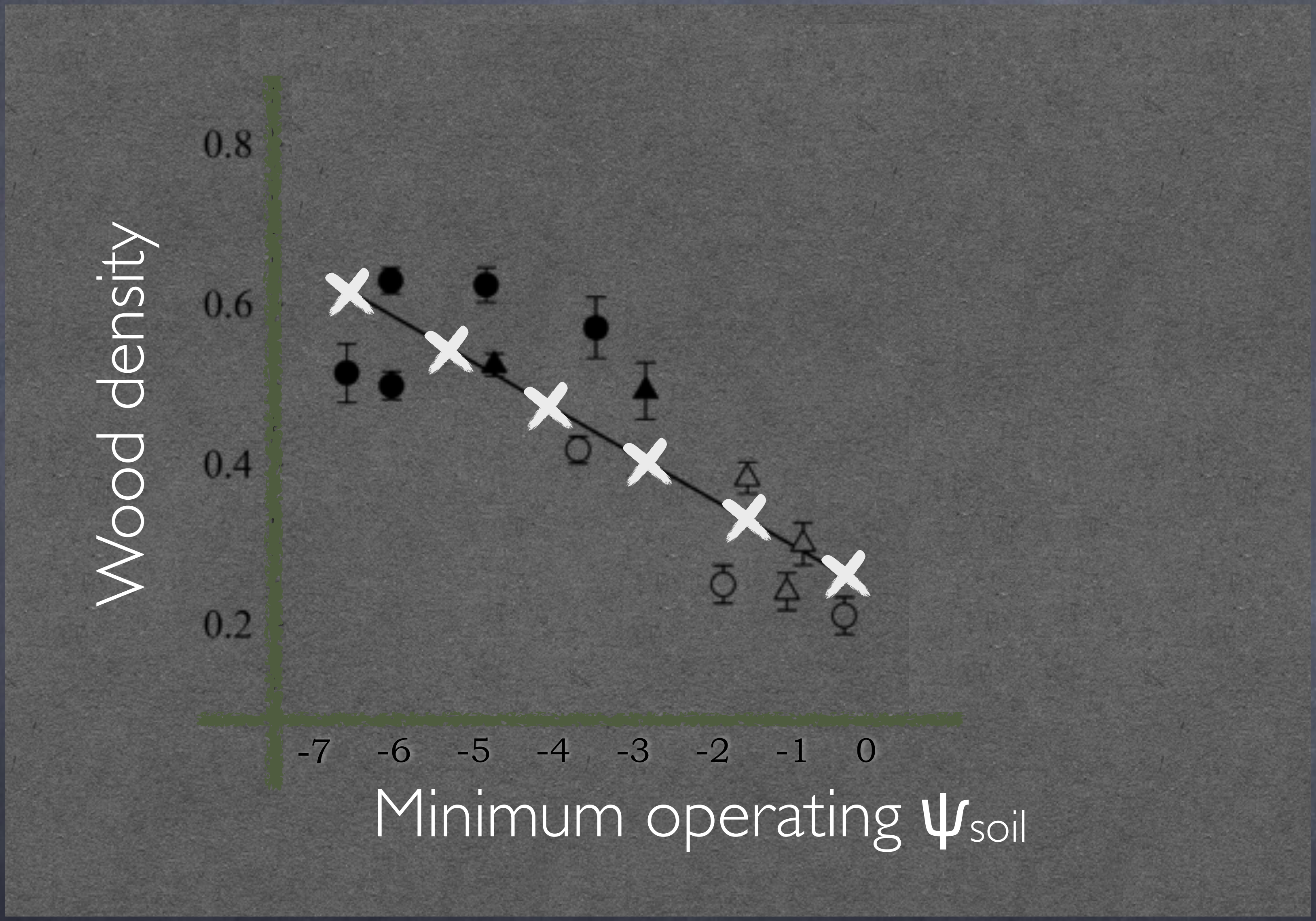


These plants do not exist because they are outside physiological limitations

Plant variation through multi-dimensional 'trait space'

