

Biodiversity and ecosystem
functioning:
a test of complementarity effects
over a large forest extent

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Biodiversity and ecosystem functioning (EF)

1. **Resilience** through functional redundancy.
 - Species lost can be replaced with similar species
2. (Bio)diversity effect. Niche **complementarity**, or complementary resource use (Hooper and Vitousek 1997)
 - A system composed of diverse species will make better use of available resources (be more productive), and supply more ecosystem services

Consensus on current knowledge

- Biodiversity effects have been detected in many ecosystems
 - but mostly under experimental conditions
 - and in herbaceous communities (e.g. BIODEPTH experiment)
- Proof is lacking in natural systems, especially **forests**
 - Vilà et al. 2007
 - Caspersen and Pacala 2001

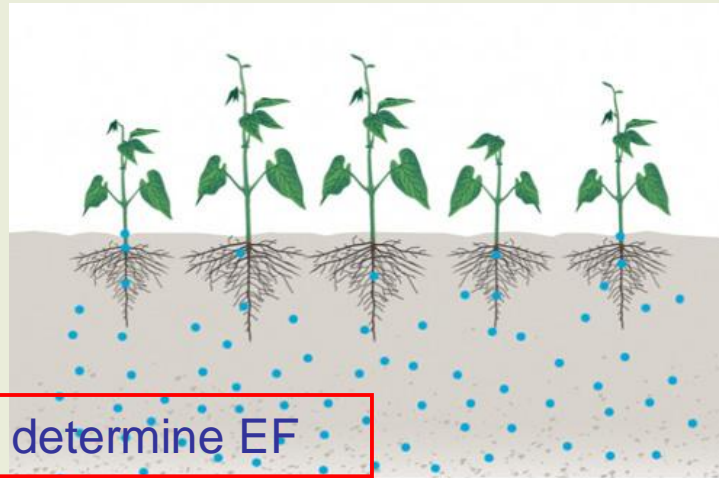
Consensus on current knowledge

- Biodiversity effects, if present, are **small and difficult to detect** in comparison with other determinants of ecosystem functions
 - Need to control for local **environment** (e.g. soil) and **climate** (temperature, precipitation, ...)
- Functional diversity (**FD**), or even phylogenetic diversity (**PD**), are better predictors of ecosystem functions than species richness (**SR**) alone

How does it work?

B) Diversity and complementarity

- Example from the BIODEPTH experiment (Max Planck Institute)



Monoculture:

Less soil volume explored

Fewer resources used

Less growth

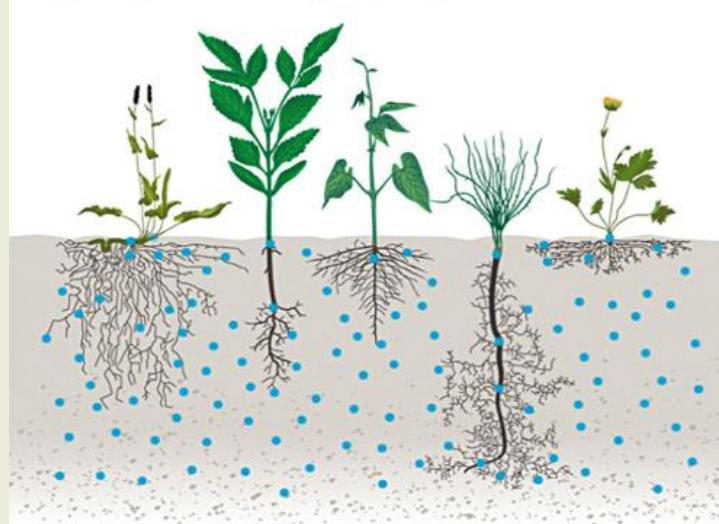
The **diversity** of traits determine EF

Polyculture:

More volume explored

Higher nutrient turnover

Greater productivity

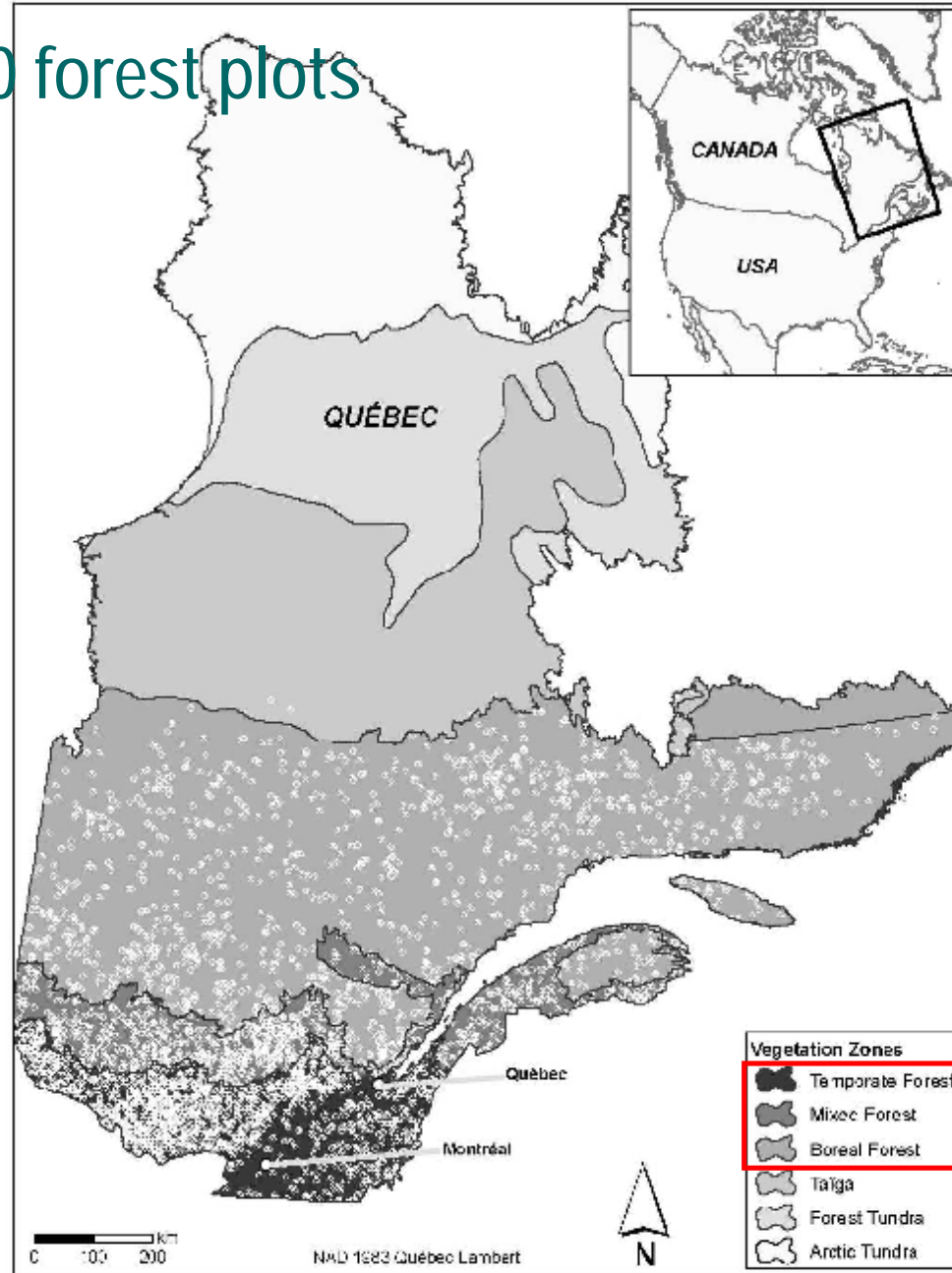


Biodiversity and forest growth:

the search for complementarity effects in Québec's forests

- MRNFQ PEP database = 36,000 permanent 400m² forest plot measurements from 1970 to 2007
- Plots are measured every 10 years (2-32 years) and new ones are added continuously
- Plots removed:
 - All human interventions
 - Significant natural disturbances (removing > 25% basal area)
 - "Non forest" (<10m²ha⁻¹) or regenerating (>25% in saplings)
- Dataset = >12000 pairs of plots (same plot measured twice)
 - 24,000 measurements; over 400,000 trees of 55 species

