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The analysis of physiological diversity: the prospects for pattern documentation and general questions in ecological physiology

MARTIN E. FEDER

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Assembly and response rules: two goals for predictive community ecology

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Synthesis

Macrophysiology: A Conceptual Reunification

Kevin J. Gaston,^{1,*} Steven L. Chown,² Piero Calosi,³ Joseph Bernardo,⁴ David T. Bilton,³ Andrew Clarke,⁵ Susana Clusella-Trullas,² Cameron K. Ghalambor,⁶ Marek Konarzewski,⁷ Lloyd S. Peck,⁵ Warren P. Porter,⁸ Hans O. Pörtner,⁹ Enrico L. Rezende,¹⁰ Patricia M. Schulte,¹¹ John I. Spicer,³ Jonathon H. Stillman,¹² John S. Terblanche,¹³ and Mark van Kleunen¹⁴



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Let the concept of trait be functional!

Cyrille Violle, Marie-Laure Navas, Denis Vile, Elena Kazakou, Claire Fortunel, Irène Hummel and Eric Garnier

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Review

Cell
PRESS

The return of the variance: intraspecific variability in community ecology

Cyrille Violle^{1,2}, Brian J. Enquist^{1,3}, Brian J. McGill⁴, Lin Jiang⁵, Cécile H. Al Catherine Hulshof¹, Vincent Jung^{8,9} and Julie Messier¹

FORUM
FORUM
FORUM

FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

Assembly rules, null models, and trait dispersion: new questions from old patterns

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3

The analysis of physiological
diversity: the prospects for pattern
documentation and general questions
in ecological physiology

MARTIN E. FEDER



Central points of Feder 1987

(1) Ecological physiology has historically emphasized the role of pattern rather than testing of hypotheses

The flowering of ecological physiology has yielded a panoply of elegant individual examples and few principles beyond the unlightening conclusion that animals work well (page 65) S.J. Gould (1980)

Move toward proposing and assessing general questions

(2) A rich documentation of physiological diversity

Variation in physiological attributes is near universal

Variation is not random

(3) Recognition of pattern in physiological diversity

Necessary for nomothetic research (identification of law-like properties)

Recognize the “general gas laws” by which species are governed

(4) Matching of physiological diversity with the environment

The physiology of organisms is in “equilibrium” with their environment

Physiologies are adequate to support maintenance, growth, reproduction

As environments vary so do the physiological characteristics

(5) The field is becoming moribund and irrelevant.. . .

Now it is time to emphasize other issues other than matching of physiology with environment

Despite lots of examples of 'convergence' in physiology (traits)
physiological variation may reflect phylogenetic relationships

Physiology can reconstruct phylogenies (Niche conservatism)

Feder dismisses this as an important area for pattern documentation

(6) Ecophysiological patterns may reveal the general principles of ecophysiology

BUT there are limitations with how the field has approached 'general principles'

To make progress in assessing general principles field needs to embrace
'strong inference'

16 October 1964, Volume 146, Number 3642

SCIENCE

Strong Inference

Certain systematic methods of scientific thinking may produce much more rapid progress than others.

John R. Platt

Scientists these days tend to keep up a polite fiction that all science is equal. Except for the work of the misguided opponent whose arguments we happen to be refuting at the time, we speak as though every scientist's field and

important to examine this method...its use and history and rationale, and to see whether other groups and individuals might learn to adopt it profitably in their own scientific and intellectual work.

In its separate element, strong

an unknown sample, where the student is led through a real problem of consecutive inference: Add reagent A; if you get a red precipitate, it is sub-group alpha and you filter and add reagent B; if not, you add the other reagent, B; and so

Platt (1964) science advances quickly when using strong inference...

The danger of single hypothesis driven science is 'confirmation bias'

Fields such as high-energy physics, molecular biology **progress faster** because they used strong inference

Strong inference **is a method by which to conduct science** – it emphasizes using alternative hypotheses rather than a single hypothesis

Compete **alternative** hypotheses or models to explain pattern

(i) To Do - Need to test the assumptions of equilibrium

Traits must vary among individuals (intraspecific variation)

We know very little about intraspecific variation

How do simple changes in DNA sequences translate into complex traits?

Is there variation in the traits related to fitness?

Issues of sample size,

Field generally assumes strong stabilizing selection

(ii) To do - What is the shape of the physiology-fitness function for traits?

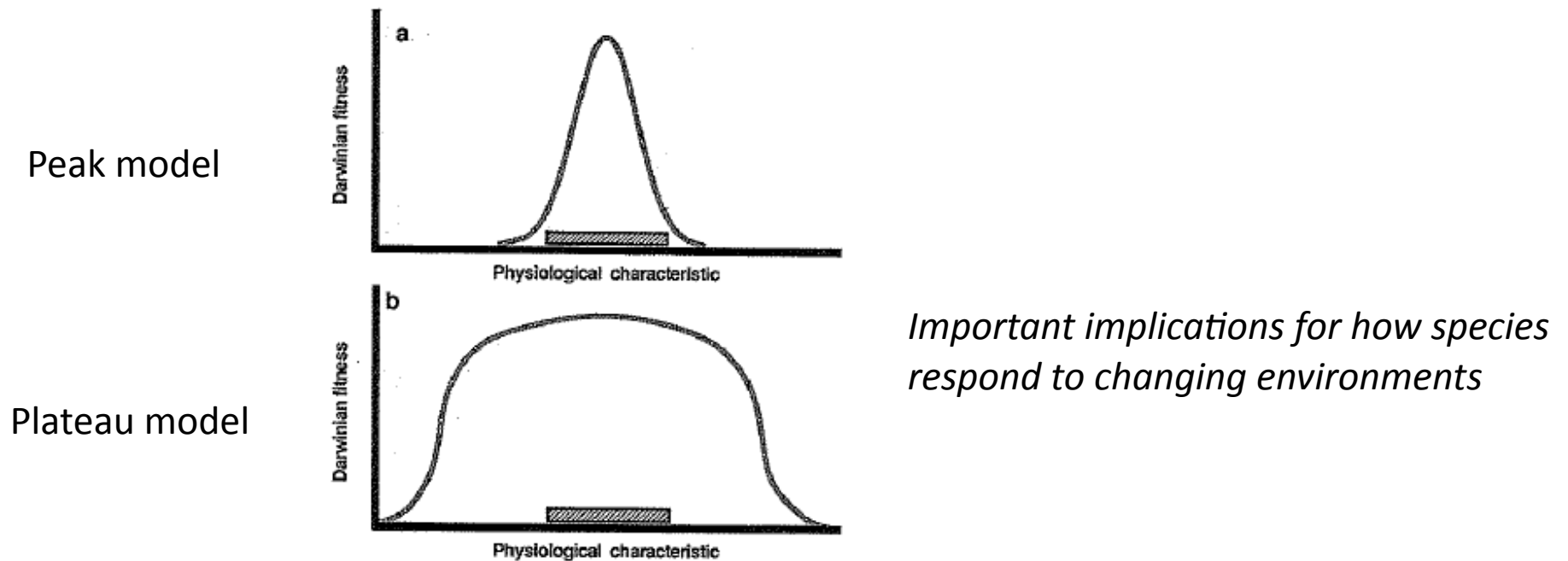
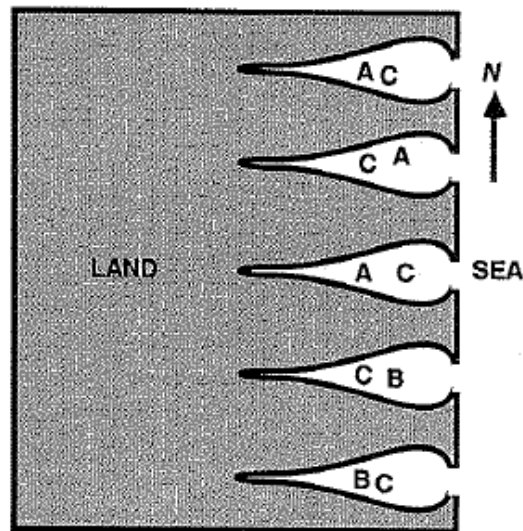