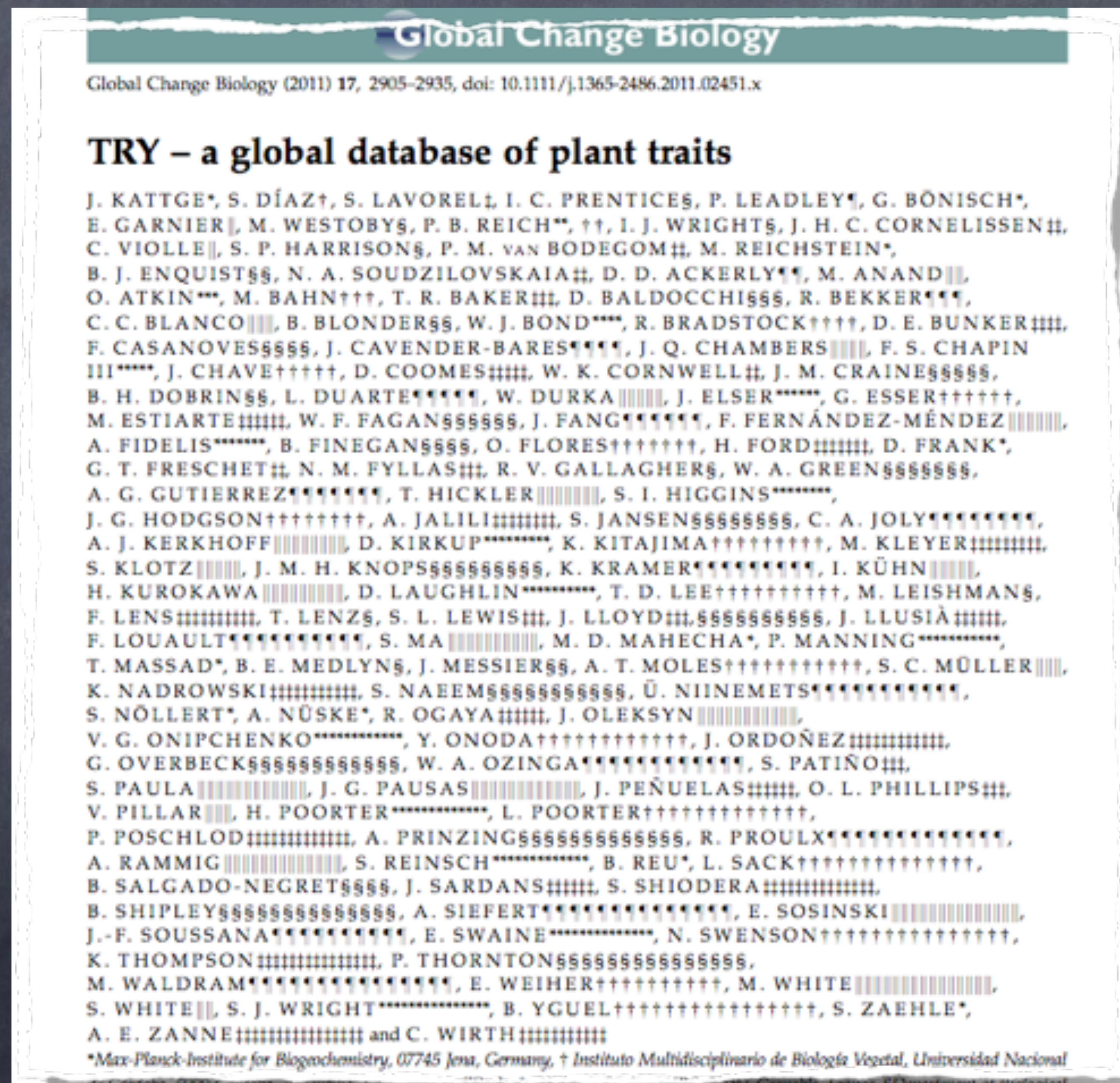


An example empirical trade-off



Example from Bolivia: Markesteijn, Poorter, et al. 2011

Our knowledge of trait space is increasing



Global Change Biology

Global Change Biology (2011) 17, 2905–2935, doi: 10.1111/j.1365-2486.2011.02451.x