Map of 12,000 forest plots



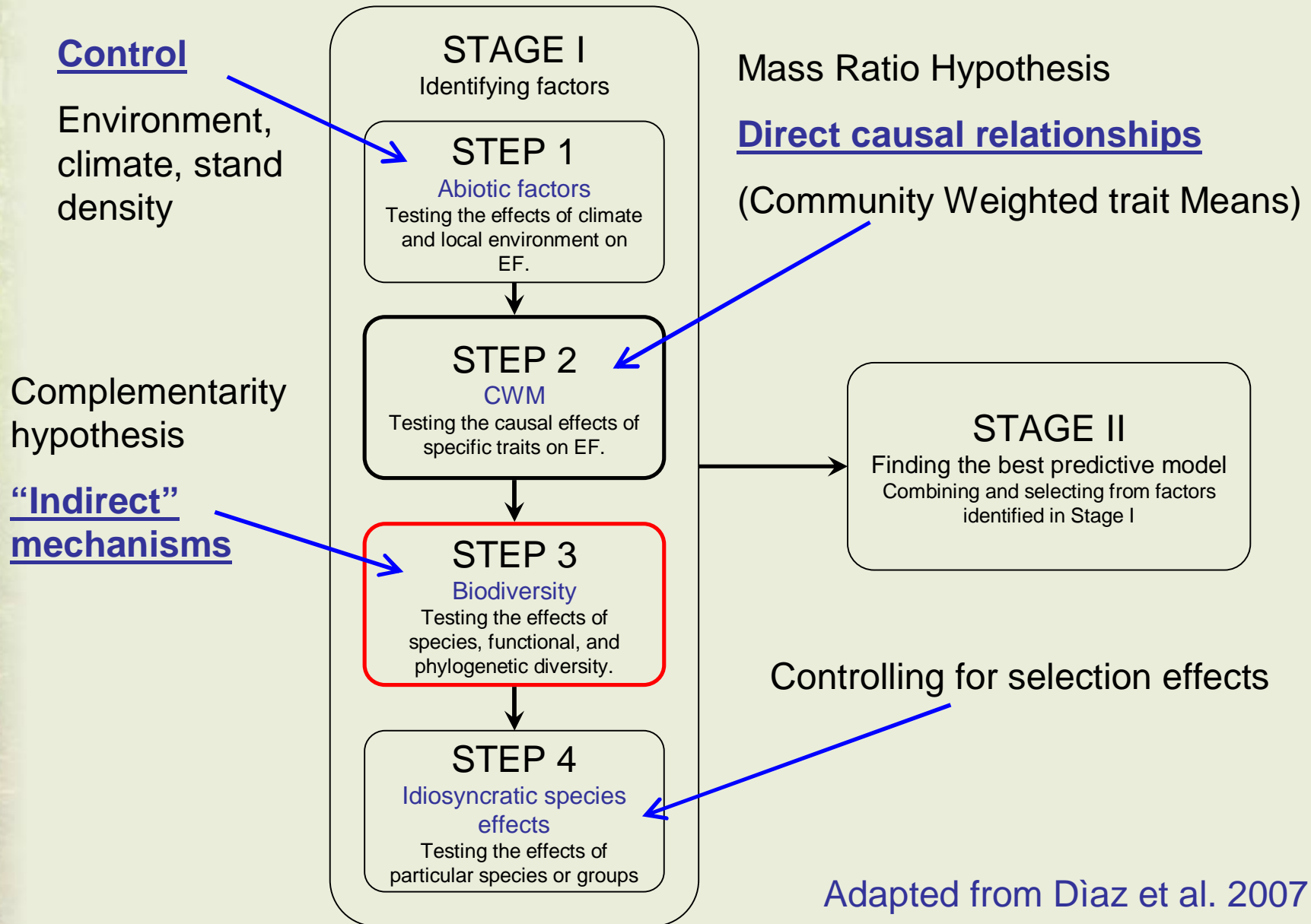
Control variables

- PEP includes *in situ* soil variables
 - LFH depth
 - Organic layer pH
 - ...
- Climate
 - ANUSPLIN interpolation of 30-year normals from all available weather stations on the territory
 - Precipitation, minimum temperature, ...
- Stand density (basal area)

