

The Reconciliation of the r-K, and C-S-R-Models for Life-History Strategies

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Abstract. The author attempts to accomplish a reconciliation of the r-K and C-S-R models to identify life-history strategies. He mapped the primary and secondary strategies of the latter model in the linear r-K continuum, using his algorithm COMPTO, for multi-attribute decision-making. He proposes a reinterpretation of the r-K model that accommodates the seven life-history strategies depicted by the C-S-R model.

Key words: C-S-R model; epistemic reconciliation; life-history strategy; r-K model

Uma Reconciliação dos Modelos r-K e C-S-R para as Estratégias Bionómicas

Sumário. O autor propõe uma reconciliação dos modelos r-K e C-S-R, para as estratégias bionómicas. Faz o mapeamento das estratégias primárias e secundárias do segundo modelo no contínuo linear r-K, recorrendo ao seu algoritmo COMPTO, para tomada de decisão em situações de atributos múltiplos. Apresenta uma reinterpretação do contínuo r-K que acomoda as sete estratégias bionómicas do modelo C-S-R.

Palavras-chave: estratégias bionómicas; modelo C-S-R; modelo r-K; reconciliação epistémica

Une Réconciliation des Modèles r-K et C-S-R pour les Stratégies Biologiques

Résumé. L'auteur propose une réconciliation des modèles r-K et C-S-R pour les stratégies biologiques. Il fait la transposition des stratégies primaires et secondaires du modèle C-S-R dans le continuum linéaire r-K, utilisant son algorithme COMPTO. Il présente une réinterprétation du continuum r-K qui accommode les sept stratégies biologiques du modèle C-S-R.

Mots clés: modèle C-S-R; modèle r-K ; réconciliation épistémique; stratégies biologiques

Introduction

KREBS (1994) defines ecology as the *scientific study of the interactions that determine the distribution and abundance of organisms*. This definition implicitly accepts that the distribution of organisms in the several environments of the Earth

is not stray or lawless, and it satisfies certain rules that ecology seeks to unveil. Thus, the study of life-history strategies (LHS) is in the core of ecology.

The models of LHS try to map environmental attributes in the space of biological traits of a species. LHS can assume the form of a regularity or law,

such as: "Environments with attributes e_1, e_2, \dots, e_n are populated by organisms with traits t_1, t_2, \dots, t_m ". Alternatively, it can be stated: "Organisms with traits t_1, t_2, \dots, t_m occupy environments with attributes e_1, e_2, \dots, e_n ".

Consensus omnium, these two equivalent laws substantiate the fundamental assumption of ecology: *environments and organisms are nomologically or lawfully related*.

It is not surprising that several authors, from different perspectives, approached the LHS issue (CRAWLEY, 1997; GRIME, 1997). Two of the most known classifications of LHS are the *r-K continuum*, seminally advanced by MacARTHUR and WILSON (1967), and the *C-S-R model* proposed by Grime, and latter well developed and illustrated in his book (GRIME, 1997).

Unity and integration is an inherent attribute of science. Its objectivity cannot tolerate the correctness of more than one theoretical non-reducible explanation for a given set of phenomena. As the same body of biological and ecological knowledge underpins models r-K and C-S-R, it must be possible to harmonize them. Otherwise, one of them must be rejected.

GRIME (1997), in pages 110-112 of his book, already attempted a preliminary reconciliation of these two models.

Tentatively, in this paper, I will expand Grime's effort. As a forester, I will use the classifications of the LHS of trees, and I will take also advantage of my background both in forest ecology (M.F., DUKE, 1968), and operations research applied to forestry (Ph. D., DUKE, 1970). Is this elaboration an interdisciplinary approach?

More specifically, here, I will attempt to establish an isomorphic mapping of the C-S-R classifications of European tree

species into the r-K continuum.

Inevitably, this reconciliation requires a reinterpretation of the r-K continuum.

As the two classifications use the same descriptive concepts, I will not accomplish a reduction (epistemic operation) but only a trivial reduction or reconciliation (AMSTERDANSKY, 1996). For an epistemological evaluation of classification see GIL (2000), and for its status and role in biology see MANHER and BUNGE (1997).

This article is a revised version of BARRETO (2003).

A Strategy for Analysis

To insert the species classified by C-R-S model into the r-K continuum, first, I must accomplish the following:

1. Put a scale in the continuum.
2. Reduce the several attributes of the C-S-R classes to a figure of the previous scale.

There is not a real pure r-strategist or K-strategist. LHS do not represent an optimum of adaptation to a given environment *sensu lato*, but a compromise solution for the several problems faced by the organisms of a species (CRAWLEY, 1997). Thus, I must create two polarized archetypes: one for the r-strategist, and another one for the K-strategist. I will describe the archetypes I developed in due time.

