8. Trait-based Ecology

Jasper Slingsby, BIO2014F

2025-05-08

Why haven't we been talking about traits?

The Grinnellian Niche

THE NICHE–RELATIONSHIPS OF THE CALIFORNIA THRASHER.[1]

BY JOSEPH GRINNELL.

THE California Thrasher (*Toxostoma redivivum*) is one of the several distinct bird types which characterize the so-called "Californian Fauna." Its range is notably restricted, even more so than that of the Wren-Tit. Only at the south does the California

> *"An explanation of this restricted distribution is probably to be found in the* ***close adjustment of the bird in various physiological and psychological respects*** *to a narrow range of environmental conditions. The nature of these critical conditions is to be learned through an examination of the bird's habitat."*

Grinnell 1917

Photo: Leslie Cavaliere, iNaturalist

The Eltonian Niche

> *"what [it] is doing in its community,... its place in the* ***biotic*** *environment, its relations to food and enemies"* - **Elton 1927**
>
> *"used in ecology in the sense that we speak of trades or professions or jobs in a human community"* - **Elton 1933**

Focuses on the organism's role or **function** in the ecosystem, often in relation to trophic position (consumers, predators, etc) and **resource use**.

Often considers the **attributes or traits** of species that allow them to fulfill their role.

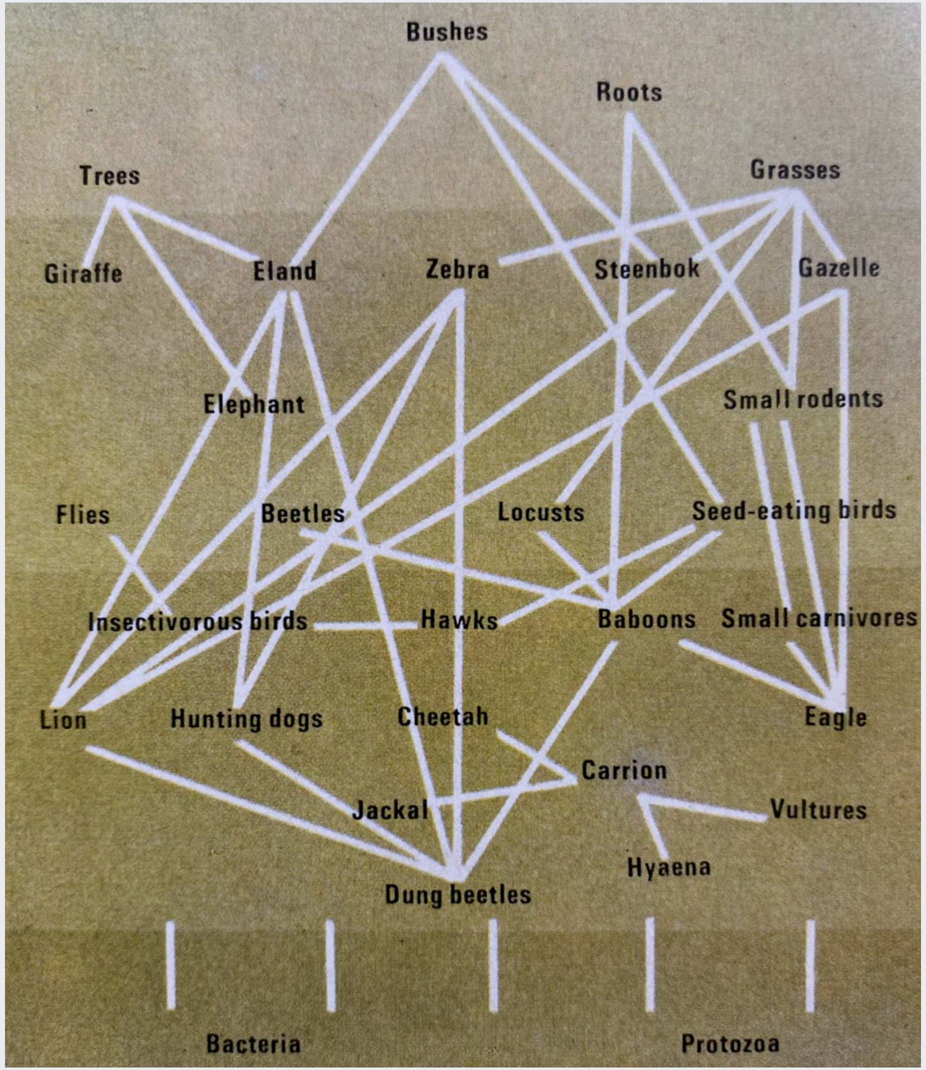


image: *The Atlas of World Wildlife* 1973

Eltonian Niche Traits

Honeycreepers evolved a range of bill forms in response to available food sources on the Hawaiian archipelago.

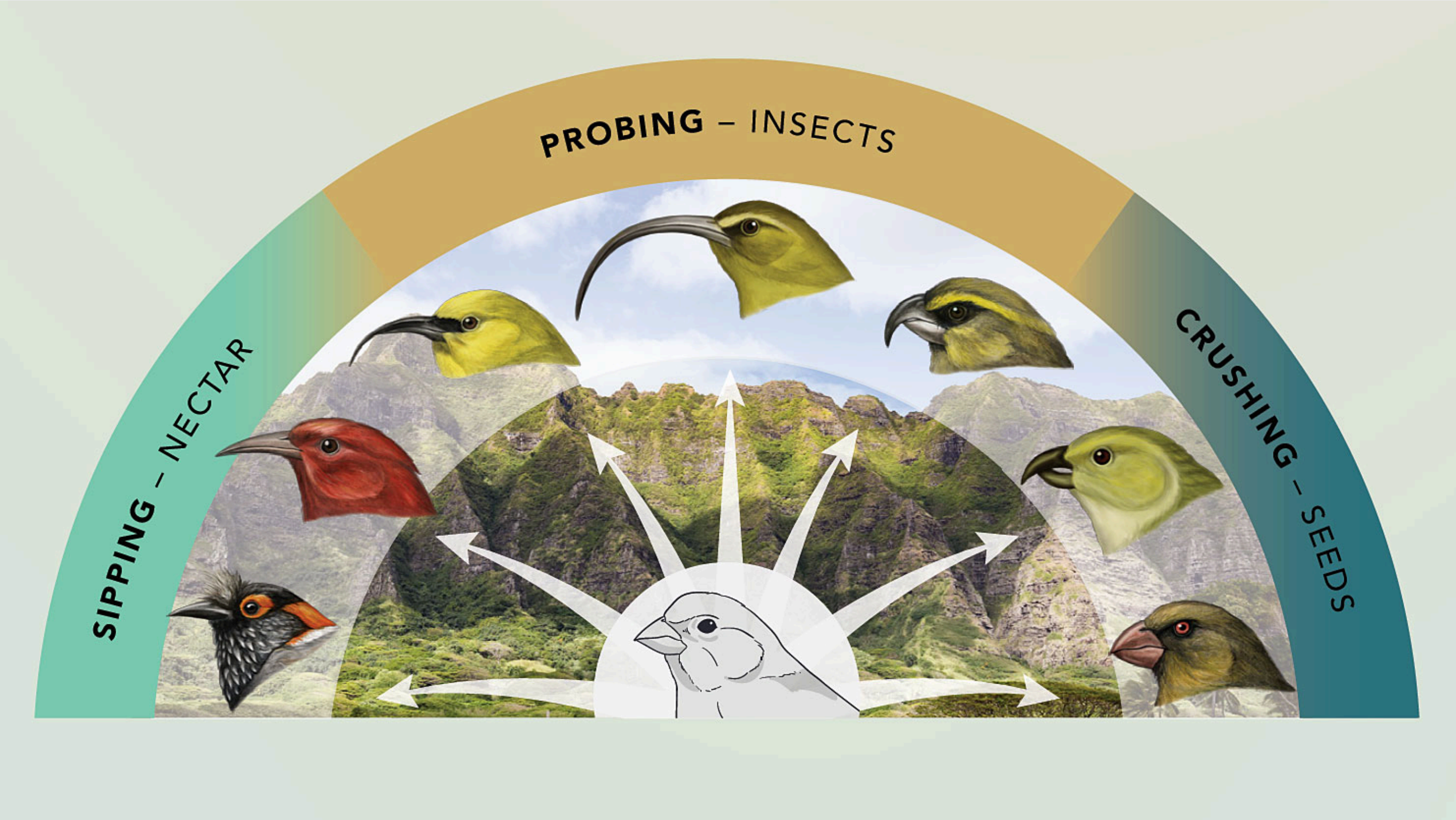


Illustration by Jillian Ditner, photo by Ashlyn Gehrett

Eltonian and Grinnellian Niche Traits?