TRY – a global database of plant traits

J. KATTGE*, S. DÍAZ†, S. LAVOREL‡, I. C. PRENTICE§, P. LEADLEY¶, G. BÖNISCH*, E. GARNIER||, M. WESTOBY§, P. B. REICH**, ††, I. J. WRIGHT§, J. H. C. CORNELISSEN‡‡, C. VIOLLE||, S. P. HARRISON§, P. M. VAN BODEGOM‡‡, M. REICHSTEIN*, B. J. ENQUIST§§, N. A. SOUDZILOVSKAIA‡‡, D. D. ACKERLY¶¶, M. ANAND||||, O. ATKIN***, M. BAHN†††, T. R. BAKER‡‡‡, D. BALDOCCHI§§§, R. BEKKER¶¶¶, C. C. BLANCO||||||, B. BLONDER§§, W. J. BOND****, R. BRADSTOCK††††, D. E. BUNKER‡‡‡‡, F. CASANOVES§§§§, J. CAVENDER-BARES¶¶¶¶, J. Q. CHAMBERS||||||||, F. S. CHAPIN III*****, J. CHAVE†††††, D. COOMES‡‡‡‡‡, W. K. CORNWELL‡‡, J. M. CRAINE§§§§§, B. H. DOBRIN§§, L. DUARTE¶¶¶¶¶, W. DURKA||||||||||, J. ELSER******, G. ESSER††††††, M. ESTIARTE‡‡‡‡‡‡, W. F. FAGAN§§§§§§, J. FANG¶¶¶¶¶¶, F. FERNÁNDEZ-MÉNDEZ||||||||||||, A. FIDELIS*******, B. FINEGAN§§§§, O. FLORES†††††††, H. FORD‡‡‡‡‡‡‡, D. FRANK*, G. T. FRESCHET‡‡, N. M. FYLLAS‡‡‡, R. V. GALLAGHER§, W. A. GREEN§§§§§§§, A. G. GUTIERREZ¶¶¶¶¶¶¶, T. HICKLER||||||||||||||, S. I. HIGGINS********, J. G. HODGSON††††††††, A. JALILI‡‡‡‡‡‡‡‡, S. JANSEN§§§§§§§§, C. A. JOLY¶¶¶¶¶¶¶¶, A. J. KERKHOFF||||||||||||||||, D. KIRKUP*********, K. KITAJIMA†††††††††, M. KLEYER‡‡‡‡‡‡‡‡‡, S. KLOTZ||||||, J. M. H. KNOPS§§§§§§§§§, K. KRAMER¶¶¶¶¶¶¶¶¶, I. KÜHN||||||, H. KUROKAWA||||||||||||||||||, D. LAUGHLIN**********, T. D. LEE††††††††††, M. LEISHMAN§, F. LENS‡‡‡‡‡‡‡‡‡‡, T. LENZ§, S. L. LEWIS‡‡‡, J. LLOYD‡‡‡,§§§§§§§§§§, J. LLUSIÀ‡‡‡‡‡‡, F. LOUAULT¶¶¶¶¶¶¶¶¶¶, S. MA||||||||||||||||||||, M. D. MAHECHA*, P. MANNING***********, T. MASSAD*, B. E. MEDLYN§, J. MESSIER§§, A. T. MOLES†††††††††††, S. C. MÜLLER||||, K. NADROWSKI‡‡‡‡‡‡‡‡‡‡‡, S. NAEEM§§§§§§§§§§§, Ü. NIINEMETS¶¶¶¶¶¶¶¶¶¶¶, S. NÖLLERT*, A. NÜSKE*, R. OGAYA‡‡‡‡‡‡, J. OLEKSYN||||||||||||||||||||||, V. G. ONIPCHENKO************, Y. ONODA††††††††††††, J. ORDOÑEZ‡‡‡‡‡‡‡‡‡‡‡‡, G. OVERBECK§§§§§§§§§§§§, W. A. OZINGA¶¶¶¶¶¶¶¶¶¶¶¶, S. PATIÑO‡‡‡, S. PAULA||||||||||||||||||||||||, J. G. PAUSAS||||||||||||||||||||||||, J. PEÑUELAS‡‡‡‡‡‡, O. L. PHILLIPS‡‡‡, V. PILLAR||||||, H. POORTER*************, L. POORTER†††††††††††††, P. POSCHLOD‡‡‡‡‡‡‡‡‡‡‡‡‡, A. PRINZING§§§§§§§§§§§§§, R. PROULX¶¶¶¶¶¶¶¶¶¶¶¶¶, A. RAMMIG||||||||||||||||||||||||||, S. REINSCH**************, B. REU*, L. SACK††††††††††††††, B. SALGADO-NEGRET§§§§, J. SARDANS‡‡‡‡‡‡, S. SHIODERA‡‡‡‡‡‡‡‡‡‡‡‡‡‡, B. SHIPLEY§§§§§§§§§§§§§§, A. SIEFERT¶¶¶¶¶¶¶¶¶¶¶¶¶¶, E. SOSINSKI||||||||||||||||||||||||||||, J.-F. SOUSSANA¶¶¶¶¶¶¶¶¶¶¶, E. SWAINE***************, N. SWENSON†††††††††††††††, K. THOMPSON‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡, P. THORNTON§§§§§§§§§§§§§§§, M. WALDRAM¶¶¶¶¶¶¶¶¶¶¶¶¶¶¶, E. WEIHER††††††††††, M. WHITE||||||||||||||||||||||||||||||, S. WHITE||||, S. J. WRIGHT****************, B. YGUEL††††††††††††††††, S. ZAEHLE*, A. E. ZANNE‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡‡ and C. WIRTH‡‡‡‡‡‡‡‡‡‡

