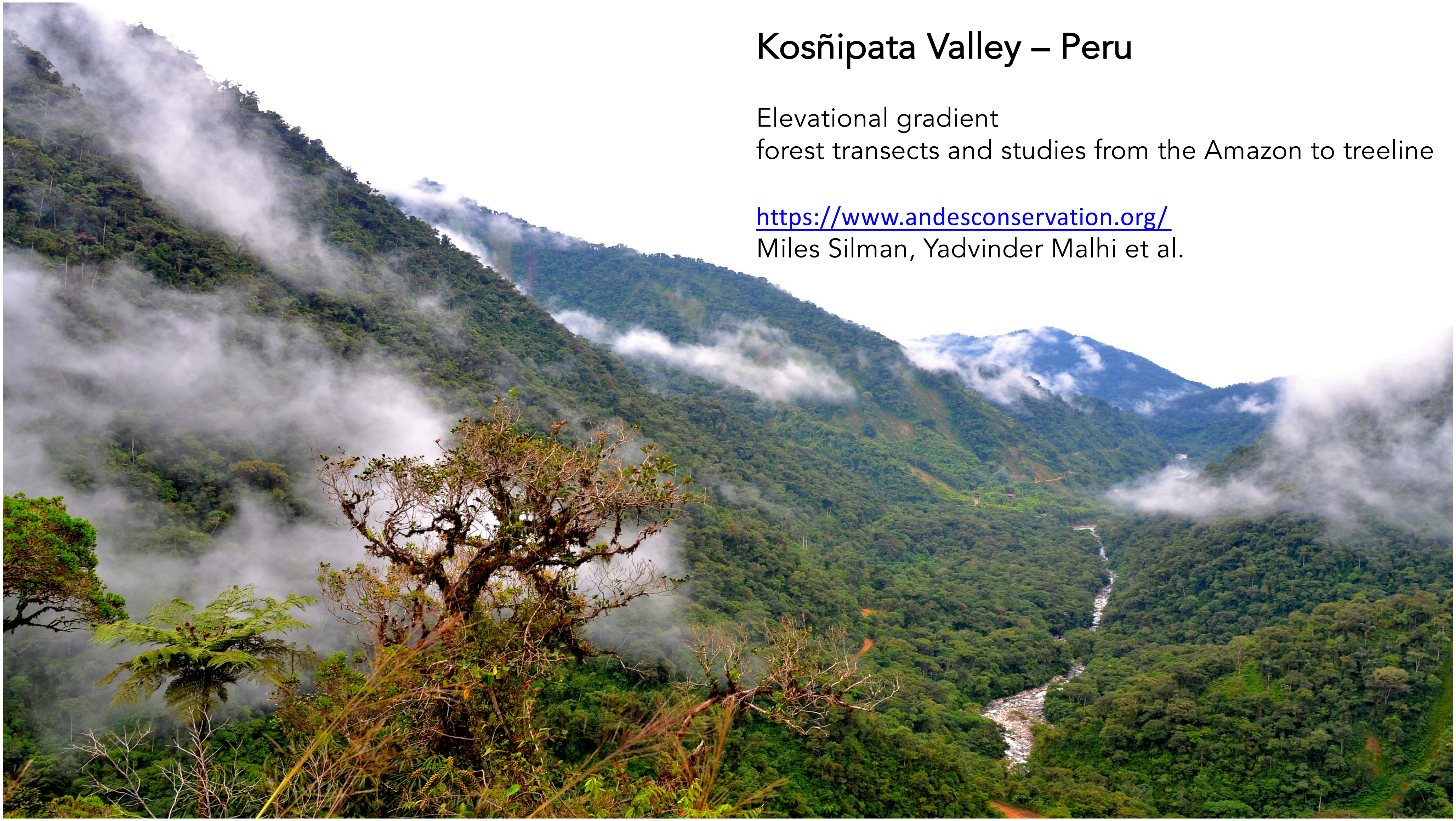
A Quick (and Rough) Introduction to Trait-based Plant Ecology

Brian J. Enquist
Dept. of Ecology and Evolutionary Biology,
University of Arizona, &
The Santa Fe Institute

THE UNIVERSITY OF ARIZONA



Kosñipata Valley – Peru

Elevational gradient
forest transects and studies from the Amazon to treeline

https://www.andesconservation.org/
Miles Silman, Yadvinder Malhi et al.

PFTC3 & 5

- We are extending the elevational gradient above treeline, in the Puna grassland, to the higher elevations in the Andes.
- We believe that this gradient is now the largest monitored elevational gradient in the world.
- ~300m to ~ 5,300m
- Large natural temperature gradient
- Monitor species, trait and functional diversity and ecosystem functioning along the entire gradient.
- We will focus on the Puna species

Introduction to Trait-based Ecology

- Why Trait-based Ecology?
- History of Trait-based Ecology
- What is a Trait?
- What Causes Variation in Traits?

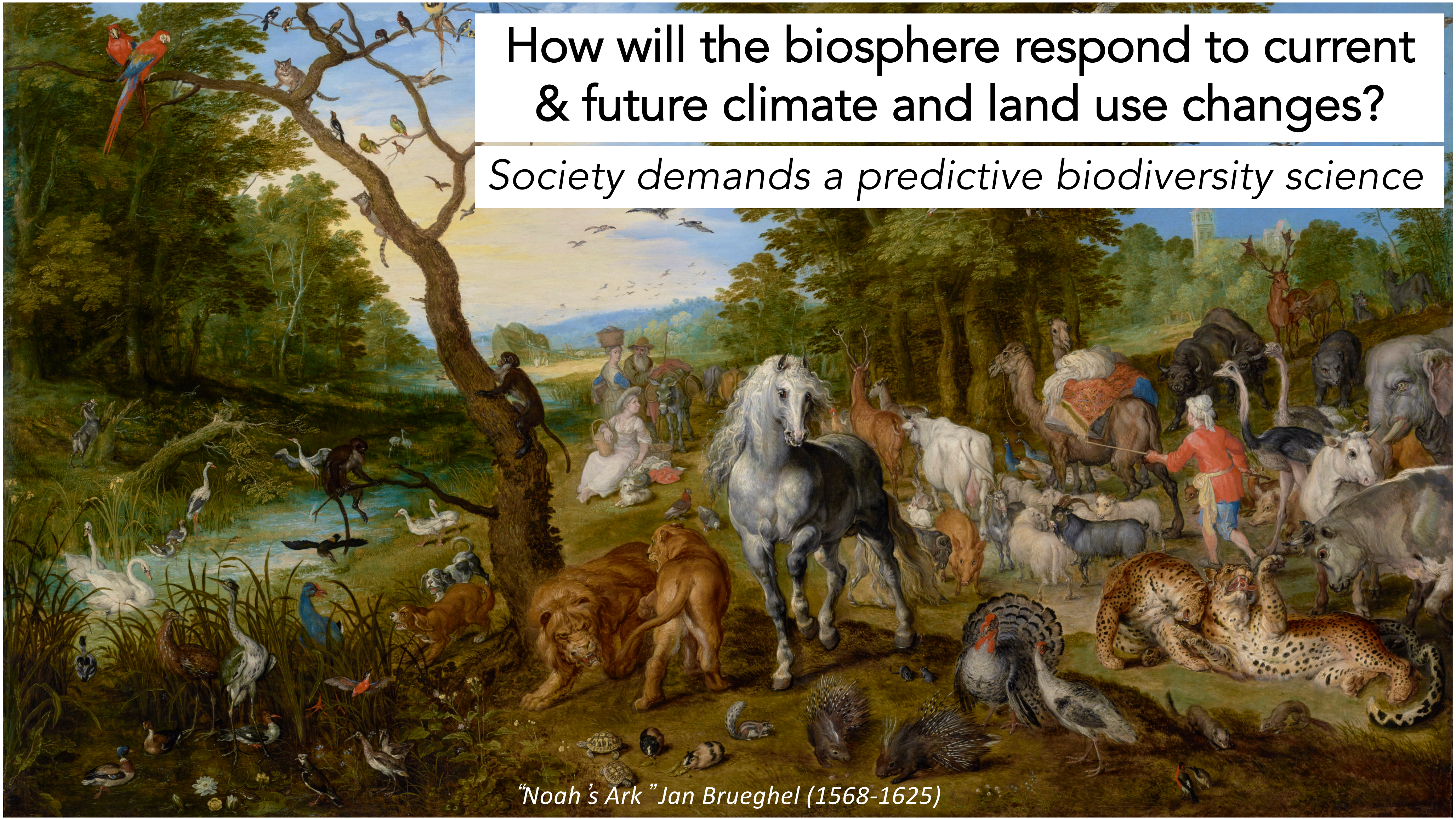
Introduction to Trait-based Ecology

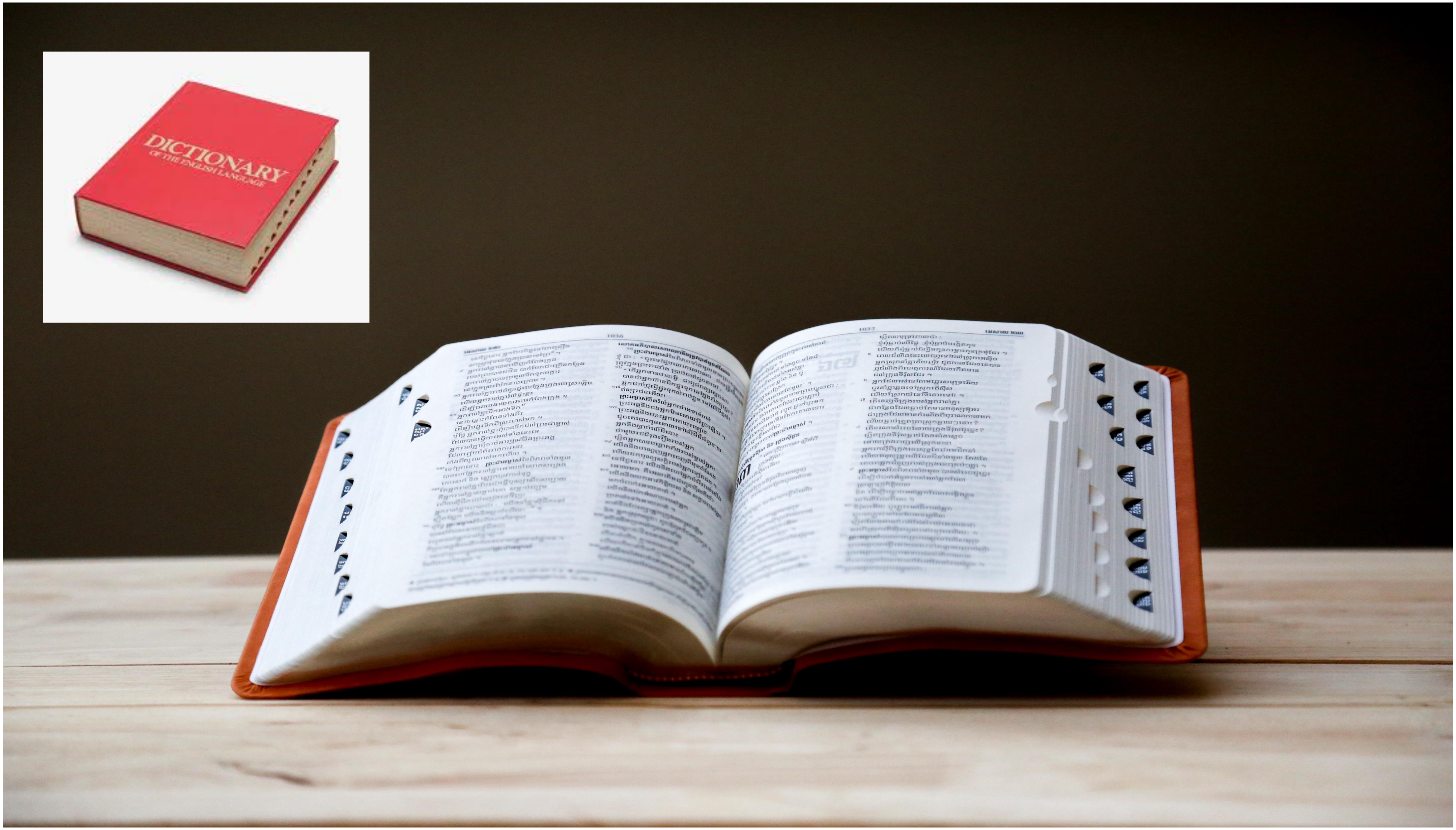
Why Trait-based Ecology?

History of Trait-based Ecology

What is a Trait?

What Causes Variation in Traits?


How will the biosphere respond to current & future climate and land use changes?
Society demands a predictive biodiversity science
"Noah's Ark" Jan Brueghel (1568-1625)


DICTIONARY
OF THE ENGLISH LANGUAGE

The phenotype is "*the observable properties of an organism that are produced by the interaction of the genotype and the environment*"[1].

- It includes all attributes of the organism that influences how an organism survives, reproduces and interacts with its environment.
- Ecology and evolutionary biology implicitly depends on the study of the diversity of phenotypes.

1. Merriam-Webster & Inc. Staff. The Merriam-Webster Dictionary, International Edition. (Merriam-Webster, Incorporated, 2016).

Why traits?

"Statements about traits give generality and predictability whereas species richness tends toward contingent rules and special cases."

Keddy (1992)

Why traits?

