Towards a theory of plant trait diversity

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Seeking general theory of vegetation structure and diversity
Limited success in predicting functional (trait) diversity

- Same few resources
- Same core physiology
- Traits vary among coexisting species
Why does competition favour diversity?
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(No diversity)
Why does competition favour diversity?

![Single winner](image1.png) ![Niche differentiation](image2.png)

(No diversity)
Why does competition favour diversity?

- Single winner: (No diversity)
- Niche differentiation: (Too simple)

- Trait → demography
- Diversity via trade-offs
- Predictable mixture
Why does competition favour diversity?

- **Single winner** (No diversity)
- **Niche differentiation**
  - Trait → demography
  - Diversity via trade-offs
  - Predictable mixture
- **Neutral drift** (Too simple)
Why does competition favour diversity?

- Single winner: (No diversity)
- Niche differentiation: Diversity via trade-offs, Predictable mixture
- Neutral drift: (Too simple)

Trait → demography
Why does competition favour diversity?

- **Single winner**
  - Trait → demography
  - Diversity via trade-offs
  - Predictable mixture

  (No diversity)

- **Niche differentiation**
  - Trait

- **Neutral drift**
  - Trait

  - Fitness equivalence
  - Diversity via chance speciation & extinction
  - Unpredictable mixture

  (Too simple)

  (Implausible)
Building an enhanced model of trait-based niche differentiation
Process 1 - Disturbance
Process 1 – Disturbance

Metapopulation

Seeds

Patch age (yr)
Process 2 - Competition for light
Process 3 – Trait-based trade-offs in plant function

- size
- thickness
- nitrogen
- vein density
- longevity

- vessel size
- lumen fraction
- wood density
- sapwood
- per leaf

- size
- thickness
- nitrogen
- longevity
Quantify key challenges, traits, & trade-offs in the life of a plant*

* At least some of them, there are more!
Seed size → Getting established

Larger seeds (seedlings) do better!

Data: Cornwell + 26 others 2014

Henary & Westoby 2001
Leaf nitrogen content per leaf area → Energy uptake

Global distribution
(n = 1975 species)

Orders of magnitude

Units: g m⁻²

Photosynthetic rate

723 species
63 sites

Leaf nitrogen per unit leaf area

Respiration rate

267 species
20 sites

Note: Apply 20-30 Kg Nitrogen/ha when Crop nutrition falls below 4.
Height per leaf area $\rightarrow$ race of light

Data: Falster + 96 others  Ecology 2015, Duurmsa & Falster bioRxiv 2015
Traits drive demography across life-cycle

- Size
- Accessory growth
- Flower
- Fruit
- Mass invested in reproduction
- Seed dispersal
- Seed in soil
- Mass invested in growth
- Net mass production
- Mortality
- Increasing size
- Construction costs

- Size
- Thickness
- Nitrogen
- Vein density
- Longevity

- Vessel size
- Lumen fraction
- Wood density
- Sapwood
- Per leaf

- Size
- Thickness
- Nitrogen
- Longevity
Three ubiquitous processes
Combine to give richer (and plausible) model of forest dynamics

Temporal dynamics within a patch

Combine to give richer (and plausible) model of forest dynamics

Temporal dynamics within a patch

Metapopulation of patches

Combine to give richer (and plausible) model of forest dynamics

Temporal dynamics within a patch

Metapopulation of patches

Question: Do trait-based trade-offs enable coexistence?

Falster et al J Ecol 2011
Trait 1: Leaf mass per unit leaf area
Leaf mass per unit leaf area → Building leaves

Cheap leaf allows fast growth when small

Global distribution (n = 6868 species)

Leaf turnover rate

Leaf–mass per unit leaf area

Data: Cornwell + 26 others 2014
Predict outcome of competition by evolving mixtures

Leaf mass per unit leaf area (kg m\(^{-2}\))

Fitness

fail ➔ neutral ➔ invade

Falster et al 2015 biorxiv 014605
Predict outcome of competition by evolving mixtures

Falster et al 2015 bioRxiv 014605
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Leaf mass per unit leaf area (kg m$^{-2}$)

Fitness

invade
neutral
fail

Falster et al. 2015 bioRxiv 014605
Predict outcome of competition by evolving mixtures

Falster et al 2015 bioRxiv 014605
Trait enables coexistence of different successional types

Falster et al 2015 biorxiv 014605
Trait 2: Size at maturation
Predict outcome of competition by evolving mixtures

- invade
- neutral
- fail

![Graph showing fitness vs. height at maturation (m)]
Predict outcome of competition by evolving mixtures

- invade
- neutral
- fail

![Graph showing fitness at different heights at maturation. The x-axis represents height at maturation (m) from 0.4 to 50, and the y-axis represents fitness from -6 to 6. There are points indicating fitness at various heights, with a trend indicating a decrease in fitness as height increases.]
Predict outcome of competition by evolving mixtures
Predict outcome of competition by evolving mixtures
Predict outcome of competition by evolving mixtures
Trait enables differentiation within successional group.

