LV simulations - effect of species' co-responses to the environment on community dynamics

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).
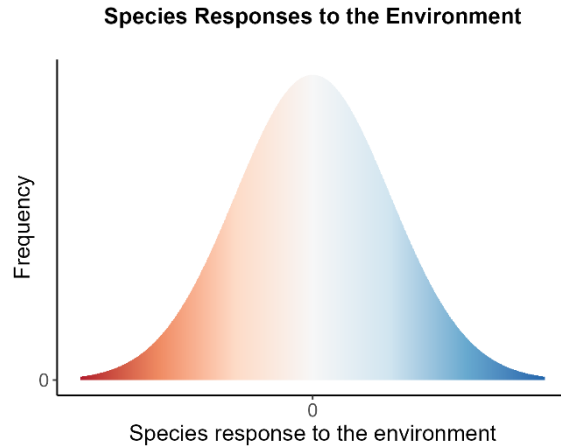
Species Responses to the Environment

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).
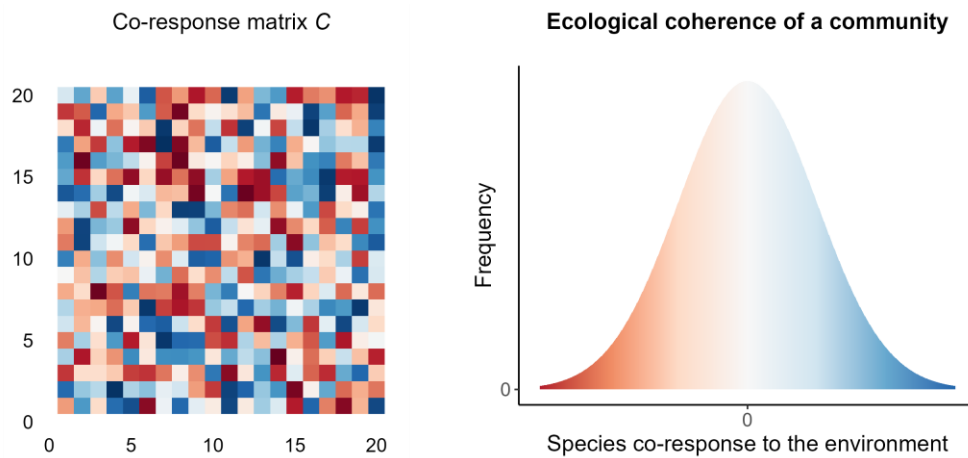

Fig. 2. A matrix of species co-responses to specific environmental variables (left) can be represented as a distribution (right), illustrating the Ecological Coherence of a community.

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.
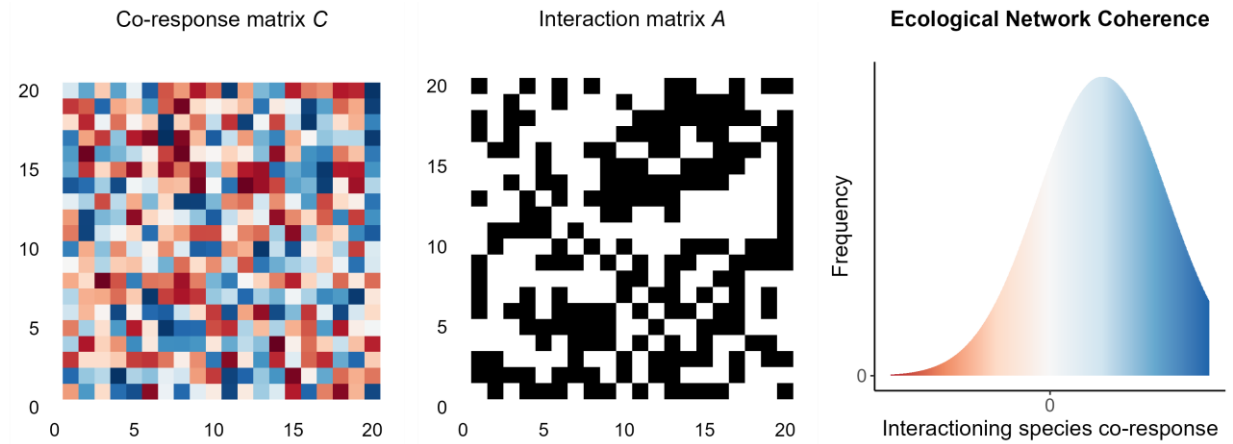

Fig. 3. By combining the co-response matrix C and the interaction matrix A (left), we derive the Ecological Coherence that accounts for interactions among species, termed the Ecological Network Coherence (ENC) of a community.

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.

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:

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

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):

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

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

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

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:

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

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.

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

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

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.

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

$$\mathbb{V}(\Delta X) = \left(\overline{\Delta \vec{X}} - \frac{1}{n}\vec{1}^T.\overline{\Delta \vec{X}\vec{1}}\right)^T.\left(\overline{\Delta \vec{X}} - \frac{1}{n}\vec{1}^T.\overline{\Delta \vec{X}\vec{1}}\right)$$

$$= \overline{\Delta \vec{X}^T}.\overline{\Delta \vec{X}} - \left(\frac{2}{n} - \frac{1}{n^2}\right)\left(\vec{1}^T.\overline{\Delta \vec{X}}\right)^2$$

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:

$$\overline{\Delta X} = \frac{1}{n}\sum_i \sum_j b_{ij} \, \Delta r_j$$

$$= \frac{1}{n}\sum_j \Delta \, r_j \left(\sum_i b_{ij}\right)$$

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):

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

Adopting the perspective where the vector $\overline{\Delta \vec{r}}$ 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:

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

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

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

Biological Interpretation of Key Equations

Through the mathematical formulation relating species' coherence in responses to environmental change to ecosystem functioning, we showed that the **Ecological Network Coherence** concept emphasizes that the impact of environmental perturbations on community structure is not only about the strength of interactions but also about how these interactions propagate through the network and influence species in a coherent or disparate manner:

Interpreting $b_{ik}b_{il}$ as Net Effects of Interactions

The terms $b_{ik}b_{il}$ reflect **net effects** within the network, accounting for both direct and indirect influences on species abundance. Unlike simply counting connections, these terms measure how **changes propagate** through all possible pathways within the network. The resulting impact of $b_{ik}b_{il}$ on variance and covariance in species abundances is therefore shaped by the entire **interaction web**:

- **Indirect Dependencies**: Values in B reflect not only direct connections but also cumulative effects, meaning that even species with few direct interactions can experience substantial influence if other species affect them indirectly.
- **Magnitude and Direction**: The values $b_{ik}b_{il}$ capture the strength and direction of these net effects, influencing how species respond to perturbations in the network.

Now, let's delve deeper into the ecological interpretation of the equations:

Equation 10: Mean Abundance Change Due to Perturbations

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

This equation shows how the **mean change** in species abundances, $\overline{\Delta X}$, depends on: -The **average impact** of perturbations ($\mathbb{E}\left[\overrightarrow{\Delta r}\right]$) across species. - and the **covariance** between perturbation effects and the column sums of B, which represents the net influence each species has in the community. In ecological terms, this tells us that both the **average direct effect** of the environment on all species and the **interaction structure** (as captured by B) jointly determine how the community's mean abundance will shift.