Opinion TRENDS in Ecology and Evolution Vol.21 No.4 April 2006
Full text provided by www.sciencedirect.com
ELSEVIER SCIENCE DIRECT

Rebuilding community ecology from functional traits

Brian J. McGill[1], Brian J. Enquist[2], Evan Weiher[3] and Mark Westoby[4]

Tucson, AZ 85721, USA
WI 54702, USA
stralia

"Although being interested in the role of traits in ecology is not new … ecologists have preferred to emphasize a nomenclatural approach by focusing on species identities, which has resulted in a loss of ecological generality …

in the context of a biotic interaction milieu. We suggest this approach can create a more quantitative and predictive science that can more readily address issues of global change.

ional traits research program

our themes that we suggest are traits, environ-al gradients, the interaction milieu and perform-currencies. These themes are linked by taking a physiological approach, by using concepts that are

ssary

unity matrix: a square (S×S) matrix describing interactions in a unity with *S* species. The community matrix, together with a vector of ic rates of increase (*r*), specifies the parameters of the generalized (*S* s) Lotka–Volterra differential equations, which can be solved for equilibrium abundances (*N*).
Distinct preference niche: a model of a niche in which each closely related species has a performance optimum at a different point along an environmental gradient (Figure 1c, main text). This model is assumed correct in most of community ecology, but might be less common than shared preferences.

Why traits?

Opinion   *TRENDS in Ecology and Evolution* Vol.21 No.4 April 2006

Full text provided by www.sciencedirect.com

ELSEVIER

Rebuilding community ecology from functional traits

Brian J. McGill[1], Brian J. Enquist[2], Evan Weiher[3] and Mark Westoby[4]

[1]Department of Biology, McGill University, Montreal, QC, Canada, H3A 1B1
[2]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA
[3]Department of Biology, University of Wisconsin – Eau Claire, Eau Claire, WI 54702, USA
[4]Department of Biological Sciences, Macquarie University, NSW 2109, Australia

In contrast…

"Statements about traits give generality and predictability, whereas nomenclatural ecology tends towards highly contingent rules and special cases."

issues of global change.

al traits research program

themes that we suggest are traits, environ- gradients, the interaction milieu and perform- rencies. These themes are linked by taking a ysiological approach, by using concepts that are

y

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Why Trait Based Ecology?

- Traditional measures based on species richness does not adequately capture predictions of our models
- Traits more directly link how species perform in differing environments
- Traits enable a more predictive ecology
- Can better link to quantitative mechanistic theory

A persistent question in ecology: How does species diversity influence ecosystem function?

Proc. Natl. Acad. Sci. USA
Vol. 94, pp. 1857–1861, March 1997
Ecology

Plant diversity and ecosystem productivity: Theoretical considerations

(biodiversity/resource competition/soil fertility/nutrient use/retention)

DAVID TILMAN†, CLARENCE L. LEHMAN†, AND KENDALL T. THOMSON‡

†Department of Ecology, Evolution and Behavior, 1987 Upper Buford Circle, University of Minnesota, St. Paul, MN 55108; and ‡Department of Chemical Engineering and Materials Science, 421 Washington Avenue SE, University of Minnesota, Minneapolis, MN 55455

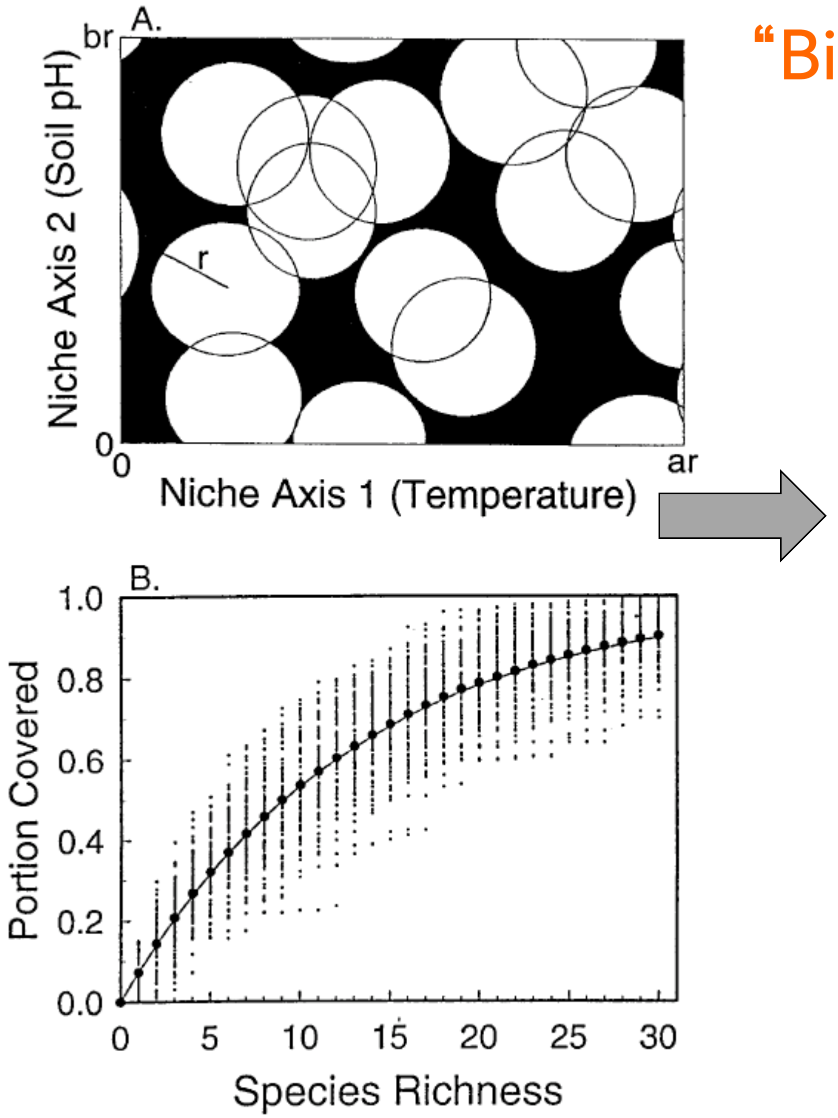
Communicated by Peter Vitousek, Stanford University, Stanford, CA, December 23, 1996 (received for review September 1, 1996)

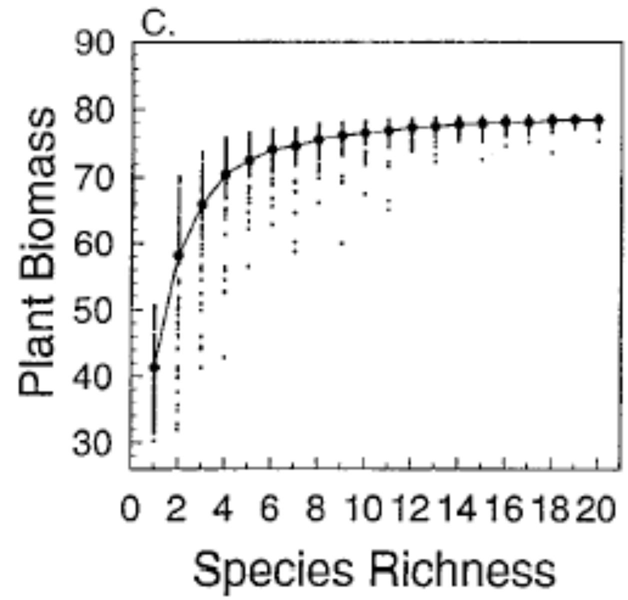
ECOLOGY

Biodiversity and Ecosystem Function: The Debate Deepens

J. P. Grime

“Biodiversity/Ecosystem Function Theory”





Tilman et al. *PNAS* (1997)

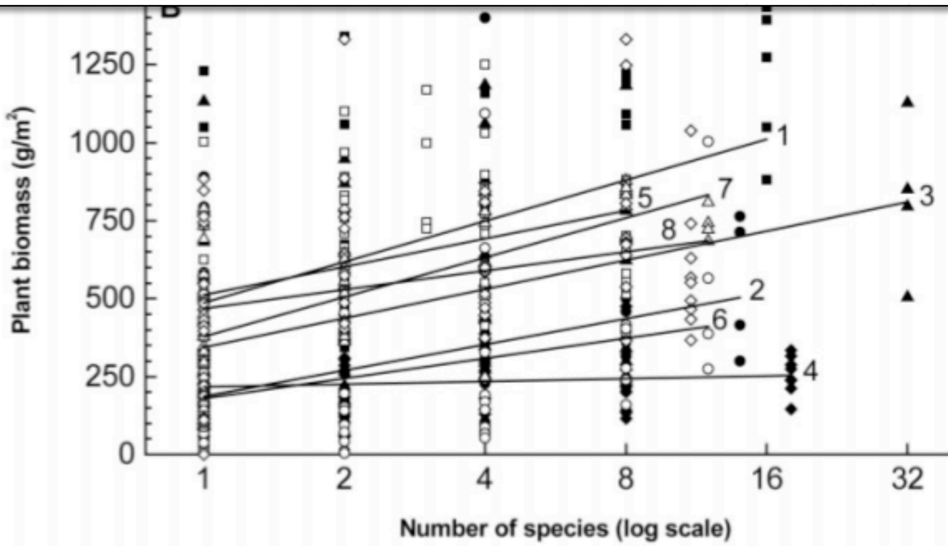
2001

SCIENCE'S COMPASS • REVIEW

REVIEW: ECOLOGY

Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges

M. Loreau,[1*] S. Naeem,[2] P. Inchausti,[1] J. Bengtsson,[3] J. P. Grime,[4] A. Hector,[5] D. U. Hooper,[6] M. A. Huston,[7] D. Raffaelli,[8] B. Schmid,[9] D. Tilman,[10] D. A. Wardle[4]



"The consequences of biodiversity has aroused considerable interest and controversy there is however, uncertainty as to how (these findings) generalize across ecosystems"

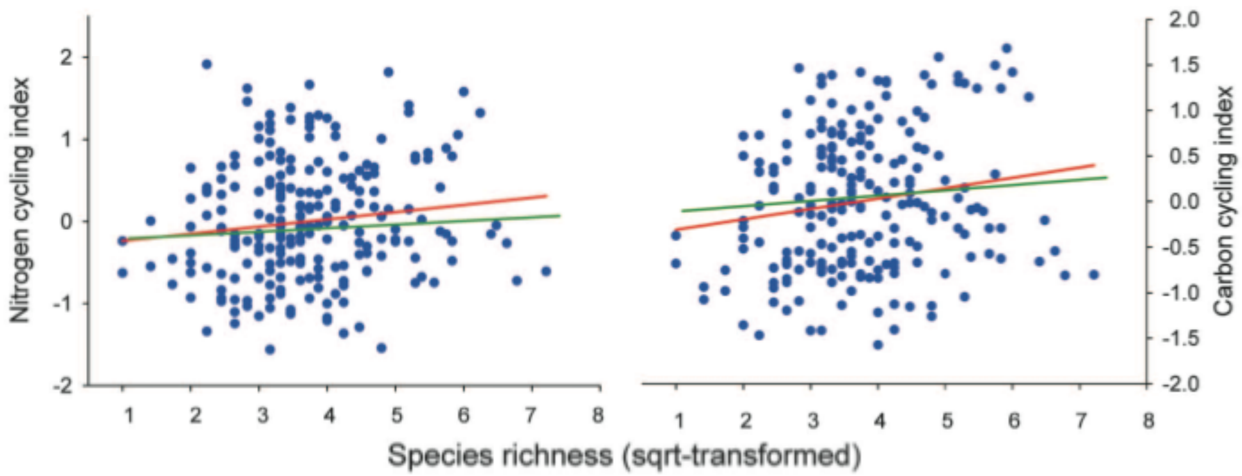
Plant Species Richness and Ecosystem Multifunctionality in Global Drylands

Science 2012

Fernando T. Maestre,[1]* José L. Quero,[1] Nicholas J. Gotelli,[2] Adrián Escudero,[1] Victoria Ochoa,[1] Manuel Delgado-Baquerizo,[3] Miguel García-Gómez,[1,4] Matthew A. Bowker,[5] Santiago Soliveres,[1] Cristina Escolar,[1] Pablo García-Palacios,[1] Miguel Berdugo,[1] Enrique Valencia,[1] Beatriz Gozalo,[1] Antonio Gallardo,[3] Lorgio Aguilera,[6] Tulio Arredondo,[7] Julio Blones,[8] Bertrand Boeken,[9] Donaldo Bran,[10] Abel A. Conceição,[11] Omar Cabrera,[12] Mohamed Chaieb,[13] Mchich Derak,[14] David J. Eldridge,[15] Carlos I. Espinosa,[12] Adriana Florentino,[16] Juan Gaitán,[10] M. Gabriel Gatica,[17] Wahida Ghiloufi,[13] Susana Gómez-González,[18] Julio R. Gutiérrez,[6] Rosa M. Hernández,[19] Xuewen Huang,[20] Elisabeth Huber-Sannwald,[7] Mohammad Jankju,[21] Maria Miriti,[22] Jorge Monerris,[23] Rebecca L. Mau,[24] Ernesto Morici,[25] Kamal Naseri,[21] Abelardo Ospina,[16] Vicente Polo,[1] Aníbal Prina,[25] Eduardo Pucheta,[17] David A. Ramírez-Collantes,[23] Roberto Romão,[11] Matthew Tighe,[26] Cristian Torres-Díaz,[18] James Val,[27] José P. Veiga,[28] Deli Wang,[29] Eli Zaady[30]

"Our results suggest that the preservation of plant biodiversity is crucial to buffer negative effects of climate change"

But, species richness only explained about 4% of variation



Thesis

Progress in biodiversity science has been limited by its primary focus on species richness (number of species per area).