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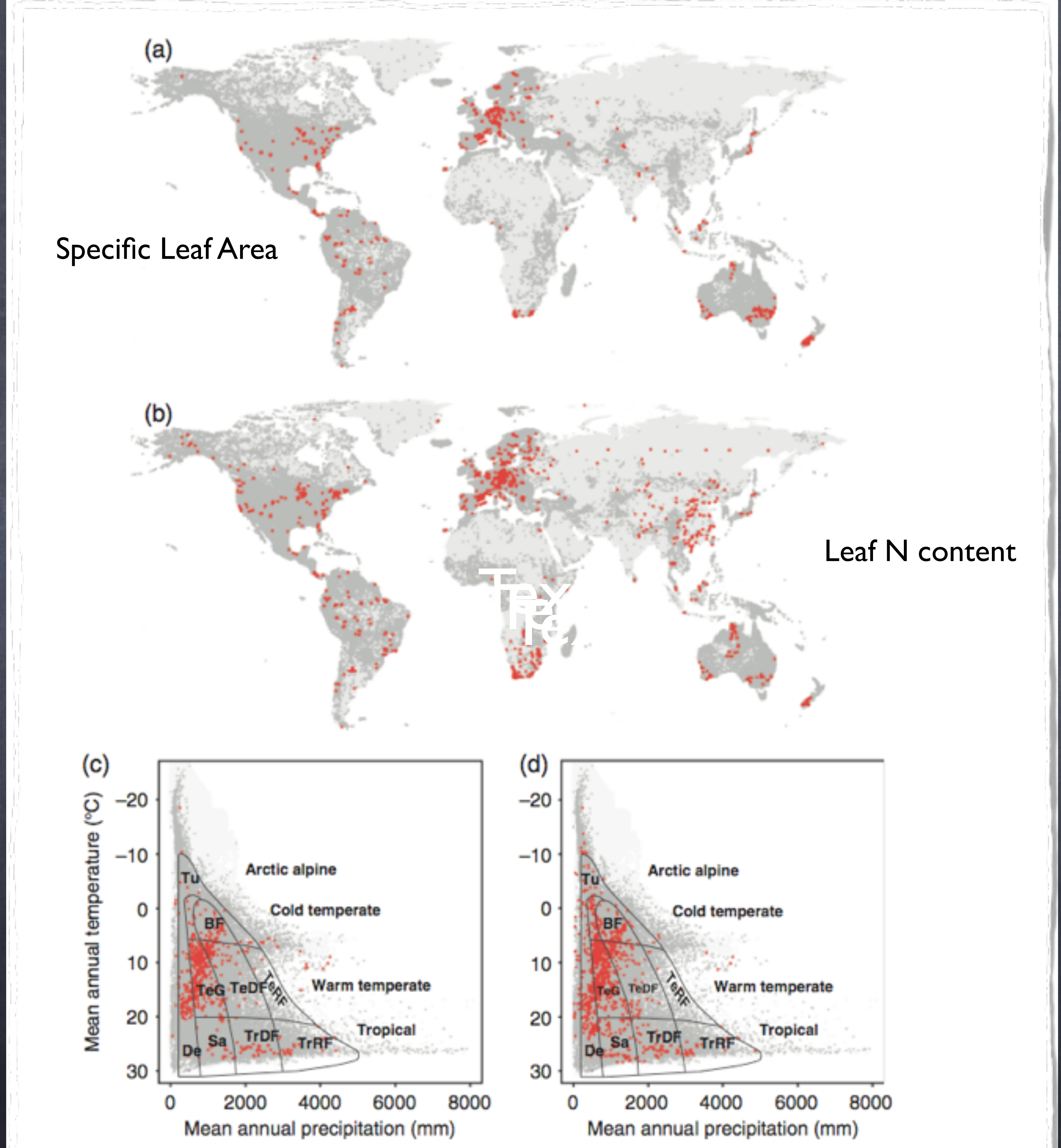
www.try-db.org



(a)
Specific Leaf Area
(b)
Leaf N content
(c)
(d)
Mean annual temperature (°C)
−20
−10
0
10
20
30
Arctic alpine
Cold temperate
Warm temperate
Tropical
Tu
BF
TeG
TeDF
TeRF
De
Sa
TrDF
TrRF
0
2000
4000
6000
8000
Mean annual precipitation (mm)