FIGURE 3.4 Two possible extreme forms of the relationship between physiological variation and fitness. For a given amount of variation in a physiological attribute (indicated by the horizontal bar), stabilizing selection would be strong in (a) ("peak" model) and weak in (b) ("plateau" model). An open question for ecological physiologists is how the actual relationships between physiological variation and fitness are distributed between the two extremes shown.

(iii) To do- Relate how variation in traits link to demography -> fitness

(iv) To do- Once a link between traits and demography and fitness is found .. follow this link to questions of species persistence through time and questions of widespread to endemic species

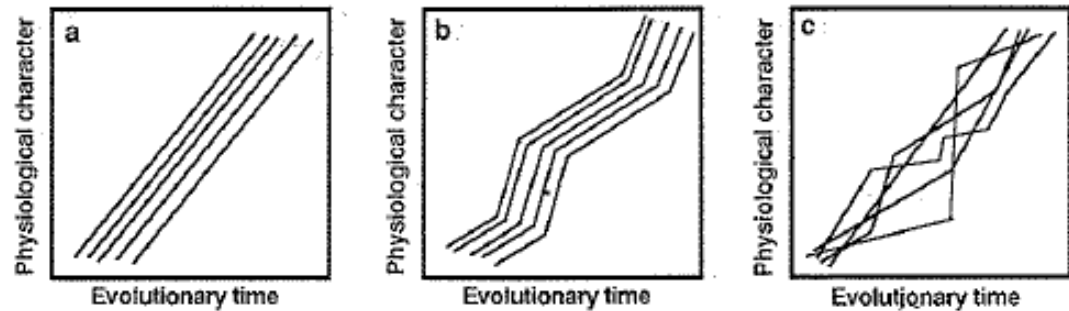


How do traits that influence dispersal or gene flow key to a taxon's long term survivorship?

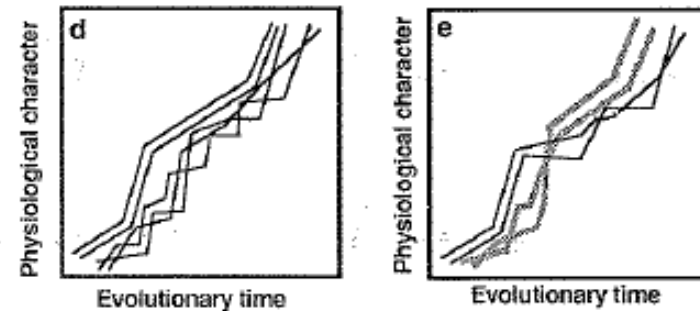
Species selection

FIGURE 3.5 A hypothetical example of "species selection" by differential extinction rates. Suppose three species of flying insects whose aquatic larvae are intolerant of seawater are distributed in estuaries along a north-south transect as shown. Suppose occasional storm fronts moving from east to west inundate the estuaries with seawater. Storms affecting the southernmost two estuaries are likely to exterminate all populations of species B but only some populations of species C. Storms affecting the northernmost three estuaries are likely to exterminate all populations of species A but only some populations of species C. All else equal, species C is likely to persist longer than the other species through the years. The physiological attributes that engender the persistence of C are those promoting dispersal of adults, not those promoting salinity tolerance of larvae.

(v) To Do – Assess trajectory of physiological traits
(how to traits covary across time – why do traits covary)



Parallelism versus independent trajectories



Documenting these trajectories
will help reveal how complex
trait correlations are regulated

Link physiology with paleobiology

FIGURE 3.6. Possible patterns of change in the components of a complex physiological trait through evolutionary time. All component traits might change in parallel, at a constant rate (a) or at a variable rate (b). Each component trait might change at its own rate, with extreme variations prevented by selection (c). Some component traits may be rate-limiting, with others free to vary as long as they do not depart drastically from the rate-limiting components (d). If so, some components may be rate-limiting early in an evolutionary transformation [solid lines in (e)], whereas others may be rate-limiting later in a transformation [shaded lines in (e)].

(vi) To Do – What is the relative importance of adaptive and nonadaptive mechanisms in generating or constraining physiological diversity?

(vii) To Do – What are the general consequences of physiological diversity for ecological and evolutionary properties of animals

What are the consequences for how species respond to environmental change?

Much as ensembles of gas molecules behave in accordance with gas laws, ensembles of species ought to behave in ecological and evolutionary time according to their physiological characteristics

Dynamics of ensembles should be predictable ...

But *there are several challenges here (see list on page 63)*

(viii) To Do – Move toward a nomothetic ecological physiology

A focus on novel and exciting questions

The field must change or it will disappear

Synthesis

Macrophysiology: A Conceptual Reunification

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A modern day reemphasis of Feder 1987?

What are the new conceptual advances since Feder 1987?

Assembly and response rules: two goals for predictive community ecology

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Overview of trait based assembly rules

Predictable attributes of species assemblages based on traits?