Species richness patterns do not offer a strong basis to develop & test theory

To better identify pattern and to link measures of the diversity of life with theory - need to incorporate additional information

Alternative measures of diversity

CHAPTER 8

Beyond Species Richness: Biogeographic Patterns and Biodiversity Dynamics Using Other Metrics of Diversity

Kaustuv Roy, David Jablonski, and James W. Valentine

Roy, Jablonski & Valentine (2004)
In: *Frontiers of Biogeography: New Approaches in the geography of nature.*

"A true understanding of the processes underlying diversity patterns requires better understanding of other aspects of organismal biology and geographic variation in these characters."

"Incorporating information on ***morphology, functional biology, and phylogenetic affinities*** *of species . . .is truly reflective of the variety (diversity) of life."*

Trait-based Biodiversity Science

A central hypothesis

Patterns of trait abundance, diversity, and dispersion can better reveal processes structuring diversity & how diversity will respond to change

Why measure functional traits?

- **Mechanistic linkages** - insight into the constraints and opportunities faced by plants in different habitats than does taxonomic identity alone (Southwood 1977; Grime 1979).

- **Link functional diversity to ecosystem processes** and the benefits that people derive from them (Chapin *et al*. 2000; Díaz *et al*. 2007)

- **Enables quantitative comparison** of distant ecosystems with little/no taxonomic overlap (Reich *et al*. 1997; Díaz *et al*. 2004; Cornwell *et al*. 2008).

Introduction to Trait-based Ecology

Why Trait-based Ecology?

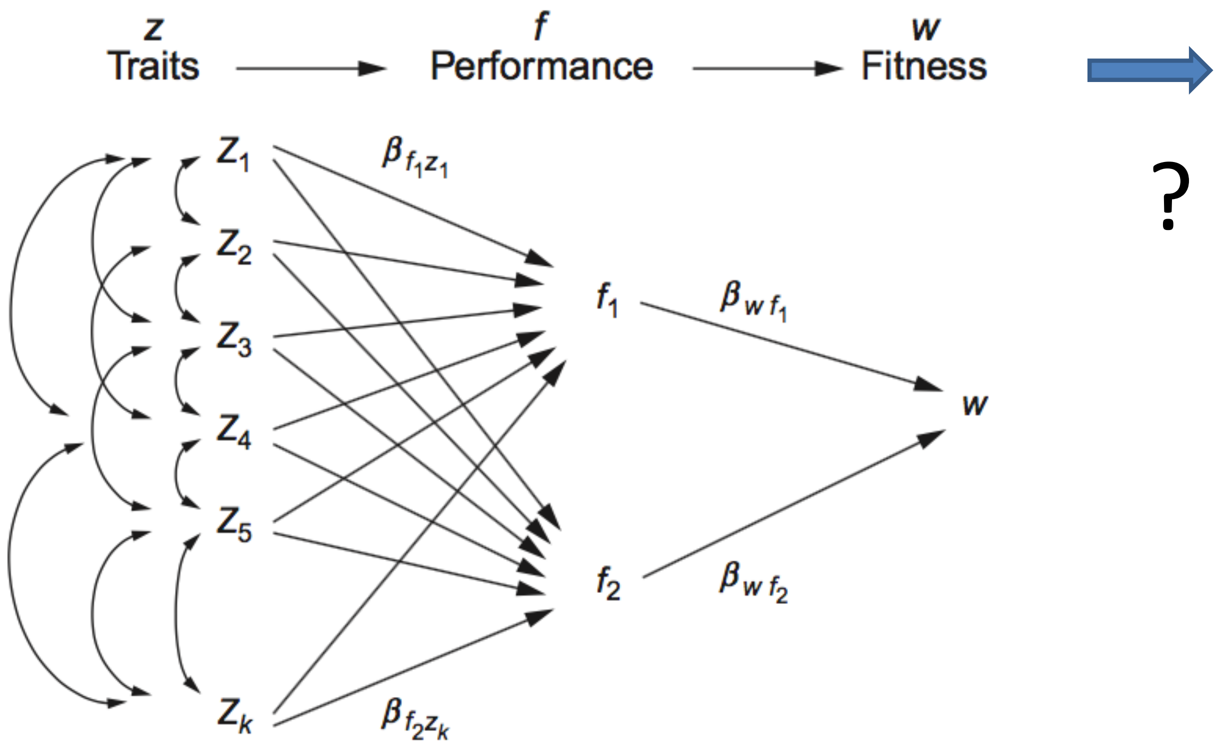
History of Trait-based Ecology

What is a Trait?

What Causes Variation in Traits?

Assumptions

Central assumption of trait-based ecology



Biodiversity
Ecology
& Ecosystems

?

From Violle et al. 2007 – based on Kingsolver and Huey (2003) and Arnold (1983)

Research focal areas

(1) Trait dispersion

Dispersion - Linking diversity, traits, competition, and phylogenetic relatedness

“The truth of the principle that *the greatest amount of life can be supported by great diversification of structure, is seen under many natural circun* ... *eely* open to immi ... al and individual mu ... s inhabitants.”

Measures of trait variation (functional diversity) often reflected in phylogenetic diversity because of **niche conservatism**

“For instance, I found that a piece of turf, three feet by four in size, which had been exposed for many years to exactly the same conditions, supported twenty species of plants, and these belonged to eighteen genera and to eight orders, which shows how much these plants differed from each other . . . .”

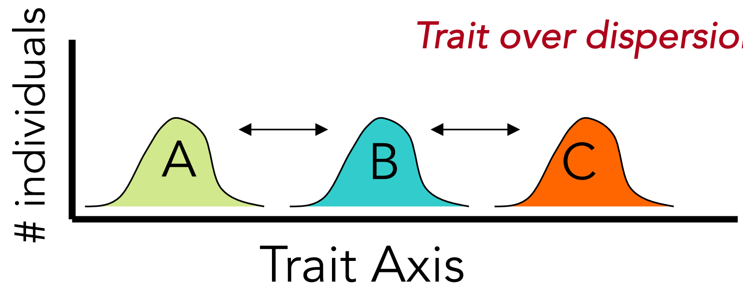
Charles Darwin 1859

Within a given ecological community, differing ecological Forces Result in Different Trait distributions

- Competitive Niche Packing

Darwin 1859, Grinnell 1914, Elton 1927, MacArthur and Levins 1967, Tilman 1982 etc. etc.

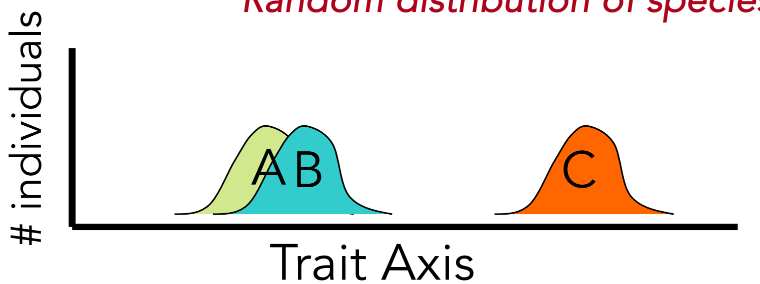
Trait over dispersion



- Random/Neutral

Hubbell 2001

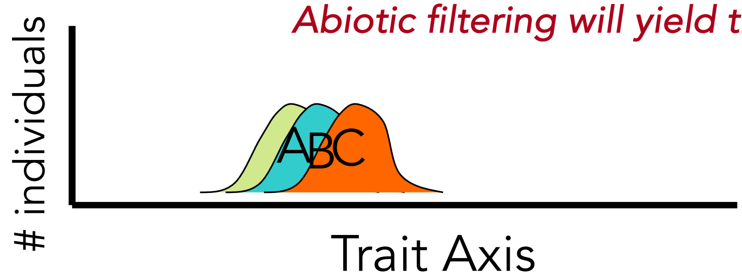
Random distribution of species trait distributions



- Abiotic filtering

Keddy et al. 1998; Weiher and Keddy 1995

Abiotic filtering will yield trait clustering



For example see Kraft et al. 2008 *Science*

Journal of Vegetation Science 17: 255-260, 2006

FORUM

Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences

Grime, J. Philip

Unit of Comparative Plant Ecology, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK; E-mail j.p.grime@sheffield.ac.uk