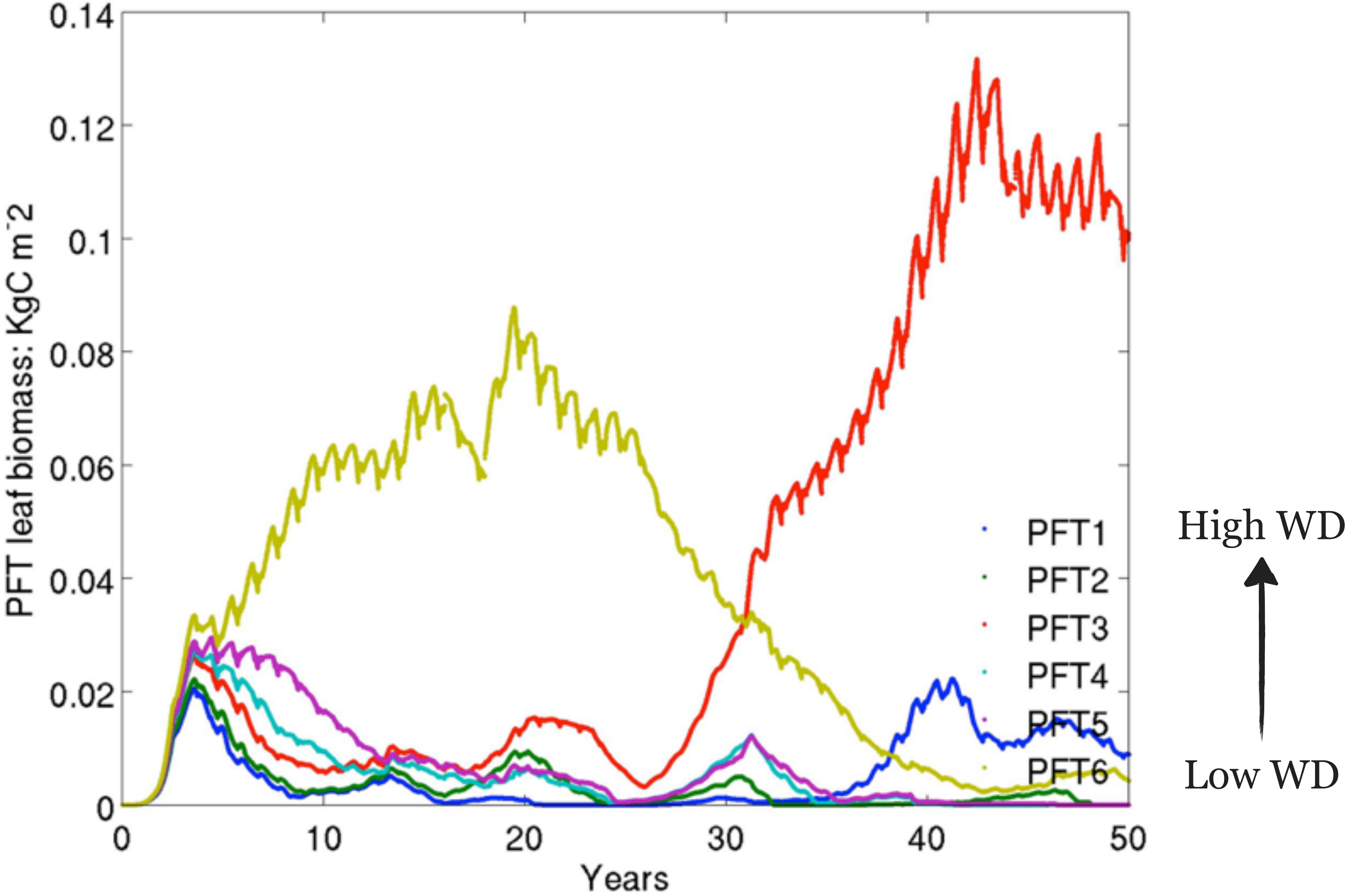
How might we use all of this data?