14 Assembly of Species Communities

Jared M. Diamond

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Ecology and Evolution of Communities

*Martin L. Cody
and Jared M. Diamond,
Editors*

Cambridge, Massachusetts, and London,
England
1975

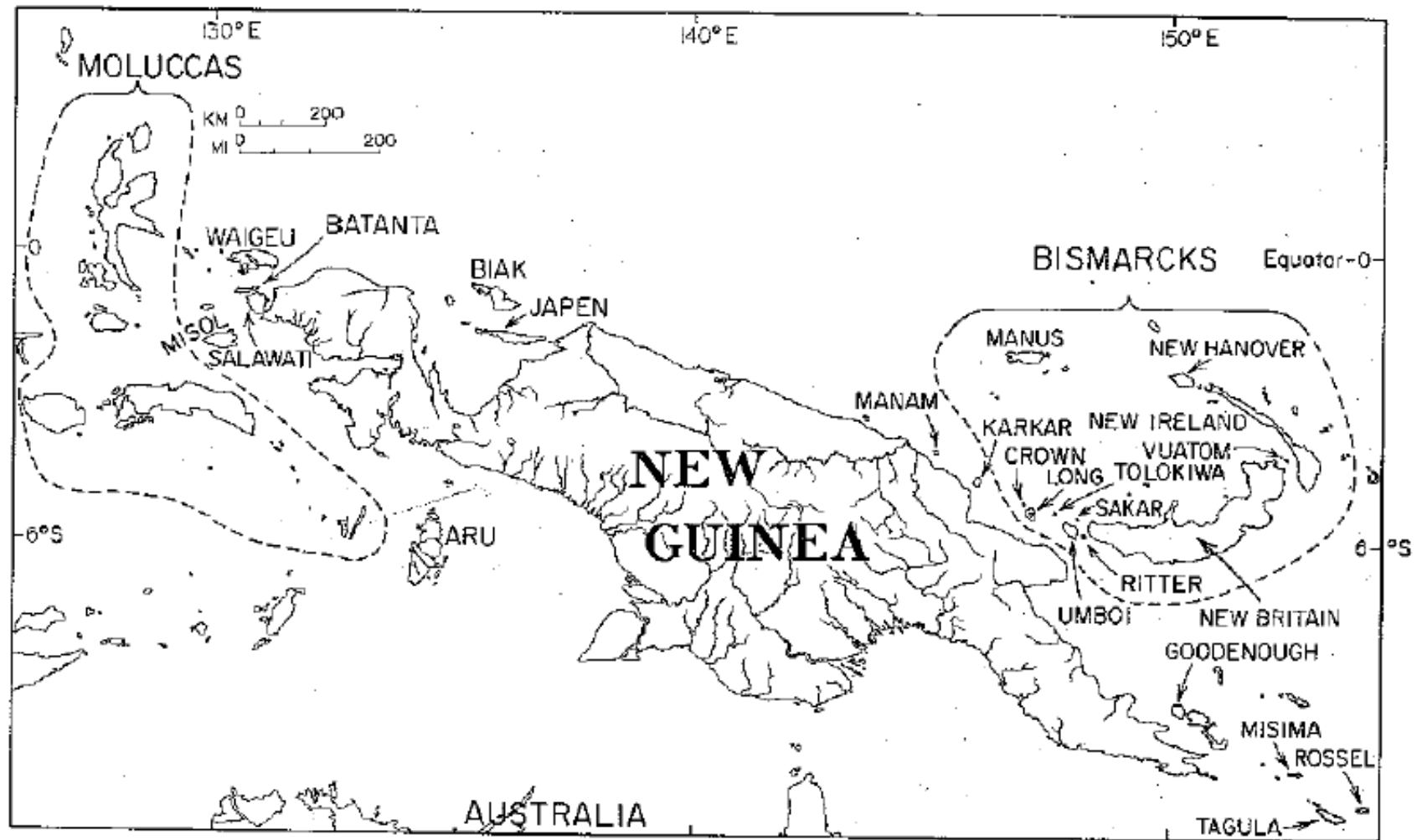


Figure 1 Map of the New Guinea region with names of some of the islands to be discussed.

species pool

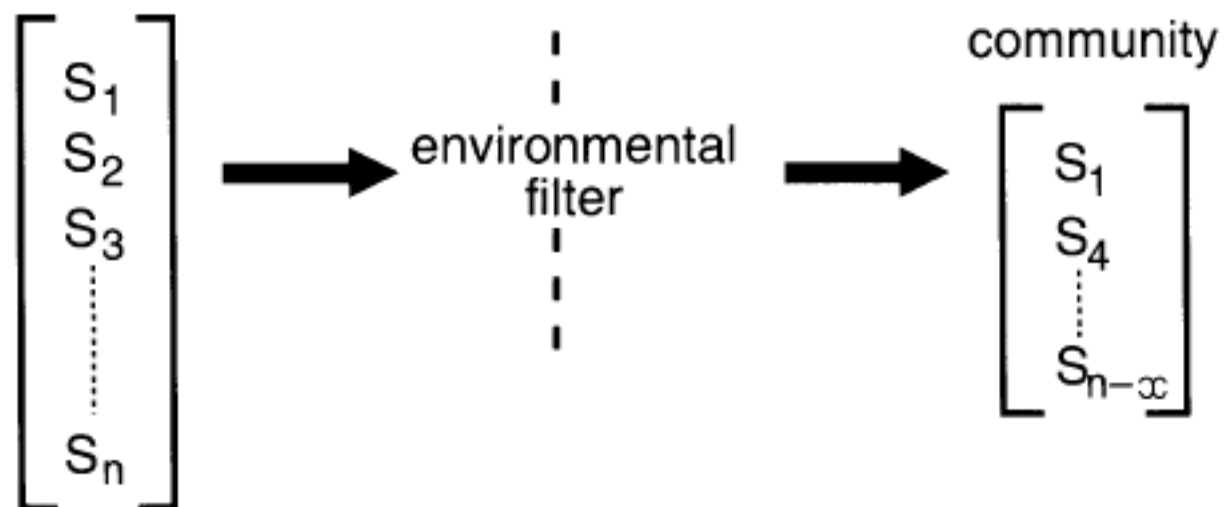


Fig. 1. Assembly rules specify which subset of species in the total pool (left) would tolerate specified conditions and form a community (right).

