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Biological self-organization and environment mediated transience in plant communities. What are the rules?

by

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Abstract. Historic and current ecological functionalities are the paper's central topics. These affect self-organization in community assembly and mediate disassembly. Much is known about the process governance rules and it is intuitive that natural governance cannot be purely random. If governance is other than completely random, then what is it? The paper describes a novel approach to identify high-level assembly/disassembly rules. It uses diagnostic 'signals' from three information sources: phylogeny, current environment, and stochasticity (symbolically *PGS, CES,* and *e*, respectively). An important property of the sources is the convolution of their effects. The paper proposes a model for this in the manner of signal superposition into total signal, *TS=PGS+CES+e.* By reasoning from facts, the paper concludes that the total signal is linked to modulation of the changing community's diversity amplitude, *PGS* to inherent self-organization, and *CES* to current environmental mediation. Signal *e* is associated with random events in community and environment. As such it is confounding both *PGS* and *CES* and controls the level of random oscillations in self regulation and environment based species trait selection and sorting on a scale from weak to near chaos. Reasoning from *TS's* link with diversity modulation hands us scalar functions on the basis of which *TS* can be measured and a signal isolation algorithm can be constructed.

Regarding the contents, the paper begins with a set of propositions which define the context of problem definition and conceptualization of the solution. Laying the theoretical foundations for signal isolation and scaling, presentation of techniques, and comprehensive discussion of an éclat example from the highly dynamic Coquihalla River floodplain[1] in British Columbia make up the paper's main text. Key literature references, and appendices of the complete numerical results round out the contents.

1 A natural forest preserved in 1975, now a residential district of Hope.

Keywords: Community assembly/disassembly, Coquihalla floodplain, Dendrogram, Diversity moderation, Evolution, Environmental mediation, Environmental signal, Governance rules, Hierarchical relevé, Partial correlation, Partial variance, Phylogenetic signal, Phylogenetic tree, Scaling functions, Signal isolation, Vegetation.

Abbreviations: CES–Current Environmental Signal, PGS– PhyloGenetic Signal, TS–Total Signal.

1

Propositions

From the results presented in the paper we have drawn specific generalizations about the assembly/disassembly rules of plant communities. We note that we consider point processes in landscape terms, therefore by definition community assembly and disassembly must occur in tandem. A consequence of this is that in reality assembly and disassembly in Nature are the same process as "succession". The process rules we state below as propositions were intended to apply in this particular context. The propositions:

1. Community assembly/disassembly is a complex-systems functionality. It is governed by system-level natural rules for which the phylogenetic signal *PGS,* the current environmental signal *CES,* and *e,* a signal associated with random events, are diagnostic.

2. Signals *PGS, CES,* and *e* occur in convolution for which the proposed model is *TS=PGS+CES+e.* The model implies linear superposition of the signals. The model does not have nor does it need an interaction term.

3. The intensity of *PGS* is indicative of the intensity of self-organization in the community forced by the interactions of the community elements.

4. The intensity of *CES* is indicative of the level of environment mediated transience in the community.

5. Consistent with the linear superposition model, two additional generalizations are suggested:

   a. When *PGS* is the dominant signal (relative to *CES*) and the *e* signal is intense, highly turbulent interactions and commensurably high community stability are expected.

   b. When *CES* is the dominant signal (relative to *PGS*) and the *e* signal is weak, transiency is intense and community instability is elevated.

In summary, while the *PGS* signal is symptomatic of the governance of self-organization in the community, the *CES* signal is symptomatic of controls in environmental mediation of community transiency.

2

Further on signal sources

We already identified the signals, now we consider sources in somewhat more detail:

1. Signal PGS. The source is the *historic phylogenetic process.* It is responsible for speciation and rather directly for the enriching the global flora. We stress that the basic taxonomic unit in the present study, unlike in earlier works which form the conceptual basis of signal isolation in this paper, and in which we used taxa that were character set types (Orlóci and Orlóci 1985, Orlóci 1991, Pillar and Orlóci 1993), at this time the taxa we use are Mendelian species. Why do we need Mendelian species? Simply stated, the definition of *PGS* and its isolation requires the taxa to be meaningful evolutionary units. Further, in signal isolation and scaling we rely on a *taxonomic dendrogram* as proxy for the *true phylogenetic tree*[2]. On this topic we refer the reader to text which presents syntheses of the evolutionary principles (Huxley 1942, Dobzhansky 1937, Stebbins 1950, Mayer 2002, Mayer and Provine 1998, Podani 2003, 2010).[3]

2. *Signal CES.* The source is the *current environmental mediation of community transience.* The signal is thus related to species trait selection, and in an indirect sense, the assortment of species traits over the landscape points into environment specific plant communities. Two points need further clarification. 'Current' is emphasizing that the environmental mediation we mention is in the 'now' *vis a*

2 The following text is quoted from http://en.wikipedia.org/wiki/Phylogenetic_tree : "A phylogenetic tree or evolutionary tree is a branching diagram or tree showing the inferred evolutionary relationships among various biological species or other entities based upon similarities and differences in their physical and/or genetic characteristics. The taxa joined together in the tree are implied to have descended from a common ancestor. In a rooted phylogenetic tree, each node with descendants represents the inferred most recent common ancestor of the descendants, and the edge lengths in some trees may be interpreted as time estimates. Each node is called a taxonomic unit. Internal nodes are generally called hypothetical taxonomic units (HTUs) as they cannot be directly observed. Trees are useful in fields of biology such as systematics and comparative phylogenetics."

3 The importation of evolutionary principles into plant taxonomy is an ongoing process ever since the seminal work of G. Bentham and J.D. Hooker (1862-1863), the first to break with the numerical system and adopt the Darwinian principles in plant taxonomy. The rules formalised gradually based on a synthesis of all evolutionary theories (Stebbins 1950) and reached mathematical definitions in Cladistics (Henning 1966, Singh 2004, Podani 2003, 2010) applying the tools of numerical taxonomy.

vis the process of 'speciation' which as it applies in our problem is in the long past. Considering that we are dealing with environmental mediation as a point process, the two processes highlighted by *PGS* and *CES* meet in the present where the species traits for which evolution is responsible are being selected and assorted by the other process, environmental mediation. The sources meeting at just one point in time, *PGS* and *CES* justifiably considered practically independent in the signal isolation problem.

3*. Uncontrollable random variation.* This is the source for *e*, encompassing all random behaviour in the plant community and environment. This source makes *TS* fuzzy and its perception as a directed (non-random) signal stream proportionately more difficult.

An important property of the sources is the superposition of their effects into a common forcing process which modulates the amplitude of species trait diversity in the community. Significantly, the diversity connection hands us scaling functions and an effective signal isolation algorithm. The framing of signal isolation in these terms is completely unlike in early attempts which Revell et al. (2008) categorically rejected.

3

Pillars of signal analysis

It flows directly from what has already been said that there has to be access to several attributes to make possible signal isolation and scaling:

1. *A species list amended with abundance estimates*. Abundance refers to any of the variables applied by Ecology (Orlóci 2010) ranging from cover/abundance (C/A) to mass or volume based biomass.

2. *A long and sharply formed environmental gradient.* The user defines the gradient and based on careful planning populates the gradient with areal sampling units, such as the ecologist's quadrats or sample plots. Gradient length is relative to the ground scale of the vegetation and environmental pattern (Greig-Smith 1952). The variance of the dominant gradient variable *U* is a measure of the gradients sharpness.

3. *An evolutionary plant taxonomic system.* It has to be assumed that species identification is based on a taxonomic system. Only when we use an evolutionary taxonomic system can we identify Mendelian species traits and construct a *taxonomic dendrogram* which may qualify as proxy for the *true phylogenetic tree.*

4. *An algorithm of signal isolation.* Our method for this is in fact relatively straight forward. Variance partitions are involved under constraints similar to what has already been discussed in earlier papers (Orlóci and Orlóci 1985, Orlóci 1991, Pillar and Orlóci 1993).