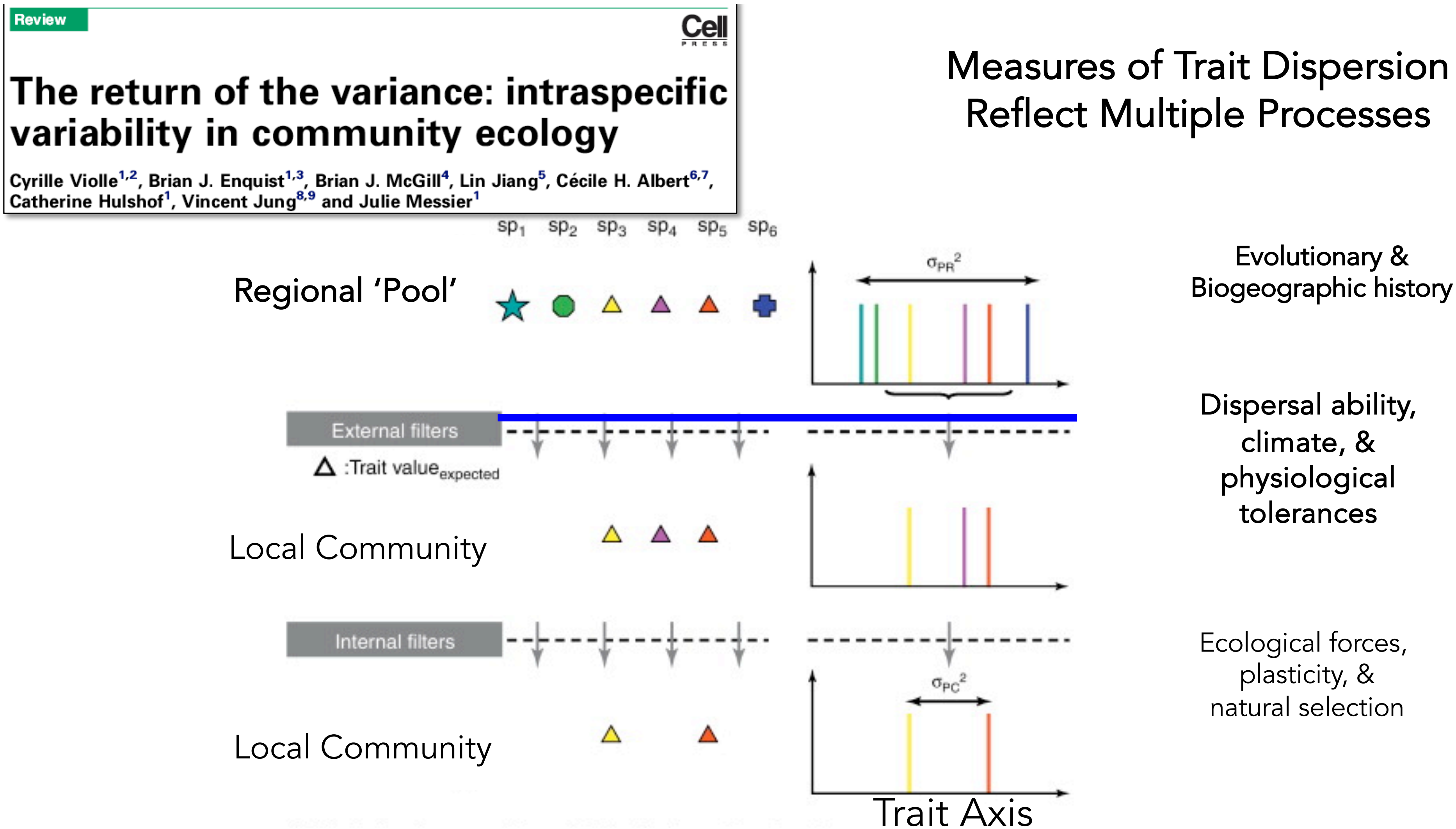
Trait Convergence

Competitive exclusion, abiotic filtering -> limits trait variation

Trait Divergence

'Niche Packing', disturbance -> increases trait variation

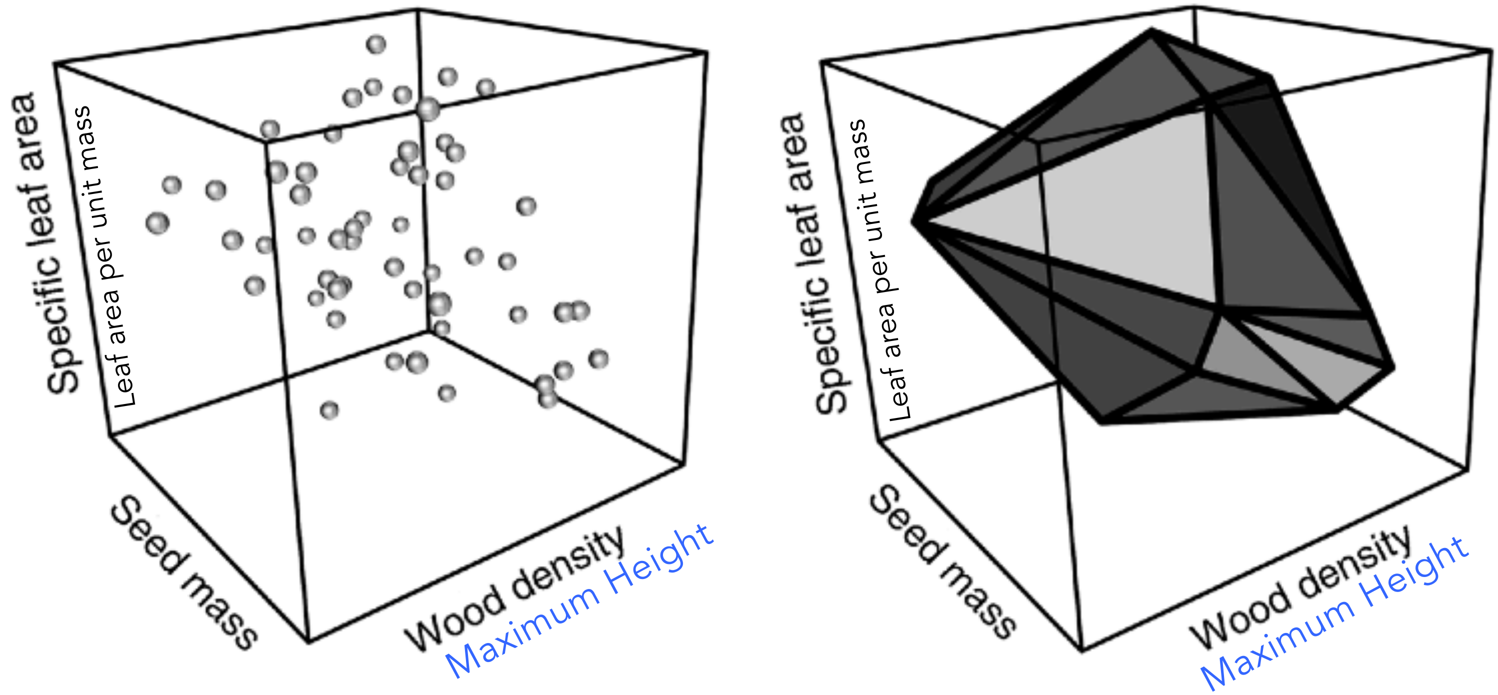
Measures of Trait Dispersion Reflect Multiple Processes



Violle, Enquist, McGill et al. (2012) *TREE*

Functional Diversity

Functional Diversity
Trait hypervolume



Trait axes reflect global variation in plant life histories

Cornwell, Schwilk, Ackerly (*Ecology* 2006)

Extending biodiversity theory via focusing on functional hypervolumes

Biotic Pressure Hypothesis

(Wallace 1878, Dobzhansky 1950, Fischer 1960, Schemske 2009)

Warm & wet environments - selection has lead to an increased range of phenotypes (traits) along various life history trade-offs

Stress dominance (Filtering) Hypothesis, (Weiher and Keddy, 1995).

Within or across clades, more stressful environments yields stronger stabilizing selection (filtering) - increasingly limits ecological and evolutionary variation in functions.

(2) Diversity of Life Histories/Ecological Strategies

Diversity of Life Histories/Ecological Strategies - The diversity of plants can be characterized by three primary strategies. *Variation in the relative importance of competition, stress, and disturbance*

C-S-R

PRIMARY STRATEGIES IN PLANTS

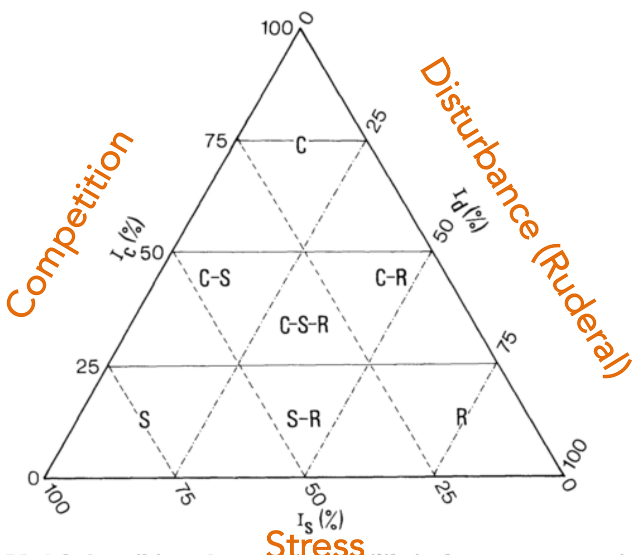


Fig. 2.—Model describing the various equilibria between competition, stress, and disturbance in vegetation and the location of primary and secondary strategies. I_c—relative importance of competition (———), I_s—relative importance of stress (– – –), I_d—relative importance of disturbance (·–·–). A key to the symbols for the strategies is included in the text.

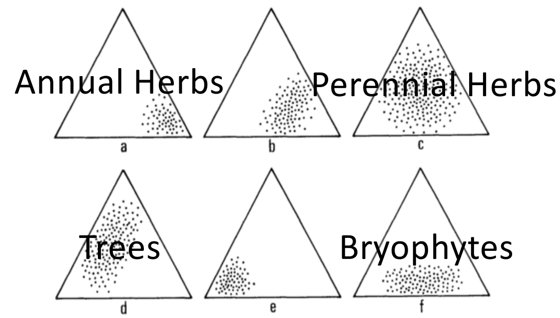
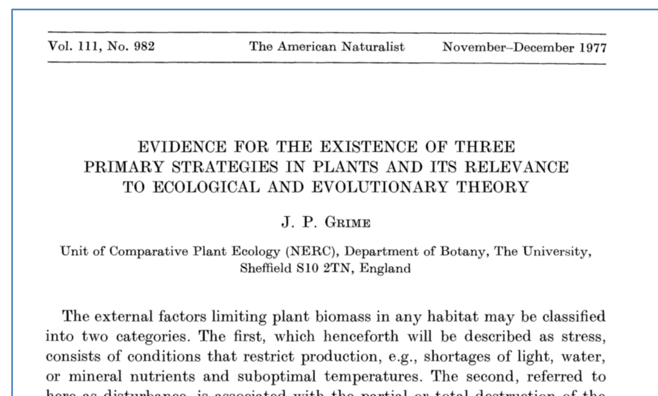


Fig. 3.—Diagrams describing the range of strategies encompassed by (*a*) annual herbs, (*b*) biennial herbs, (*c*) perennial herbs and ferns, (*d*) trees and shrubs, (*e*) lichens, and (*f*) bryophytes. For the distribution of strategies within the triangle, see figure 2.


Vol. 111, No. 982 The American Naturalist November–December 1977

EVIDENCE FOR THE EXISTENCE OF THREE PRIMARY STRATEGIES IN PLANTS AND ITS RELEVANCE TO ECOLOGICAL AND EVOLUTIONARY THEORY

J. P. Grime

Unit of Comparative Plant Ecology (NERC), Department of Botany, The University, Sheffield S10 2TN, England

The external factors limiting plant biomass in any habitat may be classified into two categories. The first, which henceforth will be described as stress, consists of conditions that restrict production, e.g., shortages of light, water, or mineral nutrients and suboptimal temperatures. The second, referred to here as disturbance, is associated with the partial or total destruction of the

(2) Diversity of Life Histories/Ecological Strategies – Fast-Slow Continuum

PNAS

Functional traits explain variation in plant life history strategies

Peter B. Adler[a,1], Roberto Salguero-Gómez[b,c], Aldo Compagnoni[a], Joanna S. Hsu[d], Jayanti Ray-M
Cyril Mbeau-Ache[f], and Miguel Franco[f]

[a]Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT 84322; [b]School of Biological Scie
Queensland, QLD 4072, Australia; [c]Evolutionary Biodemography Laboratory, Max Planck Institute for Demographic Research
[d]Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720; [e]Westville Ca
Natal, Durban 4000, Republic of South Africa; and [f]School of Biological Sciences, Plymouth University, Plymouth PL4 8AA, U

Edited by James H. Brown, University of New Mexico, Albuquerque, NM, and approved December 4, 2013 (received for revie

100 YEARS Journal of Ecology
British Ecological Society

Journal of Ecology 2014, **102**, 275–301 doi: 10.1111/1365-2745.12211

SPECIAL FEATURE – FORUM
THE TREE OF LIFE IN ECOSYSTEMS

The world-wide 'fast–slow' plant economics spectrum: a traits manifesto

Peter B. Reich[1,2]*

[1]*Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA; and* [2]*Hawkesbury Institute for the Environment, University of Western Sydney, Penrith, NSW 2751, Australia*

A continuum of life history variation

Species with fast life history
Small seeds, short-lived leaves, or soft wood.

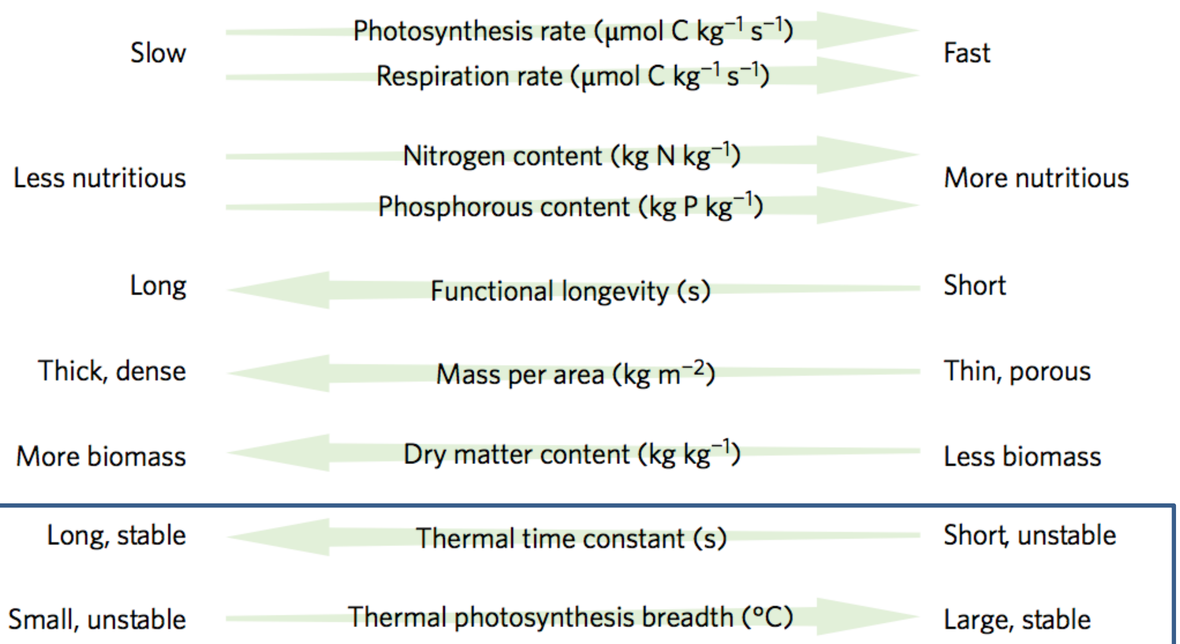
Species with slow life histories
large seeds, long-lived leaves, or dense wood

A continuum of life history variation

Species with fast life history
Small seeds, short-lived leaves, or soft wood.

Species with slow life histories
large seeds, long-lived leaves, or dense wood

Leaf Traits associated with the fast-slow continuum



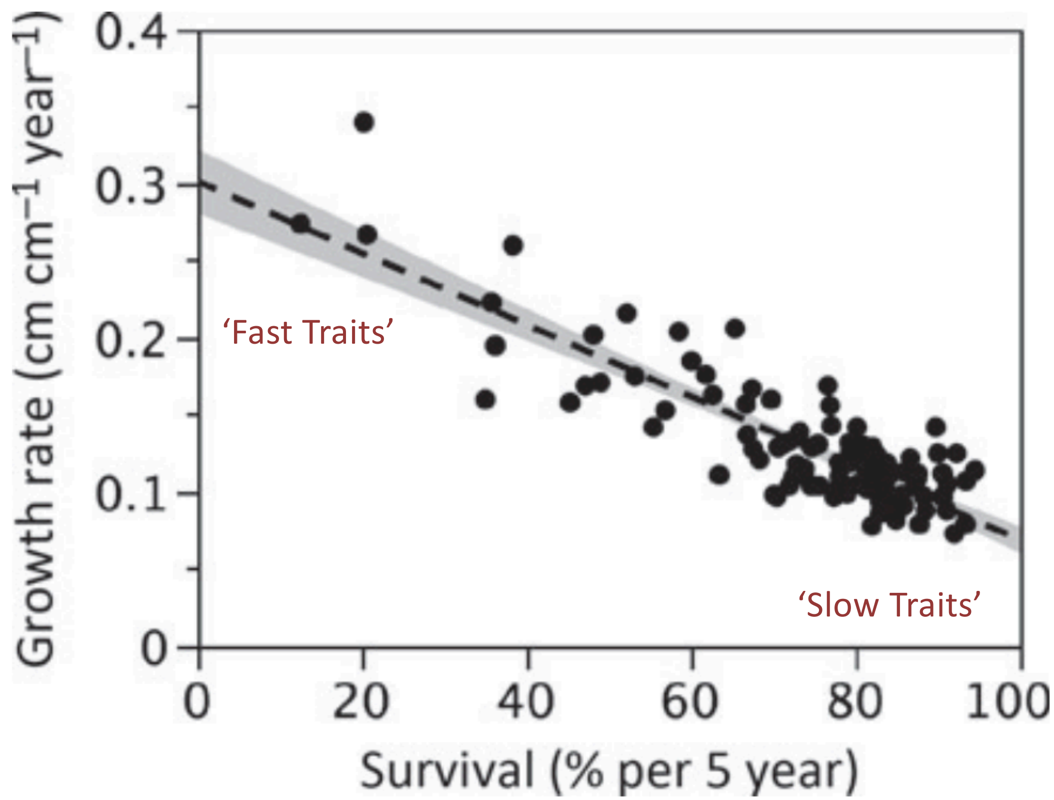
Temperature regulation

Michaletz et al. 2016 *Nature Plants*

Trade-off between growth and survival

“Traits help explain differences in growth and survival across resource gradients and thus…assembly of communities across light, water and nutrient gradients.”

