Network Coherence - current state of concept

Motivation

We currently lack theory and methods to predict community-level responses to environmental change, and the objective of our study is to develop a conceptual and mathematical framework to address this problem. To do this, we introduce a metric of Network Coherence (CN), which quantifies the degree of association between a community response to a specific environment and its biotic interactions. NC can be a direct indicator of the predictability of communities in front of environmental changes, and we think it can be important in assessing how their structure and functioning will be impacted.

Network Coherence concept

We define Network Coherence (NC) as "the degree to which the sensitivity and rate in response of a given community to specific environmental variables at a given location (defined as the instantaneous rate of change in"fitness" or abundance of each species in response to fluctuations in abiotic conditions) is associated with its species interactions."

The response is quantified incorporating both the sensitivity (i.e. how much the change in response is affected by the environment) and rate (i.e. how much time it takes to the species to develop a response), and can be either "intrinsic" or "net": intrinsic responses refer to the inherent qualities and behaviors that a species exhibits in response to specific environmental variables (i.e. fitness) independently of the effect of other species, whereas net responses correspond to the change in abundance, which result from the combined effect of multiple factors such as biotic interactions, in addition to the environment.

NC is also defined by the grain, frequency, and extend of the interactions and environmental variables. For the interactions, the grain size refers to how the information is aggregated in the network (pairwise interactions, genus, guilds, functional groups...), and for the environment, it corresponds to the resolution; the frequency to how often the environment change occurs, from rapid fluctuations to long-term trends. The choice of these scales will depend on the question under study, and because the concept arises from the concept of community, these are restricted to limits where interactions matter (e.g. trees competition occurs at regional levels).

The NC metric is computed correlating the matrix of biotic interactions A with a matrix of taxa covariances with the environment C. We can use a *Procrustes* analysis to assess the degree of correspondence between the observed species interactions and the coherence of species' responses to environmental variables.

$$NC = Procrustes(A, C)$$

Environmental coherence matrix   The environmental coherence matrix (C) should accurately represent the pairwise co-response of species to the environment.

Intrinsic responses

Because we dont have data of the fitness of multiple species across the space, we can approximate species' sensitivity to the environment employing SDMs. From the modelled suitability curves (or ocurrence probability curves), we can obtain the sensitivity of species β_i at a given spatial point x_k by calculating the first derivative of the curve $F(x_i)$.

$$\beta_i = \frac{dF(x_i)}{dx_i}\bigg|_{x=x_k}$$

$$Cov(Iresponse_i, Iresponse_j)$$

The rate at which species respond to environmental change depends on their generation time: shorter generation times allow species to respond faster. Data on species' generation time is scarce, but we can approximate it with the organism size because they are linked: smaller organisms show higher generation times due to having higher metabolic rates, higher investment in reproduction, higher resource aquisition and use, and shorter life-spans. Therefore, smaller species should respond faster and therefore show increased sensitivity to changes in the environment.

The intrinsic response $Iresponse$ to the environment at a given spatial point would then be the joint effects of the magnitude and direction of the sensitivity β_i (slope) and the rate of response which is inversely proportional to body size (l_i^{-1}):

$$Iresponse_i = sensitivity \cdot rate = \beta_i \cdot l_i^{-1}$$

Each value of the C matrix involving a pair of species would then be:

$$C_{ij} = Cov(\beta_i(x_k) \cdot l_i^{-1}, \beta_j(x_k) \cdot l_j^{-1})$$

We might compute correlations instead of covariances between pairs to standarize between the slope and body size units.

We can consider one to multiple environmental variables depending on the type of question under study (e.g. what is the NC that insect-plant pollination communities show to temperature?).

At regional scales, the responses (slopes) can vary across space. We can then take into account an average of multiple covariances at multiple points in the environmental gradient:

$$C_{ij} = \frac{\sum_{k=1}^{n} Cov(P_i'(x_k), P_j'(x_k))}{n}$$

Net responses

The matrix of covariance of net responses can be computed locally and regionally from population time series. A community-level dynamic latent trend model, which models abundance as a function of time and species as random effects, can be used to capture the joint variation between species as their biomass fluctuates through time (Hebert et al. unpubl). Species' correlation coefficients correspond to the pairwise co-response to the environment.