Early-  Mid-  Late-

Falster et al 2015 biorxiv 014605
Two axes interact to produce community with more shade tolerants

Falster et al. 2015 biorxiv 014605
Two axes interact to produce community with more shade tolerants

High diversity

Falster et al. 2015 biorxiv 014605
Diversity in tropical forests concentrated at shade tolerant end

Previously thought unlikely via niche differentiation, key motivation for neutral theory (Hubbell 2005)

Condit et al 2006 Science
Two possible outcomes of niche differentiation

- Classic niche differentiation
- Evolved fitness equivalence

Falster et al. 2015 biorxiv 014605
“Evolved neutrality” around shade-tolerant species

Ridge of fitness equivalence

Falster et al. 2015 biorxiv 014605
Outcomes of niche differentiation richer than previously thought

1. Can finally demonstrate trait-based niche differentiation
2. Find traits offer distinct pathways of differentiation
   - Leaf mass per unit leaf area (different successional types)
   - Height at maturation (differentiation within successional type)
3. Niche differentiation produces both peaked & flat landscapes
   - From same competitive & demographic processes
   - Niche & neutral processes not alternatives, both at play
4. Start to “Rebuild community ecology from traits” (McGill 2006)
Seeking general theory of vegetation structure and diversity
Forest structure & trait mixtures vary with site conditions

A  Average leaf mass per area

B  Average height at maturation

Site–productivity index

Average disturbance interval (yr)
Forest structure & trait mixtures vary with site conditions
Seeking general theory of vegetation structure and diversity

- Starting to make testable predictions
- Unclear how far we can go (is it even predictable?)
Seeking general theory of vegetation structure and diversity

- Starting to make testable predictions
- Unclear how far we can go (is it even predictable?)
- Current challenges
  - Make assembly routine
  - Evolution in multi-trait space
  - Estimating parameters for world’s species
  - Testing predictions
  - Accessing data
Knowledge is shared, peer reviewed, attributable
Openness is key to advancing ecological science

Knowledge is shared, peer-reviewed, attributable
How much of the world is woody?

Richard G. FitzJohn†, Matthew W. Pennell†*, Amy E. Zanne†, Peter F. Stevens†, David C. Tank‡ and William K. Cornell††

†Biodiversity Research Centre and Department of Zoology, University of British Columbia, Vancouver, BC V6G 1Z4, Canada; ‡Department of Biological Sciences and Institute for Bioinformatics and Evolutionary Studies, University of Idaho, Moscow, ID 83844, USA; University, Washington, DC 20052, USA; of Biological Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia

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The question posed by the title of this study is a basic one, and it is surprising that the answer is so uncertain. Recently, a number of studies have provided estimates of woody biomass and deforestation, but these datasets are fragmented and not easily comparable. Here we describe a novel approach for estimating the proportion of woody species among the vascular plant species on Earth, and we compare our results to those from previous studies.

Introduction

The question of how much of the world is woody is a basic one, and it is surprising that the answer is so uncertain. Recently, a number of studies have provided estimates of woody biomass and deforestation, but these datasets are fragmented and not easily comparable. Here we describe a novel approach for estimating the proportion of woody species among the vascular plant species on Earth, and we compare our results to those from previous studies.

Knowledge is shared, peer-reviewed, attributable

data: 10.5061/dryad.v7m14.2
code: github.com/richfitz/wood
blog: ropensci.org/blog/2014/06/09/reproducibility/
Some resources you can use, adapt, & extend!

▶ Try to make papers reproducible – code, data, R packages
   → So you never have to recreate anything we’ve done
   → Only use open data and code

▶ plant – an R package for modelling forest trait ecology & evolution
   Falster, FitzJohn, + 3 others (2016) Methods in Ecology & Evolution
   → Extend work from this talk

▶ smatr 3 – an R package for inference about allometry
   → Used in > 300 publications

▶ BAAD – a Biomass And Allometry Database for woody plants
   → Open and transparent data compilation
   (AU: Duursma, Barneche, FitzJohn, Vårhammar, Aspinwall, Battaglia, Camac, Kelly, Hamilton, Hutley, Mokany, O’Grady, Osunkoya, Tissue, Wenk, Williams, Ximenes)

▶ coraltraits.org – compilation of trait data for world’s corals
   Madin + 23 others (2016)
   → Entirely open
Seeking general theory of vegetation structure and diversity

- Starting to make testable predictions
- Unclear how far we can go (is it even predictable?)
- Current challenges
  - Make assembly routine
  - Evolution in multi-trait space
  - Estimating parameters for world’s species
  - Testing predictions
  - Accessing data
- In 5 years, I hope we ....
  - Have a shared (open) catalogue of empirical patterns (data)
  - Have a shared (open) catalogue of explanations (models)
  - Be able to predict effect of (say) high CO2 on trait mixtures
Warm thanks to ....

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