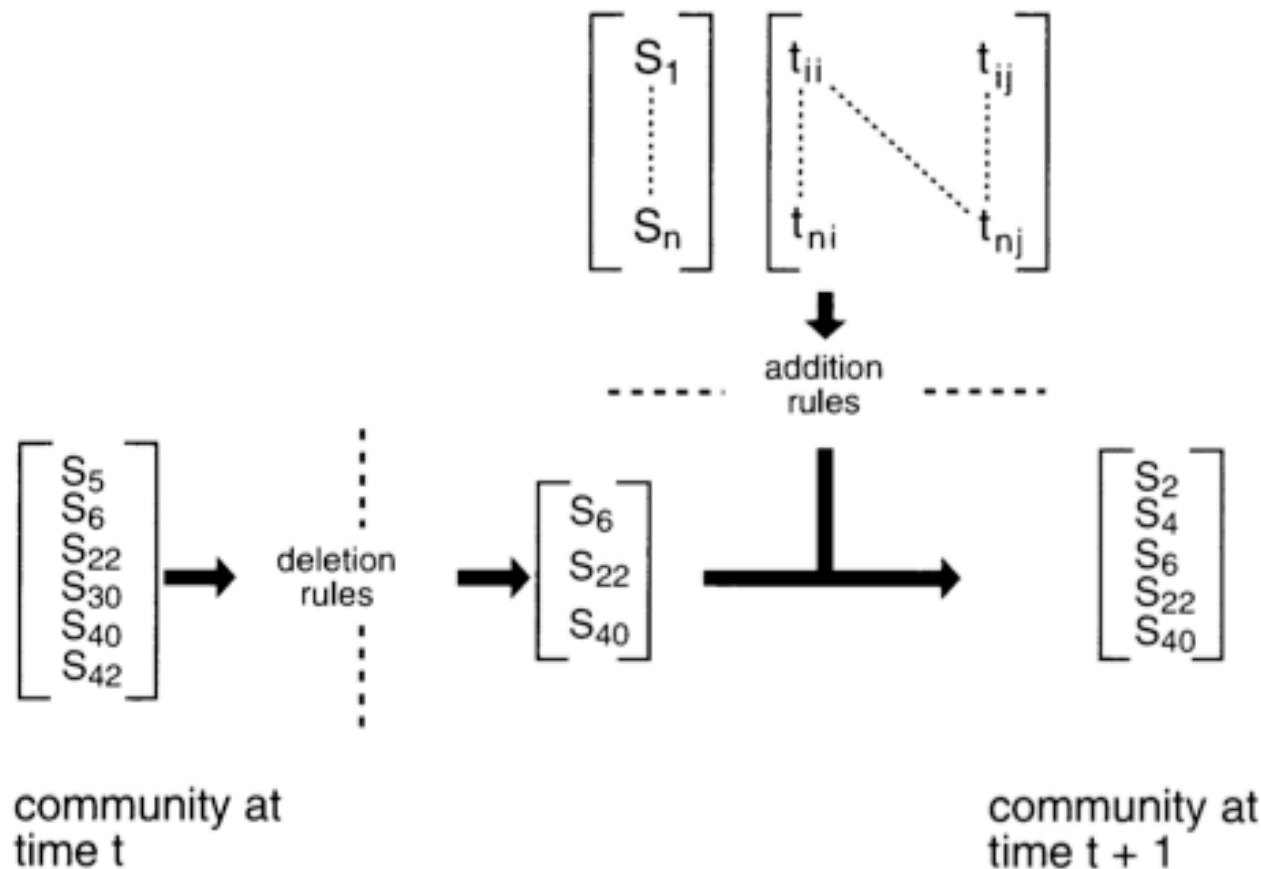


Fig. 5. General procedure for response rules. First the perturbation deletes species from the community, and then based upon the trait matrix, new species are added from the pool. In this case, the vegetation initially consists of six species. Three (S_5, S_{30}, S_{42} .) disappear from the perturbation. They are replaced by two (S_2, S_4) from the trait matrix, producing a final predicted community of five species.

Table 1. Comparison of three levels of organization in ecological research.

	State variables measured	State variable predicted	Organizing concepts
Community ecology	traits environment biomass	species present guilds present diversity	assembly rules response rules
Population ecology	birth rates death rates immigration emigration	population size age classes	life history evolution population regulation
Population genetics	gene flow heterozygosity inbreeding	breeding system mode of reproduction	evolution reproductive allocation

Null models . . .

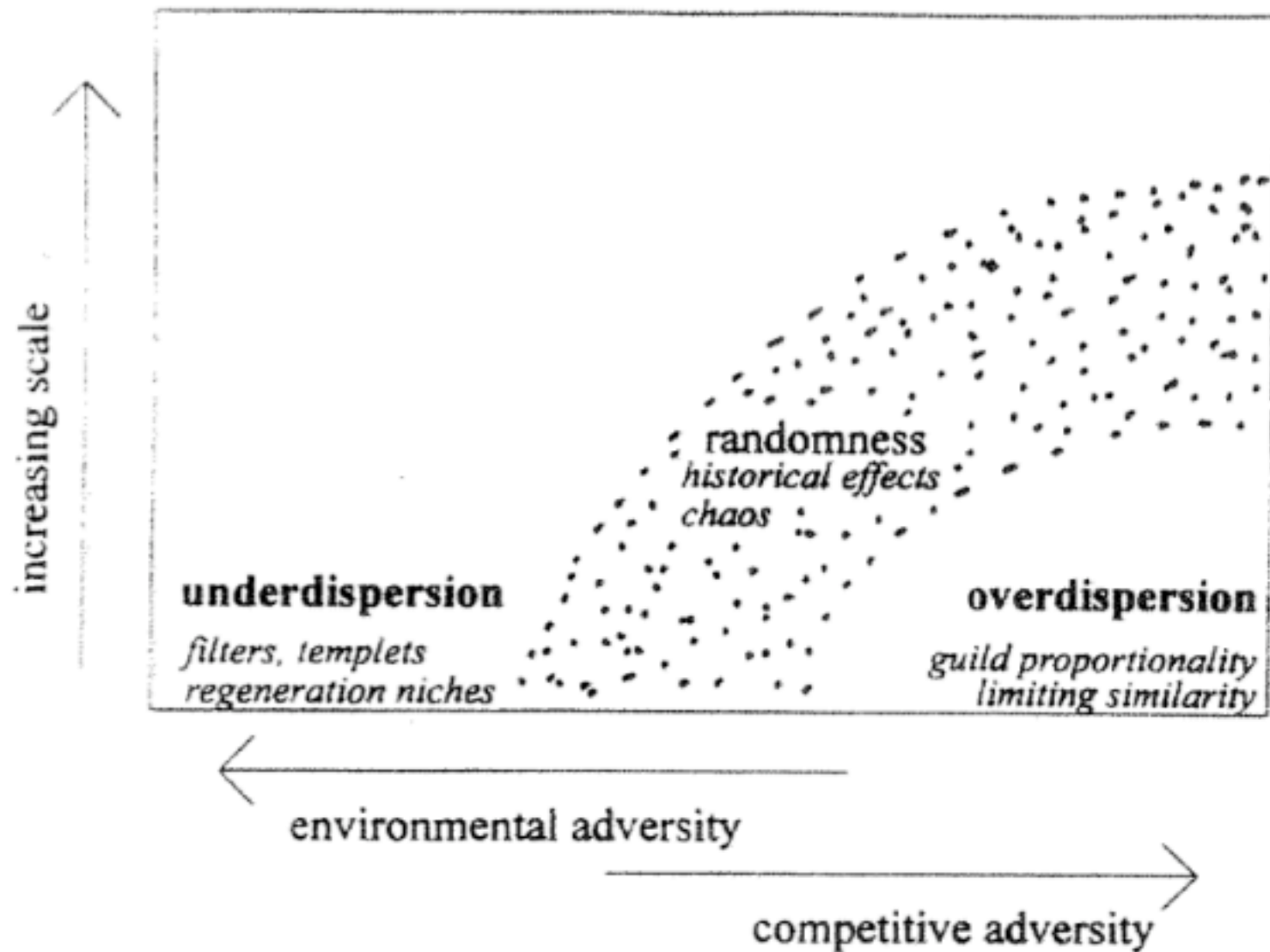


Fig. 1. A qualitative model for trait dispersion.