Breakdown of Terms:

1. **First Term**: $\mathbb{E}\left[\vec{1}^T B\right]\mathbb{E}\left[\overrightarrow{\Delta r}\right]$:
   - The component $\mathbb{E}\left[\vec{1}^T B\right]$ represents the **average influence** that each species exerts on the network. When multiplied by the average environmental impact ($\mathbb{E}\left[\overrightarrow{\Delta r}\right]$), it provides an estimate of the mean abundance change across the community.
2. **Second Term:** $\text{cov}\left(\vec{1}^T B, \overrightarrow{\Delta r}\right)$:

- This term reflects the **covariance** between species' network roles and the effects of the environmental perturbation.
- It gives insight into whether species that are **central** or influential within the network also experience **significant perturbations**.
- If this covariance is **high**, it implies that **network's most influential species** (those with larger combined interaction effects as captured by B) align closely with the environmental perturbation, potentially amplifying community-level abundance changes.

In summary, equation (10) shows that community abundance shifts are influenced by both the average effect of environmental perturbation across all species and the alignment between species' network roles and the environmental perturbation. Thus, a strong covariance between network influence and environmental perturbation magnifies changes in community abundance, especially when species central to the network experience large perturbations.

Equation 11: Variance in Abundance Change Among Species

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

This expression estimates the **variance** in the abundance change of species i. The term $b_{ik} b_{il}$ indicates that: - b_{ik} reflects the **net effect** of species k on i, considering both direct and indirect pathways. - The covariance structure $\text{cov}(\Delta r_k, \Delta r_l)$ describes the extent to which species' responses to perturbations are **correlated**, further modulated by the network's structure.

Interpretation:

This equation describes how much a particular species' abundance (X_i) is expected to fluctuate in response to a perturbation, taking into account both the species' interactions and the correlations in environmental impacts. It comprises two main components:

1. **Interaction Structure**: $\sum_k \sum_l b_{ik}\, b_{il}$
   - The summation across $b_{ik} b_{il}$ reflects how the abundance variance of species i depends on its **net effects** (direct and indirect) with other species in the network.
   - This term captures the influence that species k and l exert on i through the interaction network. Species i will have higher variance in abundance if it is experiences strong net effects (either directly or through indirect paths) from other species.

2. **Environmental Covariance**: $\text{cov}(\Delta r_k, \Delta r_l)$
   - This component describes the covariance between the impacts of the perturbation on species k and l.
   - A positive covariance suggests that k and l experience the environmental change in the same direction, which amplifies the effect on i, particularly if i is strongly influenced by k and l.

- Conversely, negative covariance can **offset** the effects on i if k and l are affected in opposing ways. This offsetting effect occurs when species linked to i are perturbed in contrasting directions, leading to a reduction in i's abundance variance.
- If environmental changes are **highly coherent** across species (i.e., large, positive covariance), species with strong connections will have increased variance, as the effect of the perturbation is compounded by the similar responses across linked species.
- **Negative covariances**, however, can reduce abundance variance through offsetting effects. For example, if species k and l respond in opposite ways to the environment and both influence species i, these opposing responses may cancel out, leading to a dampened variance in i's abundance.

Interpretation Based on Magnitudes

1. **Case 1: Strong Covariances, Regardless of Net Effects**
   - When covariances between environmental perturbations on species are high, species abundance variance increases across the network. In this case, even if a species has low net effects, it can still exhibit substantial variance in abundance due to the **highly correlated responses** of other species.
   - n this scenario, the impact of environmental perturbations on species k and l that are strongly correlated will cascade through the network, resulting in large variances for species iii. For example, even if species i has a weak direct connection with species k and l, it can still be affected significantly due to the strong environmental covariances. This occurs because i's abundance depends on k and l indirectly through other connections. As a result, if species k and l experience synchronized environmental impacts, this synchronization will propagate through their network connections, amplifying the variance in i's abundance. Therefore, in a community where environmental covariances are generally high, the entire network tends to show increased variability. This amplification occurs due to the correlated external forces affecting species simultaneously, resulting in greater community-wide fluctuations in abundance.

2. **Case 2: Strong Net Effects, Regardless of Covariances**
   - Here, the **strength of direct and indirect interactions** becomes dominant. Species that experience strong cumulative effects from others—regardless of how these effects correlate environmentally—are likely to show higher abundance variance.
   - In this scenario, a **specialist** heavily reliant on a single other species with a strong net effect might show high variance if that interacting species fluctuates significantly. Similarly, **generalist** species, even if weakly connected to many others, could exhibit high variance if the combined net effects are substantial.
   - The species' variance depends more on the magnitude of interaction effects within the network than on environmental coherence, highlighting the impact of ecological structure on stability.

3. **Case 3: Combined Strong Covariances and Strong Net Effects**

- This is the scenario where both high environmental coherence and substantial interaction strengths coexist. Species subject to **strong, correlated perturbations** and **high net effects** from others will exhibit extreme abundance variance.
- For example, a keystone species connected to several others through strong interactions would not only respond to the environmental conditions it experiences but also amplify these effects through the entire network, resulting in pronounced fluctuations across multiple species.
- This combined scenario suggests that **community stability may be highly compromised**, as species with strong net effects propagate environmentally driven changes throughout the network. The cumulative impact of coherent environmental responses and strong species interactions leads to high variability, potentially destabilizing the ecosystem.

In summary:

- **Strong covariances** lead to high variance by creating coherent responses among species.
- **Strong net effects** cause high variance due to the strength of ecological interactions.
- When **both are strong**, they compound, leading to even greater fluctuations and reduced community stability.

These insights suggest that **ecosystems with tightly coupled interactions and coherent environmental responses are more susceptible to destabilization**.

Impact of Covariance Distributions (i.e. ENC patterns) on Species Variance

The term $\text{cov}(\Delta r_k, \Delta r_l)$ in Equation 11 represents the distribution of environmental covariances across species pairs. The nature of this distribution—whether it is normally distributed, heavily skewed, or follows a particular shape (e.g., u-shaped, beta-positive, or beta-negative)—will influence the variance in abundance change for any species i in conjunction with the interaction effects from B.

1. Normally Distributed Covariances (Symmetric Distribution) with mean 0
- In this case, environmental covariances have a mean of zero with values spread symmetrically on both sides.
- **Implications:**
  - Positive and negative covariances are equally likely, meaning that effects may partially cancel each other out. This can lead to a moderation of species i's abundance variance, as some positive interactions may amplify while negative ones reduce the overall impact.
  - The overall abundance variance will depend heavily on the **interaction terms in B**. If B has both positive and negative terms, some offsetting effects will occur, potentially stabilizing the variance for species i.

- **Prediction:**
  - **P1:** With a symmetric distribution, we might observe **lower overall variance**, particularly if interaction effects are also symmetrically distributed, creating balanced amplification and dampening effects.

  - **P2:** Species may show contrasting variances if they differ in the strength of interaction effects on them (i.e. a specialist with with strong effects from one or few partners may show higher variance compared to a generalist with many weak interactions).

2. Beta-Positive Distribution (Right-Skewed)
- Covariances predominantly positive, with few negative covariances.
- **Implications:**
  - Species are generally impacted in similar directions. If species k and l share strong positive covariance, species i will likely see amplified variance if i is positively influenced by both k and l in B.
  - The **distribution of** B becomes particularly important here. If B mainly contains positive values, then the covariances will **amplify** the variance in abundance changes across the network. In contrast, if B includes negative terms, the impact may be moderated but likely still positive overall.
- **Prediction:**
  - **P3:** With mostly positive covariances, **higher abundance variance** is expected, especially if B effects are predominantly reinforcing. This is a scenario that could lead to **unstable population dynamics**, as co-amplifying effects accumulate across the network.