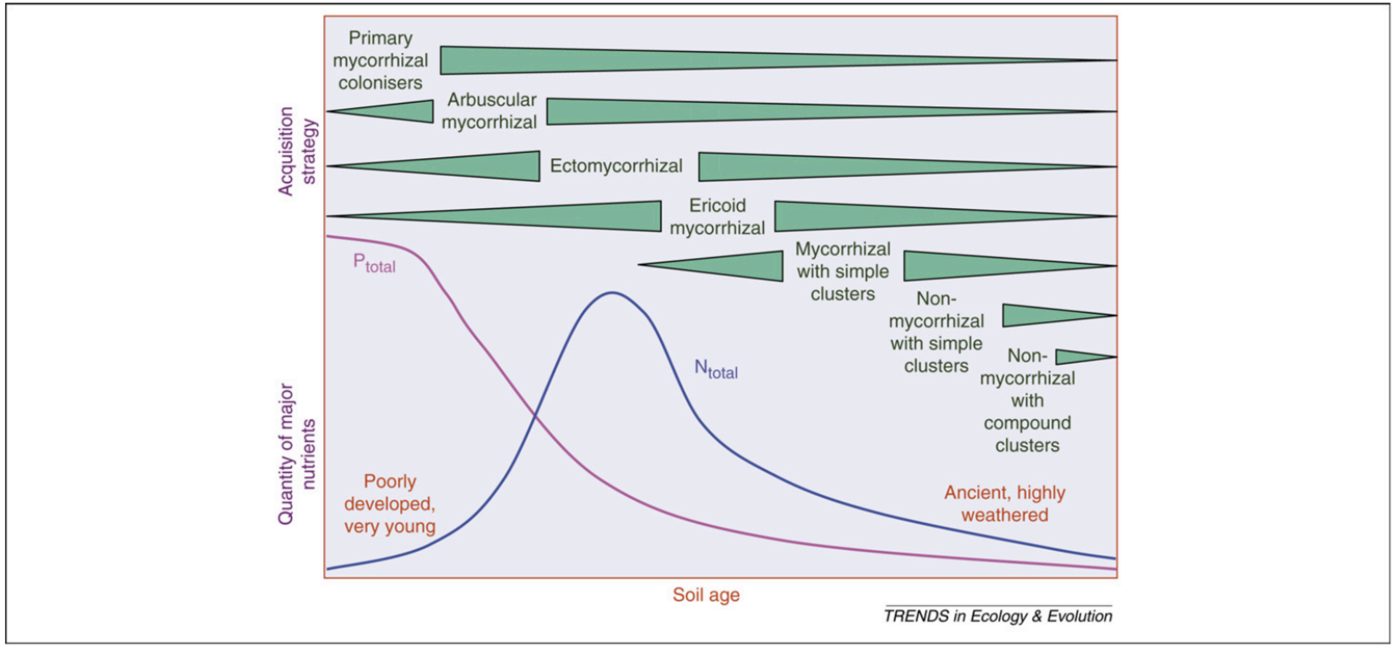
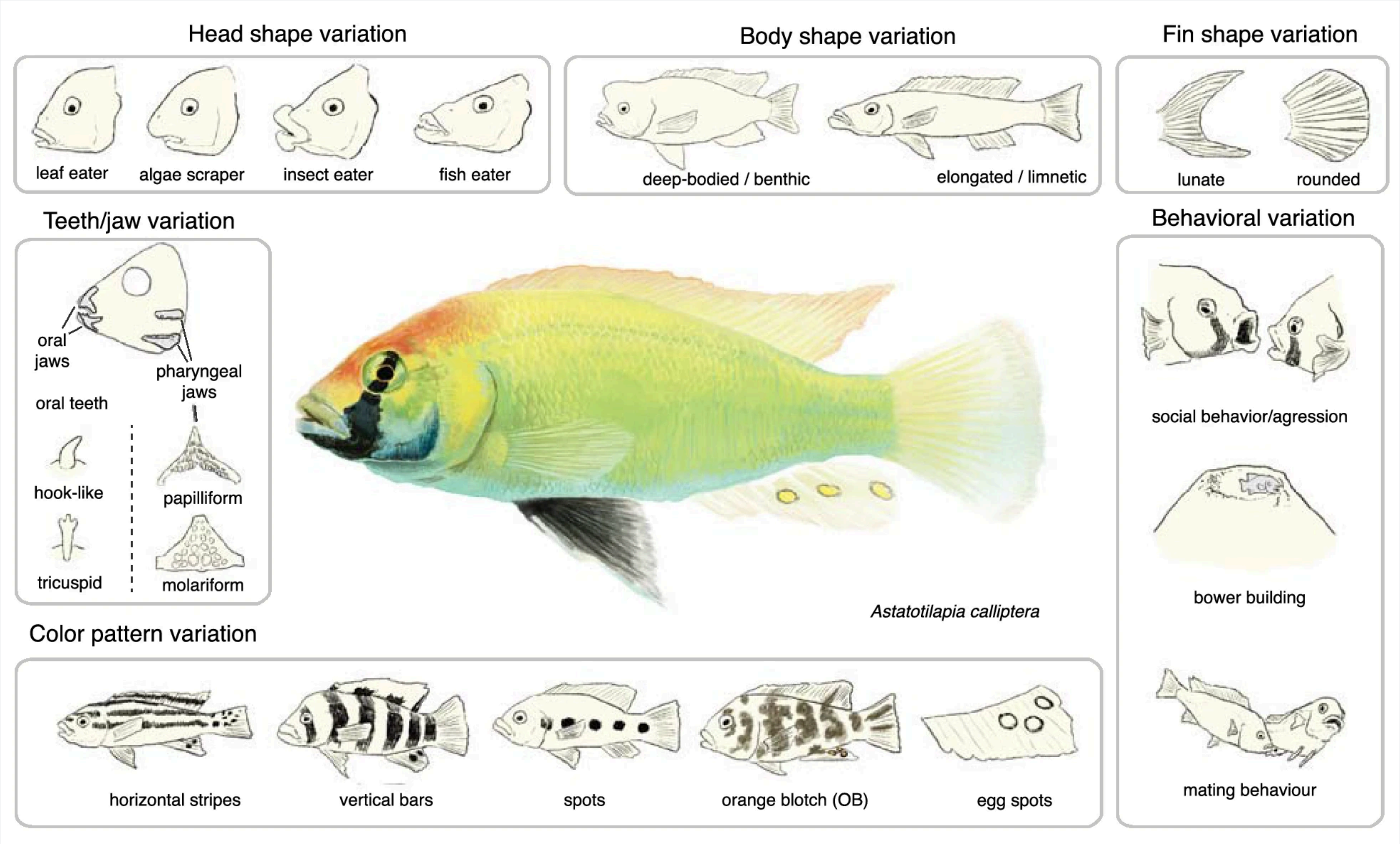


Figure 1. Changes in total soil P (purple) and N (blue) and in plant nutrient-acquisition strategies (green) as dependent on soil age, based on data in various studies [5,11,36]. 'Poorly developed, very young soils' refers to soils that result from recent volcanic eruptions; 'ancient, highly weathered soils' refers to soils that have been above sea level and have not been glaciated for millions of years. Although never becoming dominant in severely P-impoverished soils, some mycorrhizal species do co-occur with non-mycorrhizal cluster-bearing species. The highest and lowest total P levels in young and ancient soils are ~800 mg kg^{-1} soil and 30 mg kg^{-1} soil, respectively. Peak total N levels are 8 000 mg kg^{-1} soil, whereas total N levels in the very youngest soils shown here are <5 mg kg^{-1}. The width of the triangles referring to the different ecological strategies provides a (relative) measurement of the abundance of these strategies as dependent on soil age.

Plants have a range of nutrient-acquisition strategies that affect both their ability to compete for (or partition) nutrients and the soil environmental conditions where they are most likely to occur (**Lambers et al. 2008**).

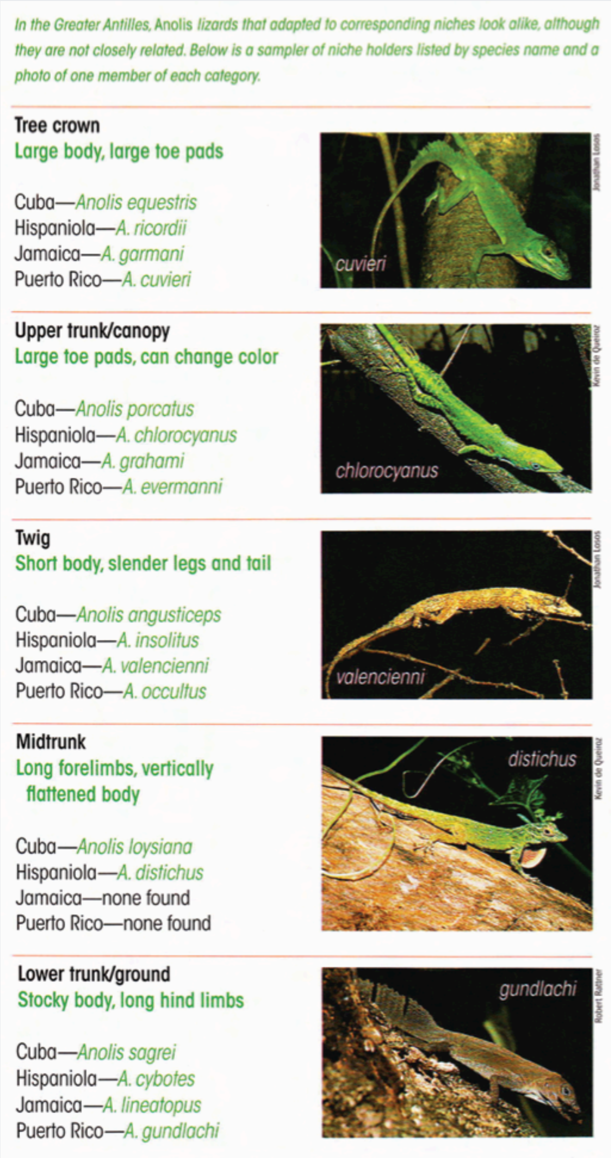
Eltonian and Grinnellian Niche Traits?



East African cichlid fishes have diverged in traits relating to diet, mating behaviour, competition and habitat.
Santos et al. 2023

Grinnellian Niche Traits?