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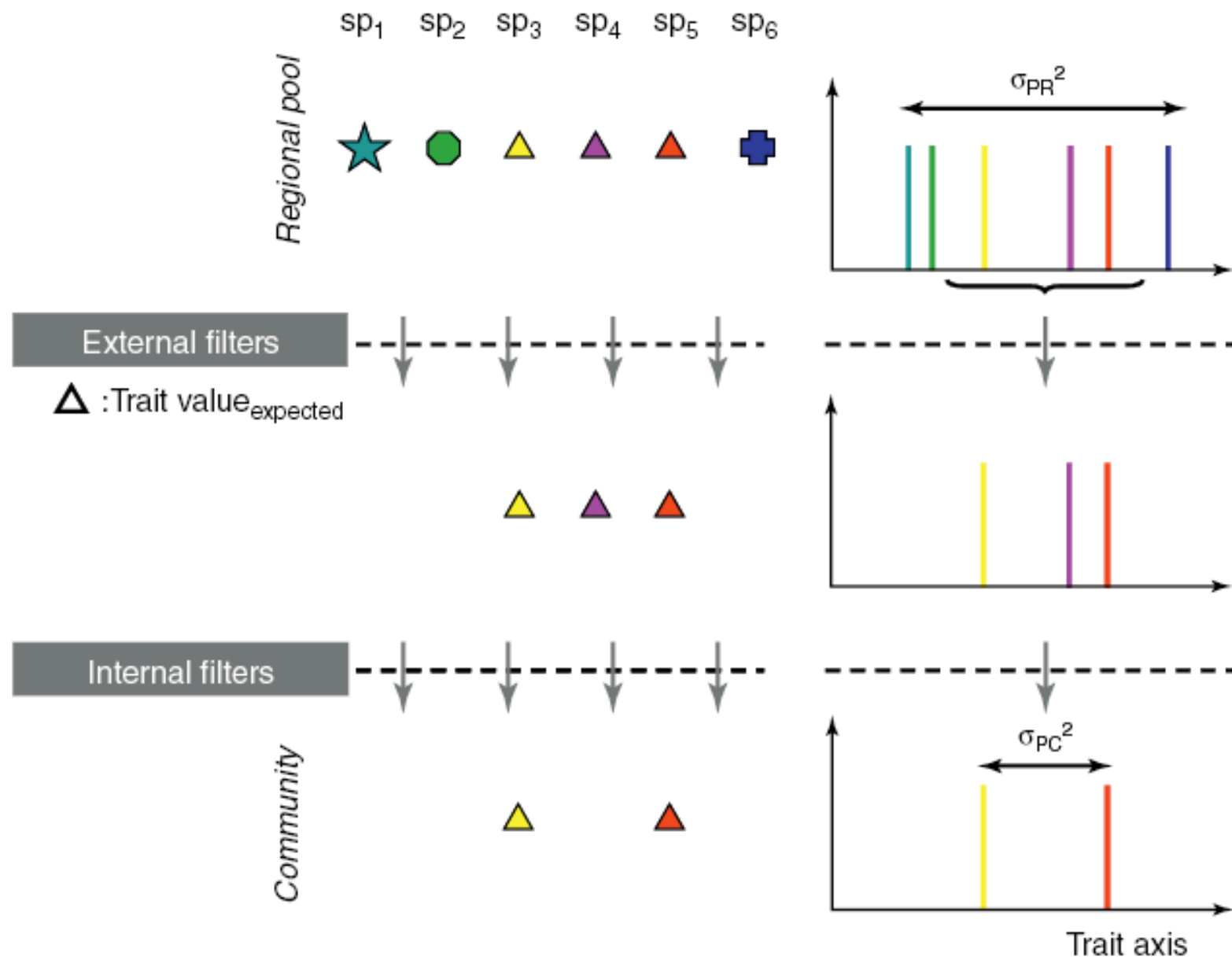
Subject Editor: Pia Mutikainen, Accepted 8 January 2007

Let the concept of trait be functional!

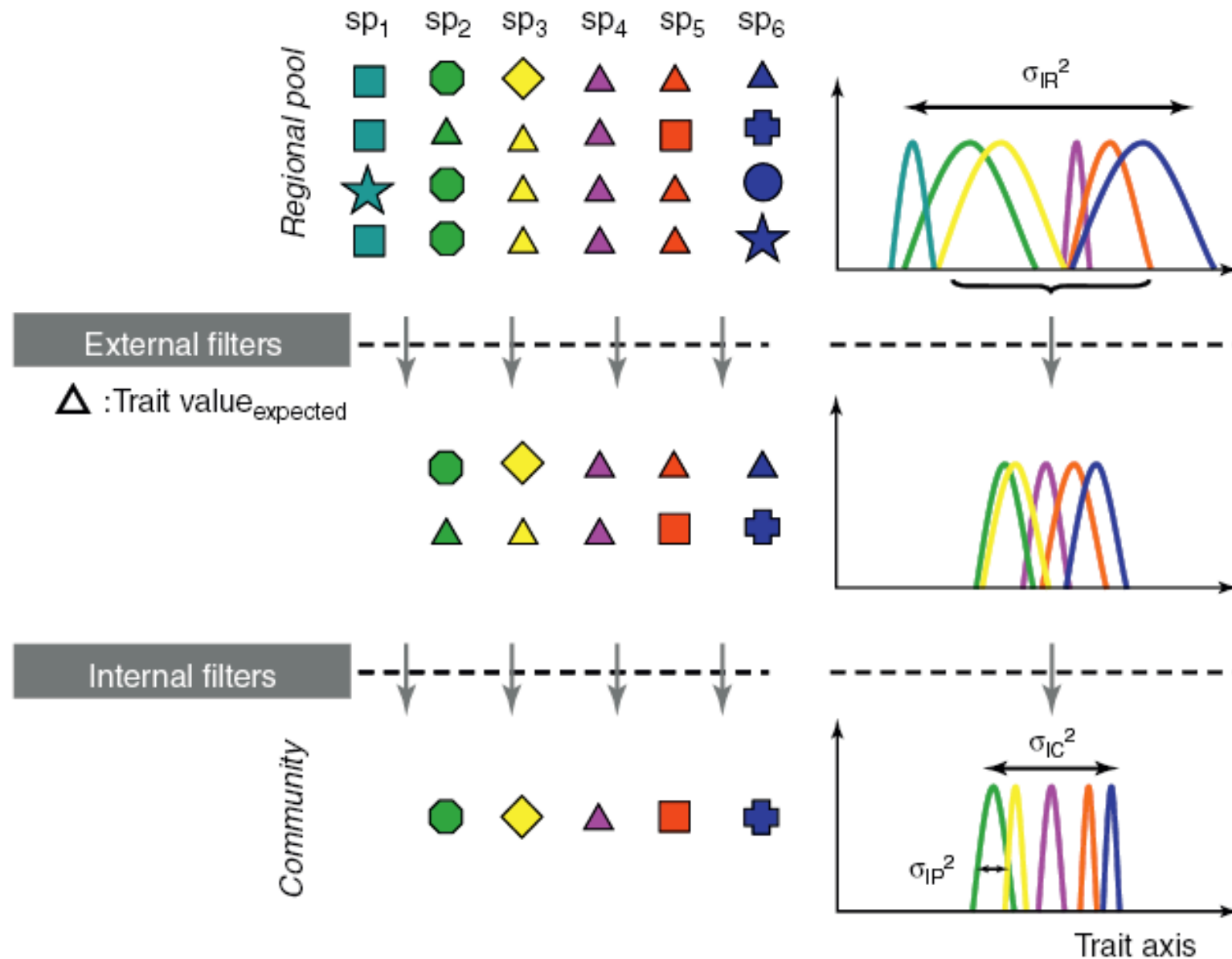
**Cyrille Violle, Marie-Laure Navas, Denis Vile, Elena Kazakou, Claire Fortunel,
Irène Hummel and Eric Garnier**

