

Estimating xylem vessel length distributions

4th Xylem International Meeting (Padua)

R. M. Link, B. Schuldt, B. Choat, S. Jansen, A. R. Cobb

University of Würzburg

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Vessel length: the neglected dimension

- "The neglected dimension" (Comstock and Sperry 2000)
- Related to **hydraulic conductivity**
 - controls contribution of pit membranes to total flow resistance¹
- Related to **embolism resistance**
 - longer vessels → more potential nucleation sites for emboli^{1,2,3}
 - role in "embolism containment"⁴

⇒ Important control variable for stability/efficiency trade-off

- Putative role in length-related artifacts in hydraulic measurements^{5,6}

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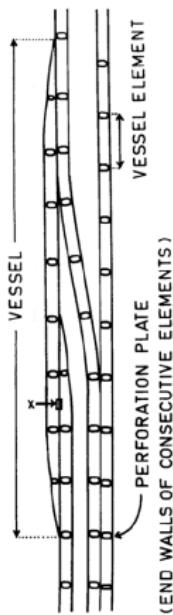
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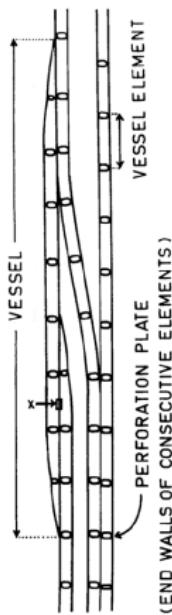
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 - not possible from longitudinal sections
 - not possible from macerations
- Instead: injection of a substance that passes through the lumen, but not pit membranes
 - Silicon/dye injection
 - Air injection

⇒ vessels have to be cut to perform measurement

... true length distribution inferred from cut-off vessels

Figure: Zimmermann & McDonough (1978); in: Cai and Tyree (2014)

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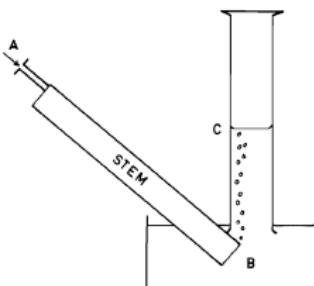


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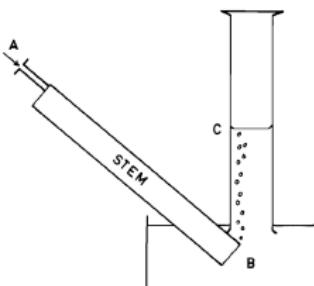


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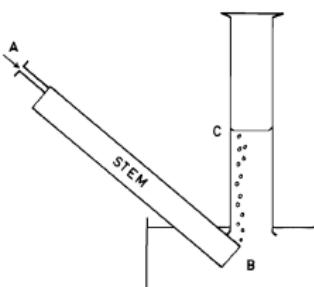


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Assumptions

Minimum set of assumptions* for VL estimates from silicon injection

- ① vessels run in parallel and are unbranched
- ② uniform distribution of end points along the stem
- ③ vessel lengths i.i.d. and independent of position
- ④ no errors in counts and length measurements



*Assumptions are based on the original papers about vessel length estimation from Skene and Balodis (1968), Milburn and Covey-Crump (1971) and Zimmermann and Jeje (1981)

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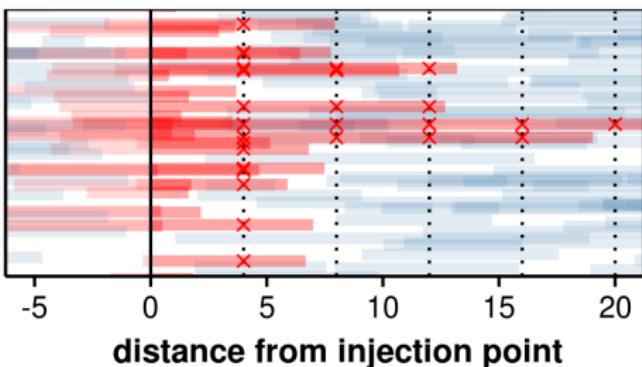
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Importance of simulation

- Indirect measurement that interferes with object of research
 - validation with "true" data impossible
- Preparation for own measurements for PhD project
 - Simulation to establish minimum sample size / number of vessels
 - But: results do not add up...