The scale for the r-K continuum is defined as the *relative proximity* p to these two archetypes. The p to the r-archetype is designated rp , and to the K-archetype Kp . For a given point in this scale it is observed $rp+Kp=1$. From here on, I will refer only to Kp . The higher is its Kp , the closer is a species to the paradigm of the K-strategist. Obviously, for the r-archetype $Kp=0$, and for the

K-archetype $K_p=1$.

To evaluate K_p I will use an algorithm I proposed a few years ago, named COMPTO (BARRETO, 1994), to generate solutions to a particular class of problems, in multi attribute decision-making. It integrates two procedures previously established by other authors: the entropy measure of importance (ZELENY, 1982), and a procedure named "Technique for Order Preference and Similarity to Ideal Solution, TOPSIS" (HWANG and YOON, 1984).

Algorithm COMPTO let me use weights (levels of importance) of the attributes of the objects (species), I am ordering in the continuum limited by the two polarized archetypes. In my analysis, I assumed equally important attributes of the species. Thus, the core of the analysis lies in the procedure TOPSIS, whose description, in English, can be find in the reference upper mentioned.

After we had chosen the attributes, units, weights, established the two polarized ideal solutions, and characterized the objects of choice, algorithm COMPTO has the following steps:

- a) Calculation of the entropy measure of the distances.
- b) Calculation of the Euclidian proximities.
- c) Calculation of the relative proximities.

The Reconciliation of a C-R-S Classification of trees

BRZEZIECKI and KIENAST (1994; BK) used the C-S-R model to classify 36 European tree species. They defined 11 attributes to characterize the ontogenesis (6 growth+5 reproduction), and more 12 ecological attributes. They used multiva-

riate statistical methods to isolate the classes of species (primary and secondary strategies). They verified that only the six growth attributes were enough for the correct ordination of the species. The vector of the growth attributes is the following one:

DMAX, maximum dbh, cm; HMAX, maximum height, cm; AMAX, maximum age, years; GMAX, growth constant (BOTKIN *et al.*, 1971); WDEN, wood density, kg/m³; WRES, wood decay resistance, 1, low, 5, high.

To apply algorithm COMPTO, I used the values of this attributes in Appendix I of BK's paper, and I established the following archetypes:

$r=[50, 20, 60, 300, 300, 1]$; $K=[200, 50, 800, 49, 700, 5]$

This classification is called **CLBK6**.

After, I used again my algorithm with the following attributes:

AMAX; GMAX; ILIGHT, shade tolerance index, 1, tolerant, 5, intolerant; SMINP, age of first seed production, years.

I replaced four growth attributes by one reproductive trait (SMINP), and one ecological trait (ILIGHT).

The archetypes defined are:

$r=[60, 300, 5, 5, 1]$; $K=[800, 49, 1, 100]$

This classification is designed **CLBK4**.

The values of K_p associated to CLBK6, K_{p6} , and CLBK4, K_{p4} , and the classifications made by BK, LHS, are exhibited in Table 1.

Let elaborate a few pertinent comments on table 1. My understanding is that CLBK4 gives the best results, although their values are very close. For instance, the values of K_{p4} for the S strategists are more coherent then those generated by CLBK6. In the following comments I will refer to K_{p4} , and LHS.

There are 13 discrepancies in the attempted reconciliation.

Table 1 - The reconciliation of the C-S-R and r-K models when applied to 36 European tree species