4

Justification of the linear superposition model

The model is *TS=PGS+CES+e,* a conceptualisation of how the different signals stack up. The reader may be wondering why the model does not include at least one product term. Not having such a term implies the assumption of the linear independence of the signals. We already explained that signal independence should not be seen as a far fledged expectation if one considers the fact of time separation of the signal sources for *PGS* and *CES*.

We mentioned also that variation along the environmental gradient is in the present, environmentally mediated selection of species traits from the available flora and assortment is very much 'current', but the evolutionary origin of the species traits that make up the local flora is far history (see section above). Questions could of course be posed to the effect that since different traits of the same species may populate different habitats, the adaptive process which produced the traits had to be linked to habitat conditions modelled on the existing ones. In other words, speciation must be in progress. These are all true, but in all likelihood the traits being currently recorded long existed and must have been the object of sorting cycles into progressively assembled and disassembled communities, including also the ones which presently exist, if by no other forcing than the feedback loop of Kernerian facilitation (Kerner 1863). Therefore, the process that produced the traits and the process which mediated current selection and assortment have to be considered independent in time.

Yet another question could bring up the fact that the species traits subjected to current environmentally mediated selection and assortments are the products of the process which gave rise to *PGS,* and for that reason the existing species traits establish a link between *PGS* and *CES*. The point here is that *PGS* and *CES* meet at one time point: the species traits which phylogeny produced in the long past are subjected to environmental mediated selection and assortment in the present. Before that singular point in time, the two processes have never met. Having said this, we are justified to regard *PGS* as being symptomatic of complex-system type self-regulation. This is different from what *CES* is involved with, namely environmental mediation, for which a typical feedback mechanism is Kernerian facilitation.

5

A path to the past – the hierarchical relevé

Each sampling unit is described by a record set called *relevé*. The most unique aspect of the Coquihalla relevés is the incorporation of a taxonomic dendrogram. Such a relevé is called a *hierarchical relevé* (see Figure 1).

The dendrogram has *m* levels (e.g., Species, Genus, Family, Class, Order, …). Each species is mapped into the dendrogram by Mendelian characters through the nodes and given an estimate of abundance *X*. Clearly when a species is found within a sample plot, *X* will be greater than zero. We re-emphasise that the hierarchical relevé amalgamates two components, the species mappings (dendrogram) and the abundance values (**X**) in a seamless manner.

In the discussed case, the dendrogram is based on an evolutionary taxonomic system and for that reason it may be used as proxy for the phylogenetic tree. But can a dendrogram which only includes the species found within a vege-

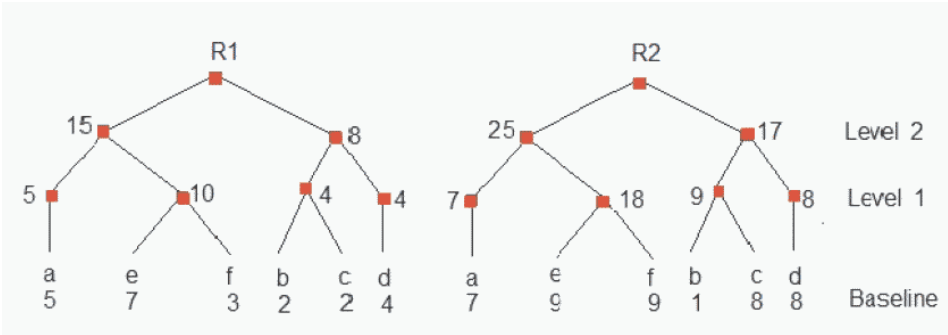

Figure 1. Two hierarchical record sets (relevés) are shown, *R1* and *R2.* The fictitious 2+1 level dendrogram incorporates 2 "Level 2" taxa (e.g., families), 4 "Level 1" taxa (e.g., genera), and 6 baseline taxa (e.g., species) a,b,c,d,e,f. The scheme is the same in *R2* as in *R1*, only the baseline data are different. The base line taxon abundance may be measured on any of different, case-specific scales. Baseline (0 level) data sets in the dendrograms: *[5 7 3 2 2 4]* and *[7 9 9 1 8 8].* Level 1 cumulants: *[5 10 4 4]* and *[7 18 9 8].* Level 2 cumulants: *[15 8]* and *[25 17].*

tation stand give us other than trivial information about the phylogenetic tree? This is true, it cannot. But the relevant point is the relevé sample's ability to give an unbiased description the vegetation. It has to be seen whether the description is biased or unbiased will depend on the sampling technique. If the sampling technique is statistical (see Orlóci 2010), the information about the description is unbiased, and by definition the dendrogram is a reliable proxy for the phylogenetic tree. But the accuracy of the proxy will depend on sample size and in our specific case on how sufficient is the length and sharpness of the gradient, in other words how well the transect captures the breadth of floristic and environmental variation within the broader landscape.

We do not analyse the basic sampling units individually. We pool adjacent sampling units into super stands, called *metacommunities.* The larger the metacommunity, the larger is the number of species and the greater is the statistical accuracy of the dendrogram to be a strong proxy. Since the dendrogram is constructed to accommodate all species in the sample, its accuracy reaches maximum when all sampling units are pooled into a single metacommunity.

At the sampling level, the elements of **X** are species abundance values estimated within the sampling units (quadrat, sample plot). After pooling the sampling units, the number of species mapped into the dendrogram may increase, and the baseline data may change. The baseline data **X** and the data cumulants at the dendrogram nodes are the basis of all analyses performed at any metacommunity size.

6

Scaling the total signal *TS*

Preliminaries

We already defined *TS* as a sum *PGS+CES+e.* We explained that in the linear superposition model *PGS* is linked directly to community self-organization, but independent from the confounding *CES,* which we associate with current environmental mediation of the assembly/disassembly process. As explained, we associate *e* with random events. We mentioned also that *TS* is directly scalable based on its link to diversity amplitude modulation within the metacommunity.

Regarding the scaling of *TS,* we observe

$TS_i=PGS_i+CES_i+e_i,\ i=0,1,2\ldots,m$

that is,

$TS=TS_0+TS_1+TS_2+\ \ldots+TS_m$

Clearly, the series

$[TS_0\ TS_1\ TS_2\ \ldots\ TS_m]$

defines an *m*-valued *temporal conditional (partial) diversity amplitude stream*. It should be noted that a suitable scaling function for *TS* should allow *m*-valued additive partitions. This condition limits our choice to three possible scaling functions:

1. *Probability.* The scaling function is a conditional probability and the series of vector elements

$[TS_0\ TS_1\ TS_2\ \ldots\ TS_m\ ]$

is a *temporal conditional probability stream.* Regarding the conditional probability concept we refer to text published elsewhere (e.g., Orlóci 2006).

2. *Logarithmic probability*. Rényi's (1961) *partial entropy of order one* (the partial Shannon diversity measure) is an example. The resulting

$[TS_0\ TS_1\ TS_2\ \ldots\ TS_m\ ]$

is a *temporal partial entropy stream* (Orlóci 2006, 2010).

3. *Sum of squares and products.* In these cases, the series

$[TS_0\ TS_1\ TS_2\ \ldots\ TS_m]$

is a *temporal partial sum of squares stream* expressible also in the form of a *temporal partial variance stream* (see definition below).