![Image Alt Text](figues/fig1.PNG)

General expectations

- Alteration in community structure and functioning with environmental change should be inversely proportional to coherence.

- The coherence between interacting species should be more important for the system dynamics than the coherence of the whole community (i.e. including non-interacting pairs).

- Species roles in driving community responses to environmental change will depend on their contribution to both network structure and coherence.

NC to anticipate consequences of environmental changes on ecosystem functioning

Objective: Derive mathematical theory that would provide an expectation on the relationship between ecological coherence and changes in ecosystem functioning

Intuition: Lack of coherence will lead to disruptions in ecosystem functioning. Expected change in ecosystem functioning is proportional to the inverse of ecological coherence.

Direct versus net interactions in foodwebs   Consider the standard Lotka-Volterra model of ecological interactions:

$$\frac{dN_i}{dt} = N_i(b_i - \sum \alpha_{ij} N_j)$$

which has for equilibrium solution:

$$\hat{N} = A^{-1} b$$

where A^{-1} is the inverse of the interaction matrix. By inversing the interaction matrix, we obtain the net effects (direct and indirect) of biotic interactions.

Ecosystem functioning   The equilibrium primary productivity is defined as the sum of influxes coming into the foodweb through primary producers (first trophic level $T1$):

$$\phi_1 = \sum_{i \in T1} b_i N_{1i}$$

And the equilibrium for secondary productivity corresponds to the total metabolic rate of heterotrophs:

$$\phi_2 = - \sum_{i \in T2U...UTn} b_i N_{2i}$$

We know from press perturbation theory (Bender et al. 1984) that changes in abundance of a species i will occur as a result of the net interaction coefficient of species i and j times the amount of change we would expect in the b coefficient:

$$\delta N_i = a_{ij}^{(-1)} \delta b_j$$

where the superscript (-1) indicates elements of the inverse interaction matrix.

The problem is: what is the expected change in density for any given species, $E[\delta N_i]$ knowing that the b coefficients are changing?

Useful properties of random variables   The expectation of a product of random variables r_1 and r_2 is:

$$E[r_1 r_2] = E[r_1] + E[r_2] + cov(r_1, r_2)$$

The variance is more difficult to assess, but in the specific case of a product of random centered normal distributions is:

$$var(r_1 r_2) = 1 + p^2$$

where p is the correlation coefficient.

$$E[\delta N_i] = E[a_{ij}^{(-1)} + E[\delta b_j] + cov(a_{ij}^{(-1)}, \delta b_j)]$$

Anticipating consequences of environmental changes Coming back to the calculation of changes in abundance

$$\delta N_{ij} = a_{ij}^{(-1)} \delta b_j$$

we get:

$$E[\delta N_{ij}] = E[a_{ij}^{(-1)} + E[\delta b_j] + cov(a_{ij}^{(-1)}, \delta b_j)]$$

Expectations

- Change in abundance will increase with the correlation between net interaction strength and the magnitude of the environmental impact. This supports the intuition that changes in the environment will be more disrupting if they happen for strong interactions than if it happens for weak interactions; or, for a given net interaction strength, we expect stronger changes in abundances if the environment changes are stronger.

- The variance in the pairwise effects will increase with the square of the correlation. Or at least, it should increase non-linearly.

Useful properties of random variables The expectation of a sum of random variables r_1 and r_2 is:

$$E[r_1 + r_2] = E[r_1] + E[r_2]$$

The variance is:

$$var(r1 + r2) = var(r_1) + var(r_2) + 2cov(r_1, r_2)$$

Anticipating consequences of environmental changes turning to exosystem functioning:

$$E[\delta \phi^1] = \sum E[\delta \phi_i^1]$$

we get:

$$var(\delta \phi^1) = \sum \delta \phi_i^1 + 2 \sum cov(\delta \phi_i^1, \delta \phi_j^1)$$

Expectations
- The expected ecosystem functioning should not be impacted by coherence.
- The variance in ecosystem functioning will be inversely proportional to coherence.

!This is counterintuitive to us and the formulas need to be revisited.

::: {style="background-color: #f2f2f2; padding: 10px;"} ### NC and network beta diversity

We currently don't have a solid mechanistic understanding on the drivers of network turnover.