Species	Kp ₄	Kp ₆	LHS
R, ruderals			
<i>Salix caprea</i>	0.02939	0.00277	R
<i>Salix alba</i>	0.06519	0.07836	R
<i>Malus sylvestris</i>	0.06979	0.06979	S-R
<i>Populus tremula</i>	0.07272	0.07164	R
<i>Sorbus aucuparia</i>	0.07765	0.02623	S-R
<i>Prunus padus</i>	0.07982	0.06384	S-R
<i>Alnus incana</i>	0.08240	0.07433	R
<i>Pyrus communis</i>	0.09784	0.09147	S-R
<i>Sorbus terminalis</i>	0.10138	0.08571	S-R
<i>Betula pendula</i>	0.10654	0.10070	R
<i>Betula pubescens</i>	0.10654	0.10070	R
S-R, stress-tolerant ruderals			
<i>Acer Campestres</i>	0.11911	0.10995	S-R
<i>Sorbus ária</i>	0.12755	0.11411	S-R
<i>Alnus glutinosa</i>	0.15342	0.15549	R
<i>Populus nigra</i>	0.15446	0.17871	R
<i>Prunus avium</i>	0.18513	0.18064	S-R
<i>Populus alba</i>	0.22855	0.26363	R
C, competitors			
<i>Picea abies</i>	0.38991	0.37800	C-S
<i>Carpinus betulus</i>	0.39197	0.37421	C
<i>Ulmus laevis</i>	0.39920	0.38527	C
<i>Fraxinus excelsior</i>	0.41772	0.43085	C
<i>Acer platanoides</i>	0.44335	0.44471	C
<i>Juniperus communis</i>	0.44857	0.42636	S
<i>Acer pseudoplatanus</i>	0.45875	0.43884	C
<i>Ulmus minor</i>	0.48918	0.48918	C
C-S-R, competitive stress-tolerant ruderals			
<i>Larix decidua</i>	0.52947	0.66625	C-S-R
<i>Tilia platyphyllos</i>	0.54261	0.43572	C
<i>Tilia cordata</i>	0.56569	0.45806	C
<i>Pinus sylvestris</i>	0.60251	0.68032	C-S-R
C-S, stress-tolerant competitors			
<i>Ulmus glabra</i>	0.62458	0.64261	C
<i>Fagus sylvatica</i>	0.63169	0.43069	C-S
<i>Quercus robur</i>	0.72872	0.77824	C-S
<i>Quercus petrae</i>	0.74988	0.78224	C-S
<i>Abies alba</i>	0.77728	0.583320	C-S
S, stress-tolerators			
<i>Taxus bacata</i>	0.84434	0.76318	S
<i>Pinus cembra</i>	0.88839	0.76518	S

Eight of them are between the strategies R and S-R. It is not easy to discriminate between these two groups.

Both applications of the algorithm COMPTO classify *Juniperus communis* as competitor, and not as stress-tolerant. This is the only discrepancy between to primary strategies.

There are two discrepancies related to C, and C-S species.

Tilia platyphyllos, and *T. cordata* are classified as C-S-R, and not as C..

Table 1 confirms the outline of reconciliation exhibited in figure 39 in GRIME (1997).

To allow a more comprehensive interpretation of table 1, I exhibit the mean values of the traits used in CLBK4, in table 2.

Table 2 shows the following:

F1. AMAX increases from r to K

F2. GMAX decreases from r to K.

F3. The behaviour of ILIGHT, and SMINP is less regular. The values of these traits, for K-1 strategists violate the pattern.

The complete clarification of these findings requires an individual analysis of each species, and more species of K-1 strategists.

An Ideal Model for Reconciliation

Let me figure an ideal reconciliation, where the space 0-1, in the r-K

continuum, is equally appropriated by the seven strategies recognized by Grime's model. In this situation the middle value of **Kp** of each class will be as follows:

R, $Kp=0.071$; S-R, $Kp=0.214$; C-R, $Kp=0.357$; C, $Kp=0.500$; C-S-R, $Kp=0.643$; C-S, $Kp=0.786$; S, $Kp=0.928$

The mean values of **Kp₄**, of the groups in table 1, are:

R, 0.081; S-R, 0.161; C-R is not represented; C, 0.430; C-S-R, 0.560; C-S, 0.702; S, 0.866.

The relative proximities are sensitive to the values of the attributes of the species, and to those of the archetypes. The analytical tools used to classify species characterised by multi attributes give relative classifications. There are not absolute classifications.

A Reinterpretation of the r-k Continuum

The reconciliation previously developed can be used for the benefit of the interpretation of the r-K continuum. It is clearly admissible to state that in this continuum there is place to accommodate rich panoply of plants with different traits, and, thus, adapted to several environments, *sensu lato*.

For the sake of rigor and correspondence, in the next statements I will follow closely the descriptions of habitats presented by GRIME (1997).

Table 2 - Mean values of **Kp₄**, and of the traits of the strategies depicted in table 1, associated to CLBK4

Strategy	Kp ₄	AMAX	GMAX	ILIGHT	SMINP
R	0.081	93.0	210.7	4.2	21.4
S-R	0.161	141.7	155.7	4.2	26.4
C	0.430	331.2	103.4	3.0	40.6
C-S-R	0.560	412.5	87.2	3.7	35.0
C-S	0.702	430.0	86.9	2.4	66.0
S	0.866	500.0	37.9	2.0	75.0

Environment I : places with both high intensity of disturbance and productivity.

Environment II: habitats lightly disturbed, but with low productivity.

Environment III: habitats where disturbance brings competition to a moderate level, and the effect of stress is low.

Environment IV: habitats showing low disturbance, and high productivity.

Environment V: environments where moderate levels of both disturbance and stress restrain the intensity of competition.

Environment VI: environments where a moderate intensity of stress, and a situation of relative-undisturbance prevail.