“Traits scale up – fast traits are associated with faster rates of ecosystem processes such as decomposition or primary productivity, and slow traits with slow process rates.”



Reich 2014 *Journal of Ecology*

(2) Diversity of Life Histories/Ecological Strategies

Ecological Strategies (An update on Grime)

ELSEVIER

Review

TRENDS in Ecology and Evolution Vol.21 No.5 May 2006

Full text provided by www.sciencedirect.com

SCIENCE DIRECT

Land-plant ecology on the basis of functional traits

Mark Westoby and Ian J. Wright

Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

First published online as a Review in Advance on August 6, 2002

PLANT ECOLOGICAL STRATEGIES: Some Leading Dimensions of Variation Between Species

Mark Westoby, Daniel S. Falster, Angela T. Moles, Peter A. Vesk, and Ian J. Wright

Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109, Australia; email: mwestoby@rna.bio.mq.edu.au

There are 4 primary trade offs that separate plant species based on traits

- The leaf mass per area-leaf lifespan dimension (LMA-LL) expresses slow turnover of plant parts (at high LMA and long LL), long nutrient residence times, and slow response to favorable growth conditions.

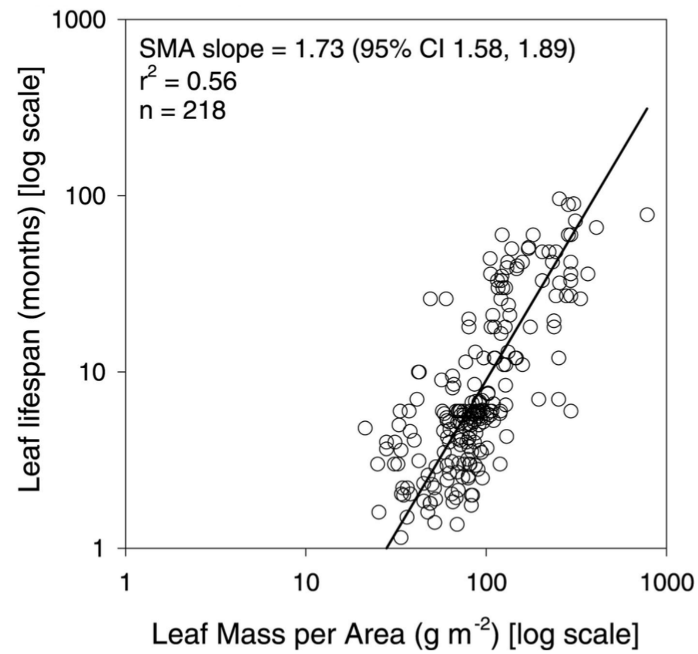
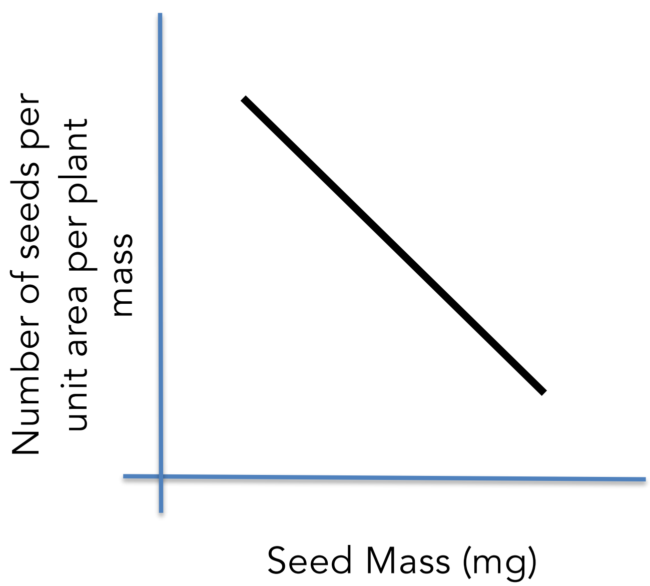


Figure 1 Correlation between leaf lifespan and leaf mass per area across 218 species from several habitats and continents. Regraphed from Reich et al. (1997); data kindly provided by the authors. SMA = Standard Major Axis; CI = confidence internal.

Westoby et al. (2002) ARES

There are 4 primary trade-offs that separate plant species based on traits

- The seed mass-seed output (SM-SO) dimension is an important predictor of dispersal to establishment opportunities (seed output) and of establishment success in the face of hazards (seed mass).



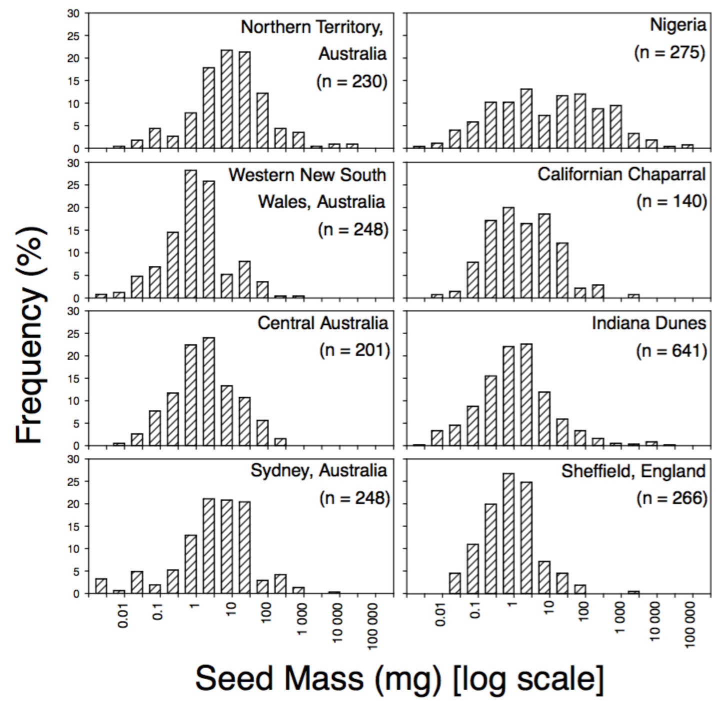


Figure 4 Cross-species frequency distributions of individual seed mass for several locations (Leishman et al. 2000). Two bars per order of magnitude of seed mass.

There are 4 primary trade offs that separate plant species based on traits

- The leaf size-twig size (LS-TS) spectrum has consequences for the texture of canopies, but the costs and benefits of large versus small leaf and twig size are poorly understood.

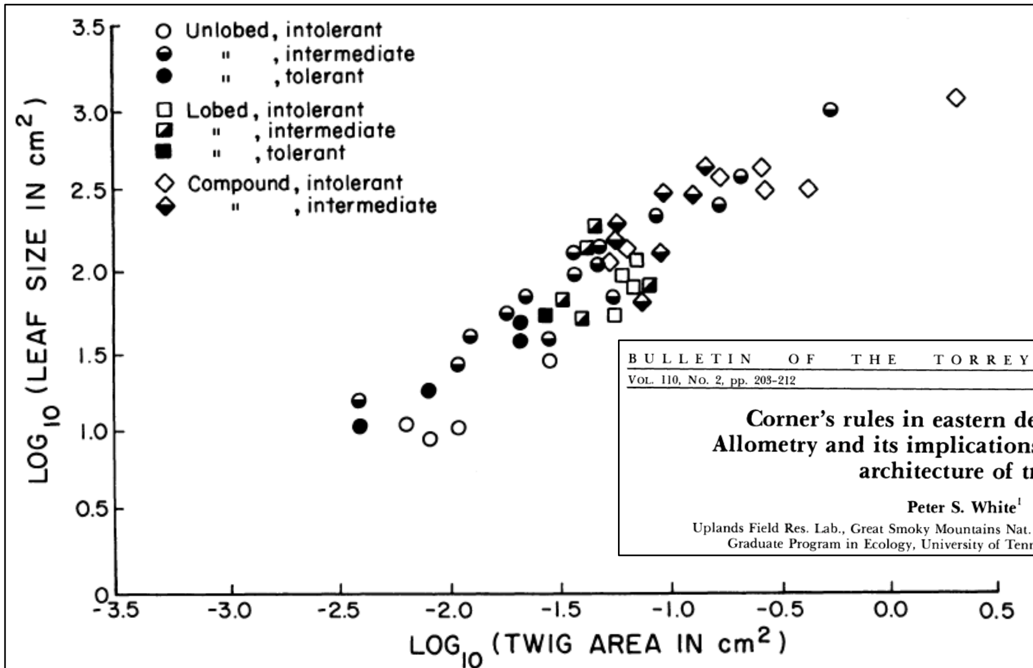


Fig. 1. A plot of the relationship between leaf size (leaf area for individual leaves) and twig cross-sectional area for 48 deciduous trees. Data are taken from Table 1. Note log scales: there is an exponential decrease in the number of species in the data base as leaf size increases.

BULLETIN OF THE TORREY BOTANICAL CLUB
Vol. 110, No. 2, pp. 203–212 April–June, 1983

Corner's rules in eastern deciduous trees: Allometry and its implications for the adaptive architecture of trees

Peter S. White[1]
Uplands Field Res. Lab., Great Smoky Mountains Nat. Park, Gatlinburg, TN 37738 and Graduate Program in Ecology, University of Tennessee, Knoxville, TN 37916

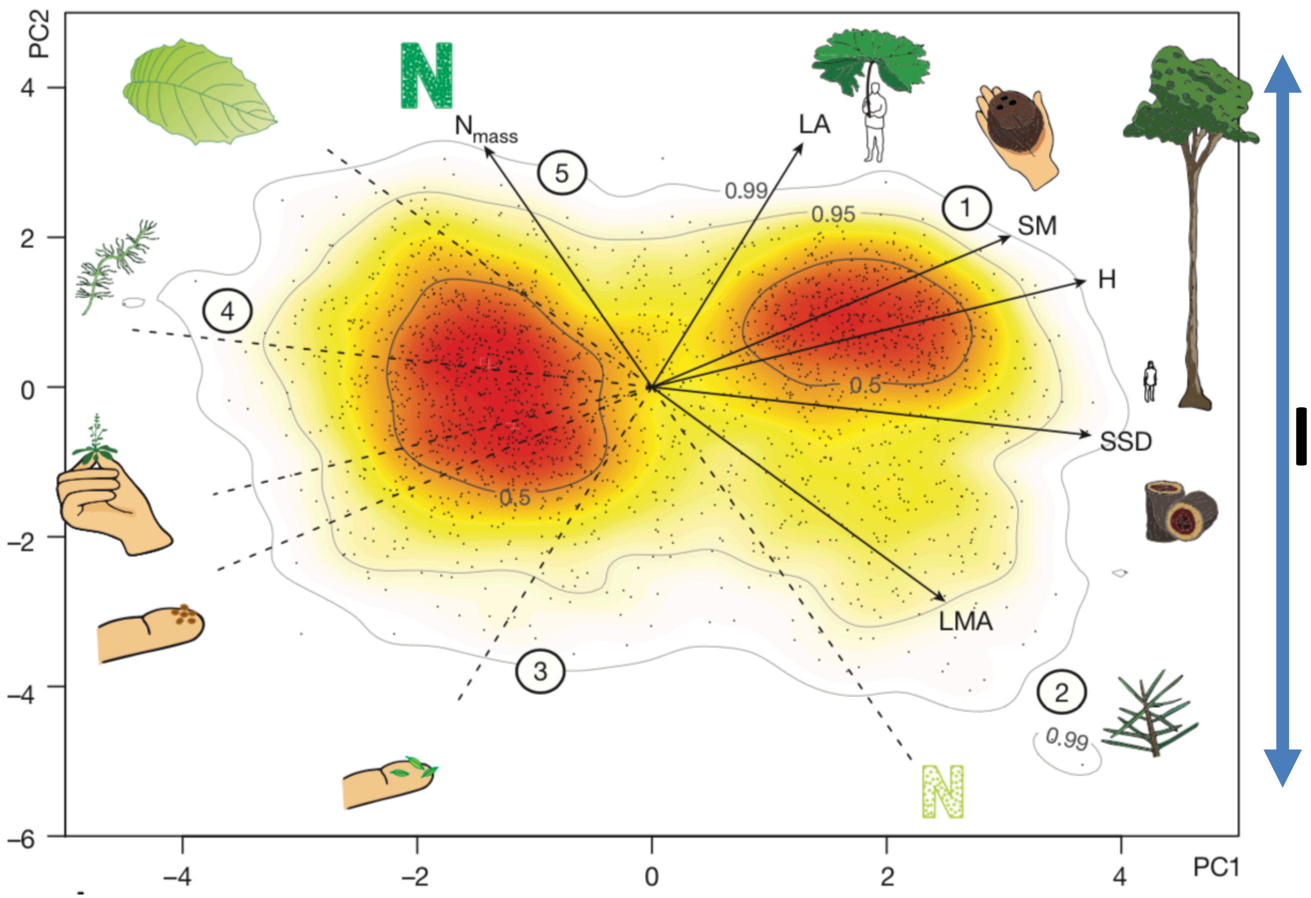
ARTICLE

doi:10.1038/nature16489

The global spectrum of plant form and function

Sandra Díaz[1], Jens Kattge[2,3], Johannes H. C. Cornelissen[4], Ian J. Wright[5], Sandra Lavorel[6], Stéphane Dray[7], Björn Reu[8,9], Michael Kleyer[10], Christian Wirth[2,3,11], I. Colin Prentice[5,12], Eric Garnier[13], Gerhard Bönisch[2], Mark Westoby[5], Hendrik Poorter[14], Peter B. Reich[15,16], Angela T. Moles[17], John Dickie[18], Andrew N. Gillison[19], Amy E. Zanne[20,21], Jérôme Chave[22], S. Joseph Wright[23], Serge N. Sheremet'ev[24], Hervé Jactel[25,26], Christopher Baraloto[27,28], Bruno Cerabolini[29], Simon Pierce[30], Bill Shipley[31], Donald Kirkup[32], Fernando Casanoves[33], Julia S. Joswig[2], Angela Günther[2], Valeria Falczuk[1], Nadja Rüger[3,23], Miguel D. Mahecha[2,3] & Lucas D. Gorné[1]