Alternative approaches to plant trait modeling

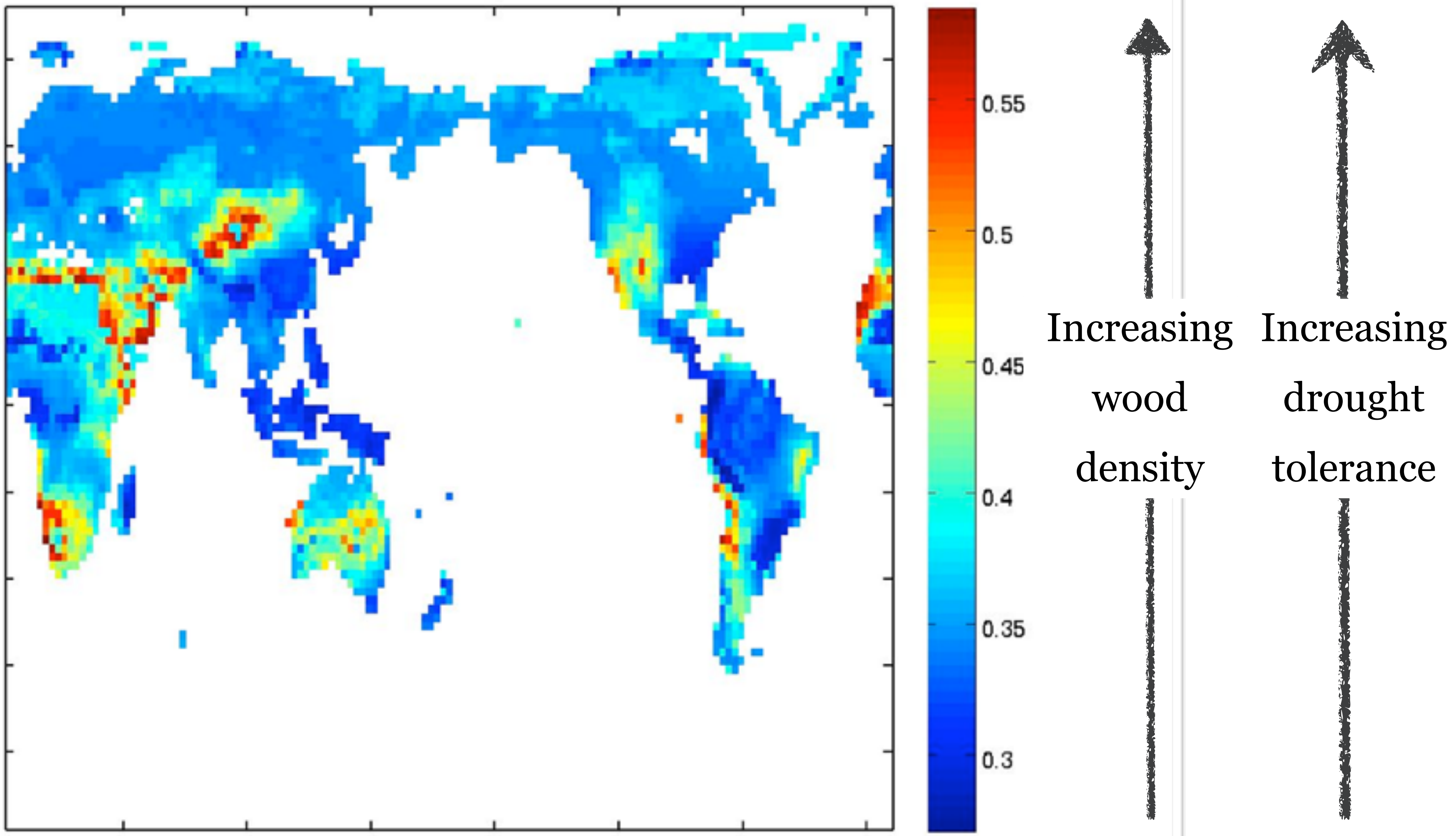
How quickly do plant traits vary?

- Model 1: Plant traits are static, adaptation happens via change in plant types
- Model 2: Plant traits optimize to prevailing environmental conditions
- Model 3: Plant traits explicitly evolve through time

Trait filtering in CLM(ED)



Wood Density Emerging from Competition



Changes in plant traits occur via changes in plant type

Optimality: an emergent property of evolution?

- All existing species are the winners of evolution
- Competition selects the fittest species
- Sub-optimal plants should be eliminated
- What should a 'fit' plant do?
- Optimality Models are hypotheses for how competitive evolution might shape plant function…
- Changes in traits occur via changes in the environment

Optimal models of plant function

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Toward a mechanistic modeling of nitrogen limitation on vegetation dynamics

Chonggang Xu[1], Rosie Fisher[2], Cathy J. Wilson[1], Stan D. Wullschleger[3], Michael Cai[1], Nate G. McDowell[1]

Leaf-trait variation explained by the hypothesis that plants maximize their canopy carbon export over the lifespan of leaves

Ross E. McMurtrie[1,3] and Roderick C. Dewar[2]

Optimal nitrogen allocation controls tree responses to elevated CO_2

Oskar Franklin[1,2]

[1]IIASA, Institute for Applied Systems Analysis, 2361 Laxenburg, Austria; [2]School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia

Resource Optimization and Symbiotic Nitrogen Fixation

E. B. Rastetter,[1]* P. M. Vitousek,[2] C. Field,[3] G. R. Shaver,[1] D. Herbert,[1] and G. I. Ågren[4]

Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees

J. Lloyd[1], S. Patiño[2], R. Q. Paiva[3,*], G. B. Nardoto[4], C. A. Quesada[1,3,5], A. J. B. Santos[3,5,†], T. R. Baker[1], W. A. Brand[6], I. Hilke[6], H. Gielmann[6], M. Raessler[6], F. J. Luizão[3], L. A. Martinelli[4], and L. M. Mercado[7]

