ENC definition
AF
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Motivation

Global change is causing significant environmental shifts to which species must adapt. These changes are dramatically altering species' populations, distributions, and phenology. Such alterations can add, eliminate, or modify the strength and sign of interactions within communities, affecting their composition, structure, and overall functioning. Given the complexity of biodiversity and the challenges associated with measuring it, the question arises: how can we anticipate changes in these properties?

Contemporary empirical investigations () and theoretical advancements () have highlighted the importance of evaluating the degree of shared responses to environmental changes across multiple species within ecological communities, commonly referred to as community synchrony (). This integrated approach underscores the interconnectedness of species dynamics and their collective impact on ecosystem stability (). Despite advancements in understanding the impacts of community synchrony, the incorporation of information on the interaction network structures remains lacking. Simultaneously, understanding how ecosystem functioning depends on network structure remains limited (Walther 2010, Montoya & Raffaelli 2010), as it necessitates information on species' dynamics driven by more factors than interactions (Lavergne et al. 2010; Tylianakis & Morris 2017; Strydom et al. 2021; Purves et al. 2013; Harfoot et al. 2014). There is therefore a pressing need for theory and tools that comprehensively integrate the interconnected dynamics of species and their collective impact on ecosystem stability to anticipate changes in the structure and function of communities.

Objective:

In this study, we introduce the concept of Ecological Network Coherence (ENC), a conceptual framework for capturing the correlational structure of species' interdependent responses to the environment in an ecological network. ENC represents an empirical community-level pattern arising from the shared responses to environmental variables among interacting species. We propose that this empirical pattern can predict potential disruptions in ecosystem functioning and serve as a foundational element for developing a new indicator of the consequences of biodiversity changes at the community level. Our primary objectives are to (1) define ENC and its components, (2) explore its quantitative application to ecosystem functioning, and (3) illustrate how to measure and analyze ENC in empirical data.

(1). Concept definition

Species responses to environmental changes include alterations in population trends, spatial distribution shifts, and phenology changes (Bellard et al., 2012). Consequently, ecological communities are characterized by heterogeneous responses, which can be summarized as a distribution of species responses (Fig. 1).

Species Responses to the Environment
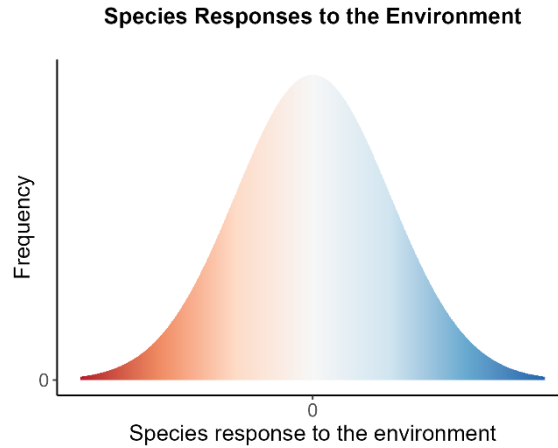
Fig. 1. A hypothetical community where species responses are perfectly balanced, with most species showing minimal response to environmental changes, while a minority exhibit strong positive or negative responses.

From this, we can assess the similarities and differences in species responses, or their co-responses. Species co-responses can be characterized based on their covariance: a positive covariance indicates that greater values of one variable typically correspond to greater values of the other, while a negative covariance suggests an inverse relationship. Correlation is a standardized version of covariance that adjusts the data to have a mean of 0 and a standard deviation of 1 (bounded between -1 and 1), providing a more straightforward interpretation of the relationship's strength and direction. Species co-responses within a community can be summarized in a matrix, C, which comprises pairwise correlations. The distribution of these co-responses forms a community pattern that we define as the Ecological Coherence of the community, reflecting how coherent species responses are to the environment (Fig. 2).
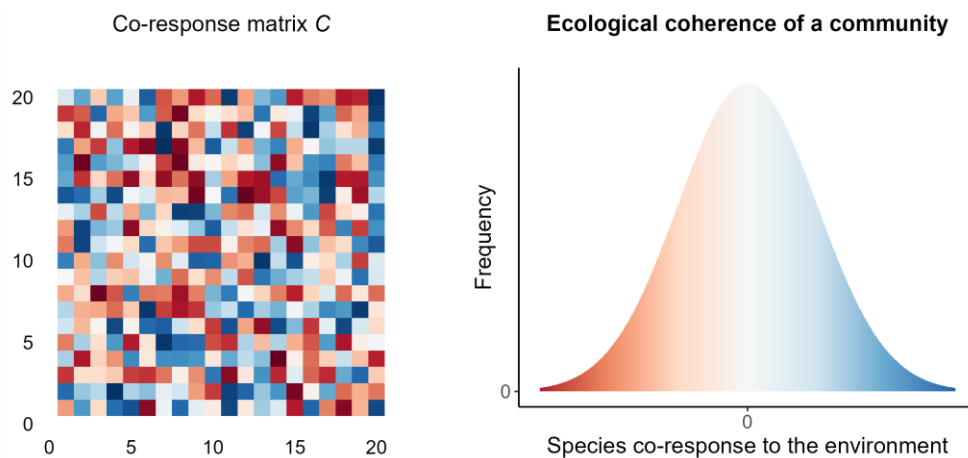
Fig. 2. A matrix of species co-responses to specific environmental variables (left) can be represented as a distribution (right), illustrating the Ecological Coherence of a community.

We can incorporate information on community structure by considering the co-responses between pairs of interacting species: the matrix C can be filtered out (multiplied) by the adjacency matrix of interactions A, which denotes the presence or absence of interactions. The distribution of the resulting filtered co-response matrix is a pattern that shows the degree of co-responses to specific environmental variables between interacting species within a community at a given location in space and time, which we define as Ecological Network Coherence.
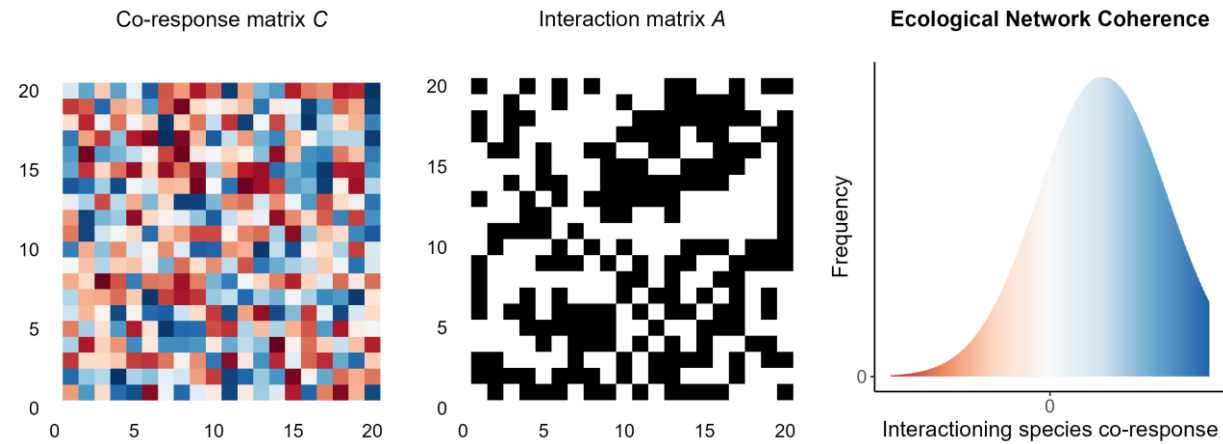
Fig. 3. By combining the co-response matrix C and the interaction matrix A (left), we derive the Ecological Coherence that accounts for interactions among species, termed the Ecological Network Coherence (ENC) of a community.