Importance of simulation

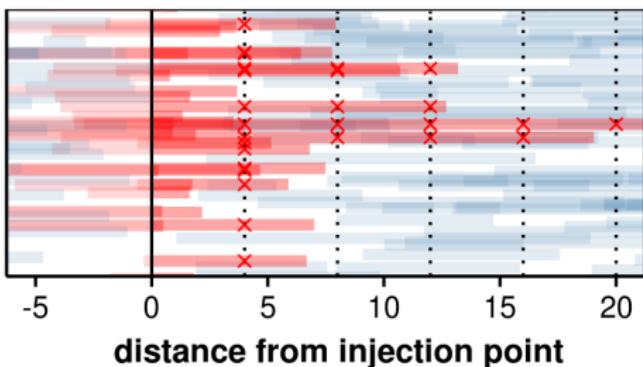
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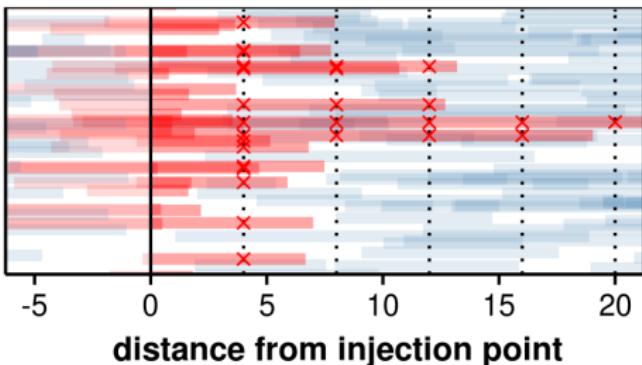
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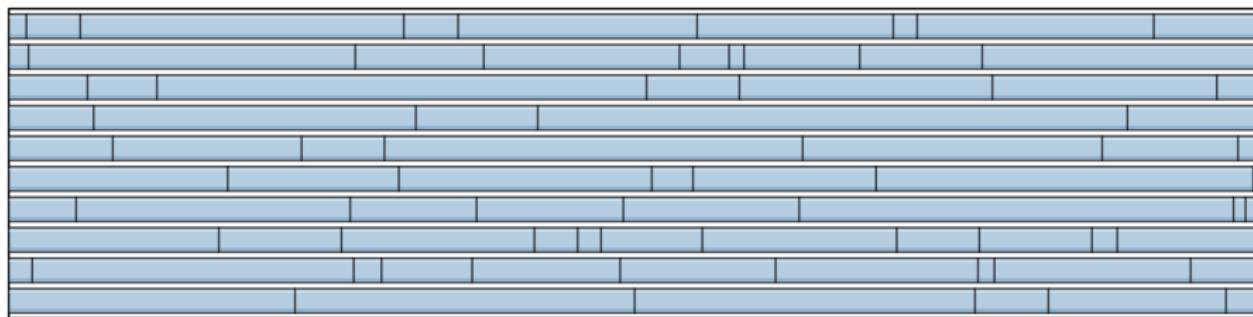
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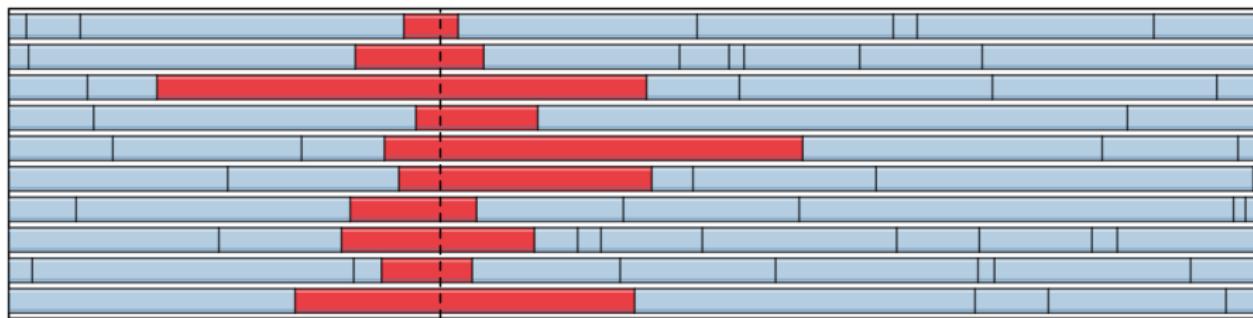
Four different ways to look at vessel length