We chose scaling functions from the last category, the same as in the Pillar and Duarte (2010) paper.[4] Our scheme differs in that it is formulated about the hierarchical relevé type description of the metacommunity. When there are *q* metacommunities, there will be *q* temporal partial variance streams and *m spatial partial variance streams*. Under the same conditions, we will have *q(q-1)/2* distinct partial covariance streams. We present the former in matrix form:

$$\begin{bmatrix} V_{10} & V_{20} & \ldots & V_{q0} \\ V_{11} & V_{21} & \ldots & V_{q1} \\ V_{12} & V_{22} & \ldots & V_{q2} \\ \ldots & \ldots & \ldots & \ldots \\ V_{1m} & V_{2m} & \ldots & V_{qm} \end{bmatrix}.$$

In analytical terms, the hierarchical partition model that hands us the elements in the *spatial partial variance streams* has ecological precedent in Greig-Smith's (1952) variance based and Orlóci's (1971) information theoretical pattern analysis. The hierarchical relevé model as presented in this paper and the temporal partial variance and covariance streams have analogues in the schemes applied by Orlóci and Orlóci (1985), Orlóci (1991, 2010), and Pillar and Orlóci (1993). The modification is in the unbalanced hierarchical embedding of taxa in the *m*-level dendrogram. The scaling functions presented in the sequel make this property of the analysis uniquely clear.

4 The Pillar-Duarte solution for signal isolation is based on three matrices of the metacommunity: *Matrix* **P –** the metacommunity's species composition. The species are given weighs according to phylogenetic trait which references the position of the species in the proxy taxonomic system. *Matrix* **T -** the metacommunity's mean vector of the functional traits of the species. *Matrix* **E** (not our *E or e)* – sample unit positions relative to an environmental gradient taken as the level of environmental effect. Within their solution, the correlation of **T** and **E,** when not trivial, supports the conjecture **E**→ **P** →**T**, that is: environmental selection of species in plant community assembly is equivalent to selection of functional traits mediated by the phylogeny of the species.

Scaling functions

The following definitions are applicable for a single hierarchical relevé of the metacommunity:

1) $S_0^2 = \sum_{j=1}^{k_0} \left(X_{0j} - \overline{X}_0 \right)^2$.

This is the total sum of squares; symbol $\overline{X}_0$ is the mean of k_0 values and X_{0j} is the *jth* element in base line **X.**

2) $S_i^2 = \sum_{j=1}^{k_i} n_{1j} \left(\frac{X_{ij}}{n_{ij}} - \overline{X}_0 \right)^2$.

This is the sum of squares based on the cumulants on dendrogram level *i;* symbol $\overline{X}_0$ is the mean of k_0 values in baseline **X**, X_{ij} a cumulant at the jth node hierarchical level *i,* and k_i the number of nodes on level *i* (see Figure 1).

3) $TS_i = S_i^2 - S_{i+1}^2$.

This is the *i*th value in the *m*-valued temporal partial sum of squares stream [TS_0 TS_1 TS_2 … TS_m]; TS_i is the diversity amplitude increase brought on when the *i+1* level taxa are split into the *i* level taxa*,* such as genera into species, family into genera, and so forth.

By definition, $TS_m = S_m^2$. The set [TS_0 TS_1 TS_2 … TS_m] is by implication a proxy map of the *temporal partial sums of squares* stream in the phylogenetic process. After division of the elements by the degrees of freedom, as in $V_i = TS_i/(k_i - 1)$ we have the temporal partial variance stream [V_0 V_1 V_2 … V_m]. We take this as a proxy mapping of the total signal stream through the nodes of the phylogenetic tree. We note for the sake of completeness that in the sample of *n* hierarchical relevés, k_i and n_{ij} remain unchanged. In other words, the design of the dendrogram is rigidly fixed to the sample's species list.

The temporal partial sum of squares stream [TS_0 TS_1 TS_2 … TS_m] is a *characteristic profile* of the *m*-level dendrogram of the metacommunity. The matrix [TS_{izy}], i=0,1,2,...,m, $z \neq y$ is a characteristic profile too, but in this the elements are partial sums of products specific to the hierarchical relevés of two metacommunities *z* and *y.* The defining equations are:

$$S_{izy} = \sum_{j=1}^{k_i} n_{ij} \left(\frac{X_{ijz}}{n_{ij}} - \overline{X}_{0z} \right) \left(\frac{X_{ijy}}{n_{ij}} - \overline{X}_{0y} \right) ,$$

$$TS_{izy} = S_{izy} - S_{i+1zy} ,$$

and

$$r_{izy} = \frac{TS_{izy}}{\sqrt{TS_{iz}TS_{iy}}}$$

The latter is a standardised co-linearity scalar known as the *partial correlation coefficient.* As defined, two metacommunities *z* and *y* are compared on dendrogram level *i*. The values of *r* range from -1 to 1. A zero value indicates no relationship, positive *r* indicates co-linearity, a form of convergence or parallelism, and negative *r* signifies proportionately intense divergence, that is, the proportional lack of positive co-linearity. The *m* sets of *q(q-1)/2* distinct correlation values can be presented for further analysis by multivariate methods (Orlóci 2010).

7

Signal isolation

As the first step in signal analysis, we pool all hierarchical relevés on the gradient into a single metacommunity with its own hierarchical relevé. We compute the temporal partial variance stream for this the same way as before:

$$\begin{bmatrix} V_{0pooled} \\ V_{1pooled} \\ \dots \\ V_{mpooled} \end{bmatrix}$$

This is the best proxy temporal partial variance stream we can get in the sample. Forging on with the calculations, we compute an *m*-valued *temporal partial variance stream* for each of the metacommunities of the *q* gradient segments. We present these as columns in matrix **V** (see above). With this step, we have all ingredients (the pooled temporal variance stream $\mathbf{V}_{pooled}$, the *m* spatial variance streams in the rows of matrix **V**, and the gradient variable *U*) needed to proceed to the next step in signal isolation: computation of the gradient based slopes of the *m* spatial partial variance streams.

For the ith of these, the gradient partial variance slope is

$$\alpha_i = abs\,arc\,tan\left(\frac{\sum_{j=1}^{q}\left(V_{ij}-\overline{V_i}\right)\left(U_j-\overline{U}\right)}{\sum_{j=1}^{q}\left(U_j-\overline{U}\right)^2}\right),\ i=0,1,\ \dots,\ m.$$

Symbols $\overline{V_i}$ and $\overline{U}$ represent mean values. The tan a_i quantity is best to obtain as a linear regression coefficient (usual symbol *b*). Regression analysis, performed on each of the *m* rows in matrix **V** using *U* as the *x* variable, hands us as a bonus some useful statistics as seen in the results.

We consider further the *m*-valued vector of regression coefficients **b**. From this using the *abs arc tan b* transformation we obtain an *m*-valued angles vector α. Based on α, two sets of *m* quantities are computed*:*

$PGS_i = V_{ipooled}$ (cos α_i), i=0,1,...,m

and

$CES_i = V_{ipooled}$ (sin α_i), i=0,1,...,m.

PGS_i is the phylogenetic signal's strength on level *i* of the dendrogram in the pooled metacommunity. Put it in another way, $100PGS_0/(PGS_0+CES_0)$% of the diversity amplitude in the metacommunity is attributable to the splitting up of genera into species. Conversely, $100CES_0/(PGS_0+CES_0)$% is the portion of the diversity amplitude attributable to environmental mediation by variable *U*. In still more general terms, the intensity of *PGS* on hierarchical level *i* is $100PGS_i/(PGS_i+CES_i)$%. The one complement of this $100CES_i/(PGS_i+CES_i)$% is the strength of *CES* referenced to variable *U.* In terms of grand totals, the proportions are

$$SSO = \frac{100 \sum_{i=0}^{m} PGS_i}{\sum_{i=0}^{m} PGS_i + \sum_{i=0}^{m} CES_i} \%$$

for self-organisation, and

$$EM = \frac{100 \sum_{i=0}^{m} CES_i}{\sum_{i=0}^{m} PGS_i + \sum_{i=0}^{m} CES_i} \%$$

for environmental mediation. In summary, *SSO* scales level of *self organization* and *EM* scales the strength of *environmental mediation* in the gradient-wide metacommunity. We may take the error terms associated with **b** as an estimate of *e* (see regression analysis in Orlóci 2010).