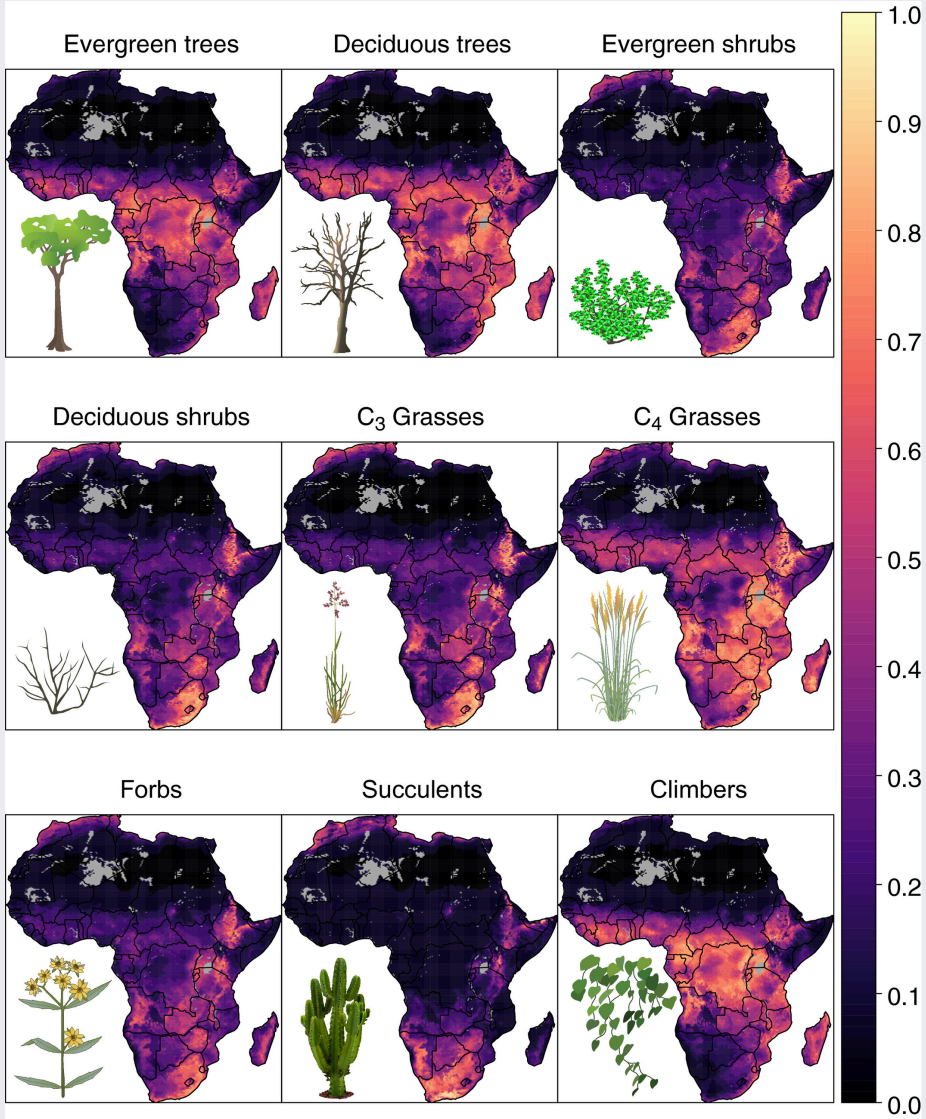
Not only have *Anolis* lizard species of the Greater Antilles specialised to use different parts of the trees they live in (niche partitioning), but these niches are filled by different species on each island and unrelated species have converged to similar morphology for each habitat type!



Losos and de Queiroz 1997

Grinnellian Niche Traits

There are clear climatic preferences among plant functional types in Africa.



Conradi et al. 2021

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

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Rebuilding community ecology from functional traits

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

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>
> *"...this can be achieved [,but] community ecology has lost its way by focusing on pairwise species interactions independent of the environment."*
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> *"...community ecology should return to an emphasis on ...*
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> [1.] *how the fundamental niche is governed by functional traits within the context of abiotic environmental gradients; and*
>
> [2.] *how the interaction between traits and fundamental niches maps onto the realized niche in the context of a biotic interaction milieu.*
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> [1.] *how the fundamental niche is governed by functional traits within the context of abiotic environmental gradients; and* [**Traits and the Fundamental Niche**]
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>
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Traits and the fundamental niche

Can traits be used to predict the fundamental niche of species?

Traits and the fundamental niche

An example from serotinous Cape Proteaceae…

RESEARCH PAPER

Global Ecology and Biogeography — A Journal of Macroecology — WILEY

Functional traits explain the Hutchinsonian niches of plant species

Martina Treurnicht[1,2,3] | Jörn Pagel[1] | Jeanne Tonnabel[4] | Karen J. Esler[2,5] | Jasper A. Slingsby[3,6] | Frank M. Schurr[1]

Related inter- and intraspecific variation in 11 functional traits to measures of the fundamental Hutchinsonian niches of 26 Proteaceae species in the Cape Floristic Region.

Treurnicht et al. 2020

image: Roets et al 2006

Traits and the fundamental niche

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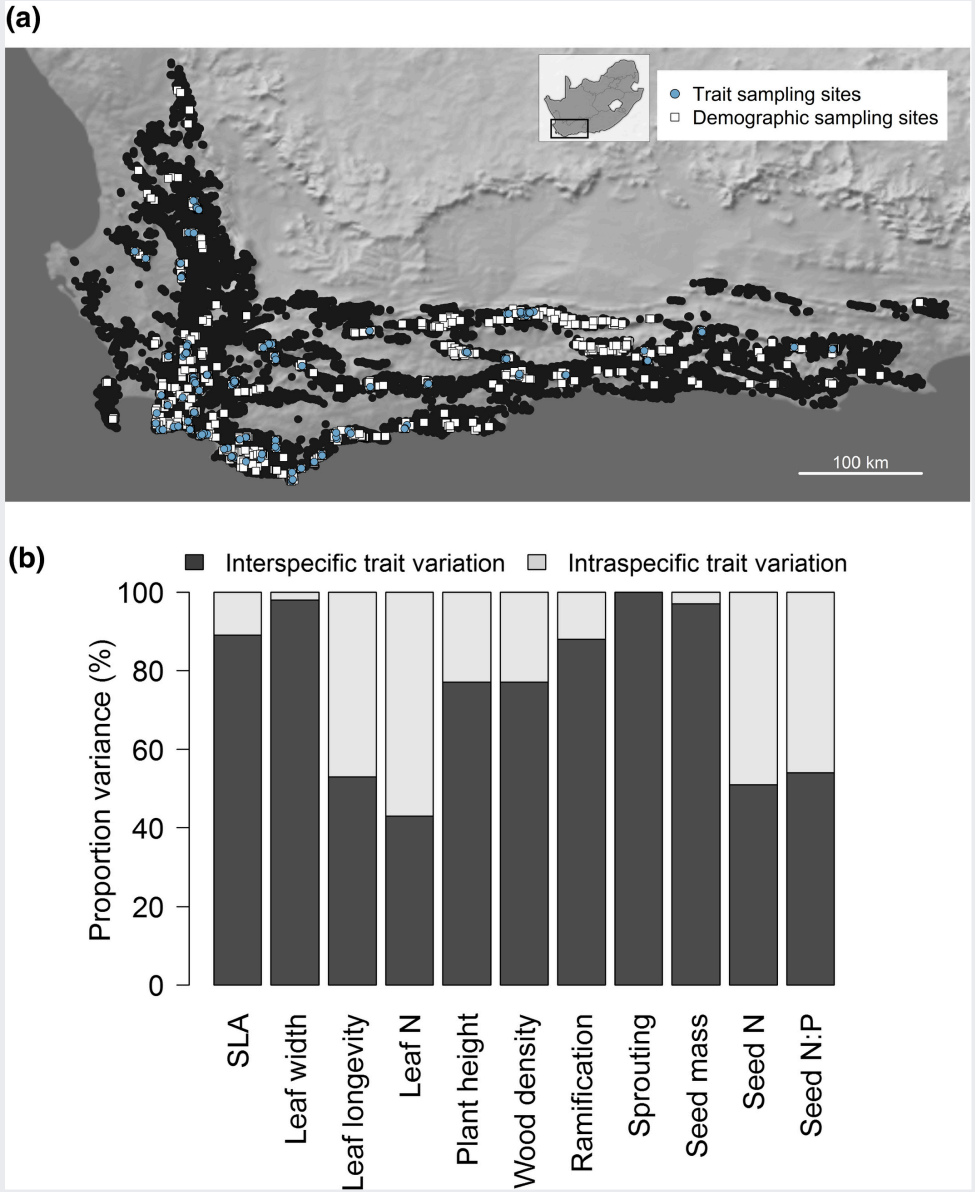
Sampled traits and demographic parameters (fecundity, recruitment and adult fire survival) for the 26 species from across their ranges.

Most of the variation in traits was between species, but some (e.g. leaf and seed N) showed high intraspecific variability.

Treurnicht et al. 2020



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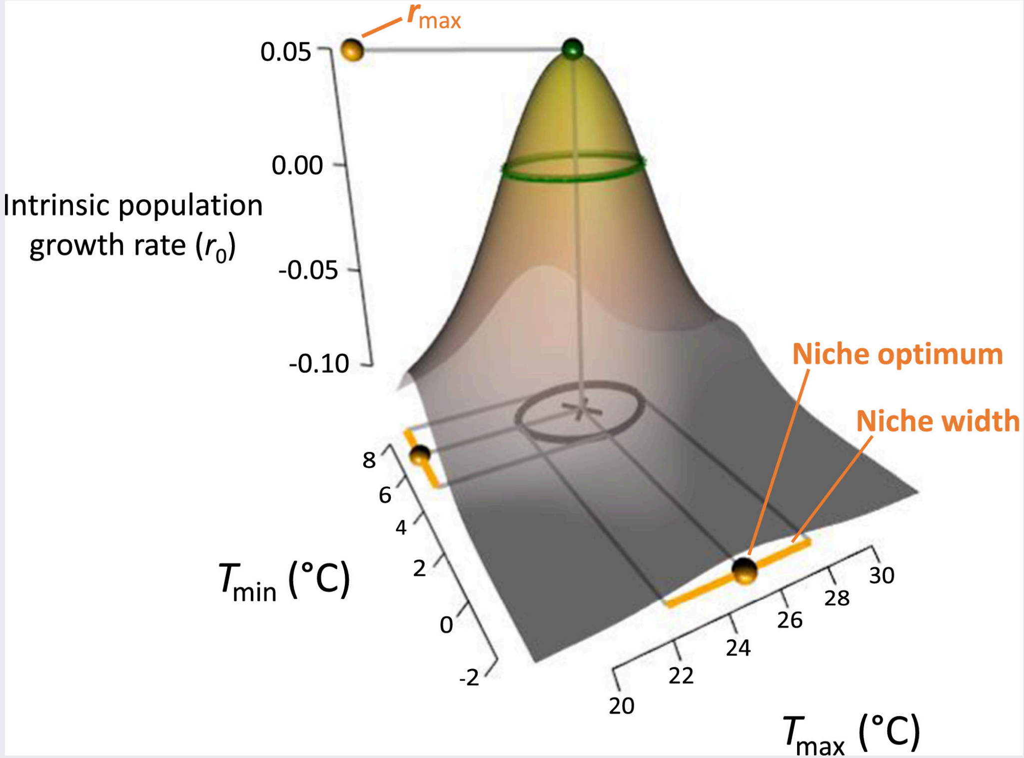

Built demographic models to estimate measures of the fundamental Hutchinsonian niche for the 26 species. These were the niche optimum and niche width for each of 5 environmental variables (aridity, minimum and maximum temperature, soil fertility and fire interval) and the r_{max} (which integrates across all variables).