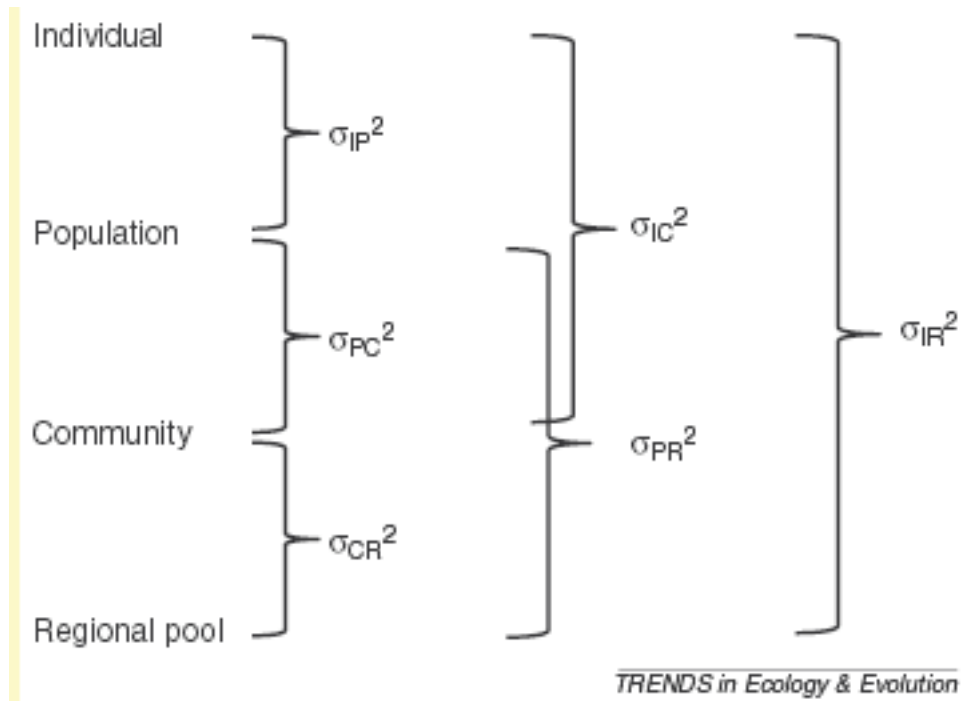
Cyrille Violle (cyrille.violle@cefe.cnrs.fr), Marie-Laure Navas, Denis Vile, Elena Kazakou, Claire Fortunel, Irène Hummel and Eric Garnier, CNRS, Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, 1919, Route de Mende, FR-34293 Montpellier Cedex 5, France. – MLN also at: Montpellier Supagro, 2 Place Viala, FR-34060 Montpellier Cedex 1, France. DV also at: Dépt de Biologie, Univ. de Sherbrooke, Sherbrooke (QC), Canada, J1K2R1.