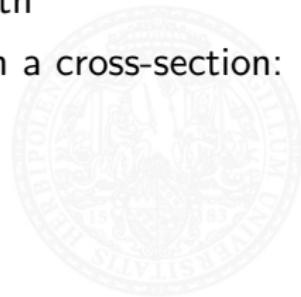
- What's there
 - Distribution of the length of all vessels in the wood sample irrespective of their position
- ⇒ **marginal vessel length distribution**



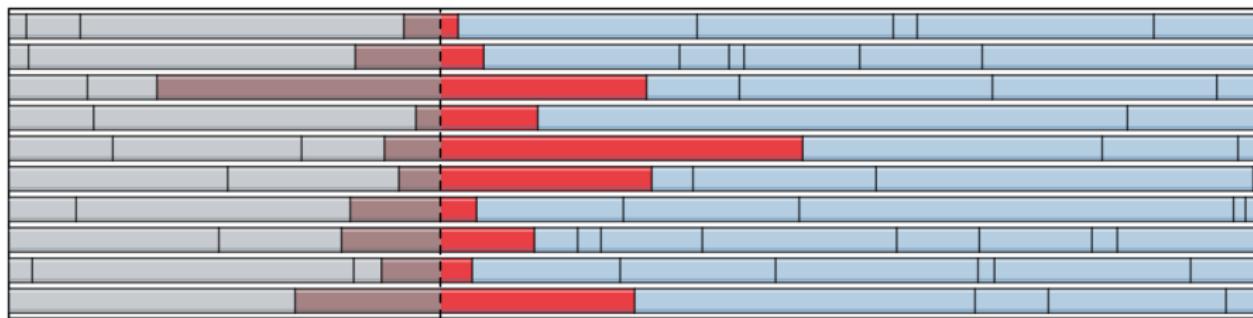
Four different ways to look at vessel length



- What's in a cross-section
- Probability of a vessel to be cut depends on its length
- Resulting conditional length distribution of vessels in a cross-section:
⇒ **"Size-biased" length distribution** (Cox 1969)



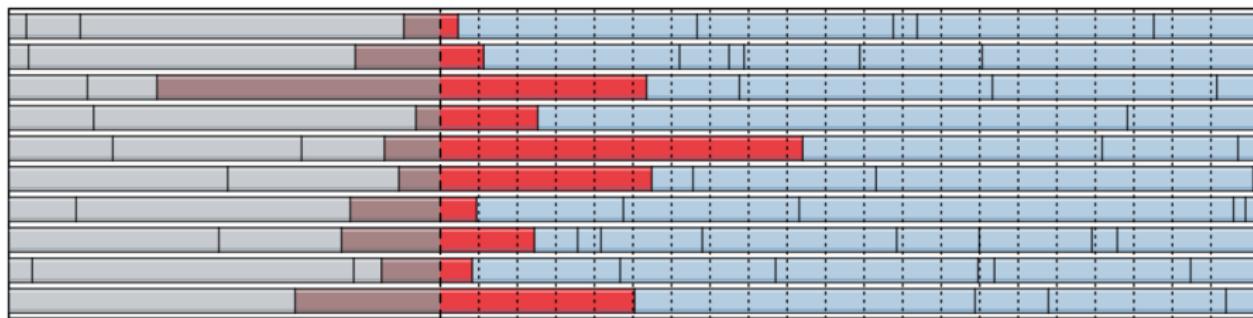
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- What's left after cutting
 - only a random fraction of the unknown original length
- ⇒ **length of cut-off vessel fragments**