Treurnicht et al. 2020

RESEARCH PAPER

Global Ecology and Biogeography A Journal of Macroecology

WILEY

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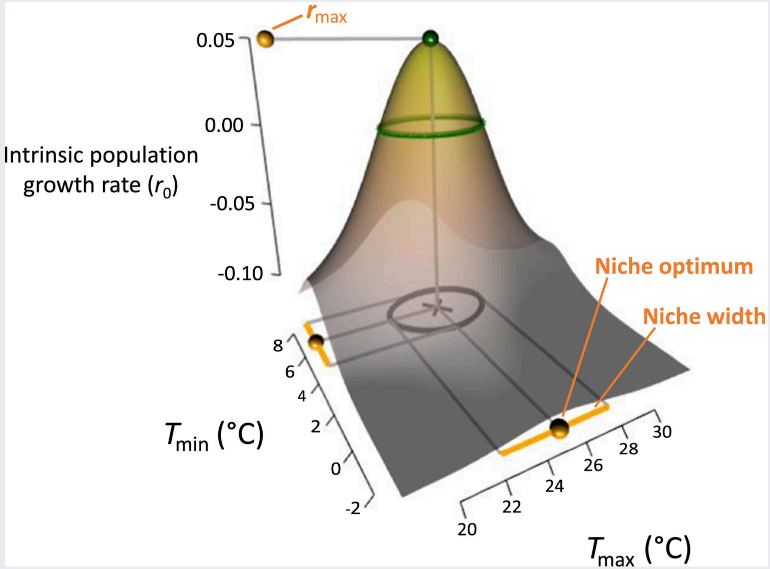
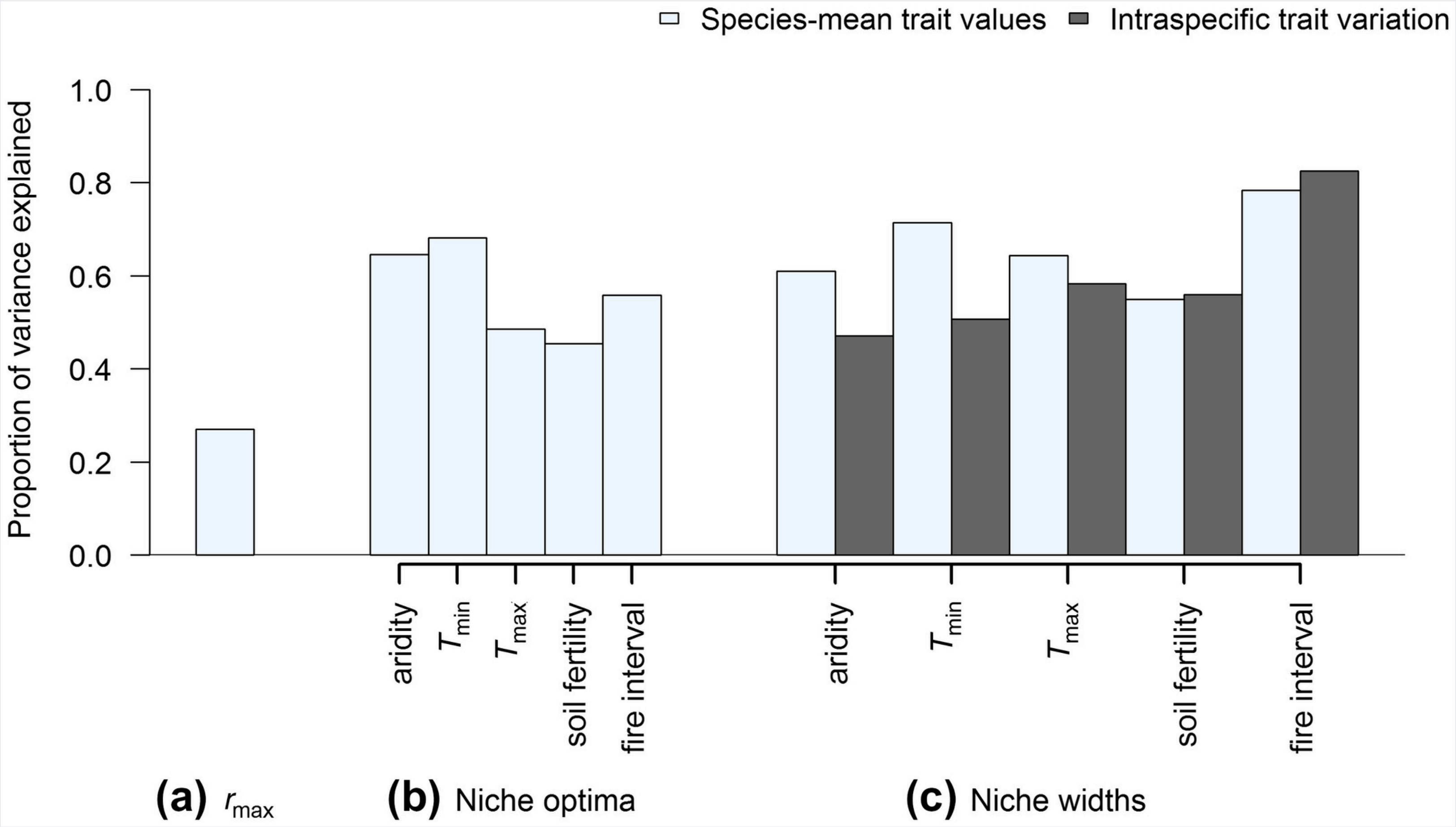
Built statistical models to predict the Hutchinsonian niche parameters as a function of the 11 functional traits.



Treurnicht et al. 2020

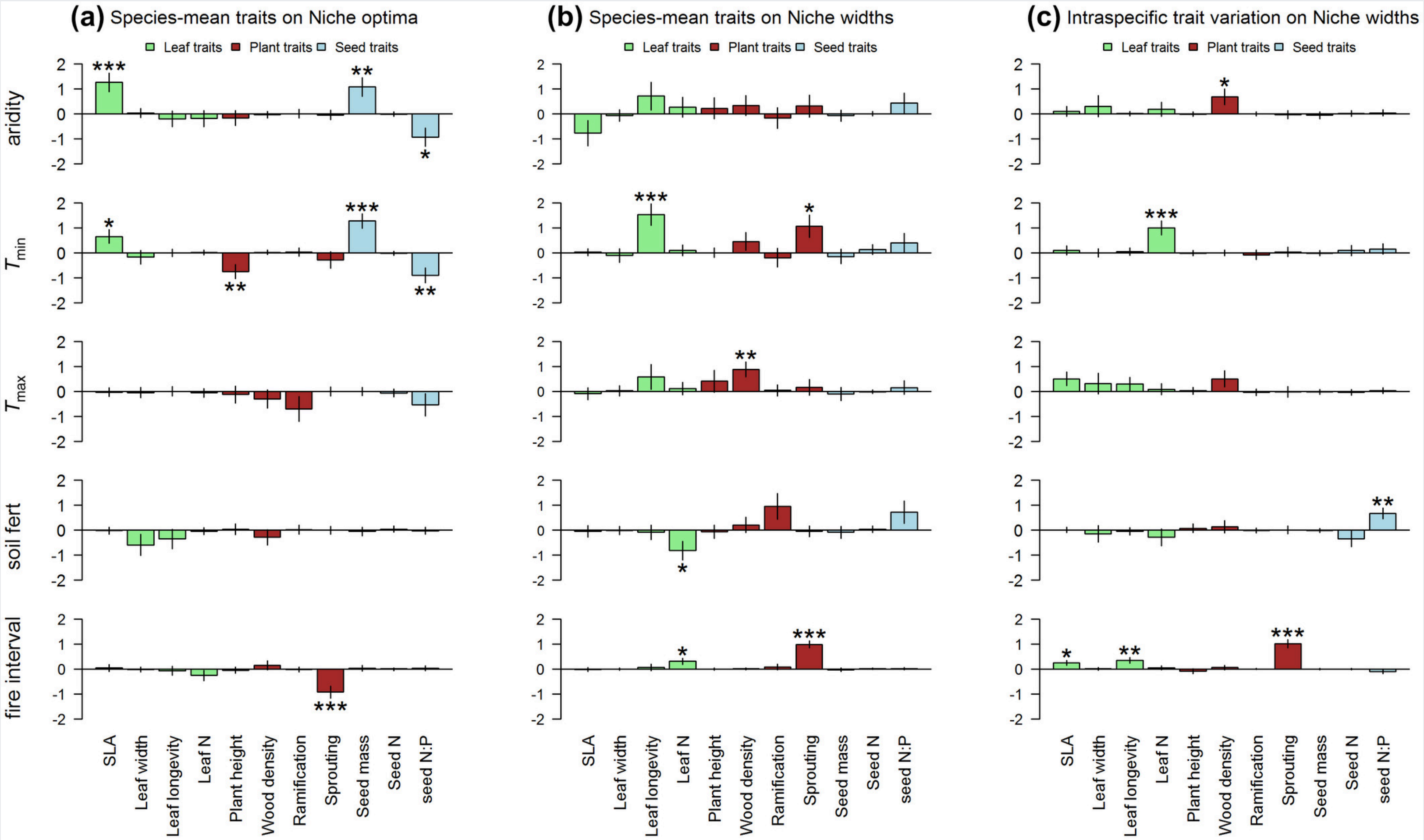
The models could explain 30% of the variance in r_{max} and >50% of the variance in the niche optima and widths of all environmental axes!