3. Beta-Negative Distribution (Left-Skewed)
- Covariances predominantly negative, with few positive covariances.
- **Implications:**
  - This distribution promotes offsetting effects within species. Negative covariances reduce the likelihood of synchronized responses, thereby dampening variance for species i.
  - If B is largely positive, these covariances will tend to **reduce the variance**, as species pairs experience opposing environmental effects. If B contains negative terms, negative covariances might as well amplify variance in abundance through indirect effects.
- **Prediction:**
  - **P4:** Abundance variances will generally be **lower** and **more stable** in the network with left-skewed covariances, particularly when combined with positive B effects. This distribution could promote **greater community resilience**, as species respond asynchronously to perturbations.

4. U-Shaped Distribution (Bimodal)
- Covariances are either strongly positive or strongly negative, with few near-zero covariances.
- **Implications:**

- This scenario creates strong amplification or offsetting effects without moderation. If species k and l are strongly positively correlated, and B reinforces these effects, variance in species i will be extreme. Conversely, if k and l are negatively correlated, offsetting effects might completely neutralize certain interactions, leading to very low or even zero variance.
        - The **interaction matrix** B is crucial here, as the extremes in covariance can either fully amplify or completely negate abundance changes depending on whether B terms align with the covariance sign.
    - In communities with U-shaped covariance distributions, **extreme variances are expected**, though the direction of these variances will depend on the interaction matrix. Strong positive or negative covariances will result in very high variances when aligned with reinforcing B terms, leading to instability.

In summary, **positive-skewed distributions** tend to amplify variance, while **negative-skewed distributions** promote stability through offsetting effects. **U-shaped distributions** create a scenario of extremes, where the interplay with B can lead to either very high or very low variance in abundance change, depending on the alignment of interactions.

These predictions highlight that **not just the magnitude but the distribution** of environmental covariances (i.e. ENC pattern), when combined with the interaction effects from B, is a key determinant of community-level stability and species resilience. Understanding these covariance structures may thus be essential for predicting how ecosystems may respond to global change and perturbations.

Equation 12: Covariance in Abundance Changes Between Species

$$\text{cov}\left(\varDelta X_i, \varDelta X_j\right) \approx \sum_k \sum_l b_{ik}\, b_{jl}\text{cov}(\varDelta r_k, \varDelta r_l)$$

This equation relates the **covariance** in abundance changes between species i and j. Here: - The **product** $b_{ik}b_{jl}$ captures how species i and j are jointly influenced by perturbations through k and l, moderated by the strength and direction of interactions as reflected in B. - This highlights how the **network structure**, in conjunction with the environmental covariance, affects how similarly (or differently) species' abundances will shift in response to perturbations.

We now test this predictions measuring changes in abundance in LV foodweb systems with varying underlying covariance structures.

LV simulations - Impact of ENC on ecosystem functioning

We further explore the impacts of ENC patterns on ecosystem functioning by conducting LV simulations.

In our simulations, we are constrained to scenarios where the covariances follow **normal distributions centered around 0** because functions like those in the clusterGeneration or randcorr packages or similar tools, which are designed to create correlation matrices, **require the matrices to be positive definite**. Positive definiteness ensures that all the eigenvalues of a matrix are positive, a property necessary for a matrix to be a valid correlation matrix.

Why Positive Definiteness is Required

Correlation matrices must be positive definite to maintain the mathematical consistency of the relationships between species. Positive definiteness implies that the matrix has only non-negative eigenvalues and that, geometrically, it defines a valid multi-dimensional ellipsoid. This requirement is essential because it guarantees that the correlation matrix is meaningful in terms of actual variances and covariances and avoid impossible or contradictory relationships.

Constraints of Non-Normal Distributions

In nature, we often observe covariance structures that resemble **beta distributions, U-shaped distributions, or other non-normal patterns**, where means are not necessarily centered at 0. These distributions can represent specialized, asymmetrical relationships or scenarios where there are highly specific, non-uniform interactions among species. However, due to the positive definiteness constraint, directly simulating these distributions for covariances can lead to inconsistencies in the correlation matrix, making the matrix unsuitable for calculations. As a result, covariance scenarios with non-zero means, such as those with highly skewed or U-shaped distributions, would typically fail the positive definiteness check required by functions like clusterGeneration.

Testing Normal Distributions Centered on 0

Focusing on normal distributions centered around 0 is still a valuable approach, even if it does not capture the full diversity of natural scenarios. Here's why:

1. **Baseline for Comparison**: Normal distributions, especially those centered on zero, provide a well-understood baseline that can help assess the general effects of **weak versus strong covariances**. By varying the standard deviation, we can explore scenarios where species have either tightly correlated (strong) or loosely correlated (weak) responses to environmental perturbations.

2. **Insight into Fundamental Dynamics**: While not capturing asymmetries, normal distributions allow you to explore essential network dynamics, such as how **variance in species abundance changes with the strength of environmental correlations**. This can reveal how interconnectedness and interaction strength influence ecosystem functioning under more general conditions.

3. **Foundation for Future Research**: By establishing a baseline with normal distributions, our simulations provide initial insights that can be built upon when extending to more complex or specific distributions.

LV Simulation - Effects on ecosystem functioning of weak vs strong covariance in normally distributed ENC pattern

The simulations consist on generating different covariance structures and analyze their impact on abundance dynamics in a foodweb – **equations 10 and 11**. To generate the correlation matrix that leads to the covariance structures (in our simulation they are the same), we use the function clusterGeneration::rcorrmatrix. Let's see how it works:

Function clusterGeneration to compute covariance matrices

https://rdrr.io/cran/clusterGeneration/man/rcorrmatrix.html

The code below shows how the function clusterGeneration::rcorrmatrix works.

Each correlation has a Beta(a,a) distribution on (-1,1) where a=alphad+(d-2)/2, where d is the dimension of the matrix.
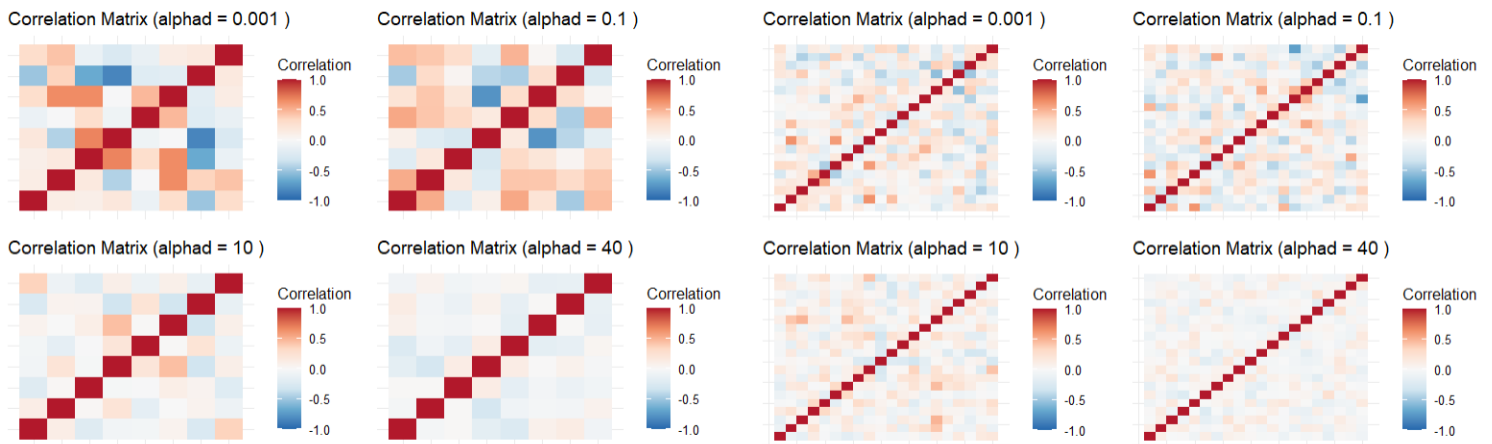
Testing different alpha_d values for 8 species:

Figure X. Correlation matrices generated with clusterGeneration::rcorrmatrix using different alpha_d values. On the left, a small community (S = 8). On the right, a larger community (S = 20).