Summarizing the pattern of species co-responses and interactions in a community distribution, ENC provides an intuitive tool for predicting the consequences of various statistical modes on ecosystem functioning. This approach offers significant advantages by bridging empirical and theoretical work. ENC is constructed from commonly measured data, making it accessible and practical for empirical researchers. At the same time, it is represented as a clear statistical object, facilitating theoretical exploration and modeling. This dual utility fosters a common framework for both empiricists and theoreticians and intuitively summarizes complex community patterns enhancing our ability to understand and predict changes in ecosystem structure and function.

(2). Linking ENC to ecosystem functioning

Let X_i be the abundance of species i in a Lotka-Volterra system, with intrinsic growth rate r_i and interaction coefficient with species j given by a_{ij}. We can write the dynamics of species i as:

$$\frac{dX_i}{dt} = X_i \left[r_i - \sum_j a_{ij} X_j \right] \tag{1}$$

Assuming the existence of an equilibrium and that all n species have non-zero abundances at equilibrium, we can write the equation for all species at equilibrium using vector notations (i.e. with arrows):

$$\vec{r} = A.\overrightarrow{X^*} \tag{2}$$

which, if the system is sufficiently not pathological, can be inverted:

$$\overrightarrow{X^*} = A^{-1}.\vec{r} \tag{3}$$

If a push perturbation $\overrightarrow{\Delta r}$ is applied to the system over a sufficiently long time, we thus expect the equilibrium to shift away from $\overrightarrow{X^*}$ by a quantity $\overrightarrow{\Delta X}$, given by:

$$\overrightarrow{\Delta X} = A^{-1}.\overrightarrow{\Delta r} \tag{4}$$

Now assuming that $\overrightarrow{\Delta r}$ is random among species, i.e. that the effect of the perturbation on each and every species is drawn from an underlying distribution, we can call $\overline{\Delta r}$ the mean push perturbation and $\mathbb{V}(\Delta r)$ the variance of push perturbation among species. For commodity, we note $\vec{1}$ the vector comprising as many 1's as the number of species in the system, and T is used as the symbol for transposition.

$$\overline{\Delta r} = \frac{1}{n}\vec{1}^T.\overrightarrow{\Delta r} \tag{5}$$

$$
\begin{aligned}
\mathbb{V}(\Delta r) \ &= \left(\overrightarrow{\Delta r} - \frac{1}{n}\vec{1}^T.\overrightarrow{\Delta r}\vec{1} \right)^T . \left(\overrightarrow{\Delta r} - \frac{1}{n}\vec{1}^T.\overrightarrow{\Delta r}\vec{1} \right) \\
&= \overrightarrow{\Delta r}^T.\overrightarrow{\Delta r} - \left(\frac{2}{n} - \frac{1}{n^2} \right) \left(\vec{1}^T.\overrightarrow{\Delta r} \right)^2 \\
&= \overrightarrow{\Delta r}^T.\overrightarrow{\Delta r} - (2n-1)\left(\overline{\Delta r} \right)^2
\end{aligned} \tag{6}
$$

In the same way, we can define $\overline{\Delta X}$ the mean abundance change due to the perturbation and $\mathbb{V}(\Delta X)$ the variance of these abundance changes among species.

$$\overline{\Delta X} = \frac{1}{n}\vec{1}^T.\overrightarrow{\Delta X} \tag{7}$$

$$\begin{aligned}
\mathbb{V}(\Delta X) \ &= \left(\overrightarrow{\Delta X} - \frac{1}{n}\vec{1}^T.\overrightarrow{\Delta X}\vec{1}\right)^T.\left(\overrightarrow{\Delta X} - \frac{1}{n}\vec{1}^T.\overrightarrow{\Delta X}\vec{1}\right) \\
&= \overrightarrow{\Delta X}^T.\overrightarrow{\Delta X} - \left(\frac{2}{n} - \frac{1}{n^2}\right)\left(\vec{1}^T.\overrightarrow{\Delta X}\right)^2
\end{aligned} \tag{8}$$

Hereafter, we use the notation $B = A^{-1}$ in order to look at the effect of A on changes in abundances at equilibrium. Getting back to equation (4) and developing the sums, we get:

$$\begin{aligned}
\overline{\Delta X} \ &= \frac{1}{n}\sum_i \sum_j b_{ij}\,\Delta r_j \\
&= \frac{1}{n}\sum_j \Delta r_j \left(\sum_i b_{ij}\right)
\end{aligned} \tag{9}$$

In this final expression, we recognize the average (*sensu* "among all species") of the product of the Δr and the column sums of B. Hence, if we further decompose this using the abusive $\mathbb{E}$ and cov notations (expectations are to be understood as averages over columns):

$$\overline{\Delta X} = \mathbb{E}\left[\vec{1}^T B\right]\mathbb{E}\left[\overrightarrow{\Delta r}\right] + cov\left(\vec{1}^T B, \overrightarrow{\Delta r}\right) \tag{10}$$

Adopting the perspective where the vector $\overrightarrow{\Delta r}$ is a random vector that follows a multivariate distribution with mean vector and covariances between vector components, we can use the propagation of uncertainty to deduce that:

$$var(\Delta X_i) \approx \sum_k \sum_l b_{ik}\, b_{il}\mathrm{cov}(\Delta r_k, \Delta r_l) \tag{11}$$

$$cov\left(\Delta X_i, \Delta X_j\right) \approx \sum_k \sum_l b_{ik}\, b_{jl}\mathrm{cov}(\Delta r_k, \Delta r_l) \tag{12}$$

with (as above) $B = A^{-1}$ the inverse of the LV interaction matrix.

(2). Predictions - effect of ENC on the predictability of community dynamics

As a first approach to investigating the consequences of ENC on ecosystem functioning, we demonstrated mathematically how it links to abundance changes and its predictability (variance in abundance changes) in a Lotka Volterra system submitted to a push perturbation.

Equation (11) captures how the covariances of perturbation responses among all species in the network contribute to the variance in abundance changes for a focal species i. The equation sums up the contributions of all pairs of species (k and l) to the variance of the abundance change of species i. This means that the variance in abundance changes for a focal species i is influenced by how all other species in the network respond to perturbations (as captured by the covariances $cov(\Delta r_k, \Delta r_l)$) and how these responses propagate through the network (as captured by the elements of the matrix B).