(a) Mean field approach to the regional pool

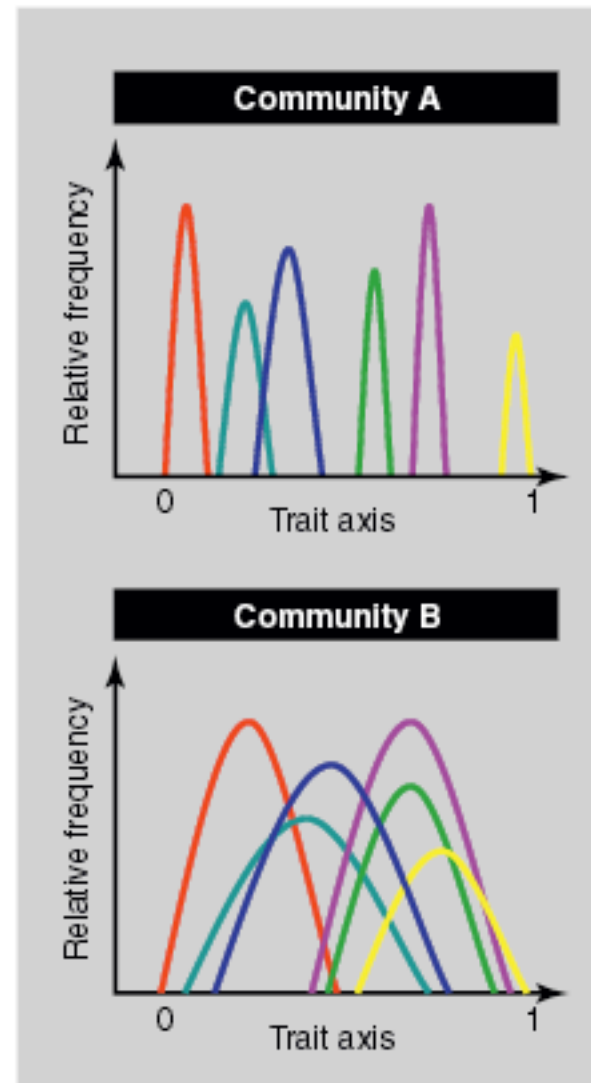
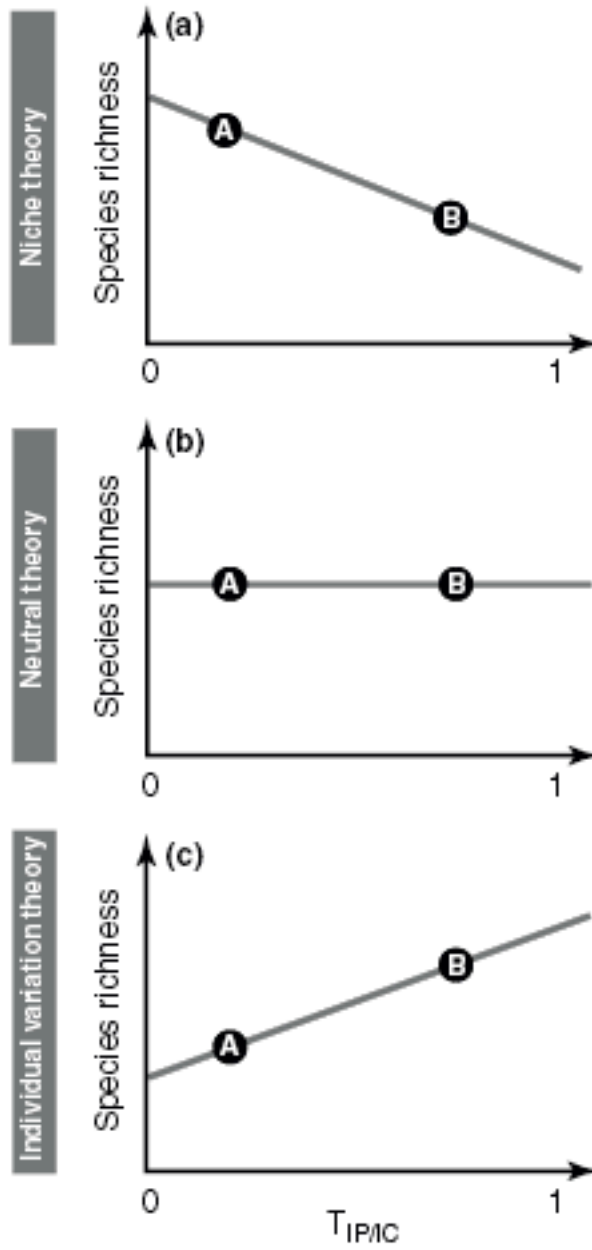


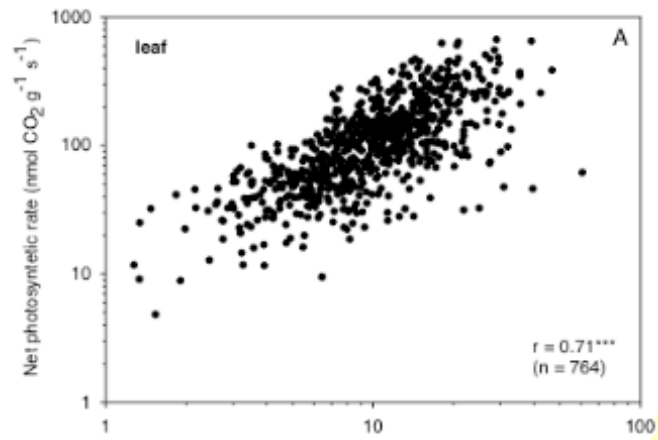
(b) Including intraspecific variability in the regional pool



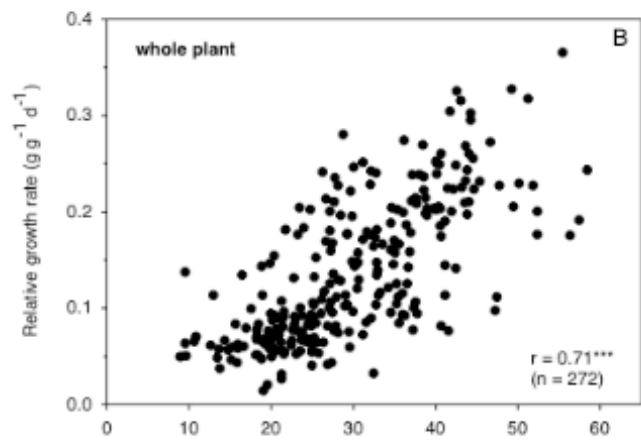


- $T_{IP/IC} = \frac{\sigma_{IP}^2}{\sigma_{IC}^2}$, the within-population variance conditional within the community;
- $T_{IC/IR} = \frac{\sigma_{IC}^2}{\sigma_{IR}^2}$, the community-wide variance relative to the total variance in the regional pool, assessed at the individual level;
- $T_{PC/PR} = \frac{\sigma_{PC}^2}{\sigma_{PR}^2}$, the community-wide variance relative to the total variance in the regional pool, assessed via population-level means.