8

Example

We use the data set which we collected July 7-8, 1976, on a transect laid on an elevation gradient inside a major meander of the Coquihalla River floodplain[5] near Hope, British Columbia. Covered by a natural high forest in its glorious mature state in 1976, now the floodplain is site of a subdivision of the city. The transect ran from the upstream section of the meander towards the old Hope-Princeton highway up to the high terrace several hundred meters away. We present data from the original survey in Table 1. The photograph of a nearby site (Figure 2) still in a reasonably natural state depicts a similar meander as the one once existed in the survey site. Both sites are within the ecological formation which Krajina (1959) described as the Coastal Western Hemlock Zone.

A common characteristic of floodplains is the presence of more or less flat benches (levels, terraces) with a slight sloping toward the adjacent higher terrain. The benches mark the joint effect of sedimentation and erosion by flood water. The benches are usually lined up on the inside of major meanders. Bench elevation increases with distance from the river. The benches' vegetation cover is remarkably different as an indication of different overflow frequency and duration, and the quality and quantity of the sediments laid down by the periodic floods.

The surface morphology of the floodplain in the study site was structured in its natural state by two active benches and one fossil terrace. The average elevation of these was 4.2 m, 5.4 m, and 10.8 m above the water level in the river when the survey began (see date above). The original survey contains 45 sample plots 10m x 10m square each and close to 100 species. The sample plots were laid on a belt transect, cover/abundance values were estimated and a composite soil sample was taken from the top 20 cm of the soil within each sample plot for chemical analysis.

5 http://maps.google.com/maps/ms?source=s_q&hl=en&geocode=&aq=&ie=UTF8&t=h&msa=0&msid=216626377309845313321.00049bf3254ab94ea225e&ll=49.376617,-121.412863&spn=0.004554,0.013078&z=17

The 3 natural sections (2 benches, 1 fossil terrace) of the elevation gradient in its natural state delineated three metacommunities (a, b, c). These are described by averages of species abundance and gradient variables (Table 1). The original gradient variables include elevation, soil nitrate nitrogen, ammoniac nitrogen, phosphorus, calcium, potassium and pH. We use the 40 most abundant species out of almost 100 and the first three of the environmental variable in the analyses. We opted for such a reduction of variables to avoid overwhelming the example with information we did not need to make our point: the environmental signal *(CES*) is strong, but the phylogenetic signal *(PGS)* is dominant.

Figure 2. The Coquihalla River floodplain near the actual survey site at Hope, British Columbia, as it has looked in its natural state. The transect's site and sampling details are described in the main text and in the caption of Table 1. The flow in the stream can be torrential and several meters higher than on day of sampling. The flow from October to March is a mere average 2 m^3/s. This can reach 12 m^3/s in May and June following runoff after warm days or rain. The river is fed by runoff from a 740 km^2 watershed in the Cascade Mountains. The highest peak in the photograph is nearly 2000 m. Photo by Maurice Jassak, Images West Marketing, Vancouver, B.C., reproduced with IWK written permission.

Table 1. Data set from the Coquihalla transect. A brief description of site, sampling design and data ownership appears in the main text. Items in table headings: # — sequence number as in M. Mihály's original records; Code – identifies species belonging among the given categories; *FT* – functional type (life-form) code and average *CA* as weight; *ET* – ecological (flood duration) type code and average *CA* as weight; a,b,c – benches low to high, average heights 4.2 m, 5.4 m, 10.8 m; Poole sample (t) drand mean *CA* – calculated for entire transect based on 45 sample plots; Soil variables – weighted mean values *CA x NN kg/ha* and *CA x AN kg/ha; NN* – nitrate nitrogen, *AM* – ammoniac nitrogen. The total number of species in the analysis is 40 and the sample size is 45 plots. The terraces a, b, c are represented by 14, 20, 11 plots in that order. Plant identification followed standard field manuals. The soil chemical analysis was performed by personnel in the Department of Agriculture, Guelph, Ontario.

#	Species	Class or higher	Code	Order	Code	Family	Code	Genus	Code
2	Acer macrophyllum	Eudicots	3	Sapindales	16	Sapindaceae	1	Acer	1
25	Galim triflorum	Asterids	1	Gentianales	10	Rubiaceae	2	Galim	11
16	Claytonia sibirica	Magnoliopsida	4	Caryophyllales	4	Portulacaceae	5	Claytonia	6
39	Osmorhiza chilensis	Asterids	1	Apiales	1	Apiaceae	21	Osmorhiza	21
37	Mnium insigne	Bryopsida	2	Eubryaales	9	Mniaceae	9	Mnium	20
3	Acer macrophyllum	Eudicots	3	Sapindales	16	Sapindaceae	1	Acer	1
15	Circaea alpina	Magnoliopsida	4	Myrtales	12	Onagraceae	7	Circaea	5
20	Dicentra formosa	Magnoliopsida	4	Ranunculales	14	Fumariaceae	12	Dicentra	8
56	Smilacina stellata	Monocots	5	Asparagales	2	Ruscaceae	21	Smilacina	29
60	Symphoricarpos albus	Asterids	1	Dipsacales	7	Caprifoliaceae	18	Symphoricarpos	31
43	Polystichum munitum	Pteridopsida	6	Dennstaedtiales	6	Dennstaedtiaceae	14	Polystichum	23
22	Disporum hookerii	Monocots	5	Liliales	11	Colchicaceae	16	Disporum	9
30	Lactuca canadensis	Asterids	1	Asterales	3	Asteraceae	20	Lactuca	16
37	Mnium spinulosum	Bryopsida	2	Eubryales	9	Mniaceae	9	Mnium	20
67	Tsuga heterophylla	Pinopsida	6	Pinales	13	Pinaceae	6	Tsuga	34
17	Clintonia uniflora	Monocots	5	Liliales	11	Liliaceae	10	Clintonia	7
54	Rubus spectabilis	Magnoliopsida	4	Rosales	15	Rosaceae	3	Rubus	28
27	Goodyera oblongifolia	Monocots	5	Asparagales	2	Orchidaceae	7	Goodyera	13
65	Trientalis latifolia	Eudicots	3	Ericales	8	Myrsinaceae	8	Trientalis	33
45	Pteridium aquilinum	Pteridopsida	6	Dennstaedtiales	6	Dennstaedtiaceae	14	Pteridium	25
49	Rhytidiadelphus loreus	Bryopsida	2	Eubryales	9	Hypnaceae	11	Rhytidiadelphus	26
34	Mahonia nervosa	Magnoliopsida	4	Ranunculales	14	Berberidaceae	19	Mahonia	19
24	Eurhynchium oreganum	Bryopsida	2	Eubryales	9	Hypnaceae	11	Eurhynchium	10
8	Amelanchier florida	Magnoliopsida	4	Rosales	15	Rosaceae	3	Amelanchier	3
70	Vaccinium parviflorum	Asterids	1	Ericales	8	Ericaceae	13	Vaccinium	35
28	Holodiscus discolor	Magnoliopsida	4	Rosales	15	Rosaceae	3	Holodiscus	12
71	Vaccinium membranaceum	Asterids	1	Ericales	8	Ericaceae	13	Vaccinium	35
57	Spiraea douglasii	Magnoliopsida	4	Rosales	15	Rosaceae	3	Spiraea	30
33	Lonicera ciliata	Asterids	1	Dipsacales	7	Caprifoliaceae	18	Lonicera	18
52	Rosa gymnocarpa	Magnoliopsida	4	Rosales	15	Rosaceae	3	Rosa	27
62	Thuja plicata (shrub)	Pinopsida	6	Pinales	13	Cupressaceae	15	Thuja	32
13	Chimaphila umbellata	Asterids	1	Ericales	8	Pyrolaceae	4	Chimaphylla	4
32	Linnaea borealis	Asterids	1	Dipsacales	7	Caprifoliaceae	18	Linnaea	17
29	Hylocomium splendens	Bryopsida	2	Eubryales	9	Hypnaceae	11	Hylocomium	15
26	Gaultheria shallon	Eudicots	3	Ericales	8	Ericaceae	13	Gaultheria	12
40	Pachistima myrsinites	Eudicots	3	Celastrales	5	Celastraceae	17	Pachistima	22
43	Pseudotsuga menziesii	Pinopsida	6	Pinales	13	Pinaceae	6	Pseudotsuga	24
3	Acer macrophyllum (shrub)	Eudicots	3	Sapindales	16	Sapindaceae	1	Acer	1
6	Achlys triphylla	Magnoliopsida	4	Ranunculales	14	Berberidaceae	19	Achlys	2
63	Thuja plicata	Pinopsida	6	Pinales	13	Cupressaceae	15	Thuja	32