Response variable

- Above-ground biomass increment of trees
 - Computed from DBH and species specific equations
 - Recruits and dead trees are (now) excluded

A model for the search of significant effects



Step 3: Biodiversity effects

- Functional diversity (FD) indices are many, and still debated, but are essentially, for a given community, the “diversity of species in the trait space”.
 - Example: spruce + fir < spruce + aspen
 - Yet SR = 2 for both
 - Incidentally, spruce-aspen was also demonstrated as more productive (Comeau et al. 2009; Légaré et al. 2005)
- FD computed from:
 - table of species abundances
 - table of functional traits (55 species x 29 functional traits)

Functional traits

Typical sources

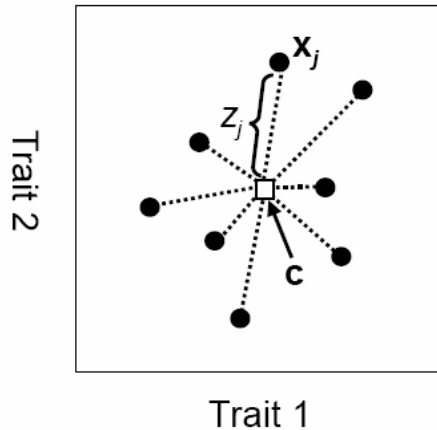
- TOPIC database from Isabelle Aubin (reproduction traits)
 - GLOPNET (leaf economics) (Wright and very many als 2004)
 - FET (Functional Ecology of Trees Database Project) (leaf and root traits) (Wirth et al., Max Planck Institute, Jena)
 - ...
- **Some problems with functional traits:**
 - Trait extent
 - Trait type. Multi-state variables → dummy variables
 - Possible ways to weight the traits (e.g. for dummy)
 - NAs: What do we do with missing values?

Functional diversity indices

- SR : species diversity (simply the number of species)
- DS : Simpson's index of diversity
- FD (Petchey et Gaston 2002)
- RaoQ - Rao's quadratic entropy (Rao 1982 , Botta-Dukát 2005)
- Villéger et al. (2008) : functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv)
- Technical questions:
 - What type of traits can be used?
 - Can weights be used?
 - Should abundances be used?
 - Should FD be unaffected by species richness?
 - Can handle NAs?

FD package for R and a new index : FDis

a



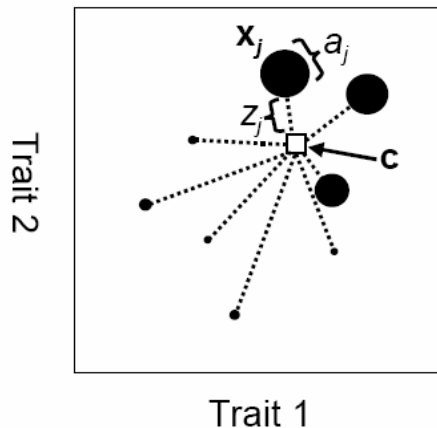
Centroid

$$\mathbf{c} = [c_i] = \frac{\sum x_{ij}}{n}$$

Functional dispersion

$$\text{FDis} = \frac{\sum z_j}{n}$$

b



Centroid

$$\mathbf{c} = [c_i] = \frac{\sum a_j x_{ij}}{\sum a_j}$$

Functional dispersion

$$\text{FDis} = \frac{\sum a_j z_j}{\sum a_j}$$

FDis

Functional dispersion

Laliberté and Legendre 2009

The larger the trait space,
and the further apart the
 species within that space,
 the greater FDis