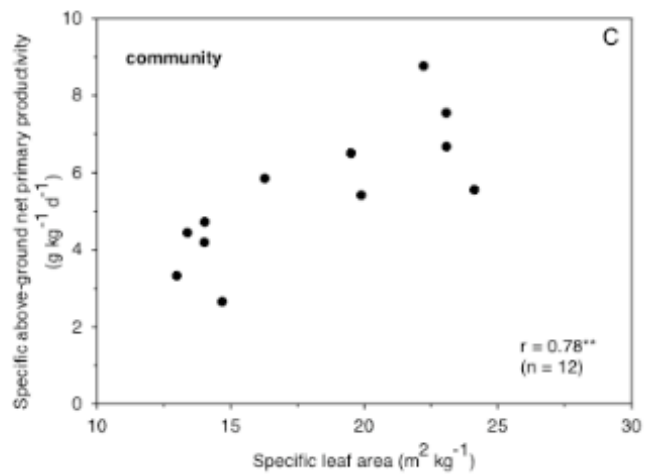




Leaf level



Whole-plant



Ecosystem

$$VM_t = VM_0 * e^{RGR * t} \tag{1}$$

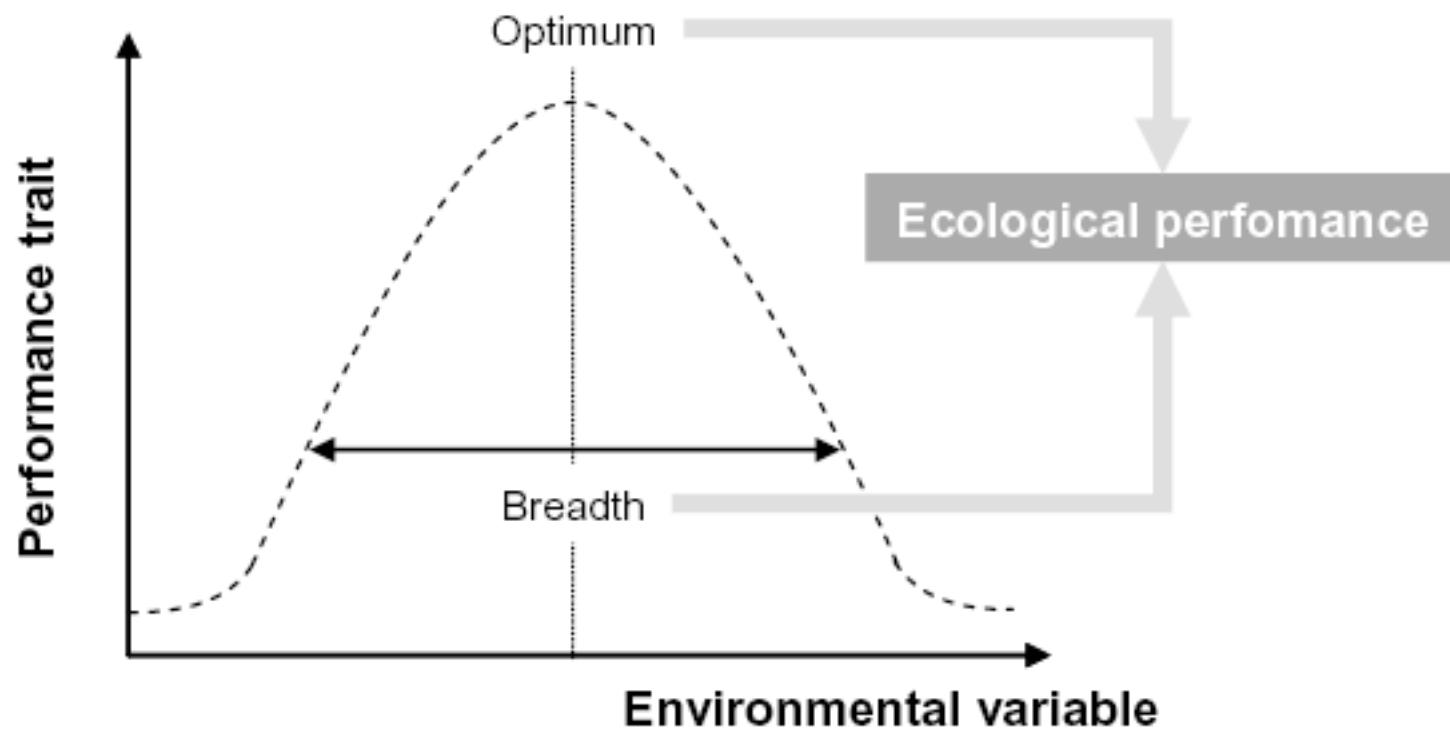


Fig. 5. Graphical definition of an ecological performance. An ecological performance can be defined as the optimum and/or the breadth of distribution of one of the three performance traits along an environmental gradient; see text for more details.

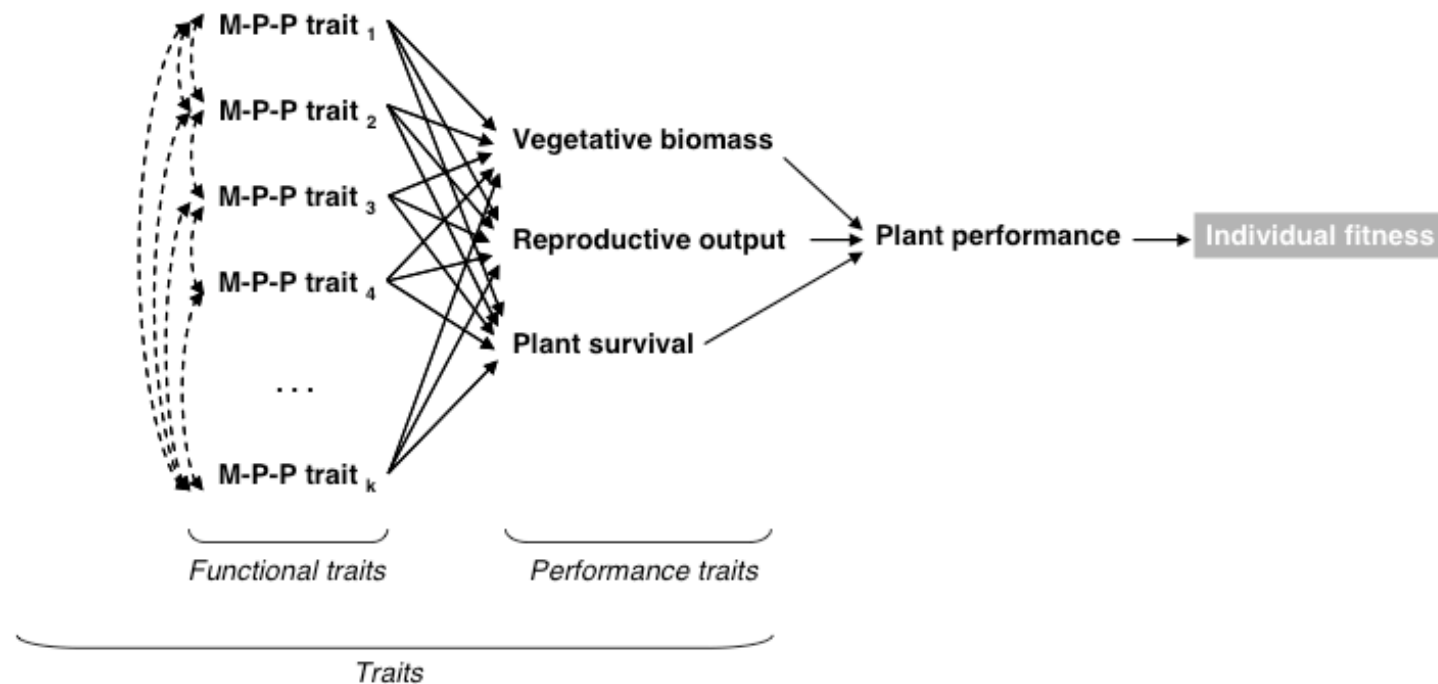


Fig. 3. Arnold's (1983) framework revisited in a plant ecology perspective. Morpho-physio-phenological (M-P-P) traits (from 1 to k) modulate one or all three performance traits (vegetative biomass, reproductive output and plant survival) which determine plant performance and, in fine, its individual 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.

$$\text{CFP}_j = \sum_{k=1}^{n_j} A_{k,j} \times \text{ET}_{k,j} \quad (4)$$