Upon a perturbation, we get Δr for each species. Therefore, the covariance matrix C is:

$$C = \begin{bmatrix} cov(\overrightarrow{\Delta r_1}, \overrightarrow{\Delta r_1}) & cov(\overrightarrow{\Delta r_1}, \overrightarrow{\Delta r_2}) & \cdots & cov(\overrightarrow{\Delta r_1}, \overrightarrow{\Delta r_k}) \\ cov(\overrightarrow{\Delta r_2}, \overrightarrow{\Delta r_1}) & cov(\overrightarrow{\Delta r_2}, \overrightarrow{\Delta r_2}) & \cdots & cov(\overrightarrow{\Delta r_2}, \overrightarrow{\Delta r_k}) \\ \vdots & \vdots & \ddots & \vdots \\ cov(\overrightarrow{\Delta r_k}, \overrightarrow{\Delta r_1}) & cov(\overrightarrow{\Delta r_k}, \overrightarrow{\Delta r_2}) & \cdots & cov(\overrightarrow{\Delta r_k}, \overrightarrow{\Delta r_k}) \end{bmatrix} \tag{13}$$

The net effect on variance is the result of complex interactions between species' responses to perturbations and their interaction coefficients, which can either amplify or reduce the variance depending on the specific configuration.

1. b_{ik} and b_{il} have the same sign
- $b_{ik}b_{il}$ is positive.
- If **positive covariance** ($cov(\Delta r_k, \Delta r_l) > 0$), the term $b_{ik}b_{il}cov(\Delta r_k, \Delta r_l)$ will be positive.
- If **negative covariance** ($cov(\Delta r_k, \Delta r_l) < 0$), the term $b_{ik}b_{il}cov(\Delta r_k, \Delta r_l)$ will be negative.

Positive covariance increases the overall variance $var(\Delta X_i)$, potentially making the system less predictable, whereas negative covariance has the contrary effect.

2. b_{ik} and b_{il} have opposite signs
- $b_{ik}b_{il}$ is negative.
- If **positive covariance** ($cov(\Delta r_k, \Delta r_l) > 0$), the term $b_{ik}b_{il}cov(\Delta r_k, \Delta r_l)$ will be negative.
- If **negative covariance** ($cov(\Delta r_k, \Delta r_l) < 0$), the term $b_{ik}b_{il}cov(\Delta r_k, \Delta r_l)$ will be positive.

Positive covariance decreases the overall variance $var(\Delta X_i)$, potentially making the system more predictable, whereas negative covariance has the contrary effect.

3. Heterogeneity of interaction effects

The scenarios discussed above apply to theoretical communities where most interactions between species are either predominantly positive or negative. However, in empirical communities, the net effects of interactions often vary widely in strength and sign:
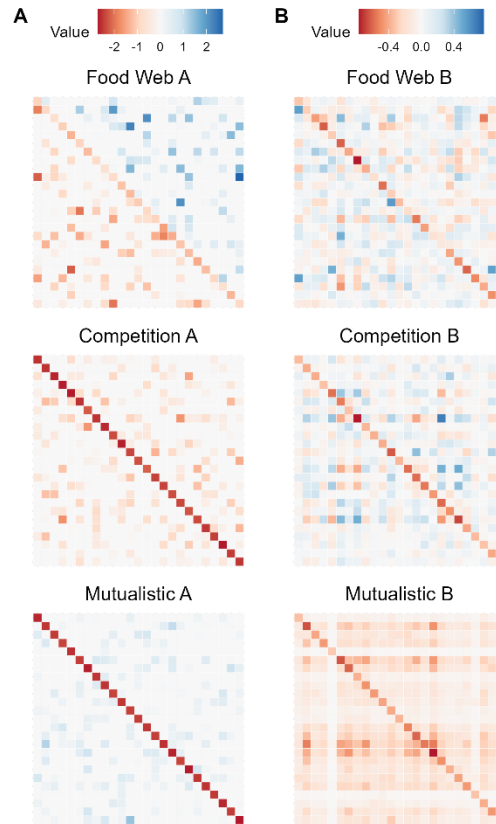
Figure 4. Interaction strengths for direct interaction matrices A (A) and net effect matrices B (B) for different types of interactions. The diagonal elements for A are adjusted by setting them to a negative value that is slightly larger than the maximum real eigenvalue plus a small random value between 0 and 0.1. This makes the diagonal elements of A negative. As a note: when the diagonal is adjusted to negative values, it introduces self-regulation. This damping effect reduces the overall interaction strengths in the matrix B. Consequently, the values in B are lower, indicating that the system is more stable and less sensitive to changes in interaction strengths.

This heterogeneity in interaction coefficients* means that any covariance structure will result in both increases and decreases in abundance variance, making it challenging to predict the outcomes. However, the strength of coherence will modulate the magnitude of these changes in variance in a consistent manner: small covariances are likely to decrease changes in variance, while large covariances will increase them.

This leads to two general predictions: first, the heterogeneous nature of real-world interactions makes the overall impact of coherence on stability complex and challenging to predict. Second, ENC patterns with strong coherence will reduce the predictability of communities and increase the potential for significant disruptions in their structure and function.

*[NOTE] Seems that this is not the case for mutualistic networks, whose *B* matrix does not contain positive values:

```r
# Function to test if a matrix contains any negative values
contains_positive_values <- function(mat) {
  any(mat > 0)
}

# Simulate 100 mutualistic networks and test for negative values

positive_values_found <- numeric(length = 1000)

for (i in 1:1000) {
  A <- sim_quantitative_network("mutualistic", S, C, aij_params, diag = "nonzero")
  B <- solve(A)
  positive_values_found[i] <- contains_positive_values(B)
}

# Check the results
sum(positive_values_found) # Number of B matrices containing negative values
## [1] 0
```

Simulations to test predictions

I simulated 100 food web structures with random interaction strengths (mean = 0, SD = 1) and computed the abundance change and variance in abundance change according to formulas (9) and (11). I tested different covariance structures*: strong positive caused by species' increases, strong positive caused by species' decreases, weak positive by species' increases, weak positive by species' decreases, null (zero covariance), weak mixed (positive and negative), and strong mixed. These are built by simulating initial and final *r* values, which determine the Δr for each species. The values in the *C* matrix are the covariance between species'Δr vectors, $cov(\overrightarrow{\Delta r_k}, \overrightarrow{\Delta r_1})$, as indicated in equation (13)).

Based on our mathematical intuition, we expect to find that the variance in abundance change is higher for the scenarios with strong positive and strong mixed covariances, and lower for weak positive, weak mixed, and null covariances.

*[NOTE] Whereas full-positive *C* matrices are feasible, full-negative ones are not. This is because negative covariance arises when species show contrary responses between them, which implies that some species will inevitably share responses among them.