Díaz et al. 2016 Nature



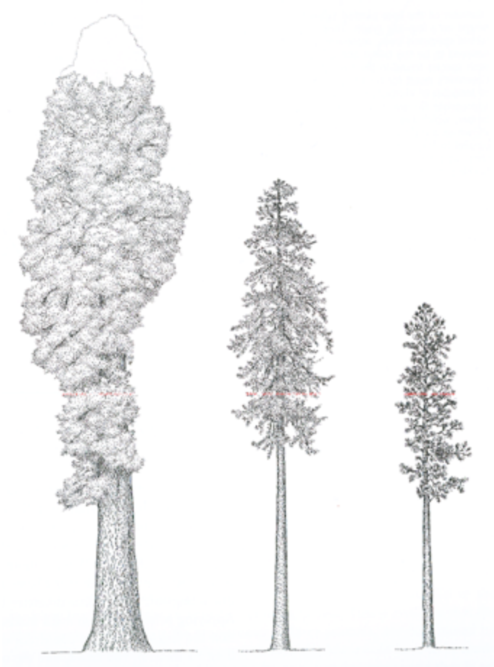
Fast-slow leaf 'economic' traits

Body size

Díaz et al. 2016 *Nature*

There are 4 primary trade offs that separate plant species based on traits

- The plant size/height dimension (Size) Perhaps the single most important trait. Strong correlate of many differences in life history and predictor of physiological rates



(3) Scaling up - Traits to ecosystems, focus on the frequency distribution of traits within a community

(3) Scaling up - Traits to ecosystems, focus on the frequency distribution of traits within a community

Journal of Ecology 1998, **86**, 902–910

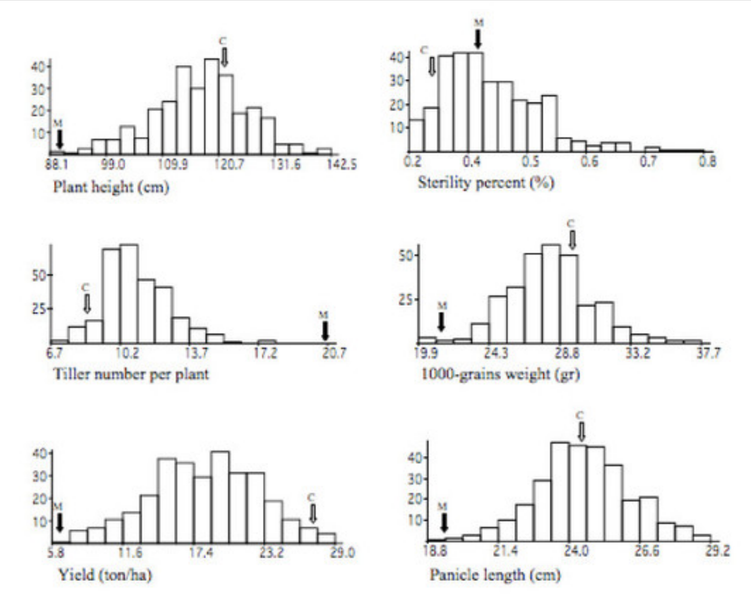
ESSAY REVIEW

Benefits of plant diversity to ecosystems: immediate, filter and founder effects

J.P. GRIME

Unit of Comparative Plant Ecology, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

In order to link traits with ecosystem functioning need abundance (need to know the abundance of trait values)



See also Enquist et al. 2015; 2017)

Introduction to Trait-based Ecology

Why Trait-based Ecology?

History of Trait-based Ecology

What is a Trait?

What Causes Variation in Traits?

What is a Trait?

A measurable (quantifiable) attribute of the phenotype

What is a Functional Trait?

A trait that influences plant function

(demography, growth rate, fitness)

Functional Traits Ultimately Link to Whole-plant Performance and Fitness

<u>Performance Traits</u>

- Growth rate
- Carbon economy
- Hydraulics
- etc

<u>Demography Traits</u>

- Survivorship
- Fecundity

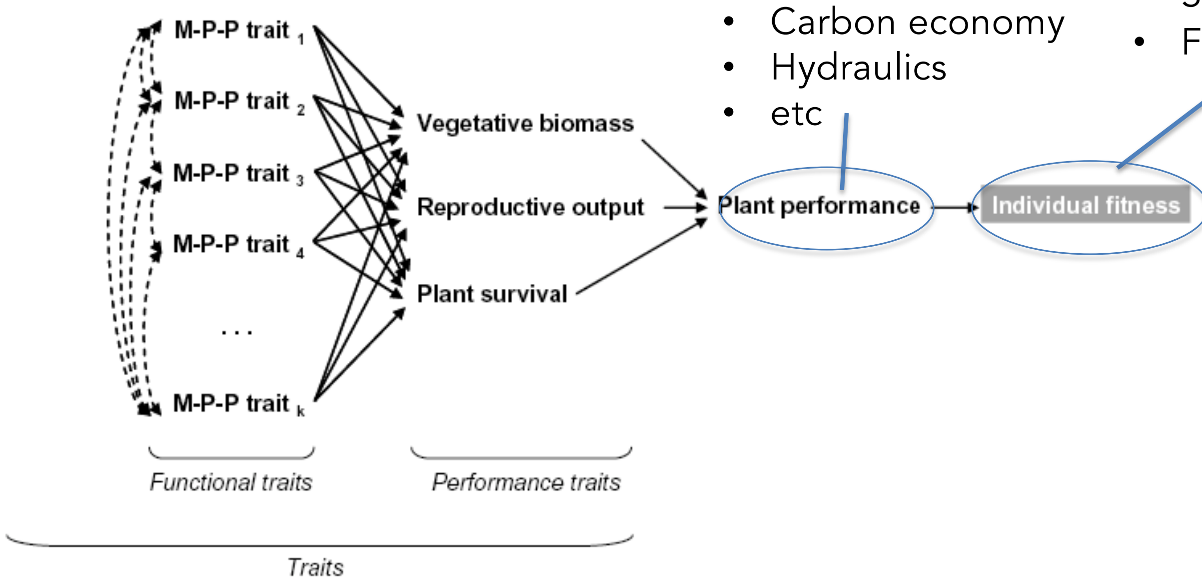


Fig. 3. Arnold's (1983) framework revisited in a plant ecology perspective. Morpho-physio-phenological (M-P-P) traits (from 1 to k) modulate one or all three performance traits (vegetative biomass, reproductive output and plant survival) which determine plant performance and, in fine, its individual fitness. M-P-P traits may be inter-related (dashed double-arrows). For clarity, inter-relations among performance traits and feedbacks between performance and M-P-P traits are not represented.

Violle et al. 2007

Seedling Traits Determine Drought Tolerance of Tropical Tree Species

Lourens Poorter[1,2,3,4] and **Lars Markesteijn**[1,2]

[1]Forest Ecology and Forest Management Group, Center for Ecosystem Studies, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands

[2]Instituto Boliviano de Investigación Forestal, P.O. Box 6204, Santa Cruz, Bolivia

[3]Resource Ecology Group, Center for Ecosystem Studies, Wageningen University, The Netherlands

Research

New Phytologist

Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests

Lourens Poorter[1,2,3]

[1]Forest Ecology and Forest Management Group, Centre for Ecosystem Studies, Wageningen University, PO Box 47, 6700 AA Wageningen, the Netherlands; [2]Instituto Boliviano de Investigación Forestal (IBIF), Casilla 6204, Santa Cruz, Bolivia; [3]Resource Ecology Group, Centre for Ecosystem Studies, Wageningen University, PO Box 47, 6700 AA Wageningen, the Netherlands

How to measure plant functional traits?

CSIRO PUBLISHING

www.publish.csiro.au/journals/ajb

Australian Journal of Botany, 2003, **51**, 335–380

A handbook of protocols for standardised and easy measurement of plant functional traits worldwide

J. H. C. Cornelissen[A,J], S. Lavorel[B], E. Garnier[B], S. Díaz[C], N. Buchmann[D], D. E. Gurvich[C], P. B. Reich[E], H. ter Steege[F], H. D. Morgan[G], M. G. A. van der Heijden[A], J. G. Pausas[H] and H. Poorter[I]

CSIRO PUBLISHING

Australian Journal of Botany, 2013, **61**, 167–234

http://dx.doi.org/10.1071/BT12225

New handbook for standardised measurement of plant functional traits worldwide

N. Pérez-Harguindeguy[A,Y], S. Díaz[A], E. Garnier[B], S. Lavorel[C], H. Poorter[D], P. Jaureguiberry[A], M. S. Bret-Harte[E], W. K. Cornwell[F], J. M. Craine[G], D. E. Gurvich[A], C. Urcelay[A], E. J. Veneklaas[H], P. B. Reich[I], L. Poorter[J], I. J. Wright[K], P. Ray[L], L. Enrico[A], J. G. Pausas[M], A. C. de Vos[F], N. Buchmann[N], G. Funes[A], F. Quétier[A,C], J. G. Hodgson[O], K. Thompson[P], H. D. Morgan[Q], H. ter Steege[R], M. G. A. van der Heijden[S], L. Sack[T], B. Blonder[U], P. Poschlod[V], M. V. Vaieretti[A], G. Conti[A], A. C. Staver[W], S. Aquino[X] and J. H. C. Cornelissen[F]

Contents

Table 2. Association of plant functional traits with (1) plant responses to four classes of environmental change (i.e. 'environmental filters'), (2) plant competitive strength and plant 'defence' against herbivores and pathogens (i.e. 'biological filters'), and (3) plant effects on biogeochemical cycles and disturbance regimes

	Climate response	CO_2 response	Response to soil resources	Response to disturbance	Competitive strength	Plant defence/ protection	Effects on biogeochemical cycles	Effects on disturbance regime
Whole-plant traits								
Growth form	*	*	*	*	*	*	*	*
Life form	*	*	*	*	*		*	*
Plant height	*	*	*	*	*	*	*	*
Clonality	*	?	*	*	*			?
Spinescence	*	?			*	*		?
Flammability		?			*	?	*	*
Leaf traits								
Specific leaf area	*	*	*		*	*	*	
Leaf size	*	?	*		*	*	*	
Leaf dry matter content	*	?	*			*	*	*
Leaf N and P concentration	*	*	*	*	*	*	*	
Physical strength of leaves	*	?	*	*		*	*	
Leaf lifespan	*	*	*	*	*	*	*	*
Leaf phenology	*		*		*		*	*
Photosynthetic pathway	*	*			*			
Leaf frost resistance	*				*	*		
Stem and belowground traits								
Stem specific density	*	?	?	*		*	*	*
Twig dry matter content	*	?	?	?		*	*	*
Twig drying time	*	?	?				?	*
Bark thickness			*	*		*		?
Specific root length	*	?	*		*	*		?
Diameter of fine root	*	?	*					
Distribution of rooting depth	*	*	*	*	*		*	*
95% rooting depth	*	?	*		*			*
Nutrient uptake strategy	*	*	*	*	*		*	
Regenerative traits								
Dispersal mode				*				
Dispersule shape and size				*				
Seed mass			*	*	*	*		
Resprouting capacity		*	*	*			*	

Key Traits Often Measured in Trait Based Ecology

Plant Traits

- **Size** (mass, diameter, height)
- **Wood/Tissue density** (hydraulic efficiency, diameter growth rate, plant life history)

$$\rho = M/V$$

- **Leaf mass fraction** (LMF) (Allocation trait (leaf mass / total plant mass)
- **Root mass fraction** (RMF) (Allocation trait)
- **Seed size, Flower size, Floral color**
- **Reproductive mass**

Root Traits

Leaf -Traits

- **Leaf size** (leaf area, leaf mass) – Life history, thermoregulation,
- Leaf thickness – Life history, photosynthesis
- **LMA - Leaf mass per unit area (leaf mass/leaf area)** – Plant life history
- **SLA - Specific leaf area** (leaf area/leaf mass) – Plant life history
- **LDMC** (Leaf Dry Matter Content) – Oven-dry mass divided by fresh mass
- **Water Content**
- **Photosynthetic rate**
- **Respiration rate**
- **%Nitrogen** (photosynthetic capacity)
- **%Carbon** (allocation)
- **%Phosphorus** (respiration efficiency)
- N/P ratio (a measure of growth efficiency, a measure of when N is limiting to growth)

Tissue Isotopes

Carbon Isotopes - carbon isotope concentration (d13C)

Describes the ratio of 13C to 12C within foliar tissue and is positively related to water use efficiency
(Donovan & Ehleringer 1994).