P.S. This is good...



Treurnicht et al. 2020

Several of the traits were significant predictors of the niche optima and widths for the 5 environmental variables.



Treurnicht et al. 2020

Traits and Community Assembly

What can traits reveal about community assembly?

Traits and Community Assembly

How would you expect traits to relate to the community assembly process?

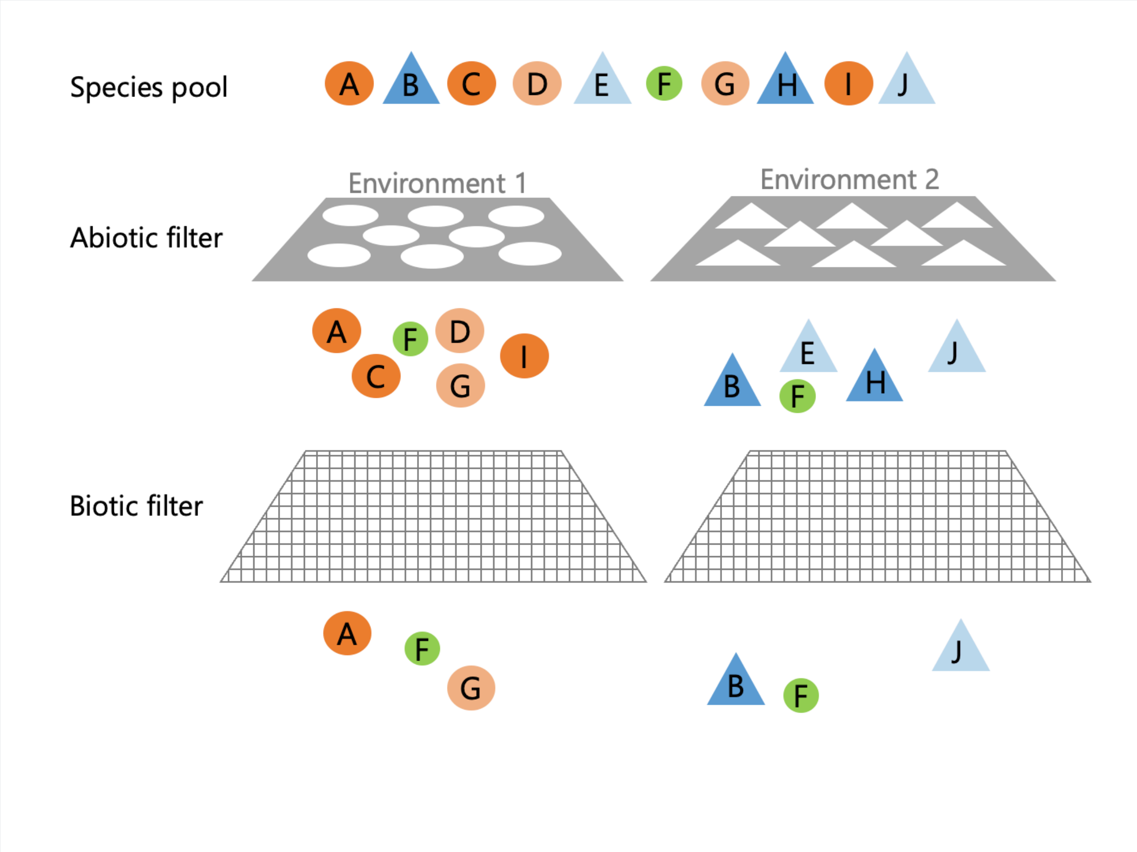


image: Tony Verboom

Traits and Community Assembly

Environmental filtering should select for species with the traits needed to survive in that environment, usually reducing the variation in traits.

Biotic interactions can have two outcomes. Competition should drive trait divergence. Conversely, a common limiting factor (e.g. a resource or shared predator) should drive convergence.

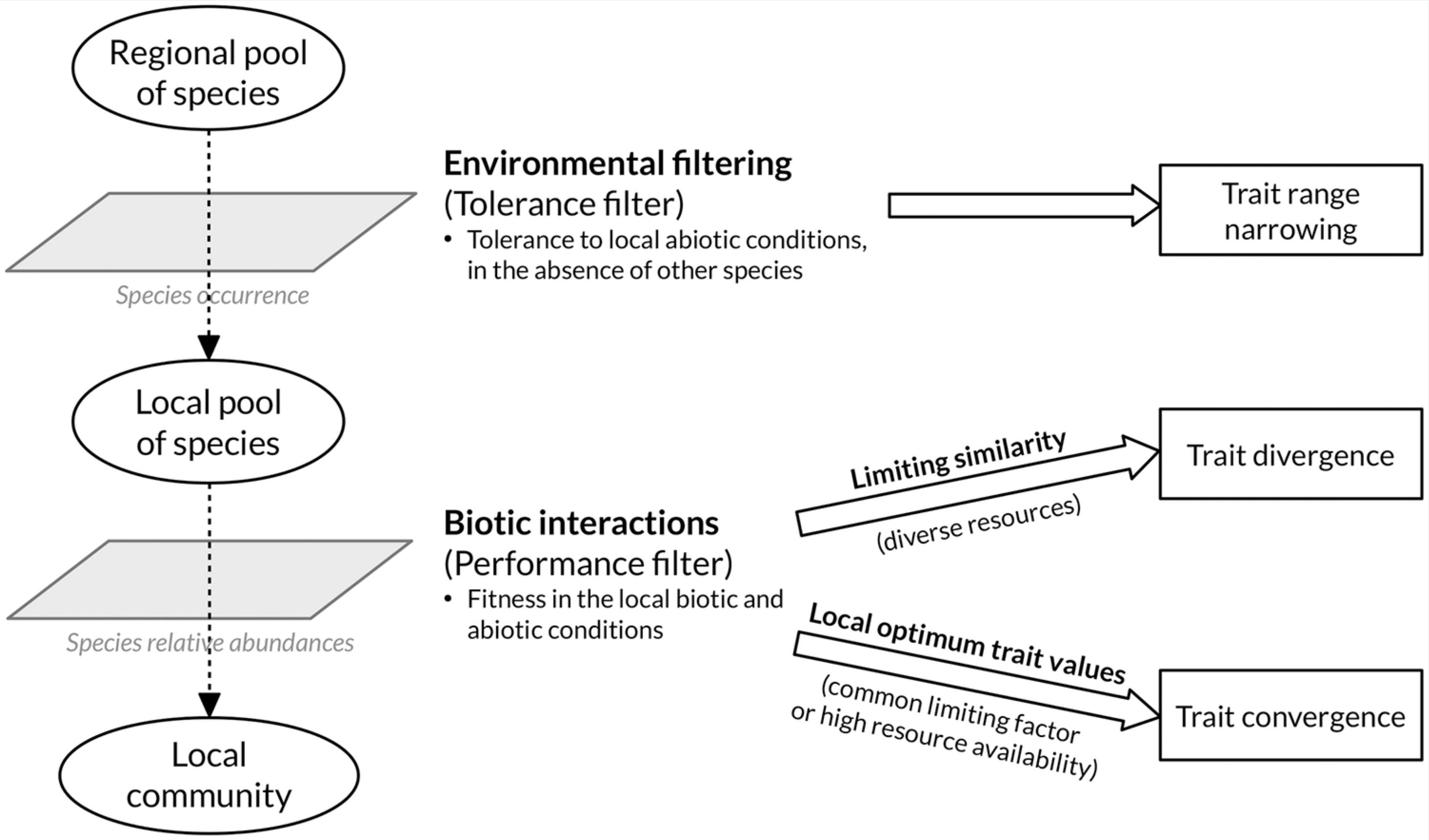


Figure from **Lechene et al 2018**

Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest

Nathan J. B. Kraft,[1] Renato Valencia,[2] David D. Ackerly[1]

It is debated whether species-level differences in ecological strategy, which play a key role in much of coexistence theory, are important in structuring highly diverse communities. We examined the co-occurrence patterns of over 1100 tree species in a 25-hectare Amazonian forest plot in relation to field-measured functional traits. Using a null model approach, we show that co-occurring trees are often less ecologically similar than a niche-free (neutral) model predicts. Furthermore, we find evidence for processes that simultaneously drive convergence and divergence in key aspects of plant strategy, suggesting that at least two distinct niche-based processes are occurring. Our results show that strategy differentiation among species contributes to the maintenance of diversity in one of the most diverse tropical forests in the world.

Kraft et al. 2009 explored trait means and variances in trees across a 25 Ha Amazonian forest plot - the ancestral home of Hubbell's Neutral Theory.

Trait means were non-random - e.g. panel A shows that SLA was lower than expected on ridgetops (pink) and higher than expected in valleys (turquoise).

They also found that the range of traits was smaller than null expectation.

This is strong evidence of niche-based trait filtering!