Covariance matrices:

```r
# Number of species
S <- 25

# Simulate initial r values (ri)
set.seed(123)
ri <- runif(S, -1, 1)

# Function to generate rf values with positive covariance
generate_rf_positive <- function(ri, mean_change, sd_variation) {
  rf <- ri + rnorm(length(ri), mean_change, sd_variation)
  return(rf)
}

# Mixed (positive and negative)
generate_rf_mixed <- function(ri, mean_change_positive, mean_change_negative, sd_variation) {
  rf <- ri
  for (i in 1:length(ri)) {
    if (i %% 2 == 0) {
      rf[i] <- ri[i] + rnorm(1, mean_change_positive, sd_variation)
    } else {
      rf[i] <- ri[i] + rnorm(1, mean_change_negative, sd_variation)
    }
  }
  return(rf)
}

# Compute the covariance matrix using delta_r vectors
compute_cov_matrix <- function(delta_r_vectors) {
  S <- nrow(delta_r_vectors)
  cov_matrix <- matrix(NA, nrow = S, ncol = S)
  for (i in 1:S) {
    for (j in 1:S) {
      cov_matrix[i, j] <- cov(delta_r_vectors[i, ], delta_r_vectors[j, ])
    }
  }
  return(cov_matrix)
}

# Generate rf values for different scenarios
mean_change_strong <- 1.2
mean_change_weak <- 0.5
sd_variation <- 0.1

# Strong positive
rf_strong_positive <- generate_rf_positive(ri, mean_change_strong, sd_variation)
delta_r_strong_positive <- rf_strong_positive - ri

# Weak positive
rf_weak_positive <- generate_rf_positive(ri, mean_change_weak, sd_variation)
delta_r_weak_positive <- rf_weak_positive - ri

# Mixed weak
mean_change_positive <- 0.5
mean_change_negative <- -0.5
rf_mixed_weak <- generate_rf_mixed(ri, mean_change_positive, mean_change_negative, sd_variation)
delta_r_mixed_weak <- rf_mixed_weak - ri

# Mixed strong
mean_change_positive_strong <- 1.2
mean_change_negative_strong <- -1.2
rf_mixed_strong <- generate_rf_mixed(ri, mean_change_positive_strong, mean_change_negative_strong, s
d_variation)
delta_r_mixed_strong <- rf_mixed_strong - ri

# Null (no change)
delta_r_null <- rep(0, S)
delta_r_vectors_null <- cbind(ri, ri)  # No change, so rf = ri
```

```r
# Create vectors delta_r for each species (each row corresponds to a species)
delta_r_vectors_strong_positive <- cbind(ri, rf_strong_positive)
delta_r_vectors_weak_positive <- cbind(ri, rf_weak_positive)
delta_r_vectors_mixed_weak <- cbind(ri, rf_mixed_weak)
delta_r_vectors_mixed_strong <- cbind(ri, rf_mixed_strong)

# Compute C matrices
cov_matrix_strong_positive <- compute_cov_matrix(delta_r_vectors_strong_positive)
cov_matrix_weak_positive <- compute_cov_matrix(delta_r_vectors_weak_positive)
cov_matrix_mixed_weak <- compute_cov_matrix(delta_r_vectors_mixed_weak)
cov_matrix_mixed_strong <- compute_cov_matrix(delta_r_vectors_mixed_strong)
cov_matrix_null <- matrix(0, nrow = S, ncol = S)  # Null scenario has no change

# Combine all covariance matrices into a list
cov_matrices <- list(
  "Strong Positive" = cov_matrix_strong_positive,
  "Weak Positive" = cov_matrix_weak_positive,
  "Mixed Weak" = cov_matrix_mixed_weak,
  "Mixed Strong" = cov_matrix_mixed_strong,
  "Null" = cov_matrix_null
)

# Prepare the plot data
prepare_plot_data <- function(cov_matrices) {
  plot_data <- lapply(names(cov_matrices), function(name) {
    matrix <- cov_matrices[[name]]
    df <- melt(matrix)
    df$Scenario <- name
    return(df)
  })
  combined_plot_data <- do.call(rbind, plot_data)
  return(combined_plot_data)
}

plot_data <- prepare_plot_data(cov_matrices)

# Generate the plot
p <- ggplot(plot_data, aes(x = Var1, y = Var2, fill = value)) +
  geom_tile(color = "white") +
  scale_fill_distiller(palette = "RdBu", direction = 1, na.value = "white") +
  labs(
    x = NULL,
    y = NULL,
    fill = "Covariance"
  ) +
  theme_minimal() +
  theme(strip.text = element_text(size = 14)) +
  facet_wrap(~ Scenario, ncol = 3, scales = "free") +
  my_theme

p
```
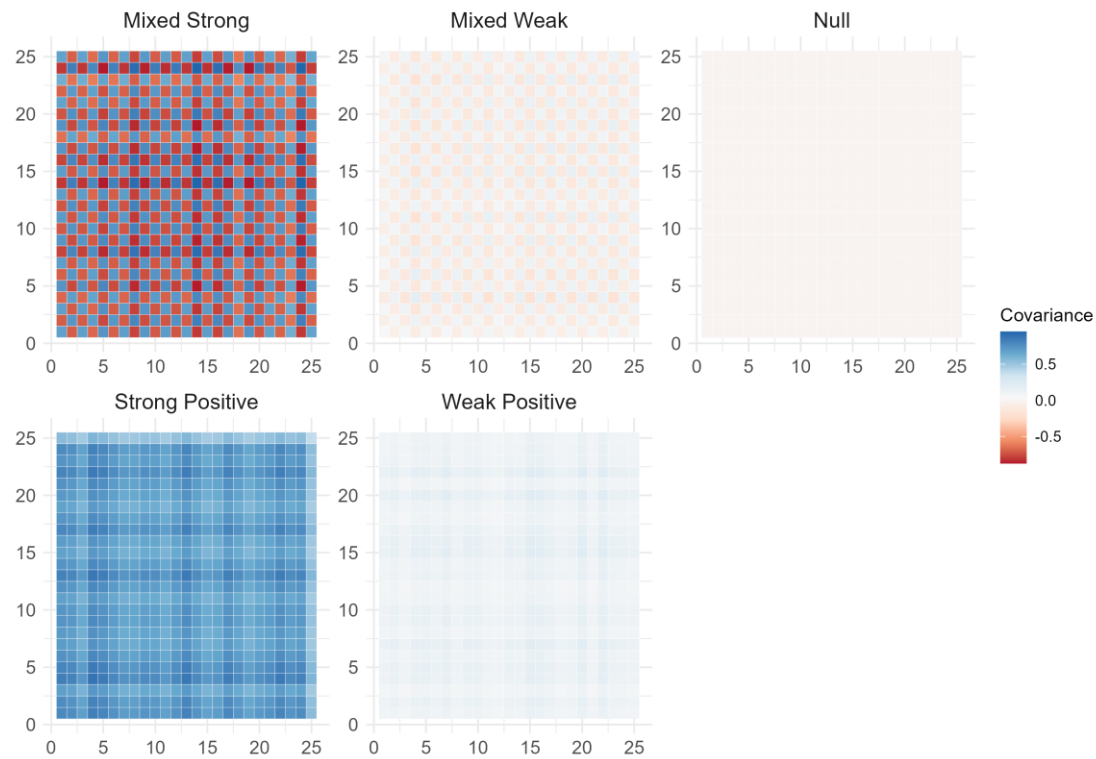
Fig 5. Covariance matrices tested in the simulation to analyze their impact on abundance change and variance in abundance change. Positive covariances may reflect species' similar increases or decreases.