Nitrogen Isotopes - nitrogen isotope concentration (d15N)

Describes the ratio of 15N to 14N within foliar tissue and can provide information on the differences in nitrogen acquisition and origin nitrogen and has been shown to be positively correlated with soil nitrogen concentration and positively correlated with nitrogen fixing bacterial associations
(Hyodo etal. 2012, Hobbie & Colpaert 2003).

Oxygen Isotopes - d18O

Can be used as a measure of plant tissue temperature (temperature at which Photosynthesis is occurring). See also Michaletz et al. 2016

Which traits should you measure?

"No methods handbook can answer the question of what are the best traits to measure, because this strongly depends on the questions at hand, the ecological characteristics and scale of the study area, and on practical circumstances."

Australian Journal of Botany, 2013, **61**, 167–234
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New handbook for standardised measurement of plant functional traits worldwide

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Which traits should you measure?

Traits to mechanistically link to organismal performance

Which traits should you measure?

Let theory guide and tell you!

Theories that link how traits and abiotic environment influences organismal performance

- **Ecophysiology/ Carbon and Nutrient Economics**
  (see Walker et al. 2014; Blonder et al. 2011)
- Energy Budgets (Temperature; see Michaletz et al. 2016)
- Carbon & Nutrient Economics (Optimization Theory; see Elser et al. 2010)
- Relative Growth Rate (RGR) - Allometry (see Enquist et al. 2015)
- Biomechanics (Niklas 1992)
- Hydraulics (e.g. Anderegg et al. 2019)
- Demography
- Trait Driver Theory (Enquist et al. 2015)

Introduction to Trait-based Ecology

Why Trait-based Ecology?

History of Trait-based Ecology

What is a Trait?

What Causes Variation in Traits?

What Causes Variation in Traits?

- Species-level differences
- Macro climatic gradients (interspecific variatioin)
- Micro climatic gradients (intraspecific variation)

Why do leaves vary in their traits?

articles

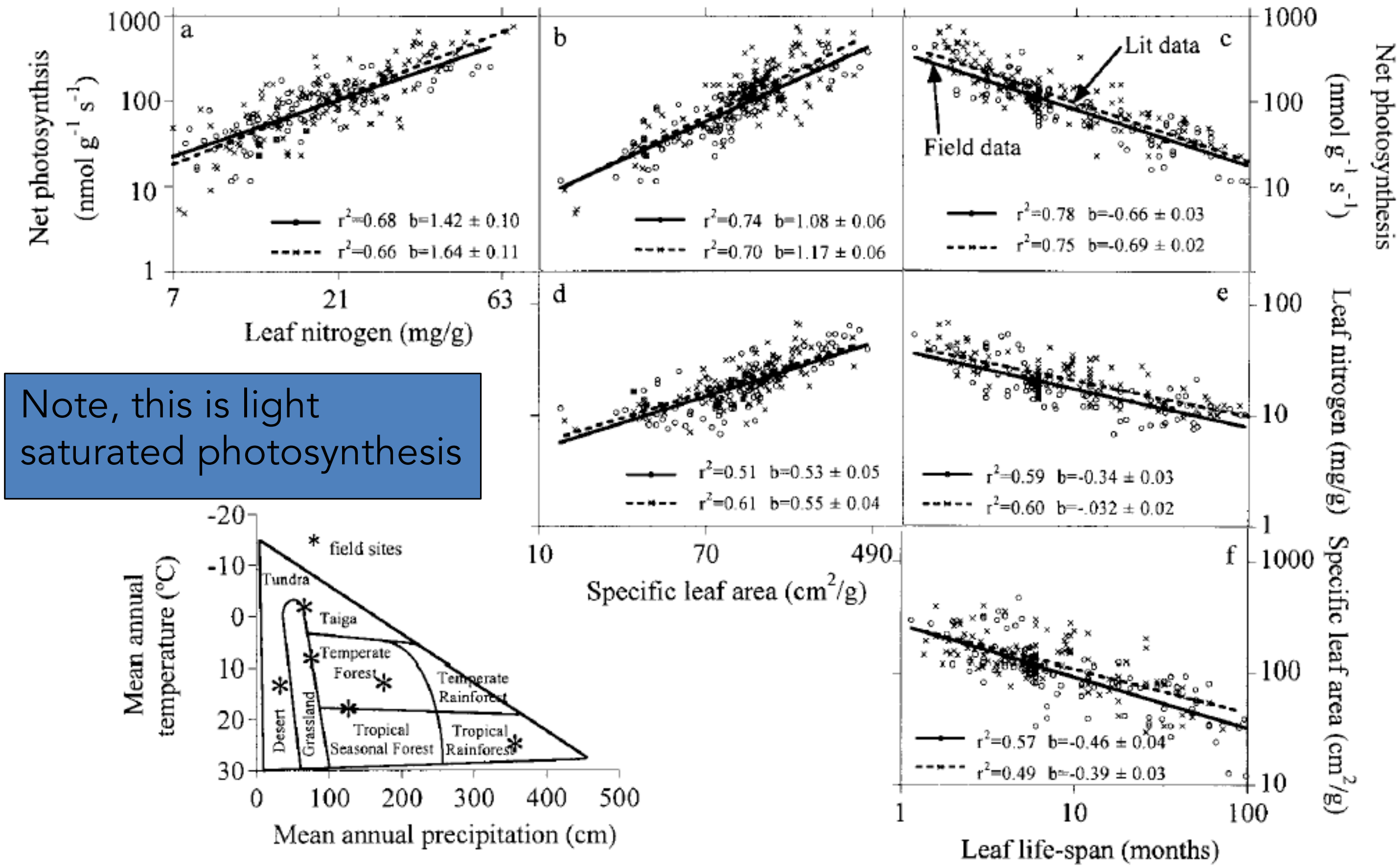
The worldwide leaf economics spectrum

Ian J. Wright[1], Peter B. Reich[2], Mark Westoby[1], David D. Ackerly[3], Zdravko Baruch[4], Frans Bongers[5], Jeannine Cavender-Bares[6], Terry Chapin[7], Johannes H. C. Cornelissen[8], Matthias Diemer[9], Jaume Flexas[10], Eric Garnier[11], Philip K. Groom[12], Javier Gulias[10], Kouki Hikosaka[13], Byron B. Lamont[12], Tali Lee[14], William Lee[15], Christopher Lusk[16], Jeremy J. Midgley[17], Marie-Laure Navas[11], Ülo Niinemets[18], Jacek Oleksyn[2,19], Noriyuki Osada[20], Hendrik Poorter[21], Pieter Poot[22], Lynda Prior[23], Vladimir I. Pyankov[24], Catherine Roumet[11], Sean C. Thomas[25], Mark G. Tjoelker[26], Erik J. Veneklaas[22] & Rafael Villar[27]

Wright et al. (2004)

Reich et al. (1997)

Differences in allocation (N, SLA) and life history (short vs. long lived) lead to differences in photosynthesis



Note, this is light saturated photosynthesis

SLA = Specific Leaf Area, LMA = Leaf Mass per unit Area= 1/SLA

SLA = leaf area divided by leaf mass

High SLA leaf

Thin and flimsy leaf

Less mass (think carbon) per unit area

But higher A_{net} and shorter lifespan

Low SLA leaf

Thick and leathery leaf

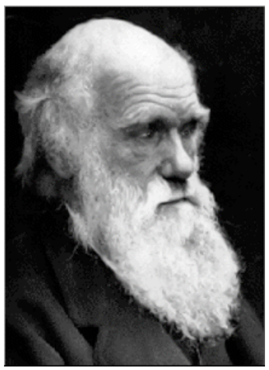
More mass (think carbon) per unit area

But lower A_{net} and longer lifespan

Think - How does SLA influence CO_2 diffusion?

Variation in leaf traits ultimately constrained by carbon economy of leaf

Natural selection has shaped leaves to have a net positive return on investment



Leaf Carbon Assimilation Rate

Leaf Life Span

$$\frac{A_a \cdot \mathrm{LL}}{\mathrm{LMA}} = A_m \cdot \mathrm{LL} \geq \kappa,$$

Leaf Mass per unit Area

Minimum lifetime leaf carbon gain (mol C g^{-1})

Chabot & Hicks 1982; Williams et al. 1989

Selection in different environments can maximize or minimize any of these leaf traits as long as κ is approx. constant

Blonder et al. (2011) Ecology Letters

The Carbon Economy of Leaves: Lifetime leaf carbon gain (mol C g^{-1})

The value of $\mathbf{K}$ is similar across diverse leaves . . .

Approximately **4 g** Carbon assimilated per **1g** Carbon invested in leaf

$$\frac{A_a \cdot \mathrm{LL}}{\mathrm{LMA}} = A_m \cdot \mathrm{LL} \geq \kappa,$$

Kikuzawa & Lechowicz (2006)

Leaf Economics Spectrum Reflects -

Why do some leaves vary in their traits?

How selection in differing environments maximizes fitness

- As reflected in different 'allocation strategies' that do best in different environments

- Numerous leaf traits that reflect total lifetime carbon gain

- Think different 'economic strategies'

For a given amount of carbon gained can 'spend' frugally and live long or 'spend' all at once and live a short time

Many traits respond to environmental gradients – but traits respond differently

Amazonian functional diversity from forest canopy chemical assembly

Gregory P. Asner[1], Roberta E. Martin, Raul Tupayachi, Christopher B. Anderson, Felipe Sinca, Loreli Carranza-Jiménez, and Paola Martinez

Department of Global Ecology, Carnegie Institution for Science, Stanford, CA 94305

Contributed by Gregory P. Asner, January 22, 2014 (sent for review November 7, 2013)

Asner et al. (2015) PNAS

Peru Elevational Gradient
3,500 m Andes-to-Amazon Gradient

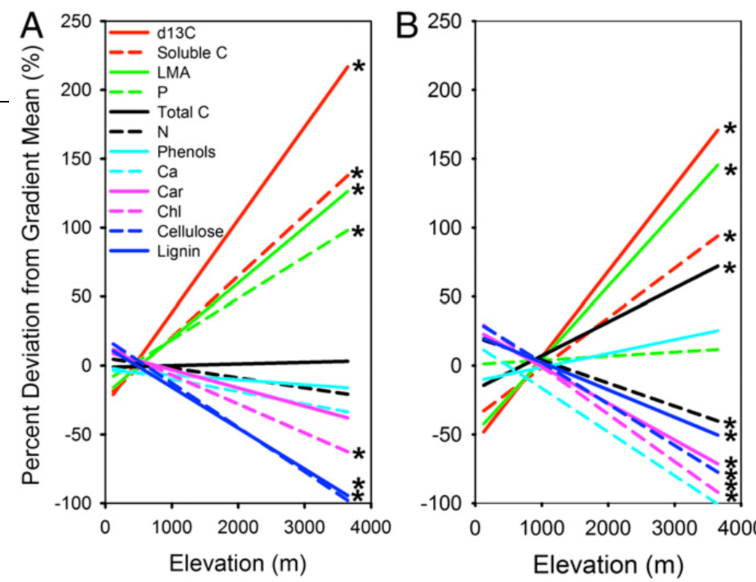
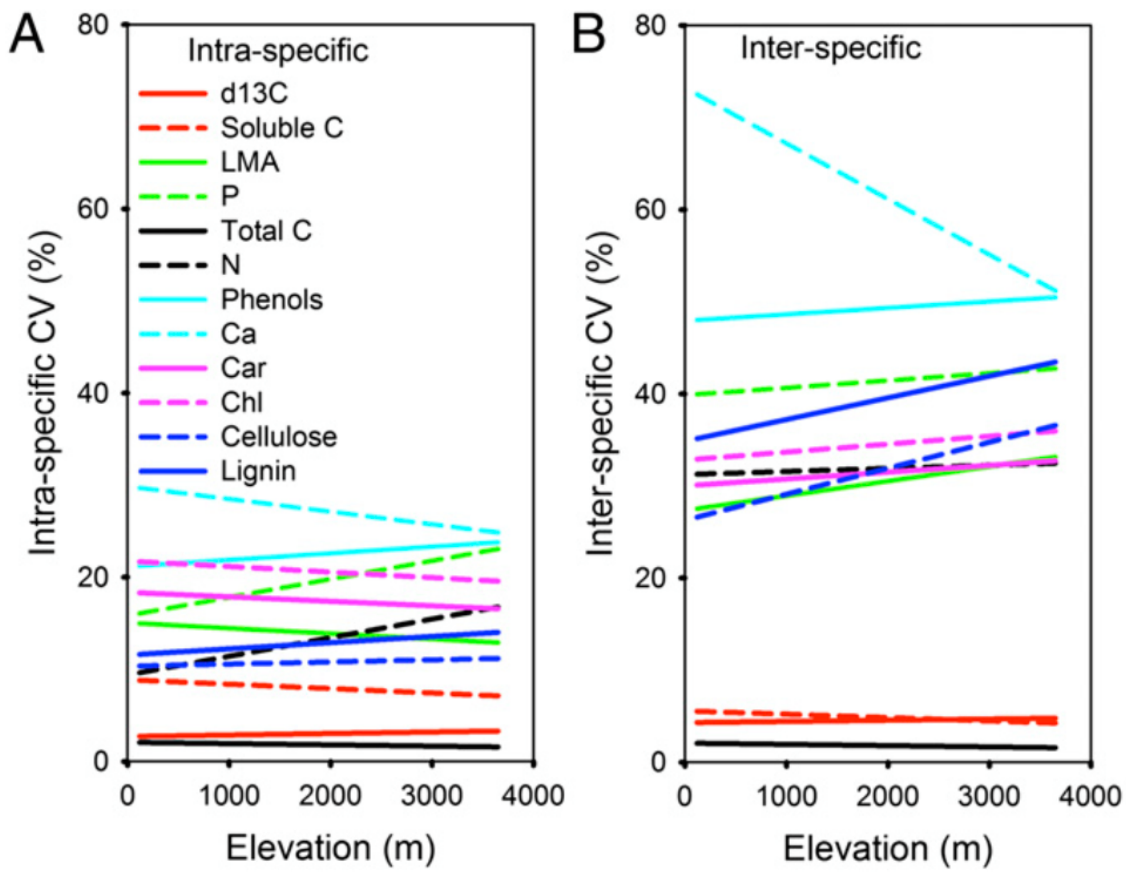