Objective: mathematically link coherence to network beta diversity

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The probability of observing an interaction between a pair of species in a given environment depends on the probability that species co-occur and thay they interact:

$$P(L_{ij}, x_i, x_j | E) = P(L_{ij}|E)P(x_i, x_j|E)$$

The probability of species co-occurring $P(x_i, x_j|E)$ can be decomposed further down into a condition probability:

$$P(x_i, x_j|E) = P(x_i|x_j, E)P(x_j|E)$$

where the first term at the right side of the equation is the probability of observing one species given the presence of the other in a given environment and the second is the probability of observing the other species.

The first term $P(x_i|x_j, E)$ is actually a measure of correlation between the two species, and therefore directly related to coherence.

We would then expect different beta diversity depending on the coherence in species responses and the structure of the L matrix.

Network beta-diversity and network properties

The correlation between beta-diversity of networks and coherence would depend on modularity and nestedness.

- β_s (species turnover) would be highly and inversely correlated to coherence, as highly coherent communities would tend to have similar responses to the environment, and, therefore, species would tend to "move" together. Low coherence in modular and nested networks would mean high species turnover, and species would be replaced as environmental conditions change.

- β_{os} (links turnover) would be higher in less modular and more nested networks, where coherence is high. That's because this measure is related to the number of similar species in any two communities: given that species A, B and C occur in any two networks, if the links between them are different, we have a high β_{os}.

- β_{wn} (network uniqueness) would be higher in highly modular networks where niche overlap is low. Coherence would he higher within each community than in the metaweb.

Expectations

- NC should decrease with modularity and increase with nestedness [CONNECTANCE, DEGREE DISTRIBUTION]
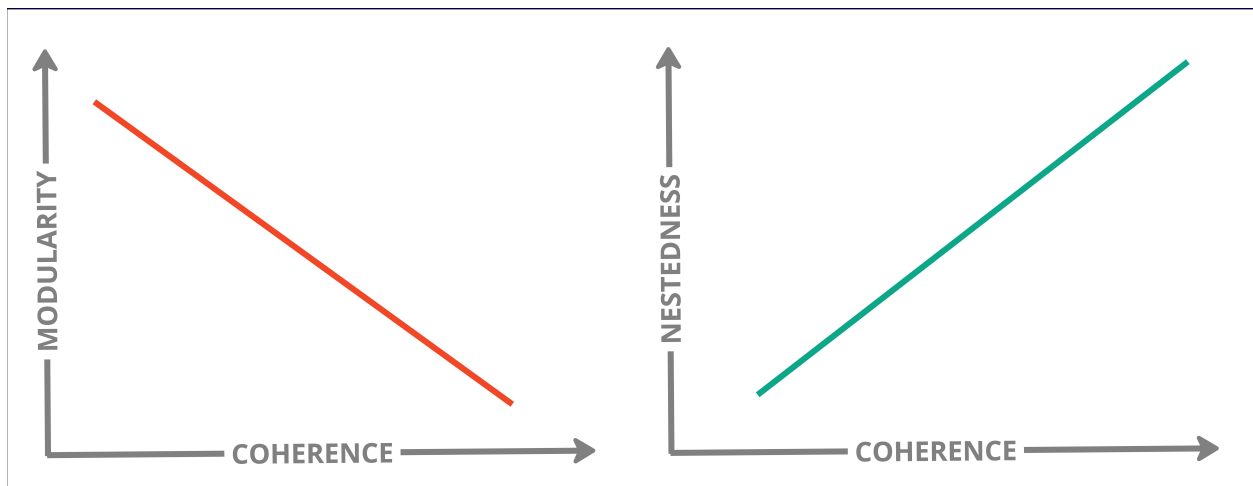
- Niche breath - low and high extremes would decrease coherence, but moderate values would increase it.
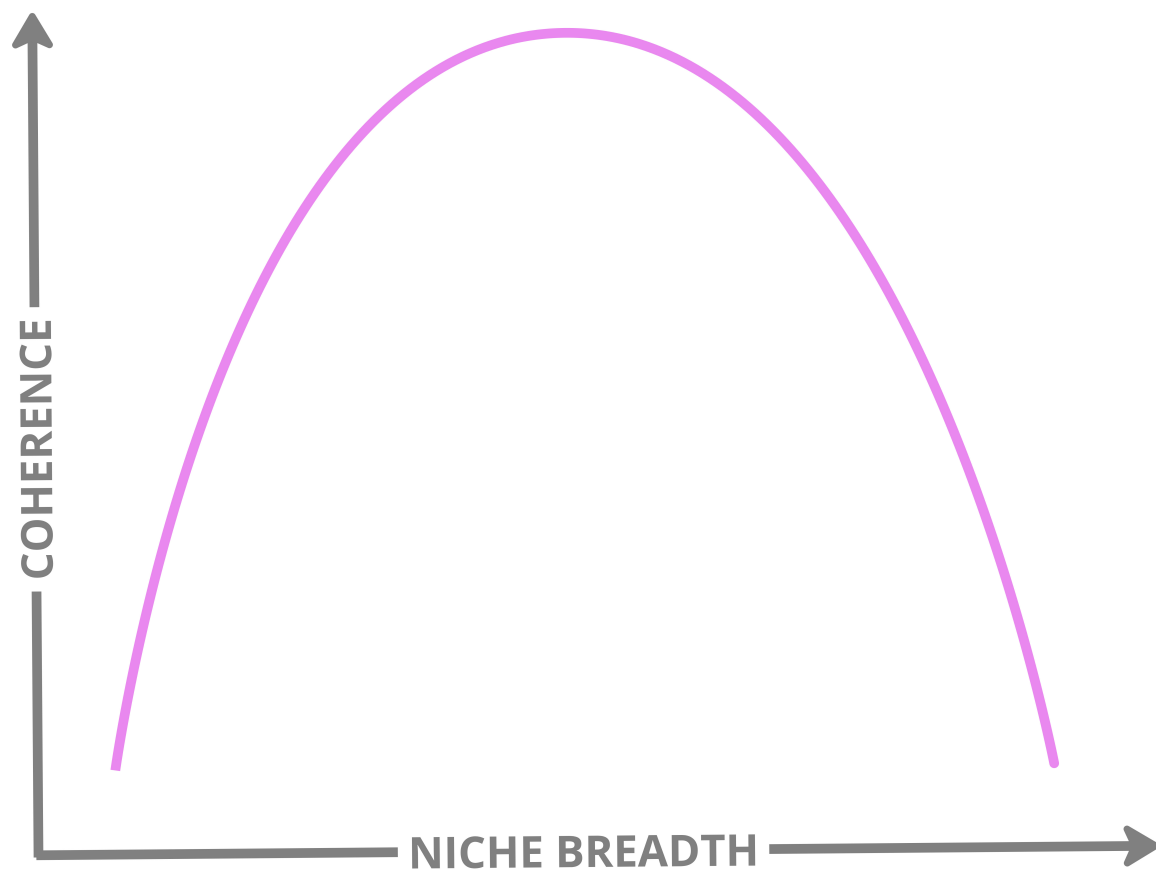
The relationship between coherence and beta diversity is contingent on how we measure beta diversity on networks - at the macro-level, there is no still convincing method to compare the structure of networks (i.e. compare species' roles rather than nodes and links).