Four different ways to look at vessel length



- What we actually measure
 - Counts of stained vessels in each of a series of consecutive cuts
- ⇒ **Injection profile**



Four different ways to look at vessel length

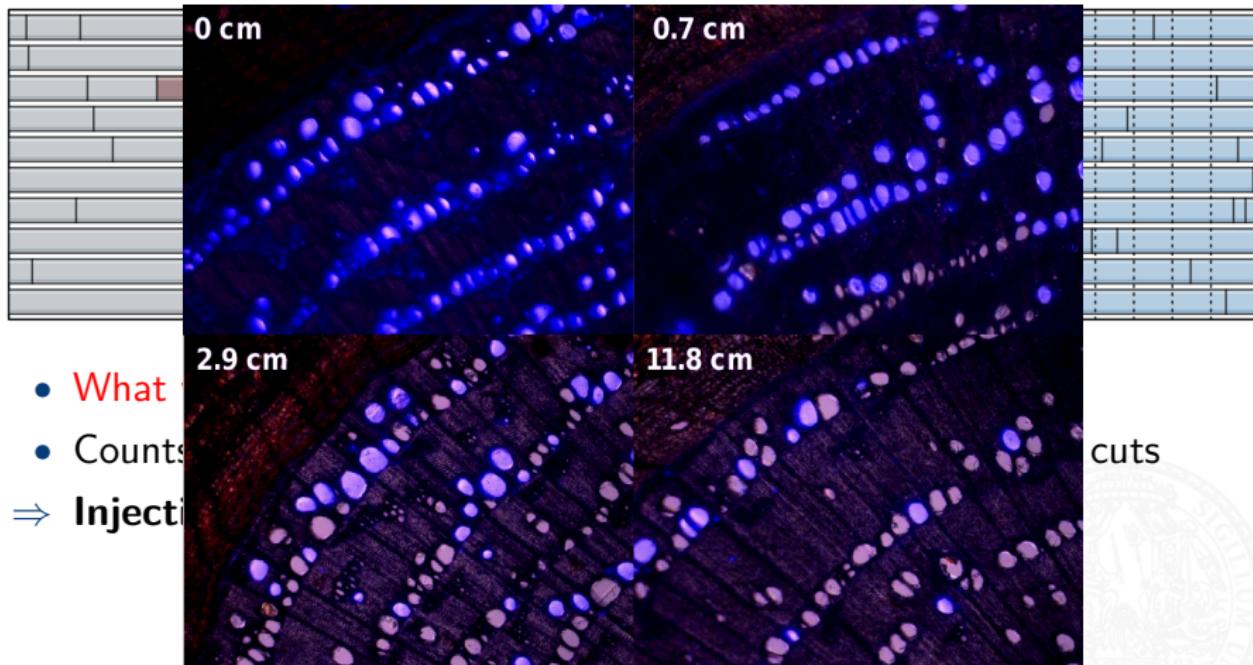


Foto: Jacobsen (2011), lab webpage (modified)