Table 1 continued

#	Species	*FT code*	*FT* Weight *CA*	ET code	ET weight *CA*	Species mean CA				*Soil* variables, weighted means	
						Bench "a"	Bench "b"	Bench "c"	Pooled Sample t	*CA x NN* kg/ha	*CA x AC* kg/ha
2	Acer macrophyllum	1	3.26	1	1.36	1.86	0.30	0.00	0.72	14.23	40.35
25	Galim triflorum	3	0.67	1	1.36	1.29	0.90	0.00	0.73	12.24	30.26
16	Claytonia sibirica	5	0.75	1	1.36	1.86	0.00	0.00	0.62	15.24	43.71
39	Osmorhiza chilensis	3	1.57	1	1.36	1.79	0.50	0.00	0.76	13.65	38.11
37	Mnium insigne	4	0.12	1	1.36	1.07	0.10	0.00	0.39	14.62	41.47
3	Acer macrophyllum	1	3.26	1	1.36	1.64	0.15	0.45	0.75	12.81	33.63
15	Circaea alpina	3	1.57	1	1.36	2.31	0.00	0.00	0.77	15.24	44.83
20	Dicentra formosa	5	1.31	1	1.36	3.36	0.25	0.00	1.20	14.74	42.59
56	Smilacina stellata	5	1.31	1	1.36	2.29	0.70	0.00	1.00	13.54	35.87
60	Symphoricarpos a.	2	1.91	1	1.36	5.00	0.90	0.36	2.09	13.64	36.99
43	Polystichum m.	4	0.12	1	1.36	7.50	2.35	0.09	3.31	13.43	34.75
22	Disporum hookerii	5	1.31	1	1.36	4.93	2.50	0.00	2.48	12.79	32.51
30	Lactuca canadensis	3	1.57	1	1.36	3.93	2.70	0.00	2.21	12.28	31.38
37	Mnium spinulosum	4	0.12	1	1.36	4.93	0.85	0.18	1.99	13.91	39.23
67	Tsuga heterophylla	1	3.26	2	1.55	0.00	3.05	0.00	1.02	7.96	19.05
17	Clintonia uniflora	5	1.31	2	1.55	0.00	4.10	0.27	1.46	7.81	16.81
54	Rubus spectabilis	2	1.91	2	1.55	0.57	2.15	1.45	1.39	8.14	21.30
27	Goodyera o.	5	1.31	2	1.55	0.00	1.95	1.36	1.10	6.99	13.45
65	Trientalis latifolia	3	1.57	2	1.55	0.50	1.90	1.73	1.38	7.86	17.93
45	Pteridium aquilinum	4	0.12	2	1.55	0.00	2.70	0.00	0.90	7.96	20.18
49	Rhytidiadelphus l.	4	0.12	2	1.55	1.79	2.35	3.09	2.41	8.75	24.66
34	Mahonia nervosa	2	1.91	2	1.55	2.64	6.60	3.91	4.38	8.72	23.54
24	Eurhynchium o.	4	0.12	2	1.55	3.00	4.95	4.64	4.20	8.83	25.78
8	Amelanchier florida	2	1.41	3	1.84	0.21	0.40	1.45	0.69	7.06	14.57
70	Vaccinium p.	2	1.91	3	1.84	0.00	0.25	2.73	0.99	5.80	7.85
28	Holodiscus discolor	2	1.91	3	1.84	0.00	0.00	1.18	0.39	5.60	1.12
71	Vaccinium m.	2	1.91	3	1.84	0.00	0.00	2.09	0.70	5.60	2.24
57	Spiraea douglasii	2	1.91	3	1.84	0.00	0.00	1.91	0.64	5.60	4.48
33	Lonicera ciliata	2	1.91	3	1.84	0.00	0.25	1.55	0.60	5.93	8.97
52	Rosa gymnocarpa	2	1.91	3	1.84	0.14	0.40	1.36	0.64	6.82	12.33
62	Thuja plicata (shrub)	2	1.91	3	1.84	0.00	0.00	0.73	0.24	5.60	3.36
13	Chimaphila u.	4	0.12	3	1.84	0.00	0.20	3.09	1.10	5.75	6.73
32	Linnaea borealis	4	0.12	3	1.84	0.00	0.10	3.00	1.03	5.68	5.60
29	Hylocomium s.	4	0.12	3	1.84	1.64	6.15	6.64	4.81	7.71	15.69
26	Gaultheria shallon	2	1.91	3	1.84	0.00	2.15	7.45	3.20	6.13	10.09
40	Pachistima m.	2	1.91	3	1.84	0.29	3.25	6.55	3.36	6.64	11.21
43	Pseudotsuga m.	1	3.26	4	5.16	8.15	6.05	8.00	7.40	9.79	26.90
3	Acer macrophyllum s.	1	3.26	4	5.16	7.57	5.25	2.64	5.15	11.13	29.14
6	Achlys triphylla	3	1.57	4	5.16	4.50	4.70	1.55	3.58	10.67	28.02
63	Thuja plicata	1	3.26	4	5.16	2.71	6.10	4.73	4.51	8.60	22.42

9

Signal numerics

All the computed results are presented in appendices. For ease of access the partial variance streams (**V** matrix, $\mathbf{V}_{pooled}$ vector) are reproduced in Table 2, a summary of results from the regression analyses in Table 3, and selected results from correlation analysis in Table 4. Empirical probability graph for the correlations, determined in a Monte Carlo experiment under the assumption of zero expectation, is presented in Figure 3.

We recall that the sample size of the grand pooled metacommunity is 45, and for the metacommunities of the a, b, c transect segments is 14, 20, 11 in that order. The number of elements in the baseline data is uniformly 40 (the number of species in the analysis). The degrees of freedom (DF) are a function of the hierarchical levels:

Level in hierarchy	Number of records in cumulants	DF	Partial DF
4	6	5	5
3	17	16	11
2	24	23	7
1	35	34	11
0	40	39	5

Considering Table 2, temporal partial variances are laid out in columns a, b, c for the metacommunities of the 3 transect segments. The rows (0 to 4) contain the spatial variance streams. We subjected each of the spatial partial variance streams to regression analysis using floodplain elevation *(U)* as the *x* variable. We present the regression results in Table 3. Our focus is on the partial variance slope (a^0), the strength of environmental mediation $(1\text{-}P^2)^{1/2}$, and the relative size of the isolated signals % *PGS and % CES*. From these values we conclude that on the baseline (Species) level and on the Family level the floodplain elevation effect is numerically high and in probability terms very robust. On the Genus level it is very low and weak in *TS*, on the Order level weak but quite robust, and on the Class level numerically weak but still quite robust. This already suggests that the relative importance of *CES* varies; strong on some levels of the dendrogram and weak on other levels. We can make a definitive statement (generaliza-

Table 2. Spatial partial variance streams is in rows (hierarchical levels 0 to 4). Temporal partial variance streams of the floodplain level metacommunities are in columns a, b, c , the pooled metacommunities partial variance stream in last column *(t)*. Gradient variable *U* is floodplain elevation. See further explanations in the main text.