The function is not very flexible, and we can only obtain contrasting scenarios if the community is small. We therefore run simulations with communities of 8 species. The simulation scheme is as follows:

1. **Define Key Functions**:
   - fw.model: Simulates the dynamics of species abundances over time based on the Lotka-Volterra model, incorporating both interaction effects (through

matrix A) and intrinsic growth rates (r). It also ensures abundances do not exceed a specified limit (100).

- o eventfun: Resets very small or negative values in the abundance matrix to zero, simulating species that have reached near-extinction.
- o simulate_dynamics_c: Runs the dynamics simulation over a specified time ($maxt$) and returns the resulting species abundances at each time step. This function uses the deSolve package to solve the differential equations defined by fw.model.

2. **Simulate Dynamics with Perturbations**:
   - o simulate_dynamics_perturbed: This function models a perturbation event by modifying the intrinsic growth rates (r) with a perturbation vector ($delta\_r$) based on the covariance matrix ($covMat$). The steps are:
     - ▪ First, an equilibrium state is established by simulating dynamics without perturbation.
     - ▪ A perturbation ($delta\_r$) is applied to r, which alters the equilibrium state of the system.
     - ▪ The new equilibrium abundances are calculated, and the change in abundances ($delta\_X$) due to the perturbation is recorded.

3. **Generate Interaction Network (A)**:
   - o The matrix A is created (outside of this code snippet) using the sim_quantitative_network function, which sets up a fixed quantitative interaction network among species based on the specified connectance and interaction parameters.

4. **Loop Through Different Covariance Scenarios**:
   - o For each value of alpha_d, a correlation matrix is generated using clusterGeneration::rcorrmatrix, where alpha_d controls the strength of covariances.
   - o The correlation matrix is scaled by sd_X to produce a covariance matrix ($covMat$). In this case, $sd\_X = 1$.
   - o For each scenario, values of the correlation matrix are stored to allow later visualization of correlation and covariance distributions across scenarios.

5. **Run Perturbation Simulations**:
   - o Within each alpha_d scenario, the simulation is run for a specified number of replicates (num_simulations).
   - o For each replicate, the dynamics are simulated pre- and post-perturbation, and the change in abundance ($delta\_X$) due to the perturbation is calculated and stored for each species.

6. **Record Results**:
   - o After running the simulations, results for each species' response to the perturbation ($Delta\_X$) are saved for analysis.
   - o The results include information about the alpha_d scenario, the specific covariance scenario, and the species affected.

Read matrix A to work on the same network

```
A <- readRDS(here::here("a_code/LV_simulations_AF/A_matrix.rds"))
```

Or create new A

```
S <- 8   # Number of species
C <- 0.4   # Connectance of the network
aij_params <- c(0, 0.5)
# Fixed interaction matrix A
A <- sim_quantitative_network(S, C, aij_params)
```
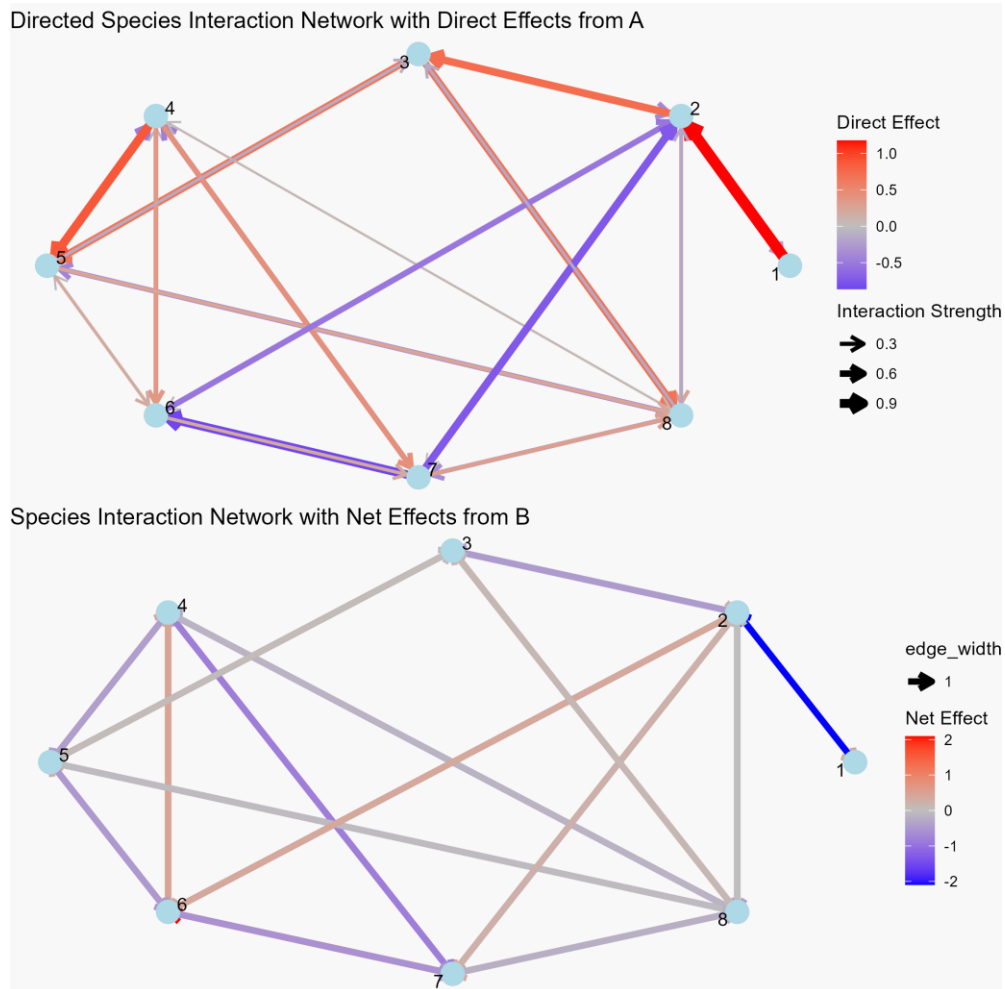
Plot network

Figure X. Interaction network used for the simulations.