[1]Earth and Biosphere Institute, School of Geography, University of Leeds, LS2 9JT, UK

[2]Grupo de Ecología de Ecosistemas Terrestres Tropicales, Universidad Nacional de Colombia, Sede Amazonia, Instituto Amazónico de Investigaciones-Imani, km. 2, vía Tarapacá, Leticia, Amazonas, Colombia

[3]Institito National de Pesquisas Amazônicas, Manaus, Brazil

Challenges and Opportunities of the Optimality Approach in Plant Ecology

Annikki Mäkelä, Thomas J. Givnish, Frank Berninger, Thomas N. Buckley, Graham D. Farquhar and Pertti Hari

Optimal co-allocation of carbon and nitrogen in a forest stand at steady state

Annikki Mäkelä[1], Harry T. Valentine[2] and Heljä-Sisko Helmisaari[3]

[1]Department of Forest Ecology, PO Box 27, 00014 University of Helsinki, Finland; [2]USDA Forest Service, 271 Mast Road, Durham, NH 03824, USA; [3]Finnish Forest Research Institute, Vantaa Research Centre, PO Box 18, 01301 Vantaa, Finland

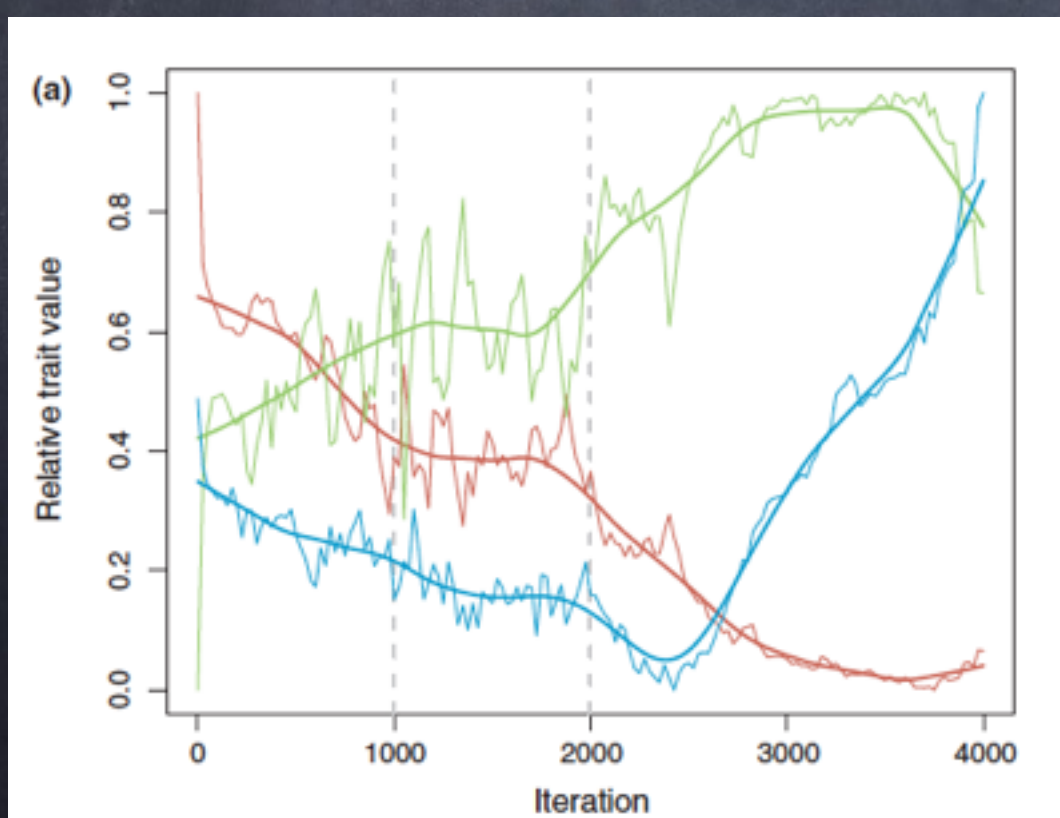
Next-generation dynamic global vegetation models: learning from community ecology