Simulations for predator-prey networks:

```r
# Number of species
S <- 25

# Simulate initial r values (ri)
set.seed(123)
ri <- runif(S, -1, 1)

# Function to generate rf values with positive covariance
generate_rf_positive <- function(ri, mean_change, sd_variation) {
  rf <- ri + rnorm(length(ri), mean_change, sd_variation)
  return(rf)
}

# Function to generate rf values with Mixed covariance (positive and negative)
generate_rf_mixed <- function(ri, mean_change_positive, mean_change_negative, sd_variation) {
  rf <- ri
  for (i in 1:length(ri)) {
    if (i %% 2 == 0) {
      rf[i] <- ri[i] + rnorm(1, mean_change_positive, sd_variation)
    } else {
      rf[i] <- ri[i] + rnorm(1, mean_change_negative, sd_variation)
    }
  }
  return(rf)
}
```

```r
# Compute the covariance matrix using delta_r vectors
compute_cov_matrix <- function(delta_r_vectors) {
  S <- nrow(delta_r_vectors)
  cov_matrix <- matrix(NA, nrow = S, ncol = S)
  for (i in 1:S) {
    for (j in 1:S) {
      cov_matrix[i, j] <- cov(delta_r_vectors[i, ], delta_r_vectors[j, ])
    }
  }
  return(cov_matrix)
}

# Simulating scenarios
mean_change_strong <- 1.2
mean_change_weak <- 0.5
mean_change_strong_decrease <- -1.2
mean_change_weak_decrease <- -0.5
sd_variation <- 0.1

# Function to simulate quantitative networks
sim_quantitative_network <- function(Net_type, S, C, aij_params, rho = 0, diag_type) {
  A <- matrix(0, S, S)
  n_pairs <- S * (S - 1) / 2
  B <- runif(n_pairs) <= C
  if (Net_type == "random") {
    A[upper.tri(A)] <- B * rnorm(n_pairs, aij_params[1], aij_params[2])
    A <- t(A)
    A[upper.tri(A)] <- B * rnorm(n_pairs, aij_params[1], aij_params[2])
  } else if (Net_type == "predator-prey") {
    aij <- -abs(rnorm(n_pairs, aij_params[1], aij_params[2]))
    A[upper.tri(A)] <- B * aij
    A <- t(A)
    aij <- abs(rnorm(n_pairs, aij_params[1], aij_params[2]))
    A[upper.tri(A)] <- B * aij
  } else if (Net_type == "competition") {
    aij <- -abs(rnorm(n_pairs * 2, aij_params[1], aij_params[2]))
    A[upper.tri(A)] <- B * aij[1:n_pairs]
    A <- t(A)
    A[upper.tri(A)] <- B * aij[(n_pairs + 1):length(aij)]
  } else if (Net_type == "mutualistic") {
    aij <- abs(rnorm(n_pairs * 2, aij_params[1], aij_params[2]))
    A[upper.tri(A)] <- B * aij[1:n_pairs]
    A <- t(A)
    A[upper.tri(A)] <- B * aij[(n_pairs + 1):length(aij)]
  } else {
    stop("Incorrect network type")
  }

  if(diag_type == "zero"){
    diag(A) <- 0
  } else {
    diag(A) <- -(max(Re(eigen(A)$values)) + runif(S, 0.1))
    while (max(Re(eigen(A)$values)) > 0) {
      diag(A) <- -(max(Re(eigen(A)$values)) + runif(S, 0.1))
    }
  }

  return(A)
}

# Function to calculate metrics
calculate_metrics <- function(B, cov_delta_r, delta_r) {
  n <- nrow(B)

  # Variance of Delta X
  var_delta_X <- numeric(n)
  for (i in 1:n) {
    var_sum <- 0
```

```r
    for (k in 1:n) {
      for (l in 1:n) {
        var_sum <- var_sum + B[i, k] * B[i, l] * cov_delta_r[k, l]
      }
    }
    var_delta_X[i] <- var_sum
  }

  # Compute column sums of B
  col_sums_B <- colSums(B)

  # Average of the sum of each column of B
  mean_sum_B <- mean(col_sums_B)

  # Mean of delta_r (assuming it is an average of a random distribution)
  mean_delta_r <- mean(delta_r)

  # Covariance between sum of each column of B and delta_r
  cov_sum_B_delta_r <- cov(col_sums_B, delta_r)

  # Calculate Abundance Change
  abundance_change <- mean_sum_B * mean_delta_r + cov_sum_B_delta_r

  return(list(Variance = var_delta_X, Abundance_Change = abundance_change))
}

# Run simulations
run_simulations_with_metrics <- function(num_simulations, Net_type, S, C, aij_params, scenario, mean
_change_strong, mean_change_weak, sd_variation) {
  results <- replicate(num_simulations, {
    # Generate new C matrix for each iteration
    if (scenario == "Strong Positive Increases") {
      rf <- generate_rf_positive(ri, mean_change_strong, sd_variation)
    } else if (scenario == "Weak Positive Increases") {
      rf <- generate_rf_positive(ri, mean_change_weak, sd_variation)
    } else if (scenario == "Strong Positive Decreases") {
      rf <- generate_rf_positive(ri, mean_change_strong_decrease, sd_variation)
    } else if (scenario == "Weak Positive Decreases") {
      rf <- generate_rf_positive(ri, mean_change_weak_decrease, sd_variation)
    } else if (scenario == "Null") {
      rf <- ri
    } else if (scenario == "Mixed Weak") {
      rf <- generate_rf_mixed(ri, mean_change_weak, mean_change_weak_decrease, sd_variation)
    } else if (scenario == "Mixed Strong") {
      rf <- generate_rf_mixed(ri, mean_change_strong, mean_change_strong_decrease, sd_variation)
    }

    delta_r <- rf - ri
    delta_r_vectors <- cbind(ri, rf)
    cov_matrix <- compute_cov_matrix(delta_r_vectors) # compute C matrix from delta_r vectors