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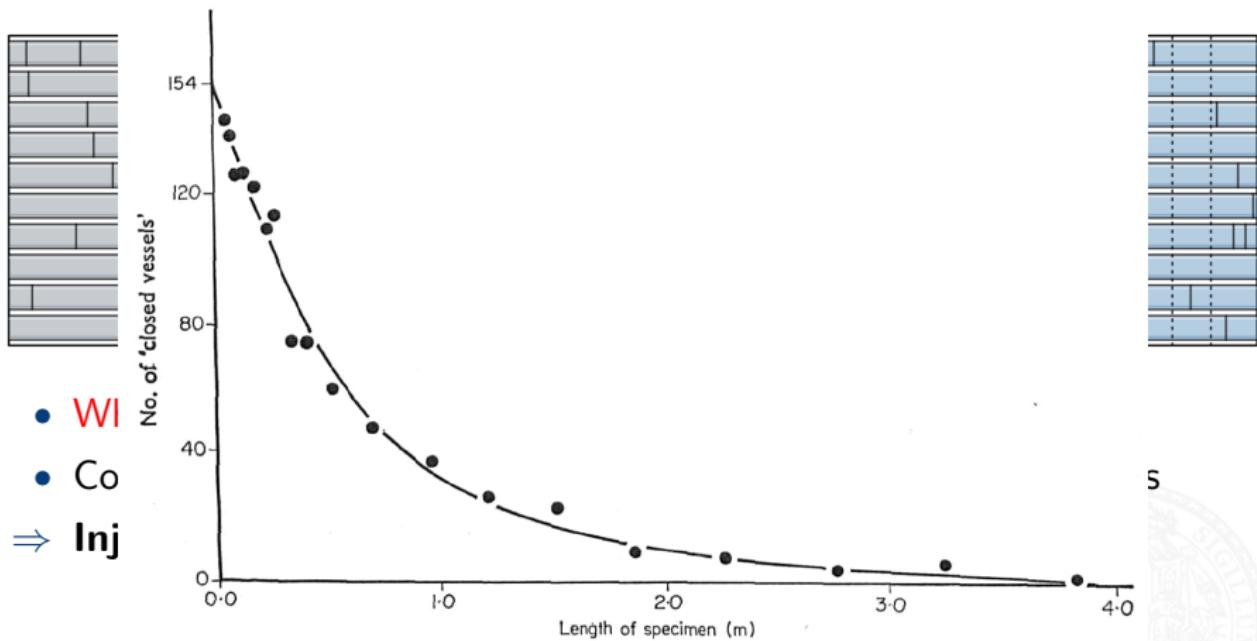


Figure: modified from Milburn and Covey-Crump (1971)

... but what length should we focus on?

- Simulation: based on the **marginal distribution**
- Literature survey: The most commonly used methods estimate the **size-biased distribution**
 - Graphical method (Milburn and Covey-Crump 1971)
 - Double-difference algorithm (Zimmermann and Jeje 1981)
 - Differential form of DD algorithm (Cohen 2003)
 - Very few exceptions^{1,2,3}

⇒ Is there a "right way"?

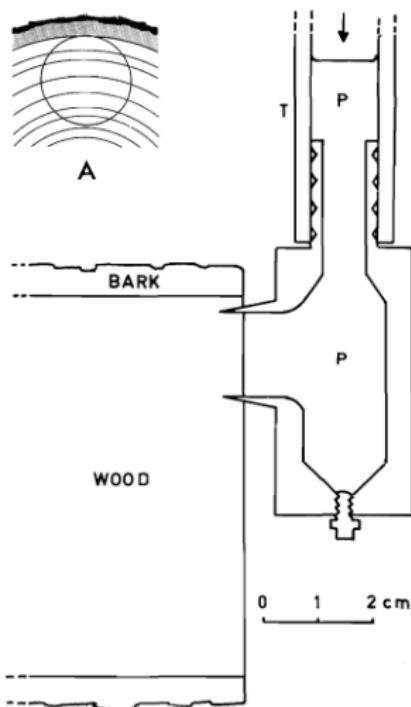


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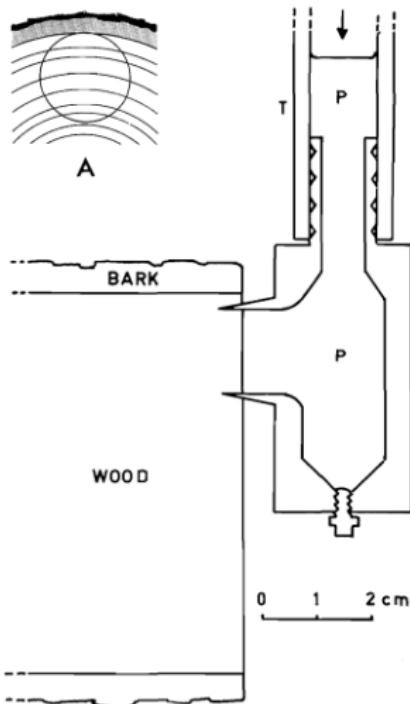