- Mutualists would show higher coherence than antagonists

- Competition interactions would show higher incoherence than predator-prey.

- Predators would have more periods of incoherence with any pair of preys if they are generalists.

- Preys would have higher periods of incoherence between them, due to niche partitioning.

NC to identify kestonne species for the response of communities to environmental change

Objective: Derive mathematical theory that would provide an expectation on species' roles in the stability of communities in the face of environmental changes.

To explore this question, we can analyze the impact of species' removal on NC.

Expectations

- Species with lower coherence and more central in the network will be responsible of the highest amount of disruptions occurring in the network in response to environmental change.

- The contribution of species to NC should depend on the size and generalism level of the network. This is because increasing size and generalism increases the redundancy on both network roles and coherence of species, which makes perturbations more diffused. In smaller networks and specialist interactions, the consequences of species' removals would have higher consequences because there would be more direct effects involved.

  It would also be interesting to investigate the correlation between species' contributions to network structure and to coherence.

[…]

Other expectations:

- Communities in more seasonal environments may show higher Network Coherence because species may be more synchronized in responding to predictable changes in the environment.

- NC may decrease with the aggregation of network-level information (taxonomic, guilds, functional groups)

Other considerations:

- We should also take into account the fact that some environmental changes are more predictable (e.g. increase in temperature) than others (e.g. drought events).

$$C_{i,j} = corr(\alpha_i, \alpha_j)$$