	V matrix			V_{pooled} vector
Levels	a	b	c	t
0 Species	6.74012	7.139820	2.437623	4.687
1 Genus	7.348533	1.586646	4.075429	2.585
2 Family	3.304415	6.150125	7.23172	2.709
3 Order	4.968971	3.435011	5.359622	1.519
4 Class	2.767431	7.020941	5.937247	3.882
Variable *U m*	4.2	5.4	10.8	

Table 3. Regression analysis summarised. The y variable is the spatial partial variance stream (rows 0 to 4 in the table). The x variable is floodplain elevation *U.* Columns in upper table: temporal partial variance streams in the metacommunities of the three transect segments (a, b, c), regression coefficients (b = tan α) , the standard deviation (SD) of tan α, coefficient of determination (R^2), spatial specific variance slopes (a^O), probability of a more extreme *a* obtained by chance ($P > \alpha$), strength of the environmental effect (variable *U)* in $(1-P^2)^{1/2}$ terms. Columns in lower table: temporal specific variances of the pooled metacommunity (*t*), the phylogenetic signal *(PGS* and *PGS %)* and the environmental signal *(CES* and *CES%)*.

Levels	a	b	c	b=tan α	*e*= SD	R^2	α^O	$P>\alpha^O$	$(1-P^2)^{1/2}$
0 Species	6.740	7.140	2.438	-0.719	0.182	0.939	35.72	0.059	0.998
1 Genus	7.349	1.587	4.075	-0.203	0.796	0.061	11.48	0.822	0.569
2 Family	3.304	6.150	7.232	0.474	0.327	0.676	25.36	0.286	0.958
3 Order	4.969	3.435	5.360	0.150	0.247	0.269	8.531	0.606	0.796
4 Class	2.767	7.021	5.937	0.272	0.567	0.187	15.22	0.678	0.735
Elev *(U)*	4.2m	5.4m	10.8m						

	*t**	*PGS = t x cos α**	*CES = t x sin α*	*% PGS*	*% CES*
0 Species	4.6868	3.8056	2.7355	65.9338	34.0662
1 Genus	2.5847	2.5329	0.5149	96.0310	3.9690
2 Family	2.7087	2.4473	1.1608	81.6353	18.3647
3 Order	1.5190	1.5022	0.2255	97.7966	2.2034
4 Class	3.8825	3.7463	1.0190	93.1113	6.8887
Average	3.0763	2.8069	1.1311	**86.9016**	**13.0984**

* Pythagorean theorem applied: e.g., $4.686753^2 = 3.805626^2 + 2.735484^2$ *******

tion) based on the isolates, *CES* from *PGS.* The sizes of these show the dominance of *PGS* (66%) to *CES* (44 %) on the Species level, and 87% to 14 % on average through all taxonomic levels.

Continuing with the interpretation of the results, we turn now to Table 4 and Figure 3. In these we can see illumination of the environmental effects on *TS*, at this time in partial correlation terms. Correlation values are based on 5 hierarchical relevés of the gradient wide metacommunity with base line variables *t, FT, ET, NN,* and *AN.* We note at the outset that our interpretation of the strength of the correlation coefficient relies on two things: the magnitude of *r* and the probability of obtaining a correlation value equal to or greater than the observed *r* when the expectation of *r* is zero, symbolically $P = P(r_{RND} \geq |r|)$ for absolute *r.* If absolute *r* is numerically strong then $R = (1–P2)^{1/2}$ approaches the upper limit in the interval 0 to 1. In formulating *R,* we use Rajski's information theoretical considerations (Orlóci 2010). We call *R* the *coherence coefficient.* Note in Rajski's scheme a lack of correlation has counterpart not in its one-complement *1- P,* but in *R.* In other words, *R* and *P* are considered orthogonal.

Dendrogram with baseline values in the *t* column of Table 1 is the base dendrogram in correlation analysis. Looking at the numerics, the correlations suggest the following strong relationships:

a. The species based hierarchy *(t)* has high coherence with the ecological type *(ET)* based hierarchy on all hierarchical levels. This suggests that the spe-

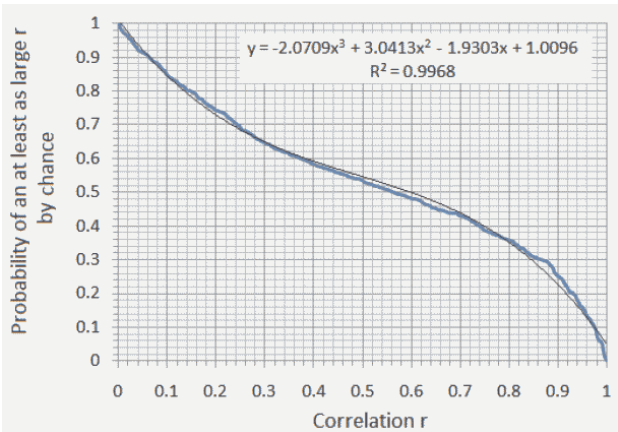

Figure 3. Empirical probabilities of a random *r* being at least as large or larger than the probability points (horizontal axis). See explanations in the main text and in Table 4. Empirical probabilities were determined in Monte Carlo experiments (see Orlóci 2010) under the assumption zero expectation. The smaller is this kind of probability the more significant is the *r* actually observed. Equation: y probability; x correlation.

Table 4. Correlation analysis of the *t, FT, ET, NN, AN* variables on floodplain elevation *U* identified in caption of Table 1. Columns: temporal partial correlation streams in top portion, probabilities of an at least as extreme absolute correlation as the observed in middle portion, correlation strengths in bottom portion. See probability equation in Figure 3 and the explanations in the main text.

Partial correlations

Level	txFT	TxET	txNN	txAA	FTxET	FTxNN	FTxAA	ETxNN	ETxAA	NNxAA
0 Species	0.624	0.970	-0.081	-0.341	0.603	0.683	-0.900	-0.091	-0.324	-0.908
1 Genus	0.066	0.490	0.434	-0.143	-0.164	0.350	-0.399	0.107	0.116	-0.883
2 Family	0.266	0.613	-0.557	0.443	0.178	-0.035	-0.063	-0.623	0.554	-0.939
3 Order	0.253	0.604	0.066	-0.144	0.818	-0.083	0.146	-0.100	0.130	-0.983
4 Class	0.078	0.573	0.221	-0.517	0.684	-0.471	0.246	-0.474	0.078	-0.744

The probability of an at least as extreme correlation as the observed occurring by chance, symbolically $P(r_{RND} \geq |r|)$ (see the main text and Figure 3)

Level	txFT	TxET	txNN	txAA	FTxET	FTxNN	FTxAA	ETxNN	ETxAA	NNxAA
0 Species	0.486	0.109	0.872	0.623	0.497	0.450	0.226	0.858	0.633	0.214
1 Genus	0.895	0.550	0.575	0.790	0.766	0.618	0.592	0.835	0.823	0.251
2 Family	0.672	0.492	0.520	0.571	0.751	0.946	0.900	0.487	0.522	0.164
3 Order	0.682	0.497	0.895	0.789	0.332	0.869	0.786	0.845	0.806	0.084
4 Class	0.877	0.512	0.709	0.538	0.449	0.559	0.688	0.557	0.877	0.404