The simulations use this fixed interaction matrix and generate different correlation structures in species' responses to the environment:

```
# Function to simulate dynamics
fw.model <- function(t, B, params) {
  with(as.list(c(B, params)), {
    B[B < 10^-8] <- 0
    B[B < 0] <- 0
    dBdt <- (params$r + params$A %*% B) * B
    dBdt[B > 100] <- 100   # Apply carrying capacity constraint   ########## !
    list(dBdt)
```

```r
  })
}

eventfun <- function(t, B, parms) {
  with(as.list(B), {
    B[B < 1e-6] <- 0
    return(B)
  })
}

simulate_dynamics_c <- function(params, model, init_biomass = runif(params$S, min = 1, max = 10)) {
  init_biomass <- as.numeric(init_biomass)
  times <- seq(from = 1, to = params$maxt)
  out <- deSolve::ode(
    y = init_biomass,
    times = times,
    func = fw.model,
    parms = params,
    events = list(func = eventfun, time = times)
  ) %>% as.data.frame()
  return(out)
}




# Function to simulate dynamics with perturbations - APPLYING DELTA_R
simulate_dynamics_perturbed <- function(params, covMat, S, maxt, perturb_scale = 1) {
  init_biomass <- runif(S, min = 1, max = 10)
  r_pre <- -params$A %*% init_biomass

  dyn_params <- list(A = params$A, r = r_pre, S = S, maxt = maxt)
  pre_perturb <- simulate_dynamics_c(dyn_params, fw.model)
  equilibrium_pre <- as.numeric(pre_perturb[nrow(pre_perturb), -1])

  # Perturbation with delta_r simulated using mvrnorm
  delta_r <- MASS::mvrnorm(n = 1, mu = rep(0, S), Sigma = covMat * perturb_scale)
  r_perturbation <- r_pre + delta_r
  dyn_params$r <- r_perturbation

  post_perturb <- simulate_dynamics_c(dyn_params, fw.model, init_biomass = equilibrium_pre)
  equilibrium_post <- as.numeric(post_perturb[nrow(post_perturb), -1])

  delta_X <- equilibrium_post - equilibrium_pre
  return(list(delta_r = delta_r, delta_X = delta_X))
}

############################################### SIMULATION

# Set simulation parameters
S <- 8   # Number of species
C <- 0.4   # Connectance of the network
aij_params <- c(0, 0.5)
sd_X <- 1   # Variance scale factor
num_scenarios <- 10
num_simulations <- 10
maxt <- 1000   # Duration of the simulation

# Fixed interaction matrix A
#A <- sim_quantitative_network(S, C, aij_params)

# Initialize data frames to store results
results <- data.frame()
correlation_distributions <- data.frame()
covariance_distributions <- data.frame()

# Loop over two alpha_d values:
for (alpha_d in c(0.001, 0.1, 1, 10, 20, 40, 60, 100)) { # or choose just 0.001 and 40
```

```r
  print(paste("alpha_d", alpha_d))

  for (scenario in 1:num_scenarios) {
    print(paste("scenario", scenario, "of", num_scenarios))

    # Generate correlation matrix and derive covariance matrix
    cor_matrix <- clusterGeneration::rcorrmatrix(d = S, alphad = alpha_d)
    covMat <- diag(sd_X, S) %*% cor_matrix %*% diag(sd_X, S)

    # Store correlation and covariance values for plotting
    cor_vals <- cor_matrix[upper.tri(cor_matrix, diag = FALSE)]
    cov_vals <- covMat[upper.tri(covMat, diag = FALSE)]

    correlation_distributions <- rbind(correlation_distributions,
                                       data.frame(Alpha_d = alpha_d, Scenario = scenario, Correlatio
n = cor_vals))
    covariance_distributions <- rbind(covariance_distributions,
                                      data.frame(Alpha_d = alpha_d, Scenario = scenario, Covariance
= cov_vals))

    for (sim in 1:num_simulations) {
      print(paste("sim", sim, "of", num_simulations))

      # Run the simulation with perturbations
      sim_result <- simulate_dynamics_perturbed(list(A = A), covMat, S, maxt)

      # Store the results for each species
      for (species in 1:S) {