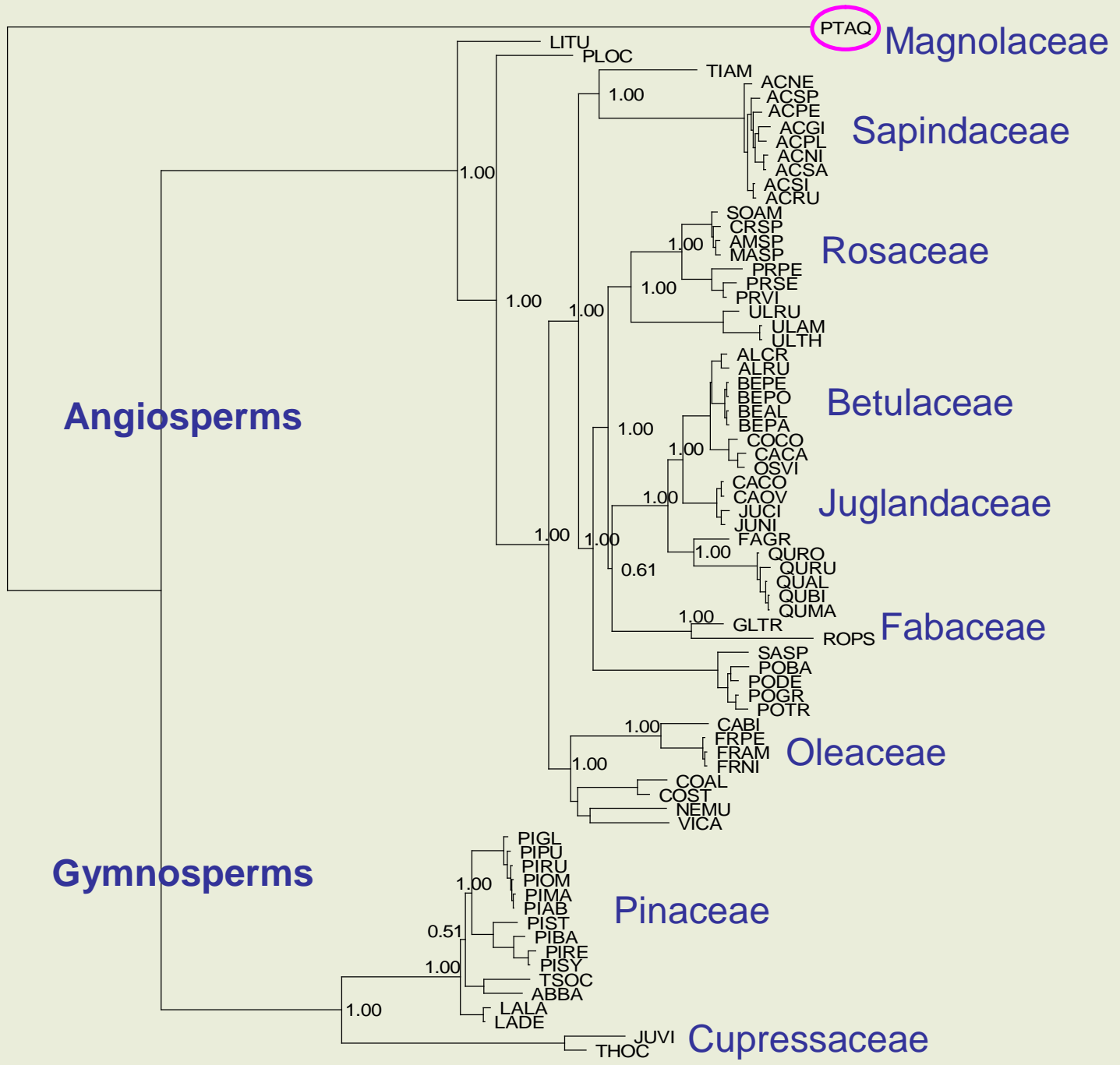
With abundances. The
 “weight” of abundant species
 draws the centroid their way

Step 3: Biodiversity effects

- **Phylogenetic diversity (PD)**, or evolutionary history, can also be computed using different, also debated, metrics.
- Essentially, PD is the variance in **evolutionary distances** between species of a given community. It is computed from a **phylogenetic tree** based on a molecular phylogeny.
- We propose that FD and PD are not opposing, but **complementary**
 - PD can tap into possible mechanisms for which we have no hypothesis or trait (yet)
 - PD has no (known) direct causal link to ecosystem function