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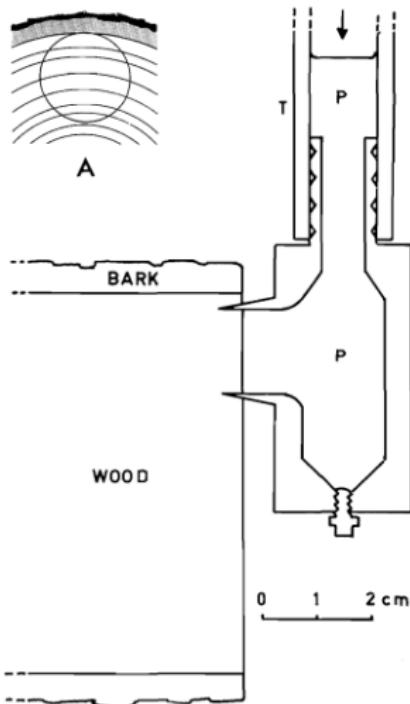
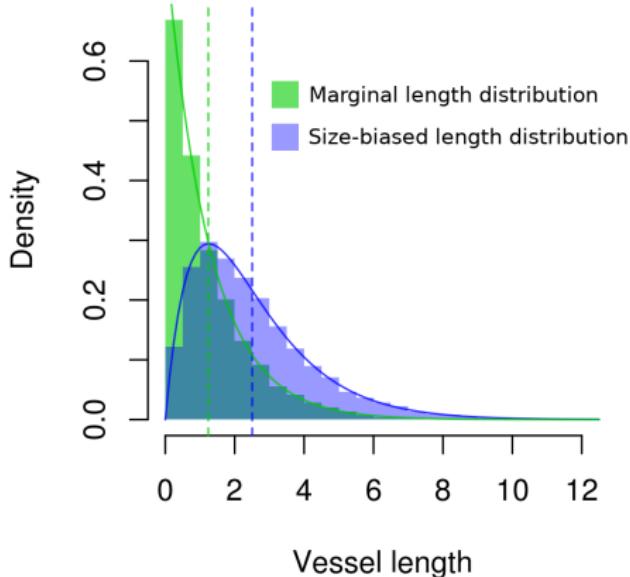


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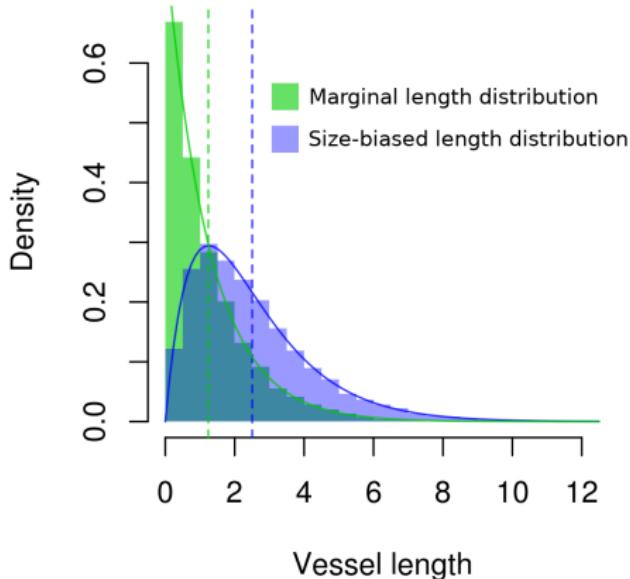
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- The average length of the marginal and size-biased VL distribution differ by **up to a factor of 2!**
- Both distributions have useful applications
 - Marginal distribution: useful when focusing at the vessel level
 - Size biased distribution: useful when comparing VL to properties measured from cross-sections