        results <- rbind(results, data.frame(
          Alpha_d = alpha_d,
          Scenario = scenario,
          Simulation = sim,
          Species = paste0("sp", species),
          Delta_X = sim_result$delta_X[species]
        ))
      }
    }
  }
}

# Compute standard deviation of Delta_X for each species, scenario, and alpha_d value
results_species <- results %>%
  group_by(Alpha_d, Scenario, Species) %>%
  summarize(variance_in_delta_X = sd(Delta_X),
            mean_delta_X = mean(Delta_X),
            .groups = "drop")

# across all scenarios
expected_delta_X <- results %>%
  group_by(Alpha_d, Species) %>%
  summarize(sd_Delta_X = sd(Delta_X),
            mean_Delta_X = mean(Delta_X))



######### ABUNDANCE delta_X

p_abund_spp <- ggplot(results_species, aes(x = Species, y = mean_delta_X, fill = as.factor(Alpha_d))
) +
  geom_boxplot(position = position_dodge(width = 0.75)) +
  labs(x = "Species", y = "Mean Delta_X", fill = "Alpha_d") +
  # scale_fill_manual(values = c("#6A0DAD", "#EAD7F5")) +
  theme_minimal() +
  ggtitle("Species-specific Mean Abundance Change Across Alpha_d Scenarios") +
  theme(legend.position = "right")

p_abund_alphad <- ggplot(expected_delta_X, aes(x = as.factor(Alpha_d), y = mean_Delta_X, fill = as.f
```

```r
actor(Alpha_d))) +
  geom_boxplot() +
  labs(x = "Alpha_d", y = "Mean Delta_X", fill = "Alpha_d") +
 # scale_fill_manual(values = c("#6A0DAD", "#EAD7F5")) +
  theme_minimal() +
  ggtitle("Comparison of Mean Delta_X Across Alpha_d Scenarios for All Species") +
  theme(legend.position = "none")


######### VARIANCE delta_X

p_sd_spp <- ggplot(results_species, aes(x = Species, y = variance_in_delta_X, fill = as.factor(Alpha
_d))) +
  geom_boxplot(position = position_dodge(width = 0.75)) +
  labs(x = "Species", y = "SD Delta_X", fill = "Alpha_d") +
 # scale_fill_manual(values = c("#6A0DAD", "#EAD7F5")) +
  theme_minimal() +
  ggtitle("Species-specific SD Delta_X Across Alpha_d Scenarios") +
  theme(legend.position = "right")


p_sd_alphad <- ggplot(expected_delta_X, aes(x = as.factor(Alpha_d), y = sd_Delta_X, fill = as.factor
(Alpha_d))) +
  geom_boxplot() +
  labs(x = "Alpha_d", y = "SD Delta_X", fill = "Alpha_d") +
  #scale_fill_manual(values = c("#6A0DAD", "#EAD7F5")) +
  theme_minimal() +
  ggtitle("Comparison of SD Delta_X Across Alpha_d Scenarios for All Species") +
  theme(legend.position = "none")

# Plot distribution of correlation values across scenarios
# ggplot(correlation_distributions, aes(x = Correlation, fill = as.factor(Alpha_d))) +
#   geom_density(alpha = 0.7) +
#   labs(x = "Correlation Value", y = "Density", fill = "Alpha_d") +
#   scale_fill_manual(values = c("#6A0DAD", "#EAD7F5")) +
#   xlim(-1, 1) +
#   ggtitle("Distribution of Correlation Values Across All Scenarios") +
#   theme_minimal()

# Plot distribution of covariance values across scenarios
plot_Cdistr <- ggplot(covariance_distributions, aes(x = Covariance, fill = as.factor(Alpha_d))) +
  geom_density(alpha = 0.7) +
  labs(x = "Covariance Value", y = "Density", fill = "Alpha_d") +
#   scale_fill_manual(values = c("#6A0DAD", "#EAD7F5")) +
  xlim(-1, 1) +
  ggtitle("Distribution of Covariance Values Across All Scenarios") +
  theme_minimal()


arranged_plot <- ggarrange(
  p_abund_spp,
  p_abund_alphad,

  p_sd_spp,
  p_sd_alphad,

  ncol = 2,
  nrow = 2,

  labels = LETTERS[1:4])

print(plot_Cdistr)
print(arranged_plot)
```
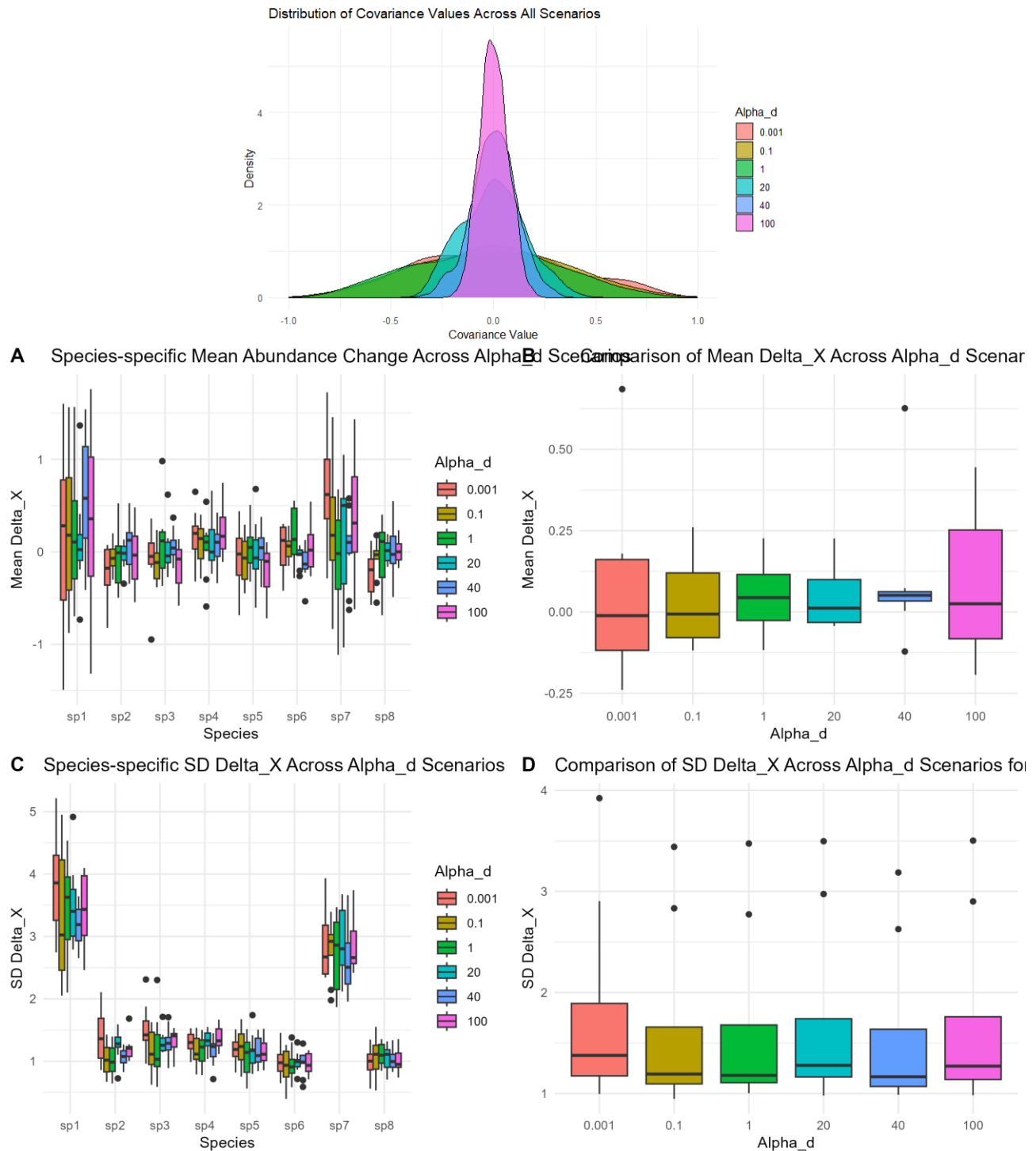
Figure X. Results from simulation where covariance structure changes: weaker to stronger SD from normally distributed set of covariances. Interaction matrix A is fixed (previous plot).