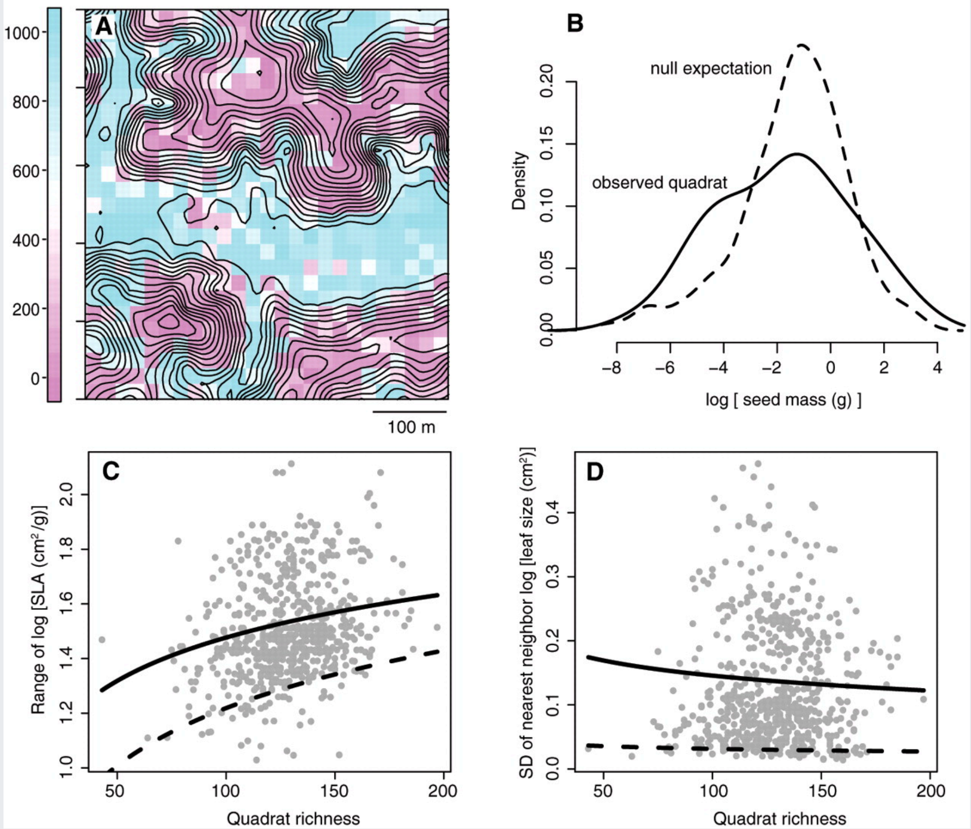


Fig. 1. Examples of community trait patterns at Yasuní. See figs. S1 to S3 for complete results. (**A**) The rank of observed mean SLA in the null distribution for all 625 quadrats. Contours indicate topography within the plot (interval = 2 m); thus, ridgetops have lower than expected SLA and valleys have higher. (**B**) Observed (solid line) and expected (dashed line) distribution of seed masses in one quadrat with significantly low kurtosis. (**C**) Points indicate the observed range of SLA (log-transformed) in each quadrat as a function of quadrat richness. The solid line indicates the expected range value predicted by the null model, and the dashed line indicates the 5% confidence interval of the null distribution used to assess significance in Table 2. Only one interval is indicated because the test is one-tailed. The distribution of observed points is significantly shifted below the null expectation (Table 1), suggesting that in aggregate, quadrat-level SLA ranges are smaller than expected across the forest. (**D**) Same plot for the SD of nearest-neighbor distances for leaf size (log-transformed). The distribution of observed points is significantly shifted below the null expectation (Table 1), indicating that in aggregate, quadrat-level leaf size distributions are more evenly spread than expected.

Traits and Community Assembly

There have been quite a few tests! Here is just a small sample from plant communities.

o = overdispersion (or evenness) = trait divergence

u = underdispersion = trait convergence

Results are clearly quite mixed!!!

Unfortunately, we're not always able to make sense of the patterns and reconcile them with the expected ecological processes... but we're learning!

Table 1 Examples of studies documenting trait and/or phylogenetic "overdispersion" and "underdispersion" (clustering) in plant communities

Type of study	Habitat	Dispersion (o, over; u, under)	Source
Traits	California grasslands[a]	o, u	Ackerly & Cornwell 2007, Cornwell & Ackerly 2009
	Spanish pastures[a]	o, u	de Bello et al. 2009
	Amazonian palms	u	Anderson et al. 2011
	North American trees	u	Swenson & Weiser 2010
	Australian subtropical forests	u	Kooyman et al. 2010
	Amazonian tropical forests[a]	o, u	Kraft et al. 2008
	Tropical successional communities (Mexico)	u	Lebrija-Trejos et al. 2010
	Tropical cloud forests (China)	u	Long et al. 2011
	Tropical rain forest (French Guyana)	o, u	Paine et al. 2011
	Neotropical dry forest[a]	o, u	Swenson & Enquist 2009
	Costa Rican nontree communities	u	Mayfield et al. 2005
Phylogeny	Disturbed old fields (Canada)	u	Dinnage 2009
	California plant communities[a]	o, u	Cadotte et al. 2010
	Brazilian cerrado	u	Silva & Batalha 2009
	Bornean rainforest	u	Webb 2000
	Amazonian forests[a] (Peru)	o, u	Fine & Kembel 2011
	Neotropical forests[a] (Panama)	o, u	Kembel & Hubbell 2006
	Subtropical forests[a] (China)	o, u	Pei et al. 2011
	Tropical forests (Panama, Puerto Rico, Costa Rica)	o, u	Swenson et al. 2007
	Costa Rican secondary forests	o	Letcher 2010
Traits and phylogeny	Serengeti grasslands[a]	o, u	Anderson et al. 2011
	Algerian Xeric communities	u	Pavoine et al. 2011
	Cape Floristic region	o	Slingsby & Verboom 2006
	Dutch plant communities[a]	o, u	Prinzing et al. 2008
	Mediterranean communities[a] (Spain)	o, u	Verdu & Pausas 2007, Ojeda et al. 2010
	Minnesotan oak savannahs	u	Willis et al. 2010
	Floridian oaks[a]	o, u	Cavender-Bares et al. 2004a,b
	Floridian forests	u	Cavender-Bares et al. 2006
	Tropical Inga trees	o, u	Kursar et al. 2009
	Tropical fern communities[a] (Costa Rica)	o, u	Kluge & Kessler 2011
	Amazonian forests[a] (Ecuador)	o, u	Kraft & Ackerly 2010
	Costa Rican nontree communities	u	Mayfield et al. 2009

[a]Opposite patterns at different spatial scales, in different habitats, for different groups of species, or for different traits.

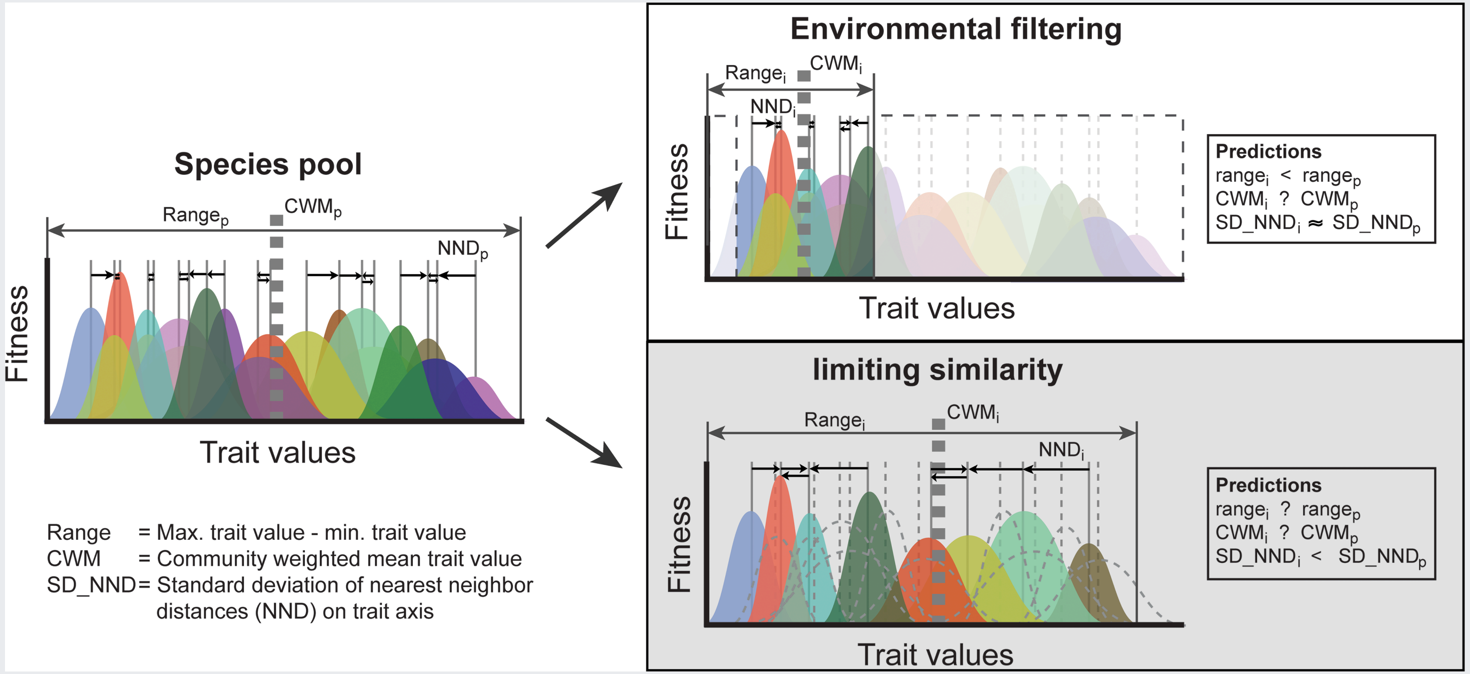
HilleRisLambers et al. 2012

Traits and Community Assembly

One issue is that these things are complex to measure! Different measures (or metrics) may be more or less suitable for different datasets, biotic communities or processes, and can give different outcomes...

For example, limiting similarity may result in a greater range of traits, but there's a lot going on within that range too.

Only species with overlapping niches should compete, so many species within the range should be competitively excluded...