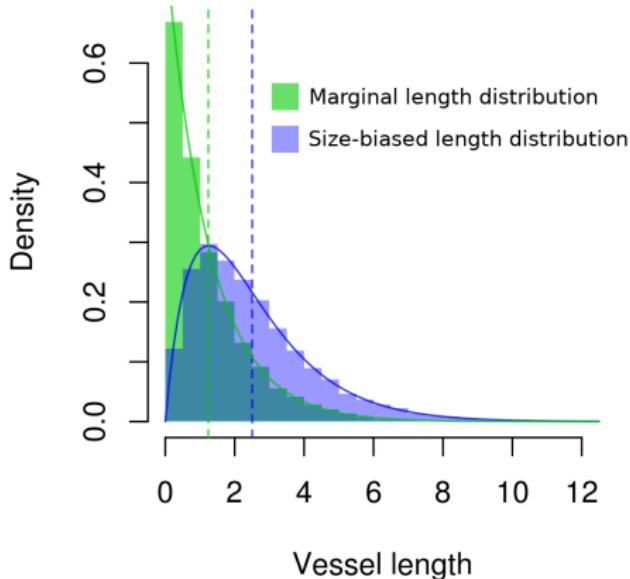
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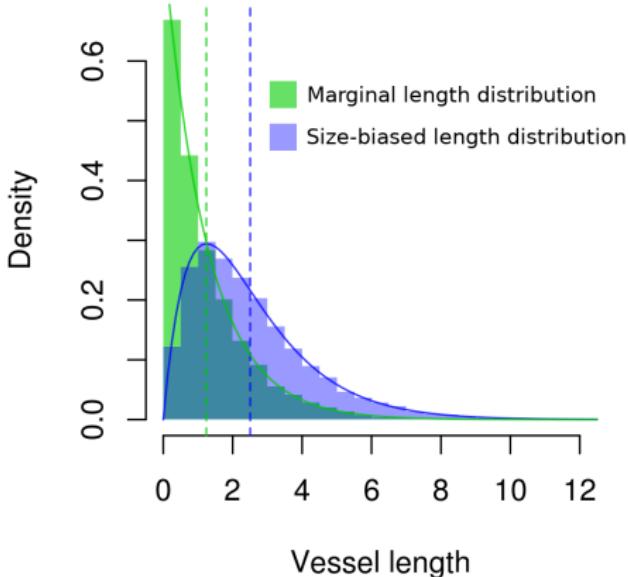
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Important considerations for VL studies



① Which **population** of vessels you want to characterize?

- example: allometric diameter-length scaling laws affect all vessels, not just the sample situated in a cross-section
- wrong reference frame can obscure or even invert relationships

② What **scale** is relevant for the processes you are studying?

- example: allometric constraints act at the single-vessel level
- inferring scaling rules from plant- or species-level aggregate variables: risk of **ecological fallacies** (Robinson 1950)
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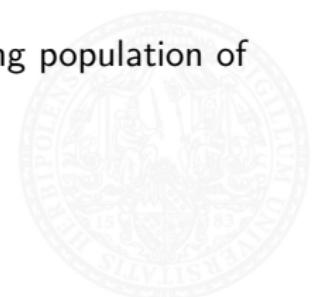
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 - Estimates of average vessel diameter etc. are potentially size-biased
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Summary

- Vessel length can be characterized by different distributions
 - Marginal distribution: focus on vessel level
 - "Size-biased" distribution (e.g. DD algorithm): focus on cross-sections
→ Choice of focus has important implications
- Theory and tools for vessel length estimation: Link et al. (2018)
- Possible directions for future studies
 - Model extension: more realistic model of vessel length
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Github: r-link



Twitter: @RomanMLink

Bibliography I

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