    interaction_matrix <- sim_quantitative_network(Net_type, S, C, aij_params, diag_type = "nonzero"
)
    inverse_matrix <- solve(interaction_matrix)
    if (is.null(inverse_matrix)) {
      return(list(Variance = rep(NA, S), Abundance_Change = NA))
    }

    metrics <- calculate_metrics(inverse_matrix, cov_matrix, delta_r)
    list(metrics = metrics, A_matrix = interaction_matrix, B_matrix = inverse_matrix, C_matrix = cov
_matrix)
  }, simplify = FALSE)

  list(results = lapply(results, function(res) res$metrics),
       A_matrices = lapply(results, function(res) res$A_matrix),
       B_matrices = lapply(results, function(res) res$B_matrix),
       C_matrices = lapply(results, function(res) res$C_matrix))
}
```

```r
# Generate results for each scenario
Net_type <- "competition"
C <- 0.2
aij_params <- c(0, 0.1)
num_simulations <- 100

scenarios <- c("Strong Positive Increases", "Weak Positive Increases", "Strong Positive Decreases",
"Weak Positive Decreases", "Null", "Mixed Weak", "Mixed Strong")

simulation_results_with_metrics <- lapply(scenarios, function(scenario) {
  run_simulations_with_metrics(num_simulations, Net_type, S, C, aij_params, scenario, mean_change_st
rong, mean_change_weak, sd_variation)
})


# Prepare the matrices data
prepare_matrices_data <- function(simulation_results) {
  df_list_matrices <- lapply(names(simulation_results), function(scenario) {
    A_matrices <- simulation_results[[scenario]]$A_matrices
    B_matrices <- simulation_results[[scenario]]$B_matrices
    C_matrices <- simulation_results[[scenario]]$C_matrices
    df <- data.frame(
      Scenario = rep(scenario, length(A_matrices)),
      A_matrix = I(A_matrices),
      B_matrix = I(B_matrices),
      C_matrix = I(C_matrices)
    )
    return(df)
  })
  combined_df_matrices <- bind_rows(df_list_matrices)
  return(combined_df_matrices)
}


combined_matrices_data <- prepare_matrices_data(setNames(simulation_results_with_metrics, scenarios)
)


###########################################################


# Prepare the data for plotting
prepare_combined_plot_data <- function(simulation_results) {
  df_list_var <- lapply(names(simulation_results), function(scenario) {
    data <- simulation_results[[scenario]]$results
    df <- data.frame(
      Scenario = scenario,
      Variance = unlist(lapply(data, function(res) res$Variance)),
      Abundance_Change = unlist(lapply(data, function(res) res$Abundance_Change))
    )
    return(df)
  })
  combined_df_var <- bind_rows(df_list_var)
  combined_df_var <- combined_df_var %>% filter(!is.na(Variance) & !is.na(Abundance_Change))

  return(combined_df_var)
}


combined_plot_data <- prepare_combined_plot_data(setNames(simulation_results_with_metrics, scenarios
))


# Plot results
scenario_order <- c(
  "Strong Positive Increases",
  "Weak Positive Increases",
  "Null",
  "Strong Positive Decreases",
```

```r
  "Weak Positive Decreases",
  "Mixed Weak",
  "Mixed Strong"
)

combined_plot_data$Scenario <- factor(combined_plot_data$Scenario, levels = scenario_order)

# Define color palette based on RdBu
color_palette <- scales::brewer_pal(palette = "RdBu", direction = -1)(7)
mixed_weak_color <- "violet"
mixed_strong_color <- "magenta4"

# Define scenario colors
scenario_colors <- setNames(c(color_palette[1], color_palette[2], color_palette[5], color_palette[1]
, color_palette[2], mixed_weak_color, mixed_strong_color), scenario_order)

# Plot abundance change
p1 <- ggplot(combined_plot_data, aes(x = Scenario, y = Abundance_Change, fill = Scenario)) +
  geom_jitter(width = 0.2, alpha = 0.1, shape = 21, size = 2, aes(color = Scenario)) +
  scale_fill_manual(values = scenario_colors) +
  scale_color_manual(values = c(setNames(ifelse(scenario_order == "Null", "black", scenario_colors),
scenario_order), "black")) +
  geom_hline(yintercept = 0, linetype = "dashed", color = "red") +
  labs(x = " ", y = "Abundance Change") +
  theme_classic() +
  theme(axis.text.x = element_text(angle = 45, hjust = 1), legend.position = "none")

# Plot variance in abundance change
p2 <- ggplot(combined_plot_data, aes(x = Scenario, y = Variance, fill = Scenario)) +
  geom_jitter(width = 0.2, alpha = 0.1, shape = 21, size = 2, aes(color = Scenario)) +
  scale_fill_manual(values = scenario_colors) +
  scale_color_manual(values = c(setNames(ifelse(scenario_order == "Null", "black", scenario_colors),
scenario_order), "black")) +
  labs(x = " ", y = "Variance in Abundance Change") +
  theme_classic() +
  theme(axis.text.x = element_text(angle = 45, hjust = 1), legend.position = "none")


ggarrange(p1, p2, nrow = 2, ncol = 1, labels = LETTERS[1:2])
```
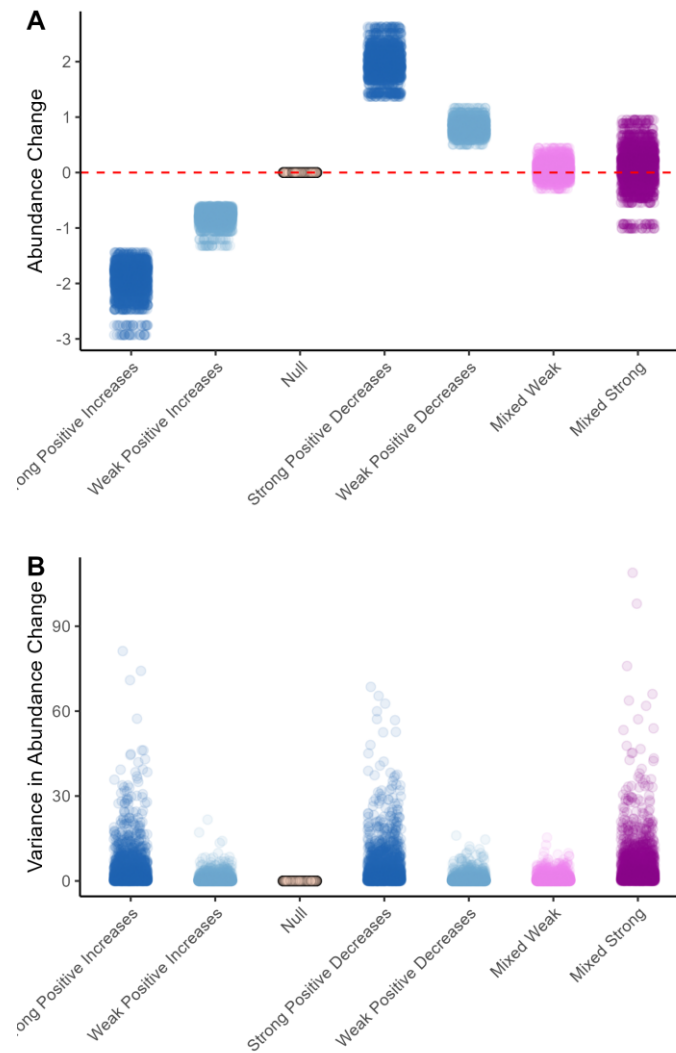
Fig 6. Effects of community covariance structure on the change in abundance of species in foodwebs (A) and the variance of abundance changes (B). Each dot represents a species within one of the 100 simulated foodwebs.