- Scenarios have pretty much the same mean, probably because, as predicted, the symmetric distribution of covariances centered on 0 cancels out the effects.

- However, under wider distributions (presence of stronger correlations, alpha_d = 0.001), we find that the most explosive and unpredictable dynamics can occur (largest outliers).

- The dynamics of specialist species 1 become more unpredictable in the covariance scenario with stronger correlations, alpha_d = 0.001. This may be, as predicted, because it experiences stronger interaction effects that can combine with strong covariances.

Other explorations - Dummy correlations to test effect of increasing mean correlation

We cannot generate beta distributions where most species have positive covariances and only a few negative because of positive definitness problems with the correlation matrix. Instead, we can generate correlation matrices where all the values are the same, increasing from 0 to 0.9:

```r
generate_cov_matrix2 <- function(S, corr, sd_x) {
  cor_matrix <- matrix(1, nrow = S, ncol = S)
  cor_matrix[upper.tri(cor_matrix)] <- cor_matrix[lower.tri(cor_matrix)] <- corr
  sd_X <- rep(1, S)
  cov_matrix <- diag(sd_X) %*% cor_matrix %*% diag(sd_X)
  return(cov_matrix)
}

# Set simulation parameters
S <- 8  # Number of species
C <- 0.4  # Connectance of the network
aij_params <- c(0, 0.5)
sd_X <- 1  # Variance scale factor
num_scenarios <- 10
num_simulations <- 10
maxt <- 1000  # Duration of the simulation

# Fixed interaction matrix A
#A <- sim_quantitative_network(S, C, aij_params)

# Initialize data frames to store results
results <- data.frame()
correlation_distributions <- data.frame()
covariance_distributions <- data.frame()

# Loop over two alpha_d values: 0.001 and 40
for (corr in seq(0, 0.9, by = 0.1)) {
  print(paste("corr", corr))

  for (scenario in 1:num_scenarios) {
    print(paste("scenario", scenario, "of", num_scenarios))

    # Generate correlation matrix and derive covariance matrix
    cor_matrix <- generate_cov_matrix2(S, corr = corr, sd_x = 1)
    covMat <- diag(sd_X, S) %*% cor_matrix %*% diag(sd_X, S)

    # Store correlation and covariance values for plotting
    cor_vals <- cor_matrix[upper.tri(cor_matrix, diag = FALSE)]
    cov_vals <- covMat[upper.tri(covMat, diag = FALSE)]

    correlation_distributions <- rbind(correlation_distributions,
                                       data.frame(Alpha_d = alpha_d, Scenario = scenario, Correlatio
n = cor_vals))
    covariance_distributions <- rbind(covariance_distributions,
                                      data.frame(Alpha_d = alpha_d, Scenario = scenario, Covariance
= cov_vals))

    for (sim in 1:num_simulations) {
      print(paste("sim", sim, "of", num_simulations))

      # Run the simulation with perturbations
      sim_result <- simulate_dynamics_perturbed(list(A = A), covMat, S, maxt)

      # Store the results for each species
      for (species in 1:S) {
```

```r
      results <- rbind(results, data.frame(
        corr = corr,
        Scenario = scenario,
        Simulation = sim,
        Species = paste0("sp", species),
        Delta_X = sim_result$delta_X[species]
      ))
    }
   }
  }
}

# Compute standard deviation of Delta_X for each species, scenario, and alpha_d value
results_species <- results %>%
  group_by(corr, Scenario, Species) %>%
  summarize(variance_in_delta_X = sd(Delta_X),
            mean_delta_X = mean(Delta_X),
            .groups = "drop")

# across all scenarios
expected_delta_X <- results %>%
  group_by(corr, Species) %>%
  summarize(sd_Delta_X = sd(Delta_X),
            mean_Delta_X = mean(Delta_X))



######### ABUNDANCE delta_X

p_abund_spp <- ggplot(results_species, aes(x = Species, y = mean_delta_X, fill = as.factor(corr))) +
  geom_boxplot(position = position_dodge(width = 0.75)) +
  labs(x = "Species", y = "Mean Delta_X", fill = "corr") +
 # scale_fill_manual(values = c("#6A0DAD", "#EAD7F5")) +
  theme_minimal() +
  ggtitle("Species-specific Mean Abundance Change Across corr Scenarios") +
  theme(legend.position = "right")

p_abund_alphad <- ggplot(expected_delta_X, aes(x = as.factor(corr), y = mean_Delta_X, fill = as.fact
or(corr))) +
  geom_boxplot() +
  labs(x = "corr", y = "Mean Delta_X", fill = "Alpha_d") +
 # scale_fill_manual(values = c("#6A0DAD", "#EAD7F5")) +
  theme_minimal() +
  ggtitle("Comparison of Mean Delta_X Across corr Scenarios for All Species") +
  theme(legend.position = "none")

######### VARIANCE delta_X

p_sd_spp <- ggplot(results_species, aes(x = Species, y = variance_in_delta_X, fill = as.factor(corr)
)) +
  geom_boxplot(position = position_dodge(width = 0.75)) +
  labs(x = "Species", y = "SD Delta_X", fill = "corr") +
 # scale_fill_manual(values = c("#6A0DAD", "#EAD7F5")) +
  theme_minimal() +
  ggtitle("Species-specific SD Delta_X Across corr Scenarios") +
  theme(legend.position = "right")


p_sd_alphad <- ggplot(expected_delta_X, aes(x = as.factor(corr), y = sd_Delta_X, fill = as.factor(co
rr))) +
  geom_boxplot() +
  labs(x = "corr", y = "SD Delta_X", fill = "Alpha_d") +
  #scale_fill_manual(values = c("#6A0DAD", "#EAD7F5")) +
  theme_minimal() +
  ggtitle("Comparison of SD Delta_X Across corr Scenarios for All Species") +
  theme(legend.position = "none")
```

```r
# Plot distribution of correlation values across scenarios
# ggplot(correlation_distributions, aes(x = Correlation, fill = as.factor(Alpha_d))) +
#   geom_density(alpha = 0.7) +
#   labs(x = "Correlation Value", y = "Density", fill = "Alpha_d") +
#   scale_fill_manual(values = c("#6A0DAD", "#EAD7F5")) +
#   xlim(-1, 1) +
#   ggtitle("Distribution of Correlation Values Across All Scenarios") +
#   theme_minimal()


# Plot distribution of covariance values across scenarios
plot_Cdistr <- ggplot(covariance_distributions, aes(x = Covariance, fill = as.factor(corr))) +
  geom_density(alpha = 0.7) +
  labs(x = "Covariance Value", y = "Density", fill = "corr") +
#  scale_fill_manual(values = c("#6A0DAD", "#EAD7F5")) +
  xlim(-1, 1) +
  ggtitle("Distribution of Covariance Values Across All Scenarios") +
  theme_minimal()


arranged_plot <- ggarrange(
  p_abund_spp,
  p_abund_alphad,

  p_sd_spp,
  p_sd_alphad,

  ncol = 2,
  nrow = 2,

  labels = LETTERS[1:4])

print(plot_Cdistr)
print(arranged_plot)
```
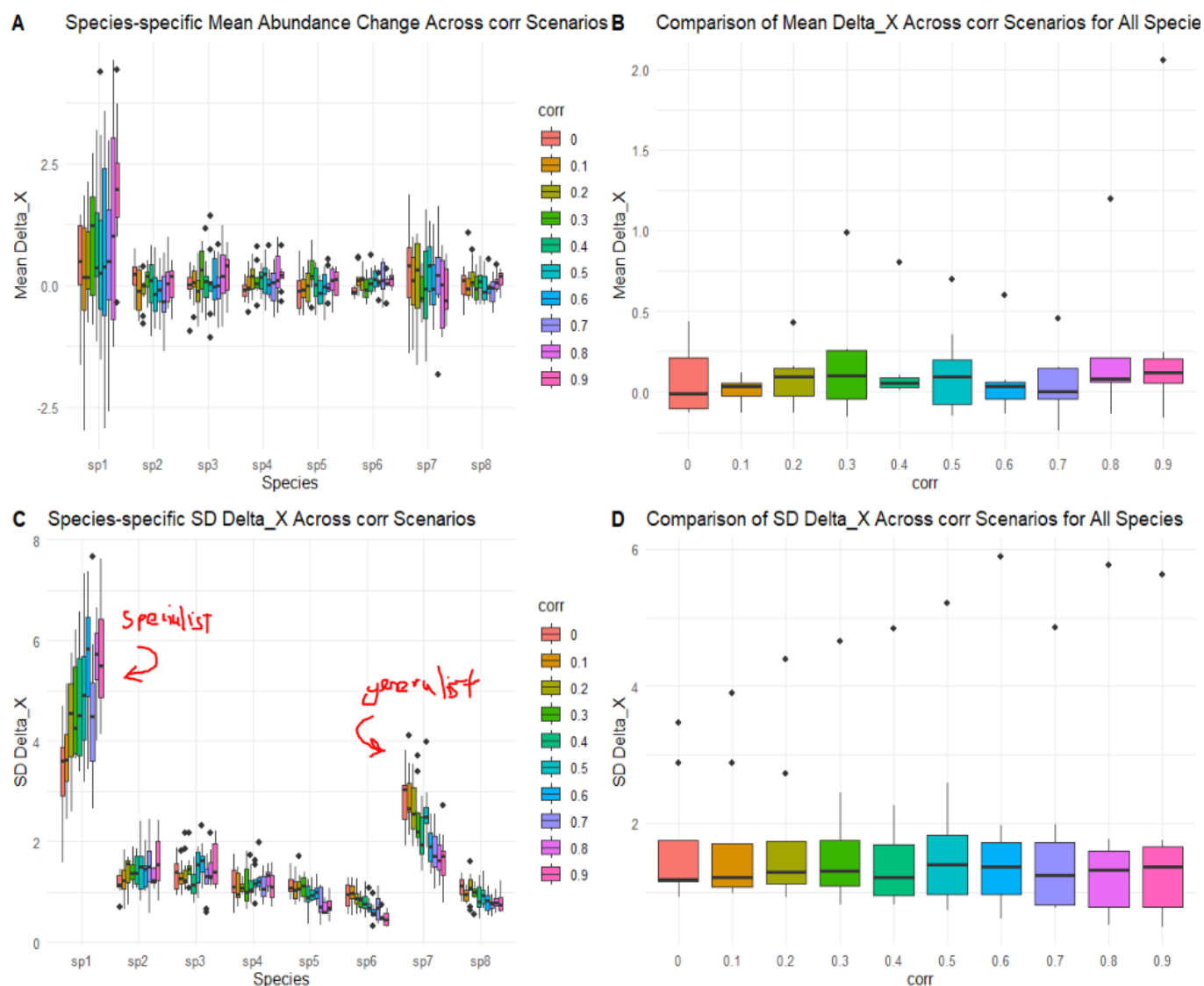
Figure X. Results form simulation with dummy correlation matrices with all equal values ranging from 0 to 0.9 correlations.