Fig. 1. Changes in average canopy foliar traits along a 3,500-m Andes to Amazon elevation gradient for (*A*) all sites on all soil types and (*B*) a subset of sites on high-fertility soils. The lines are ordinary least squares regression fits for each trait after normalization of the data to their elevation gradient mean values (site mean − gradient mean)/gradient SD (*SI Methods*). *Linear regression fits to foliar data that are significant at the $P < 0.05$ level. Car, carotenoid; Chl, chlorophyll.

A significant fraction of the variation in traits is intraspecific



Asner et al. (2015) PNAS

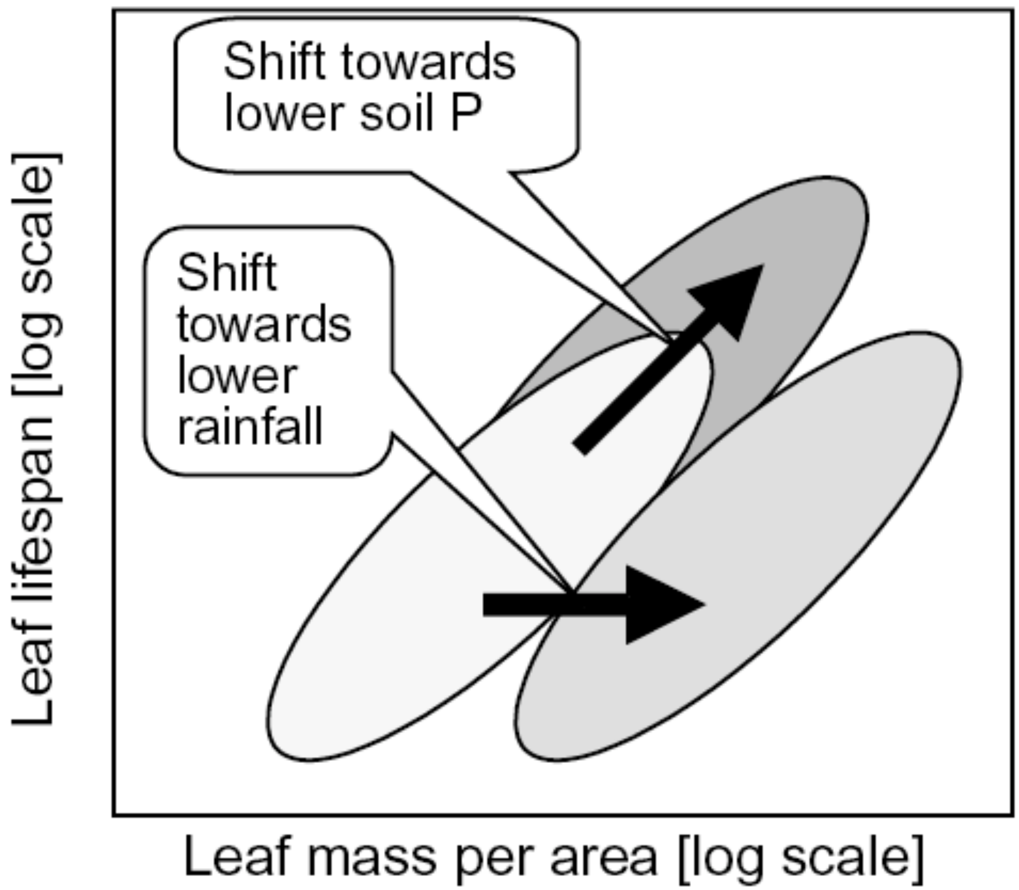
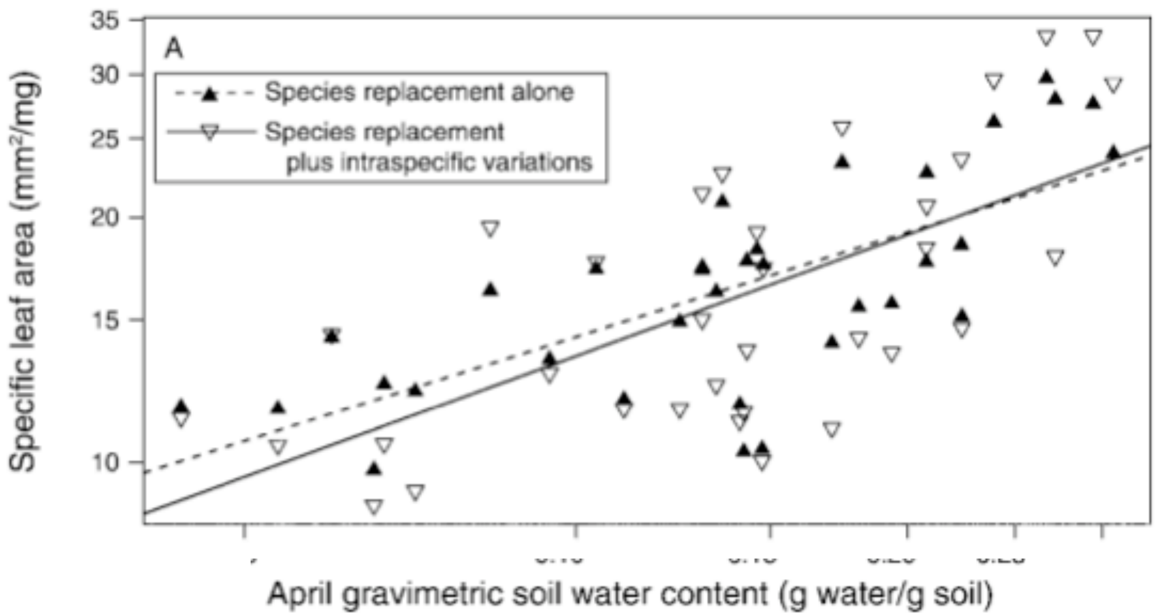


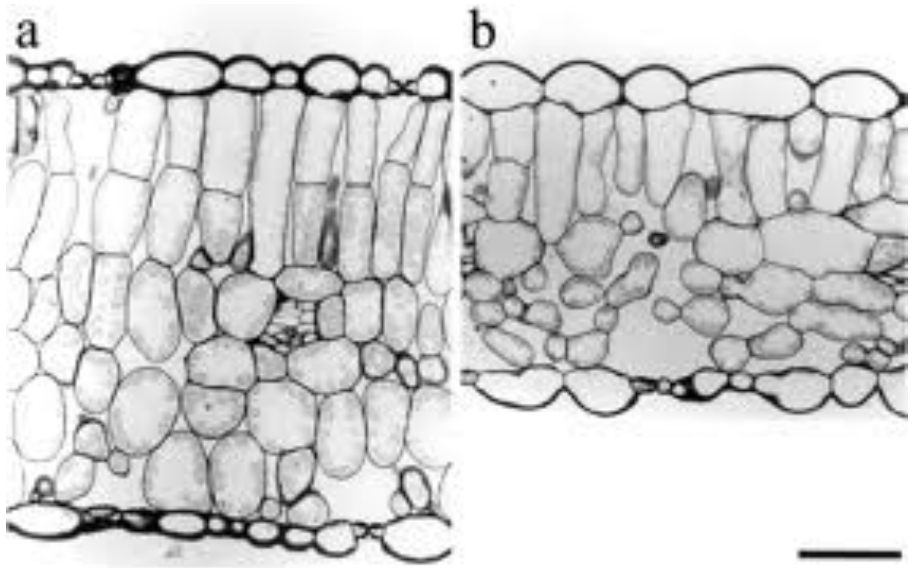
Figure 3 Schematic of leaf lifespan: leaf mass per area (LMA) relationships observed by Wright et al. (2002). Each oval cloud represents the scatter of species in a given habitat. Species occurring at lower soil P tend to have higher LMA, and leaf lifespan is also higher, corresponding to the same LMA-LL relationship observed across species within habitat. Species occurring at lower rainfall also tend to higher LMA but have

Ecological Monographs
Vol. 79, No. 1



Leaf Traits (SLA) vary along moisture, temperature, and nutrient gradients. Why?

SLA varies in sun versus shade leaves



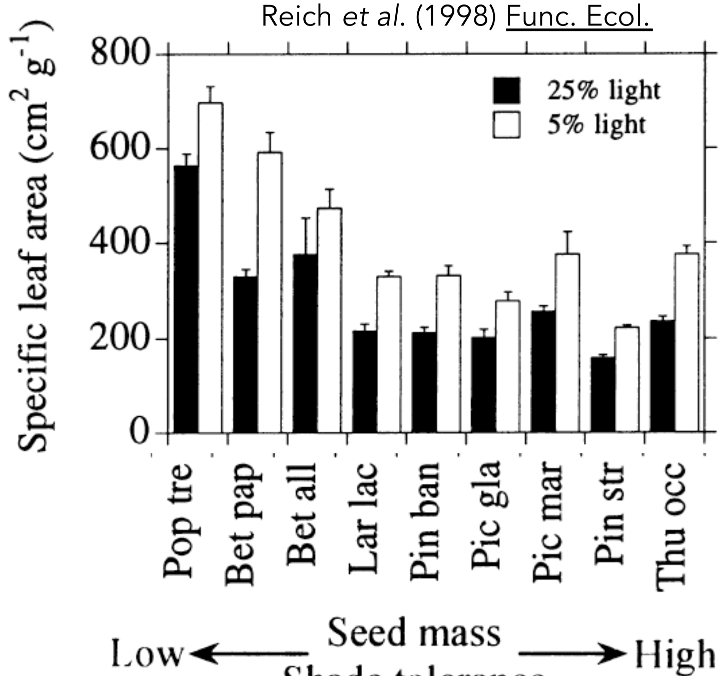
Cross-section of Sun (a) versus Shade (b) Leaf

Specific leaf area is determined by leaf area and leaf mass (thickness x tissue density)

http://pcp.oxfordjournals.org/content/42/12/1303/F1.expansion

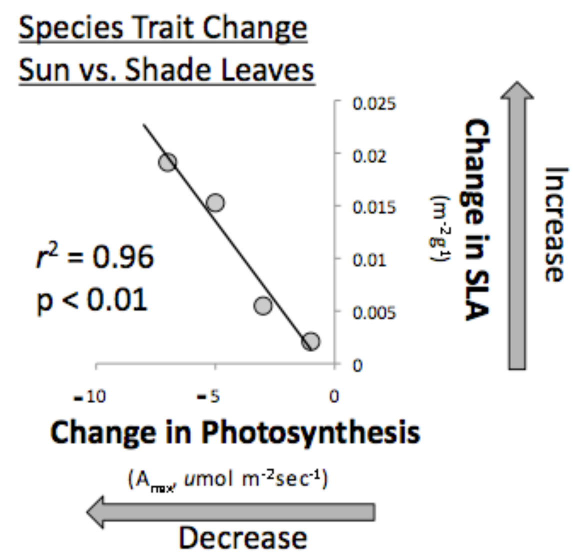
Different light environments 'select' for differing traits

Reich *et al*. (1998) Func. Ecol.



Fast Growth Slow Growth

Data from Kitajima *et al*. (2005) Ecology



Plastic and adaptive differences consistent with shift in leaf traits in differing light environments

Trait change influence plant production in different light conditions?

Introduction to Trait-based Ecology

Why Trait-based Ecology?

History of Trait-based Ecology

What is a Trait?

What Causes Variation in Traits?

Conclusions

Why measure traits ?

- **Plant functional traits give better insight** into the constraints and opportunities faced by organisms than does taxonomic identity alone (Southwood 1977; Grime 1979).

- They also provide understanding of how functional diversity in the broad sense underpins ecosystem processes and the benefits that people derive from them
- (Chapin *et al*. 2000; Diaz *et al*. 2007).

- Traits offer the possibility of comparing distant ecosystems with very little taxonomic overlap
- (Reich *et al*. 1997; Diaz *et al*. 2004; Cornwell *et al*. 2008).


Thank you!

References – read up to learn more!

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