Correlation strength expressed by the coherence coefficient $R = \sqrt{1 - P^2}$

Level	txFT	TxET	txNN	txAA	FTxET	FTxNN	FTxAA	ETxNN	ETxAA	NNxAA
0 Species	0.874	0.994	0.489	0.782	0.868	0.893	0.974	0.514	0.774	0.977
1 Genus	0.446	0.835	0.818	0.613	0.643	0.786	0.806	0.550	0.567	0.968
2 Family	0.740	0.871	0.854	0.821	0.661	0.325	0.437	0.874	0.853	0.986
3 Order	0.731	0.868	0.446	0.615	0.943	0.495	0.618	0.535	0.593	0.996
4 Class	0.481	0.859	0.705	0.843	0.893	0.829	0.726	0.830	0.481	0.915
Average	**0.655**	**0.885**	**0.663**	**0.735**	0.802	0.666	0.712	0.661	0.654	0.969

cies represent strong ecological traits as Pillar and Duarte (2010) concluded. The *t* hierarchy scores high coherence also with functional type *(FT)* based hierarchy on the hierarchical levels except Genus and Class.

b. Soil nitrate nitrogen *(NN)* fails in similar terms as *FT,* but the coherence of *t* based hierarchy and ammoniac nitrogen *(AN)* based hierarchy is strong.

c. In other comparisons, the coherence of *AN* and *NN* based hierarchies is very high but negative. This is not surprising when we consider the change in humus type from the quickly decomposing kind on the functioning floodplain benches to the deep raw humus on the fossil terrace.

10

A discussion

Kerner's (1863) ideas on the assembly of species into environment specific communities and his assertion that plant communities develop *in situ* in the sense of undergoing compositional transitions owing to a feedback mechanism which he discovered and we call facilitation was truly the kernel for modern dynamic ecology. Kerner's work is seminal on environmental mediation rules and starting point toward finding general rules in the governance of the plant community assembly/disassembly process. Now it is clear that to find general rules the search has to go beyond environmental mediation of species trait selection and assortment, into the dual process, powered by interactions of the community elements (Stachowicz 2001) and we call self-organization (Camazine et al. 2003). Wilson (2009) makes these remarks:

> "... Two basic kinds of community pattern can be envisaged, with different causes:
>
> (a) Environmentally mediated patterns, i.e., correlations between species due to their shared or opposite responses to the physical environment. Ecologists have long tried 'to find out which species are commonly associated together upon similar habitats' (Warming, 1909). Modern methods allow more subtle questions to be examined, such as the shape of environmental responses (e.g., Bio et al., 1998), the niche widths (e.g., Diaz et al., 1994), and how repeatable the associations of species are (e.g., Wilson et al., 1996c). However, the simple existence of environmentally mediated patterns is now too obvious to need demonstrating; Warming (1909) described it as 'this easy task'.
>
> (b) Assembly rules, i.e., patterns due to interactions between species, such as competition. These patterns, when we can find them, are fascinating evidence that competition, allelopathy, facilitation, mutualism, and all the other biotic interactions that we know about in theory, actually affect communities in the real world.
>
> Of course, to make this distinction, it has to be known what processes have caused each pattern – physical environment or biotic interactions – but that is our task as community ecologists. Both types of process may occur."

Wilson's point (a) confirms environmental mediation by mechanisms such as facilitation and his (b) addresses self organization by biological interactions. Obviously, Wilson perpetuates a perennial shortcoming in the English language

literature by pointing to Warming (1909) as his historic reference rather than mentioning Kerner's (1863) work from half a century earlier in which environmental mediation is discussed. In fact, Kerner discusses the process in the feedback context of facilitation, narrating how plant species can change the environment to their own demise in the site. Based on our results, it can be seen quite clearly that environmental mediation, such as in facilitation, promotes community's transience, and self-organization tends to support increased stability and permanence. Both processes are point processes and for that reason have to be running in tandem. Actually measuring the level of environmental mediation and self-organization takes us a mega step further. We use for this a methodology which is centred on the signal superposition model *TS=PGS+CES+e.*

The isolation and scaling of signals is a topic which is discussed in current papers (see Pillar and Duarte 2010 and references therein) with varying success (Revell et al. 2008). Pillar and Duarte (2010) see the phylogenetic signal's role in the community assembly process in the manner of species being selected by their environmental traits. This is an important assembly rule which our results support by showing the dominance of *PGS* related self organization over *CES* related transience. Formally recognizing this is a strong statement contrary to the spreading arguments which give dominance to the rule of randomness.

Why is this surge of interest in the isolation of the different signals? An answer to this question is the ecologists' intention to discover and then incorporate provisions for the phylogenetic signal into the main corpus of governance principles in community functioning (Orlóci and He 2009). Pillar and Duarte (2010) mention several benefits to be gained from signal research: the comparison of metacommunities, the discovery of new community assembly rules, the identification of plant species traits most responsible for the phylogenetic signal, the illumination of the trait-filtering process along ecological gradients, and not the least, the addressing of questions regarding phylogenetic niche conservatism.

We go a step further. Based on our finding, we have a strong reason to stand behind the propositions we listed at the beginning of the main text. Some of our Coquihalla results are simply astonishing. The many fold dominance the phylogenetic signal strength (*SSO* = 86.6%) over environmental signal strength (*EM* = 13.1%) is nothing less than such. We conclude on that basis that the importance of self-organization overwhelms the importance of environmental mediation. The forgoing implies that community transience is not as strong a tendency as competition based self-organization which may counteract community transience. The forgoing also implies that the moderation of the diversity amplitude in meta-

communities may be far more a phylogenetic functionality than it is an environmental mediation functionality.

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Appendices

Appendix 1. Numerical values in this table are partial sums of squares in columns a, b, c, and t, and products in columns ab, ac, at, bc, bt, ct in Part I; partial variances and covariances in Part II; and partial product moment correlations in Part III. The individual columns are temporal streams which map the total signal in the taxonomic dendrogram. The numerical results are based on the three metacommunities for which the hierarchical relevés are given in Table 1. Symbols a, b, and c are labels for the flood plain levels (3 transect segments and metacommunities occupying the segments) and for the pooled metacommunity of the entire transect (t). The basic data on which these results are based are in Table 1.

Part I	Temporal partial sum of squares and product streams									
Level	a	ab	ac	at	b	bc	bt	c	ct	t
0 Species	33.701	29.183	15.031	25.979	35.699	20.361	28.425	12.188	15.869	23.434
1 Genus	80.834	12.666	23.765	39.147	17.453	19.725	16.631	44.830	29.441	28.432
2 Family	23.131	-4.720	-4.558	4.640	43.051	36.080	24.823	50.622	27.379	18.961
3 Order	54.659	23.440	-35.199	14.275	37.785	11.304	24.171	58.956	11.699	16.709
4 Class	13.837	20.954	11.147	15.315	35.105	15.822	23.974	29.686	18.909	19.412

Part II	Temporal partial variance and covariance streams									
Level	a	ab	ac	at	b	bc	bt	c	ct	t
0 Species	6.740	5.837	3.006	5.196	7.140	4.072	5.685	2.438	3.174	4.687
1 Genus	7.349	1.151	2.160	3.559	1.587	1.793	1.512	4.075	2.676	2.585
2 Family	3.304	-0.674	-0.651	0.663	6.150	5.154	3.546	7.232	3.911	2.709
3 Order	4.969	2.131	-3.200	1.298	3.435	1.028	2.197	5.360	1.064	1.519
4 Class	2.767	4.191	2.229	3.063	7.021	3.164	4.795	5.937	3.782	3.882

Part III	Temporal partial correlation streams					
level	ab	ac	at	bc	bt	ct
0 Species	0.841	0.742	0.924	0.976	0.983	0.939
1 Genus	0.337	0.395	0.817	0.705	0.747	0.825
2 Family	-0.150	-0.133	0.222	0.773	0.869	0.884
3 Order	0.516	-0.620	0.472	0.239	0.962	0.373
4 Class	0.951	0.550	0.934	0.490	0.918	0.788