The simulations reveal that:

- Abrupt changes in abundances occur when species exhibit strong co-responses. When these responses are predominantly positive, there are significant increases or decreases in species abundance. Conversely, when co-responses are both positive and negative, the outcomes are more varied, including both major increases and decreases in abundance, but at a smaller scale than when they are predominantly positive.

- Variance in abundance changes is higher when species display strong co-responses, particularly in scenarios with strong mixed co-responses.
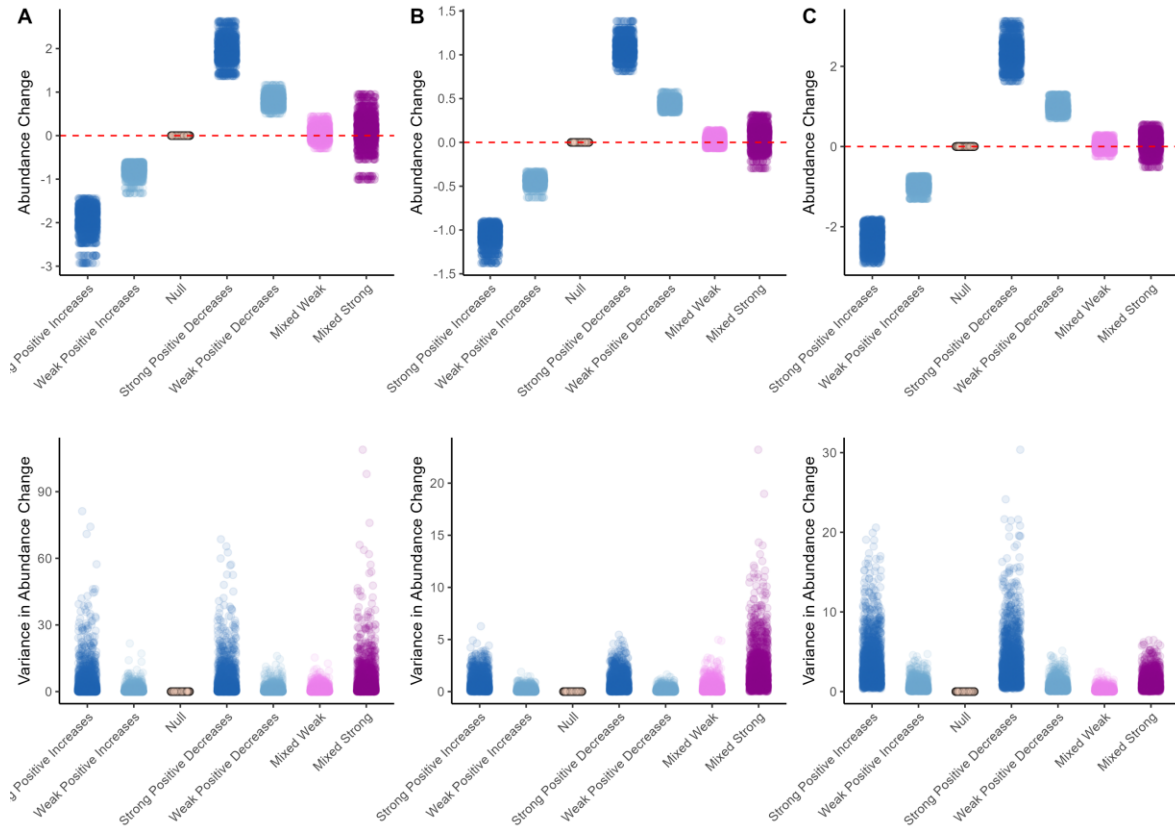
Fig. 7. Comparison of simulation results between predator-prey (A), mutualistic (B), and competition (C) networks. Mutualistic networks show a slightly different pattern than predator-prey and competition: in positive covariance scenarios, they show stronger decrease in abundance, and the variance in abundance change is higher in strong positive covariance scenarios than in mixed strong.

We can see how the different scenarios of *C* matrix structures translate to ENC:
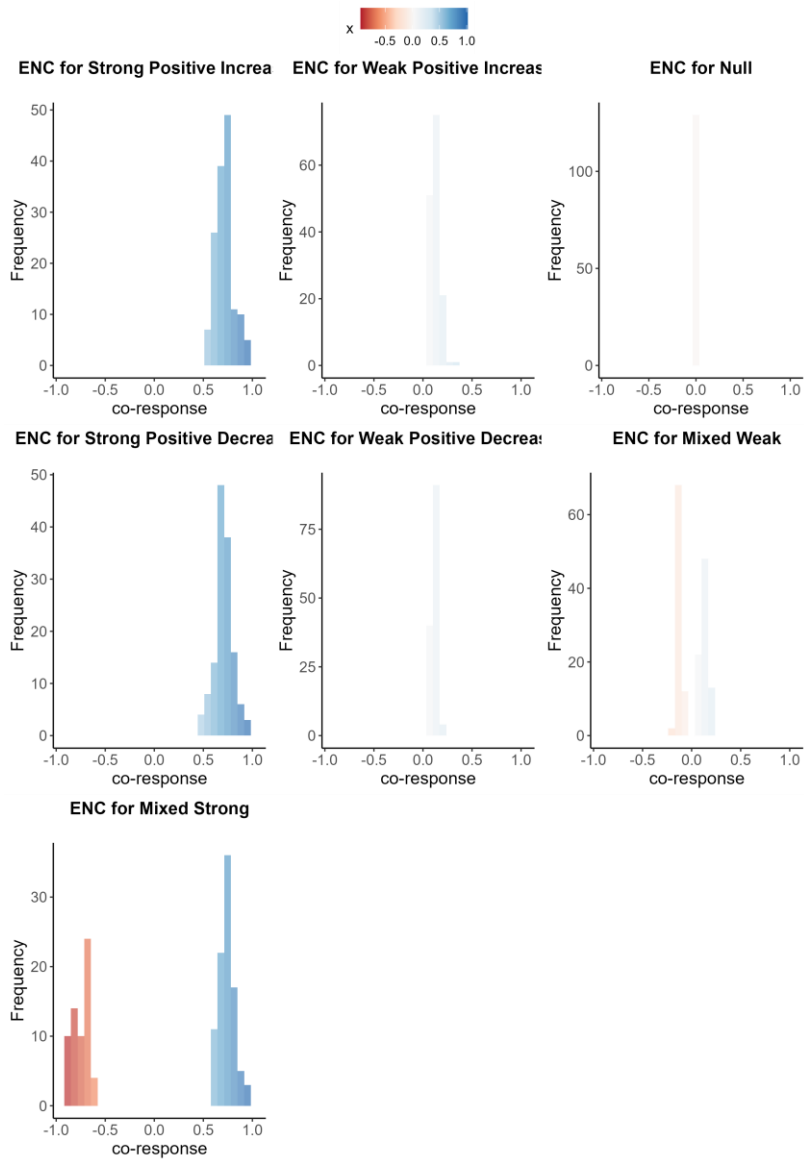
Fig. 8. Examples of an ENC for a single simulation in each covariance scenario tested.