Phylogeny used to compute PD indices

- 73 species, including exotics for a better resolution
- Two gene sequences (*rbcL* and *matK*) with complementary resolution
 - Both are chloroplastic sequences that code for something important. Mutations are slow and follow species evolution
 - Commonly available from Gene Bank
 - *rbcL* evolves more slowly and resolves deeper phylogenetic relationships
 - *matK* provides better resolution among more closely related species
- Rooted on a common fern (*Pteridium aquilinum*)
- Aligned in Muscle and converged using Bayesian techniques in MrBayes
- Major groups strongly supported



Phylogenetic diversity indices (PD)

- The classic = Faith's PD (e.g. Cadotte et al. 2008)
 - very dependant on SR
- We also computed the phylogenetic species variability index (PSV) (Helmus et al. 2007)
 - PSV can be considered pure phylogenetic signal that is not confounded with species richness or abundance
- Computed using the "picante" package for R (Kembel et al. 2009)

Results (Stage II – combined effects)

Mean temp

Stand density

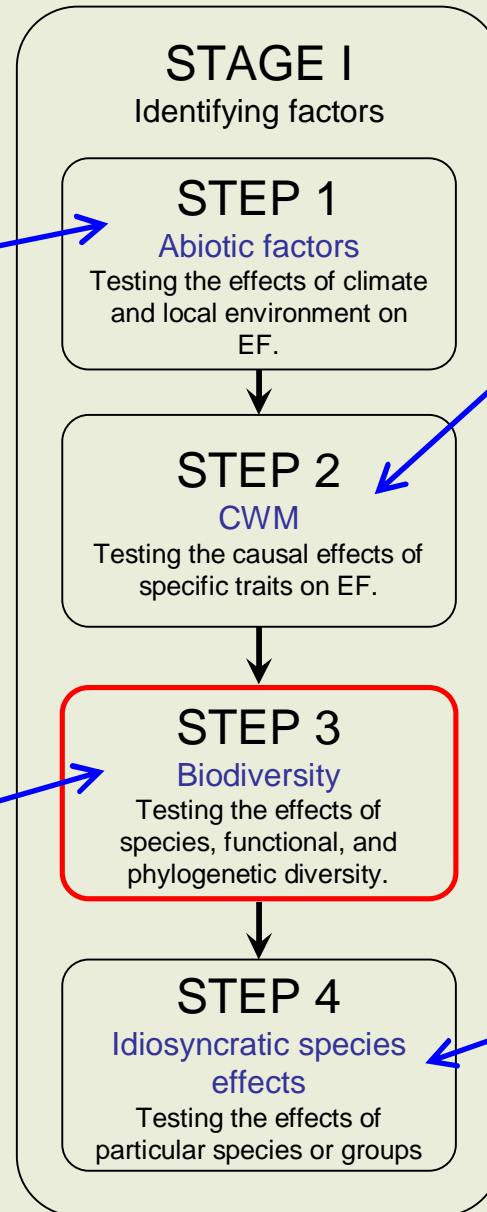
Organic layer depth

$R^2 : 0.59$

PD + FD

$R^2 : 0.30$

About half as much as climate!



LMA, MaxH, WD,
Leaf [N], ...

$R^2 : 0.49$

All $p < 0.0001$
Model $R^2 : 0.68$

Maples, Pioneer, Fir,
Spruces

$R^2 : 0.50$

Bioclimatic zones

- Malgré le contrôle des variables climatiques, il semble y avoir un fort effet du domaine bioclimatique
- Plus important encore, l'effet de la biodiversité ne devient significatif qu'à partir de la sapinière à bouleau jaune, et prend de l'ampleur jusque dans la pessière à mousse.
 - La biodiversité ne devient importante que lorsqu'elle se fait plus rare?
 - La diversité dans l'érablière est mal rendue par les arbres seulement?

Conclusions

- Positive effect of biodiversity on forest growth was detected
- One more argument against the **normalization** of forests
- Argument in favour of **mixed plantations**, even in intensive setups

Future work

- Diversity in structure, not just species, at other spatial scales
- Biodiversity effect on resilience (resistance to pest outbreaks)
- Specific roles of PD and FD yet to be determined
- Formal tests with trees are needed to identify mechanisms
 - BIOTREE and Sardinillia experiments, and others?
- For all forest ecologists 😊
 - A lot of variance still unexplained!

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