Luo et al 2016

Traits and Community Assembly

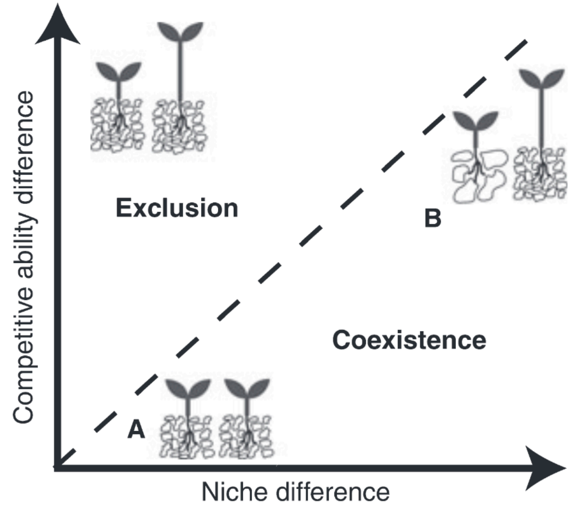


Figure 2 Coexistence occurs when niche differences exceed competitive ability differences among competitors, the region below the dashed 1 : 1 line (the line shows where growth rates when rare are zero). Variation in soil texture preference is presented as a niche difference, while variation in height is presented as a competitive ability difference. Letters A and B indicate different coexistence scenarios. Species can coexist when they are relatively similar when subtle niche differences overcome small competitive ability differences (location A). They can also coexist when they are quite different when large niche differences overcome large competitive ability differences (location B).

Another issue is that Modern Coexistence Theory (MCT) has shown that the relationship between traits and coexistence is not straightforward.

Recall that MCT considers both niche differences and fitness (competitive ability) differences. Larger niche differences allow stable coexistence, while larger competitive ability differences (i.e. fitness differences) favor competitive exclusion. Coexistence can be achieved by various combinations of the two, with smaller fitness differences allowing smaller niche differences.

The predictions are thus:

- The fundamental niches of species and the traits that determine them should differ to some degree.
- Species that co-occur should be more similar in their traits that determine competitive ability...

Mayfield and Levine 2010

But how do we know which are the right traits?

...for prediocting the fundamental niche and/or competitive ability?

Traits and Community Assembly

If one has a clear understanding of the system and necessary traits, you could be more specific in your predictions than just changes in trait convergence or divergence.

e.g. This example shows the need for plants to have aerenchyma to survive in inundated wetlands, because otherwise they can't get oxygen to their roots and they would rot.

Unfortunately, it is rare to have this detailed an understanding of the biology *a priori*. It is also difficult to generalise this rule beyond wetland plants...

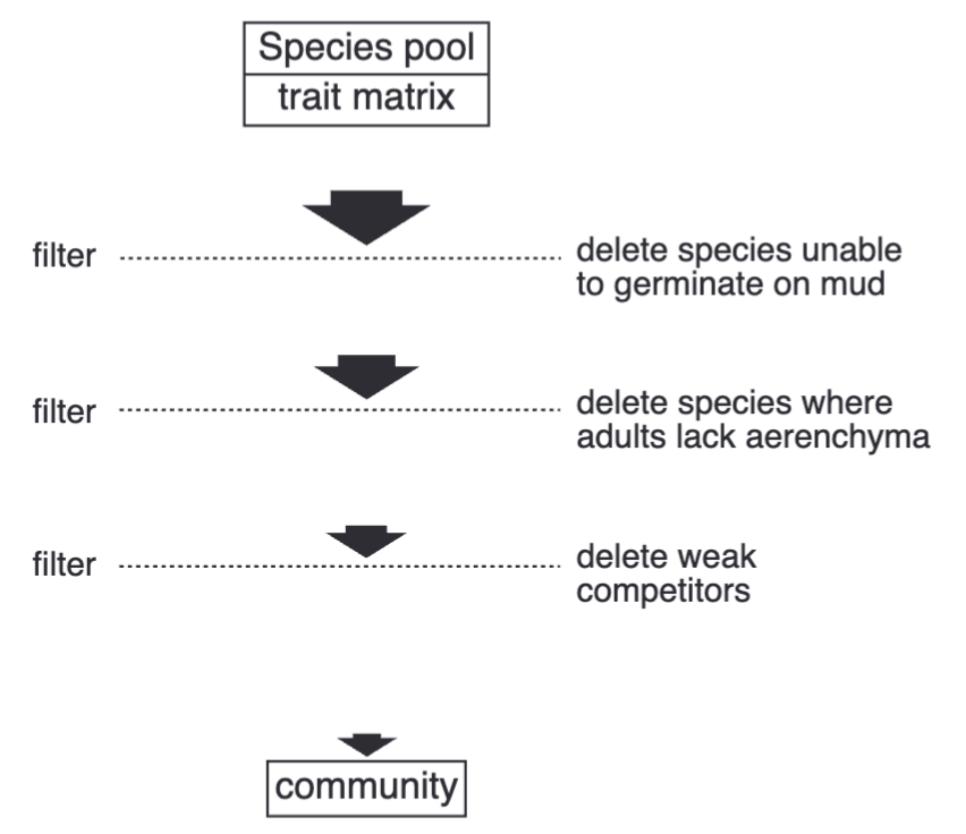
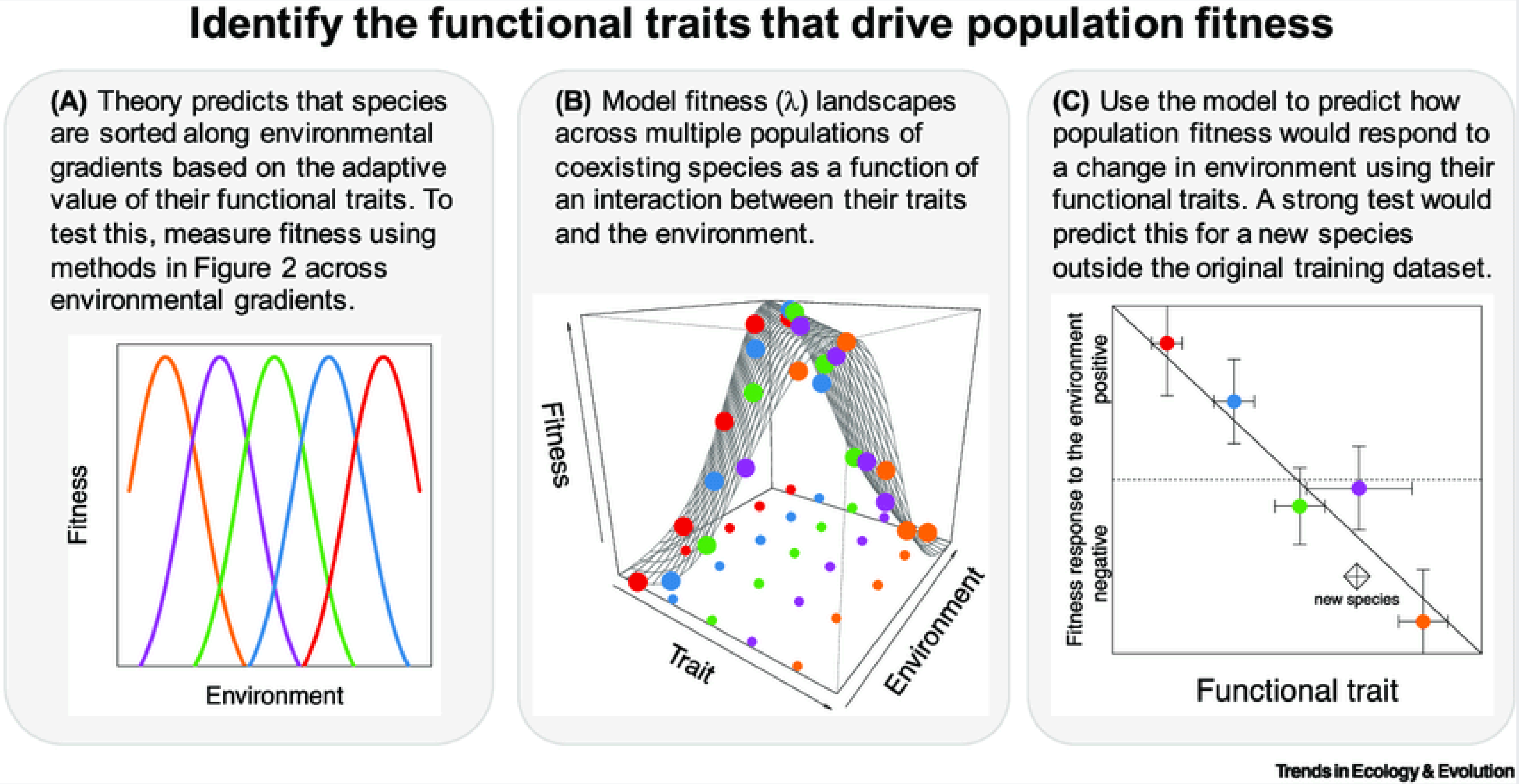


Figure from **Keddy 1992**

But how do we know these are the right traits?

This is why step 1 is looking at the relationship between traits and fundamental niches!

Selecting the right traits



This is essentially the process we followed in **Treurnicht et al. 2020**. Figure from **Laughlin et al. 2020**.

Other considerations and advantages of trait-based ecology?

Traits and scaling

Example traits	Organismal processes	Community processes	Ecosystem processes
Leaf chemistry and longevity	Carbon balance Disease resistance Growth rate	Competition Herbivory Succession	Decomposition Nutrient cycling Productivity
Leaf and stem hydraulic traits	Drought tolerance	Competition and facilitation	Hydrology Precipitation patterns
Fine root traits	Soil resource uptake Growth rate	Competition and facilitation Community invasibility	Decomposition Soil development

Fig. 1. Functional traits can be used to understand a wide range of ecological processes occurring at organismal, community, and ecosystem scales. Examples are given here of how leaf, stem, and fine root traits influence a variety of ecological processes.