Environment VII: habitats with low productivity and low level of disturbance.

My reinterpretation of the r-K continuum, and my reconciliation of the two models are presented in Table 3.

A more suggestive representation of the reconciliation is displayed in Figure 1.

Probably, there is a problem of semantics, in this issue.

Table 3 - The reinterpretation of the r-K continuum, and the reconciliation of this model with model C-S-R

Environment	Theoretical Kp	LHS of the r-K Model	LHS of the C-S-R Model
-	0	r-archetype	-
I	0.000001-0.142857	r-3	R
II	0.142858-0.285714	r-2	S-R
III	0.285715-0.428571	r-1	C-R
IV	0.428572-0.571428	r↔K	C
V	0.571429-0.714285	K-1	C-S-R
VI	0.714286-0.857142	K-2	C-S
VII	0.857143-0.999999	K-3	S
-	1	K- archetype	-

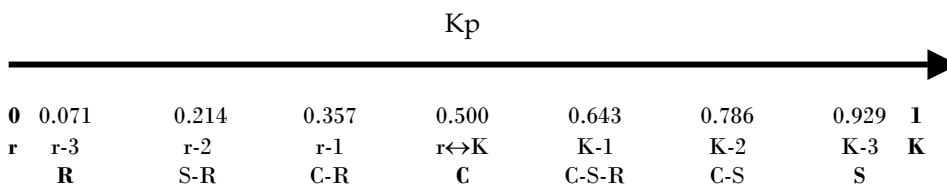


Figure 1 - A tentative reinterpretation of the r-K continuum. See the text for the meaning of the symbols

Final Comments

I close this paper with the following conclusive remarks:

C1. Probably, only a parsimonious number of (*strategic or primary*) attributes of the species are enough to depict the LHS of plants, if adequate and efficient analytical tools are used (table 1).

The distinction between primary or strategic and secondary traits is defensible because it is observed that there are not pure strategists, and some species have traits admitted to be strategically antagonist. I admit that BK's paper also points in this direction.

C2. The complete reconciliation, or equivalence, between the r-K and C-S-R models was established. The triangular space of the C-S-R strategists can be mapped into the linear r-K continuum, without loss of information (table 3, figure 1).

C3. It deserves to be mentioned that ecology, as a science, is the greatest beneficiary of the reconciliation I attempted to accomplish. Its coherence and consistency was evinced, and eventually strengthened.

References

- AMSTERDANSKY, S., 1996. Redução. In *Enciclopédia Enaudi. Volume 33. Explicação*. Imprensa Nacional – Casa da Moeda, Lisboa, Portugal. pp. 478-491.
- BARRETO, L.S., 1994. *Alto Fuste Regular. Instrumentos para a sua Gestão*. Publicações Ciência e Vida, Lda., Lisboa, Portugal.
- BARRETO, L.S., 2003. *The Reconciliation of the r-K, and C-S-R Models for Life-History Strategies*. Research Paper SB-01/03. Departamento de Engenharia Florestal, Instituto Superior de Agronomia, Lisboa.
- BOTKIN, D.B., JANAK, J.F., WALLIS, J.R., 1971. *Some Ecological Consequences of A Computer Model of Forest Growth*. IBM Research, RC 3493, IBM Thomas J. Watson Research Center, Yorktown Heights, U.S.A.
- BRZEZIECKI, B., KIENAST, F., 1994. Classifying the Life-History Strategies of trees on the Basis of the Grimean Model. *Forest Ecology and Management* **69** : 167-187.
- CRAWLEY, M.J., 1997. Life History and Environment. In M.J. Crawley, Ed., *Plant Ecology*, second edition. Blackwell Science, Oxford, United Kingdom. pp. 73-131.
- GIL, F., 2000. Classificações. In *Enciclopédia Enaudi. Volume 41. Conhecimento*. Imprensa Nacional – Casa da Moeda, Lisboa, Portugal. pp. 90-110.
- GRIME, J.P., 1997. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. Second edition. John Wiley & Sons, Ltd, Chichester, United Kingdom.
- HWANG, C.L., YOON, K., 1984. *Multiple Attribute Decision Making*. Springer-Verlag, New York, U.S.A.
- KREBS, C.J., 1994. *Ecology*. Fourth edition. Harper Collins, New York, U.S.A.
- MACARTHUR, R.H., WILSON, E.D., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, U.S.A.
- MAHNER, M., BUNGE, M., 1997. *Foundations of Biophilosophy*. Springer-Verlag, Berlin, Germany.
- ZELENY, M., 1982. *Multiple Criteria Decision Making*. McGraw-Hill, New York, U.S.A.

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