Summary

ENC provides a robust framework for summarizing the co-responses of interacting species within a community, derived from common empirical data, and offers properties that can be analyzed using established theoretical models to understand their impact on ecosystem functioning. We demonstrated that the relationship between the elements constituting ENC—the structure of species interactions and their co-responses to environmental changes—significantly influence Lotka-Volterra (LV) dynamics in a community. In empirical systems, predicting these effects is challenging due to the heterogeneous nature of interaction effects. However, a general prediction emerges: stronger coherence among species' responses will lead to greater disruptions in community structure, making the system less predictable, irrespective of the direction of coherence. Simulations across various scenarios of species co-responses partly confirmed this prediction, revealing that the most significant changes in abundance occur when strong coherence is unidirectional. Additionally, the system becomes least predictable when coherence is strong in both directions, with the effects varying depending on the type of interaction.

**Extension – species' roles and impact on community dynamics**

The covariance contribution in Formula (10), $cov(\vec{1}^T B, \vec{\Delta r})$, suggests that species with higher influence (influence measured as the sum of all row values for a given column or species) within the interaction network (as captured by the B matrix) and their corresponding responses Δr will contribute more to this term than other species. Consequently, these species are more relevant in significantly impacting the overall change in abundance. In other words, changes in community abundance will largely depend on the responses of these central species within the interaction network.
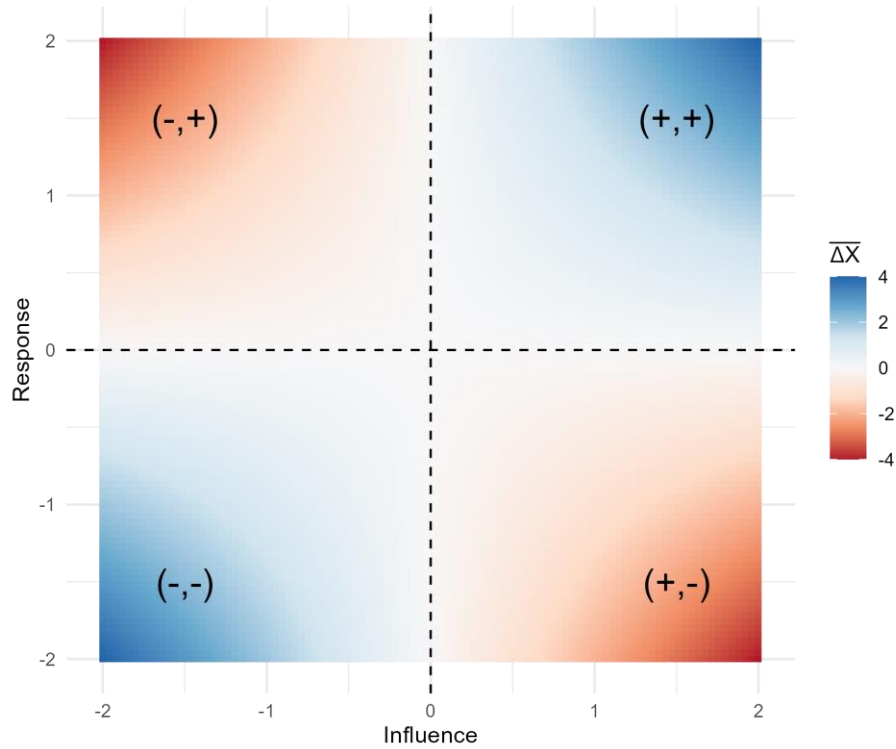
Fig. 9. Diagram showing the impact of the combined effect of species' influence in the interaction matrix (column sum of net interaction effects matrix B) and their response to the environment (Δr) on the mean abundance change of the community, following formula (9). The signs in parentheses indicate the values along the response and influence axes.

The pattern formed by the location of species within this diagram could provide new insights in spotting risks of community disruptions:
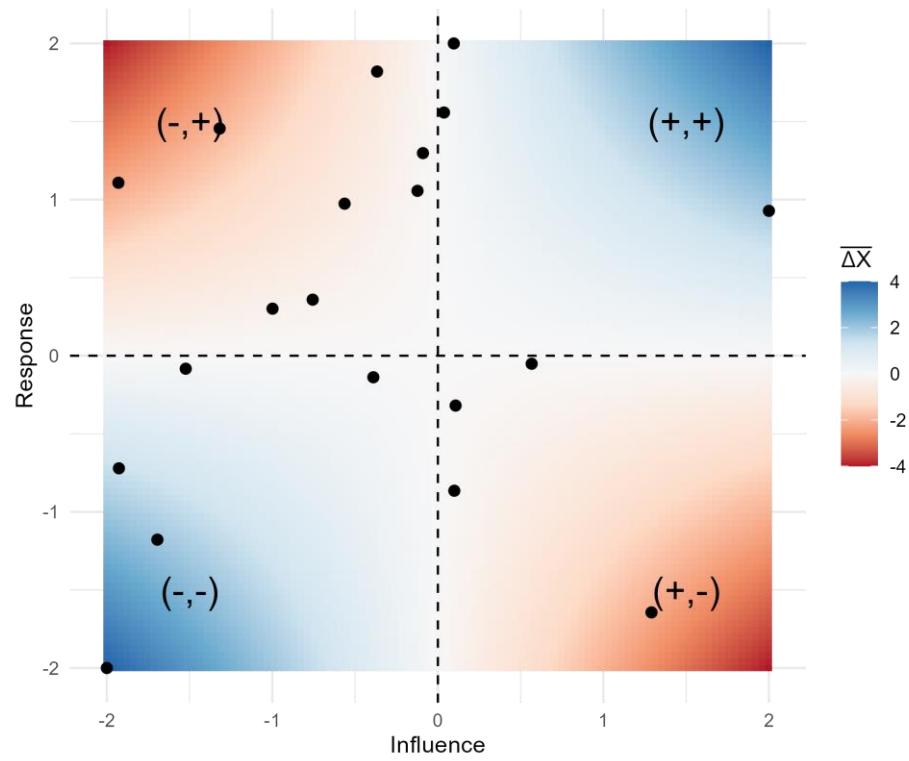
Fig. 10. Diagram showing values for species from a simulated foodweb.