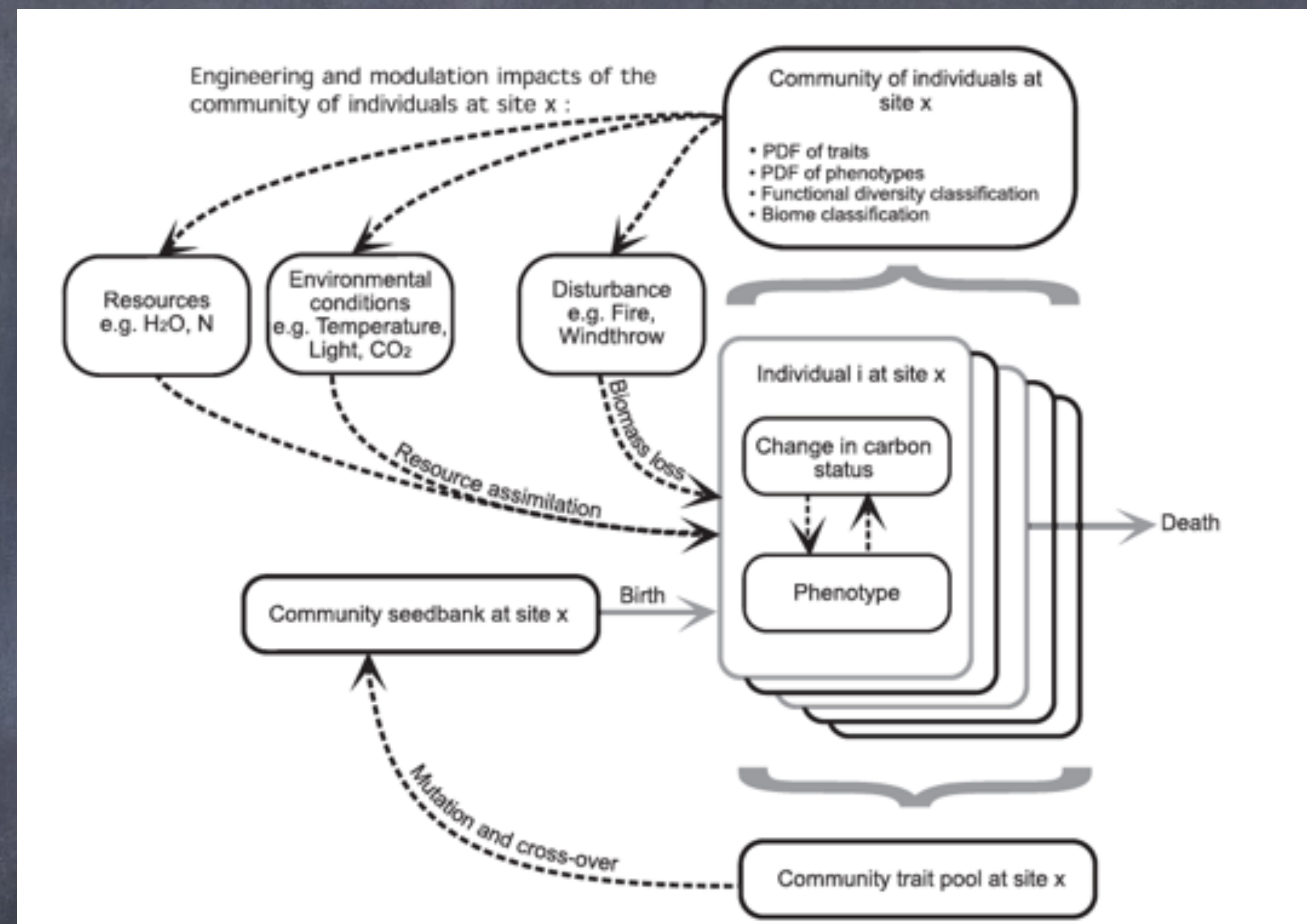
Simon Scheiter[1], Liam Langan[2] and Steven I. Higgins[2]

[1]Biodiversität und Klima Forschungszentrum (LOEWE BiK-F), Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, D-60325, Frankfurt am Main, Germany; [2]Institut für Physische Geographie, Goethe-Universität Frankfurt am Main, Altenhöferallee 1, D-60438, Frankfurt am Main, Germany

The 'aDGVM2' model

Traits can't just optimize, they need to evolve through time…





Individual, population and community trait values adapt to conditions

Modelling plant diversity

- Trait filtering models allow traits to vary with changing frequency of plant types
- Optimal models allow traits to vary as the environment changes
- Evolving models allow plant traits to vary in space and time
- No models have a concept of phenotypic plasticity

Summary

- Vegetation Dynamics models vary according to how they aggregate plants

- And according to whether they include climate envelope concepts

- And depending on how they model recruitment and mortality…

- Biome boundaries are actually extremely poorly understood, but without testing them we have limited confidence in future predictions.