Traits affect processes from the organism to ecosystem and should help us scale across the hierarchy or ecology, **Funk et al. 2017**

Traits and ecosystem function

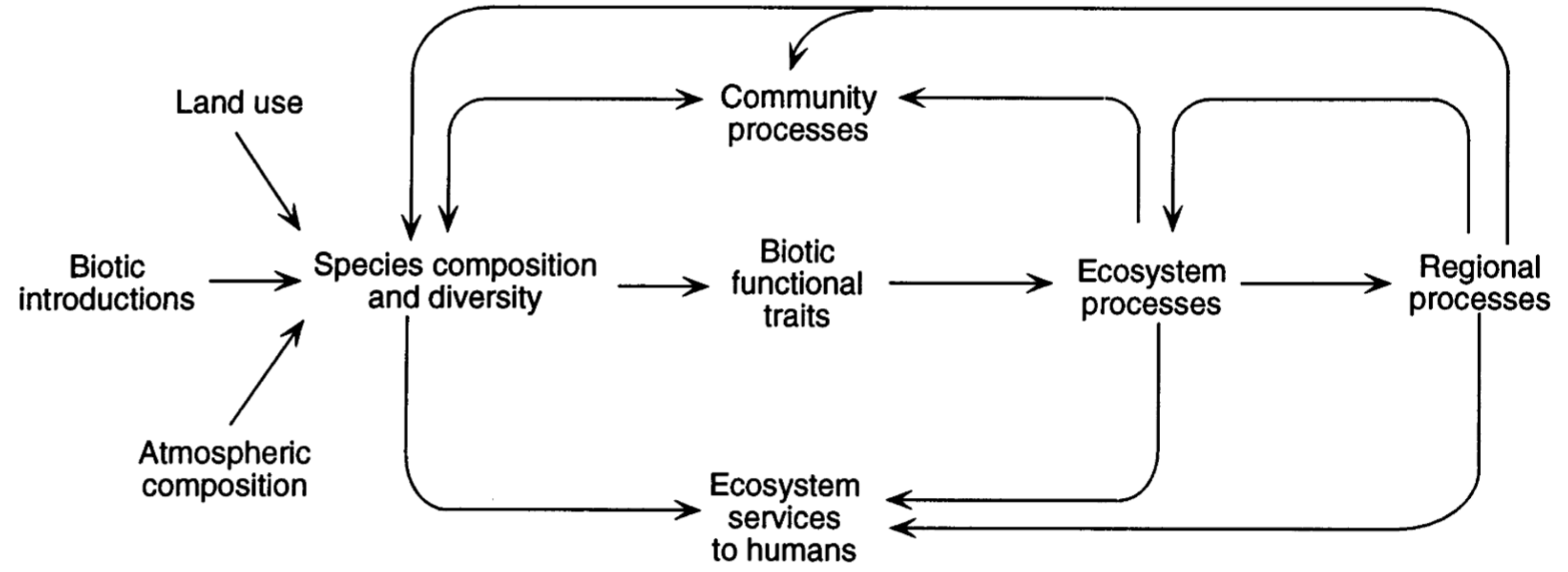


Fig. 1. Linkages involving species composition and diversity and ecosystem processes. Ecosystem processes include productivity and nutrient cycling. Regional processes include trace gas fluxes to the atmosphere and nutrient fluxes from terrestrial to aquatic systems. Community processes include competition and predation. Ecosystem services are the benefits derived by humans from ecological processes.

A focus on traits allows us to link community assembly and outcomes for ecosystem function, **Chapin et al 1997**

Trade-offs among traits

A trade-off occurs when one trait cannot increase without a decrease in another. This can put profound limitations on the ecology of organisms.

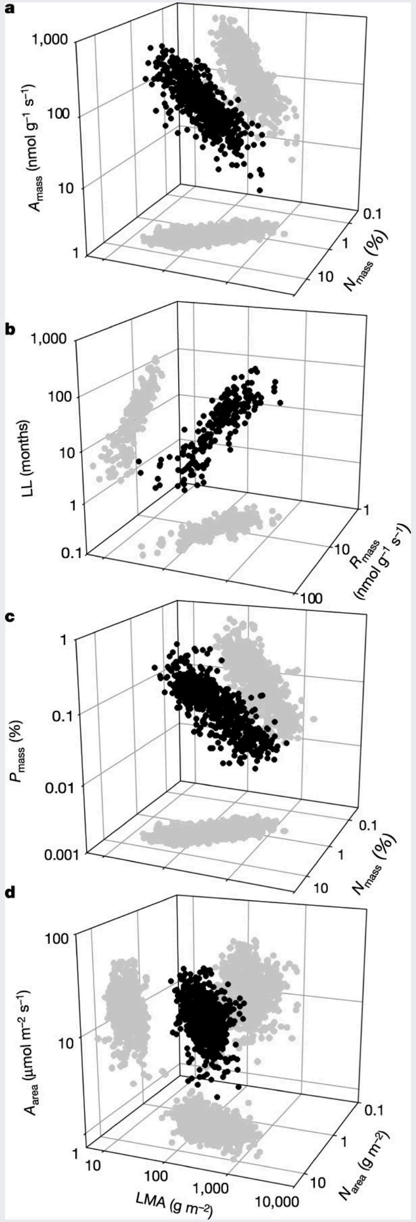
E.g. Leaf dry mass per unit area (LMA) positively correlates with:

- Nitrogen content
- photosynthetic capacity
- relative growth rate

But is negatively correlated with:

- leaf longevity

The leaf economics spectrum (LES) - Wright et al. 2004

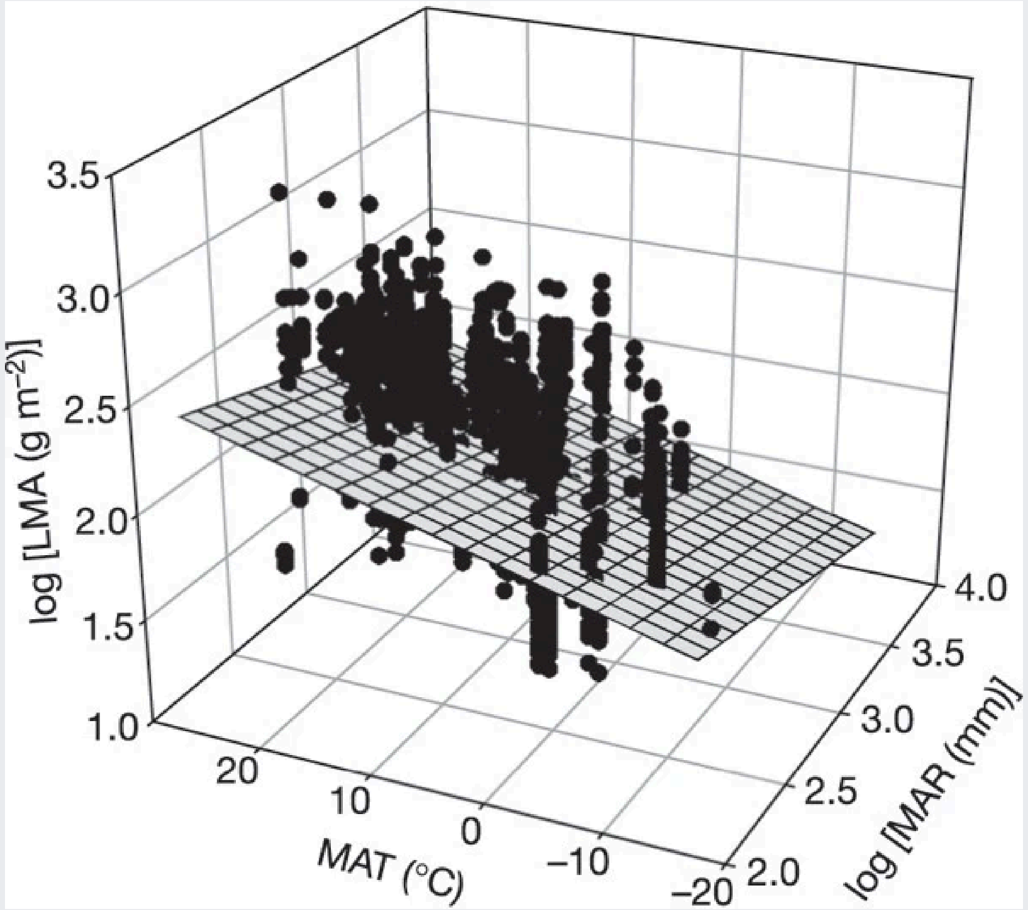


Trade-offs among traits

LMA correlates with environment (temp and rainfall)

- Higher LMA in hot, dry places

This also represents a trade-off in that specific traits can limit species to specific resource/habitat requirements (water, light, nutrients). i.e. the trade-offs in traits can have a direct effect on species niches!



The leaf economics spectrum (LES) - Wright et al. 2004

Where to for trait-based ecology and niche theory?

> *"Opinions regarding the relative importance of the niche, and hence traits, to community dynamics fall loosely into three camps.*
>
> - *The first argues that trait differences among individuals are largely irrelevant at the community level compared to factors such as demographic stochasticity (e.g. Neutral Theory: Hubbell, 2001).*
> - *The second argues that traits are relevant to individuals, but the complexity of biotic and abiotic interactions precludes us from scaling individual processes to the community level (e.g. Lawton, 1999).*
> - *The final camp argues that traits provide a path forward to a unified theory of community ecology by providing a taxon-independent means for generalizing the structure and/or functioning of communities that is based on functional traits rather than species identity (e.g. Westoby & Wright, 2006; McGill et al., 2006a)."*

- **Funk et al. 2017**

Take-home

> *Traits were clearly included in early definitions of the niche by Grinnell and Elton.*
>
> *While some traits may be more Grinnellian (relating to environmental conditions) and other more Eltonian (relating to resource exploitation and the species functional role), they are often difficult to classify as they may be related to both.*
>
> *Integrating traits into niche theory requires being able to predict (a) aspects of the niche, and (b) community assembly processes, based on traits.*
>
> - *We're having mixed results here, but we are making progress...*
>
> *A focus on traits allows us to integrate across the hierarchy of ecology from the individual to whole ecosystems.*
>
> *A focus on traits allows us to link community assembly, ecosystem function and nature's contributions to people.*

Thanks!

Slides created via the R packages:

xaringan
gadenbuie/xaringanthemer

The chakra comes from remark.js, **knitr**, and R Markdown.