Appendix 2. Result of linear regression analysis. The spatial partial variance streams on which the analysis was performed are taken from Appendix 1.

x data: 4.2m, 5.4m, 10.8m
y data by dendrogram level :

0 Species	6.74012	7.139820	2.437623
1 Genus	7.348533	1.586646	4.075429
2 Family	3.304415	6.150125	7.23172
3 Order	4.968971	3.435011	5.359622
4 Class	2.767431	7.020941	5.937247

Hierarchical level 0

r^2 Coef Det	DF Adj r^2	Fit Std Err	F-val
0.9396348213	0.8792696427	0.9058709452	15.565841800

Parm	Value	Std Error	t-value	95% Confidence Limits		P>|t|
a	10.32725653	1.344809123	7.679347469	-6.76016354	27.41467661	0.01654
b	-0.71883366	0.182197367	-3.94535699	-3.03387071	1.596203398	0.05865

Hierarchical level 1

r^2 Coef Det	DF Adj r^2	Fit Std Err	F-val
0.0611763926	0.0000000000	3.9598506641	0.0651628188

Parm	Value	Std Error	t-value	95% Confidence Limits		P>|t|
a	5.719363854	5.878589358	0.972914335	-68.9751962	80.41392394	0.43322
b	-0.20330802	0.796442771	-0.25527009	-10.3230729	9.916456910	0.82237

Hierarchical level 2

r^2 Coef Det	DF Adj r^2	Fit Std Err	F-val
0.6757177649	0.3514355298	1.6337135066	2.0837335254

Parm	Value	Std Error	t-value	95% Confidence Limits		P>|t|
a	2.336700874	2.425326521	0.963458262	-28.4799945	33.15339626	0.43697
b	0.474321440	0.328587975	1.443514297	-3.70078466	4.649427536	0.28568

Hierarchical level 3

r^2 Coef Det	DF Adj r^2	Fit Std Err	F-val
0.2690170542	0.0000000000	1.2300725218	0.3680209719

Parm	Value	Std Error	t-value	95% Confidence Limits		P>|t|
a	3.567277126	1.826102005	1.953492804	-19.6355489	26.77010311	0.18998
b	0.150086893	0.247403867	0.606647321	-2.99347730	3.293651088	0.60578

Hierarchical level 4

r^2 Coef Det	DF Adj r^2	Fit Std Err	F-val
0.1871937354	0.0000000000	2.8182138367	0.2303054781

Parm	Value	Std Error	t-value	95% Confidence Limits		P>|t|
a	3.392132709	4.183774409	0.810782891	-49.7677616	56.55202701	0.50263
b	0.272020631	0.566825931	0.479901530	-6.93018570	7.474226967	0.67866

Appendix 3. Correlation analysis of variables t, FT, ET, NN, and AN. Symbols in column heading and associated data in Table 1: t - average cover abundance values of species in the pooled, gradient wide metacommunity; FT - functional type, cover abundance; ET - ecological type, cover abundance; NN - weighted nitrate nitrogen; AN - weighted ammonic nitrogen. The entries in main body of table are partial sum of squares and partial products in Part I, partial variances and co-variances in Part II, partial correlations and associated probabilities of an at least as extreme correlation by chance (Figure 3) in Part III. Note, when we shift from the species based hierarchy (t) to another type, for example to the FT based hierarchy, the dendrogram remains the same as defined for species. Only the numerical values change in the baseline data and in the cumulants.

Part I

Level	txt	txFT	txET	txNN	txAN	FTxFT	FTxET	FTxNN	FTxAN
0 Species	23.434	2.882	18.273	-1.089	-30.662	0.911	2.241	1.802	-15.964
1 Genus	28.432	0.542	9.540	16.611	-29.053	2.394	-0.929	3.887	-23.430
2 Family	18.961	2.022	4.508	-21.222	73.051	3.043	0.523	-0.536	-4.142
3 Order	16.709	4.033	7.493	3.855	-45.973	15.188	9.669	-4.575	44.449
4 Class	19.412	1.452	6.758	3.474	-60.683	17.975	7.765	-7.116	27.835

ETxET	ETxNN	ETxAN	NNxNN	NNxAN	ANxAN
15.138	-0.976	-23.426	7.631	-46.626	345.592
13.327	2.808	16.122	51.644	-241.114	1443.217
2.851	-9.206	35.407	76.666	-311.131	1433.339
9.207	-4.320	30.807	201.993	-1088.501	6064.259
7.159	-4.524	5.552	12.722	-70.735	710.285

Part II

Level	txt	txFT	txET	txNN	txAN	FTxFT	FTxET	FTxNN	FTxAN
0 Species	4.691	0.577	3.657	-0.218	-6.135	0.182	0.448	0.360	-3.193
1 Genus	2.585	0.049	0.867	1.510	-2.641	0.218	-0.084	0.353	-2.130
2 Family	2.709	0.289	0.644	-3.032	10.436	0.435	0.075	-0.077	-0.592
3 Order	1.519	0.367	0.681	0.350	-4.179	1.381	0.879	-0.416	4.041
4 Class	3.882	0.290	1.352	0.695	-12.137	3.595	1.553	-1.423	5.567

ETxET	ETxNN	ETxAN	NNxNN	NNxAN	ANxAN
3.028	-0.195	-4.685	1.526	-9.325	69.118
1.212	0.255	1.466	4.695	-21.919	131.202
0.407	-1.315	5.058	10.952	-44.447	204.763
0.837	-0.393	2.801	18.363	-98.955	551.296
1.432	-0.905	1.110	2.544	-14.147	142.057

Part III

Level	txFT	txET	txNN	txAN	FTxET	FTxNN	FTxAN	ETxNN	ETxAN	NVxAN
0 Species	0.624	0.970	-0.081	-0.341	0.603	0.683	-0.900	-0.091	-0.324	-0.908
1 Genus	0.066	0.490	0.434	-0.143	-0.164	0.350	-0.399	0.107	0.116	-0.883
2 Family	0.266	0.613	-0.557	0.443	0.178	-0.035	-0.063	-0.623	0.554	-0.939
3 Order	0.253	0.604	0.066	-0.144	0.818	-0.083	0.146	-0.100	0.130	-0.983
4 Class	0.078	0.573	0.221	-0.517	0.684	-0.471	0.246	-0.474	0.078	-0.744

Probability P of an at least as extreme correlation as the observed occurring by chance

Level	txFT	txET	txNN	txAN	FTxET	FTxNN	FTxAN	ETxNN	ETxAN	NVxAN
0 Species	0.486	0.109	0.872	0.623	0.497	0.450	0.226	0.858	0.633	0.214
1 Genus	0.895	0.550	0.575	0.790	0.766	0.618	0.592	0.835	0.823	0.251
2 Family	0.672	0.492	0.520	0.571	0.751	0.946	0.900	0.487	0.522	0.164
3 Order	0.682	0.497	0.895	0.789	0.332	0.869	0.786	0.845	0.806	0.084
4 Class	0.877	0.512	0.709	0.538	0.449	0.559	0.688	0.557	0.877	0.404

Strength of correlation expressed by the coherence coefficient $R = \sqrt{1 - P^2}$

Level	txFT	txET	txNN	txAN	FTxET	FTxNN	FTxAN	ETxNN	ETxAN	NVxAN
0 Species	0.874	0.994	0.489	0.782	0.868	0.893	0.974	0.514	0.774	0.977
1 Genus	0.446	0.835	0.818	0.613	0.643	0.786	0.806	0.550	0.567	0.968
2 Family	0.740	0.871	0.854	0.821	0.661	0.325	0.437	0.874	0.853	0.986
3 Order	0.731	0.868	0.446	0.615	0.943	0.495	0.618	0.535	0.593	0.996
4 Class	0.481	0.859	0.705	0.843	0.893	0.829	0.726	0.830	0.481	0.915