- Specialist species 1 vs generalist species 7: sp1 and 7 show the contrary pattern. For the specialist sp1, increasing covariances increases its SD Delta_X, whereas it decreases sp7 one. This is in line with our predictions.
- outliers in SD Delta X plot shows that in more positive correlations, there is the chance to have a more explosive dynamics.

Other explorations - simulation with equation terms

One way to get insights into the effect of different distributions that we cannot use because of positive definitness issues is to simply generate the covariance distribution values and apply them to equation 11 directly (without simulations):

```r
# Function to generate a symmetric correlation matrix based on different distributions
createSymmetricCorMat <- function(S, distribution_type = "normal", mean = 0, sd = 1, beta_shape1 = N
ULL, beta_shape2 = NULL, ushape1 = NULL, ushape2 = NULL) {
  n_off_diag <- S * (S - 1) / 2

  if (distribution_type == "normal") {
    cor_values <- rnorm(n_off_diag, mean = mean, sd = sd)
  } else if (distribution_type == "beta") {
    cor_values <- rbeta(n_off_diag, shape1 = beta_shape1, shape2 = beta_shape2)
    cor_values <- 2 * (cor_values - 0.5)
  } else if (distribution_type == "u_shaped") {
    cor_values <- rbeta(n_off_diag, shape1 = ushape1, shape2 = ushape2)
    cor_values <- 2 * (cor_values - 0.5)
  } else {
    stop("Invalid distribution type specified.")
  }

  cor_values[cor_values < -1] <- -1
  cor_values[cor_values > 1] <- 1

  corMat <- diag(1, nrow = S, ncol = S)
  corMat[upper.tri(corMat)] <- cor_values
  corMat[lower.tri(corMat)] <- t(corMat)[lower.tri(corMat)]

  return(corMat)
}


# Function to variance in abundance change based on formula 11
calculate_variancedelta <- function(B, cov_delta_r) {
  n <- nrow(B)

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

  Variance = var_delta_X
}


# Define scenarios for covariance distributions
scenarios <- list(
  list("label" = "normal weak",
       "distribution_type" = "normal",
       "mean" = 0,
       "sd" = 0.1),

  list("label" = "normal strong",
       "distribution_type" = "normal",
```

```r
        "mean" = 0,
        "sd" = 0.6),

  list("label" = "beta -",
        "distribution_type" = "beta",
        "beta_shape1" = 2,
        "beta_shape2" = 5),

  list("label" = "beta +",
        "distribution_type" = "beta",
        "beta_shape1" = 5,
        "beta_shape2" = 2),

  list("label" = "u-shaped",
        "distribution_type" = "u_shaped",
        "ushape1" = 0.1,
        "ushape2" = 0.1)
)

# Prepare data for plotting individual replicate results
plot_data <- data.frame(Scenario = character(), Variance_Change = numeric())

# List to store covariance matrices for each scenario for plotting later
covariance_storage <- list()


# Run simulation for each scenario
for (scenario in scenarios) {

  variance_changes <- numeric(20)
  cov_matrices <- list()

  for (i in 1:300) {
    # Generate covariance matrix
    cov_delta_r <- createSymmetricCorMat(S = 20,
                                         distribution_type = scenario$distribution_type,
                                         mean = scenario$mean,
                                         sd = scenario$sd,
                                         beta_shape1 = scenario$beta_shape1,
                                         beta_shape2 = scenario$beta_shape2,
                                         ushape1 = scenario$ushape1,
                                         ushape2 = scenario$ushape2)
    cov_matrices[[i]] <- cov_delta_r

        # Simulate interaction network A and invert it to get B
    A <- sim_quantitative_network("predator-prey", S = 20, C = 0.2, aij_params = c(0.5, 0.1))
    B <- solve(A)

    # Calculate metrics
    variance_changes[i] <- mean(calculate_variancedelta(B, cov_delta_r))

  }

  # Store individual replicate results for plotting
  plot_data <- rbind(plot_data,
                     data.frame(Scenario = scenario$label,
                                Variance_Change = variance_changes))

  # Store covariance matrices for later plotting
  covariance_storage[[scenario$label]] <- cov_matrices
}

# Plotting the covariance distributions
for (scenario_label in names(covariance_storage)) {
  cov_matrices <- covariance_storage[[scenario_label]]

  # Extract off-diagonal elements from each covariance matrix and create a dataframe
```

```r
  off_diag_values <- sapply(cov_matrices, function(mat) mat[upper.tri(mat)])
  off_diag_df <- data.frame(Value = as.vector(off_diag_values),
                            Matrix = rep(1:20, each = length(off_diag_values) / 20))

  # Generate density plots for each of the 20 matrices
  p_list <- lapply(1:20, function(i) {
    ggplot(subset(off_diag_df, Matrix == i), aes(x = Value)) +
      geom_density(fill = "skyblue", alpha = 0.5) +
      labs(title = paste("Matrix", i), x = "Covariance Value", y = "Density") +
      xlim(-1, 1) +
      theme_minimal() +
      theme(axis.title.x = element_text(size = 10),
            axis.text.x = element_text(size = 8),
            axis.title.y = element_text(size = 10),
            axis.text.y = element_text(size = 8),
            plot.title = element_text(size = 8, hjust = 0.5))
  })

  # Arrange the 20 density plots into a grid
  plot_grid <- ggarrange(plotlist = p_list, ncol = 5, nrow = 4,
                         top = paste("Covariance Distribution for Scenario:", scenario_label))
  print(plot_grid)
}

# Define colors for each scenario
scenario_colors <- c("normal weak" = "skyblue", "normal strong" = "orange",
                     "beta -" = "purple", "beta +" = "green", "u-shaped" = "red")
scenario_order <- names(scenario_colors)


p2 <- ggplot(combined_plot_data, aes(x = Scenario, y = Variance_Change, fill = Scenario)) +
  geom_violin(trim = FALSE, alpha = 0.5) +  # Add violin plot to show the distribution
  geom_jitter(width = 0.2, alpha = 0.1, shape = 21, size = 2, aes(color = Scenario)) +  # Overlay individual points
  scale_fill_manual(values = scenario_colors) +
  scale_color_manual(values = scenario_colors) +
  geom_hline(yintercept = 0, linetype = "dashed", color = "red") +
  labs(x = " ", y = "Variance in Abundance Change") +
  theme_classic() +
  theme(axis.text.x = element_text(angle = 45, hjust = 1), legend.position = "none") +
  ylim(0, max(combined_plot_data$Variance_Change))

print(p2)
```
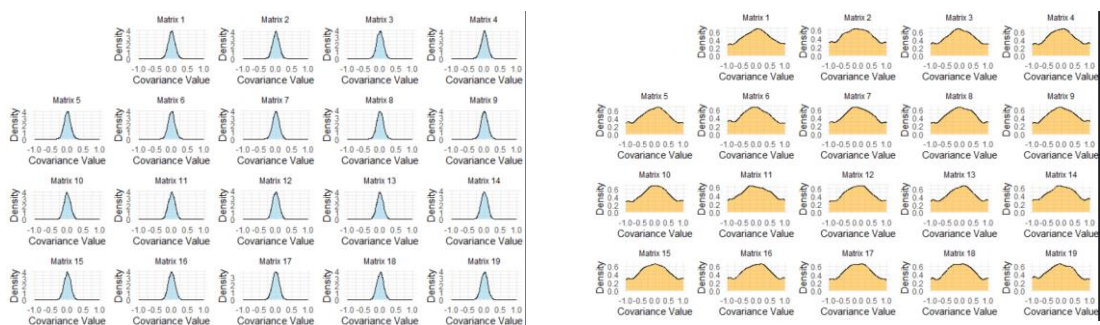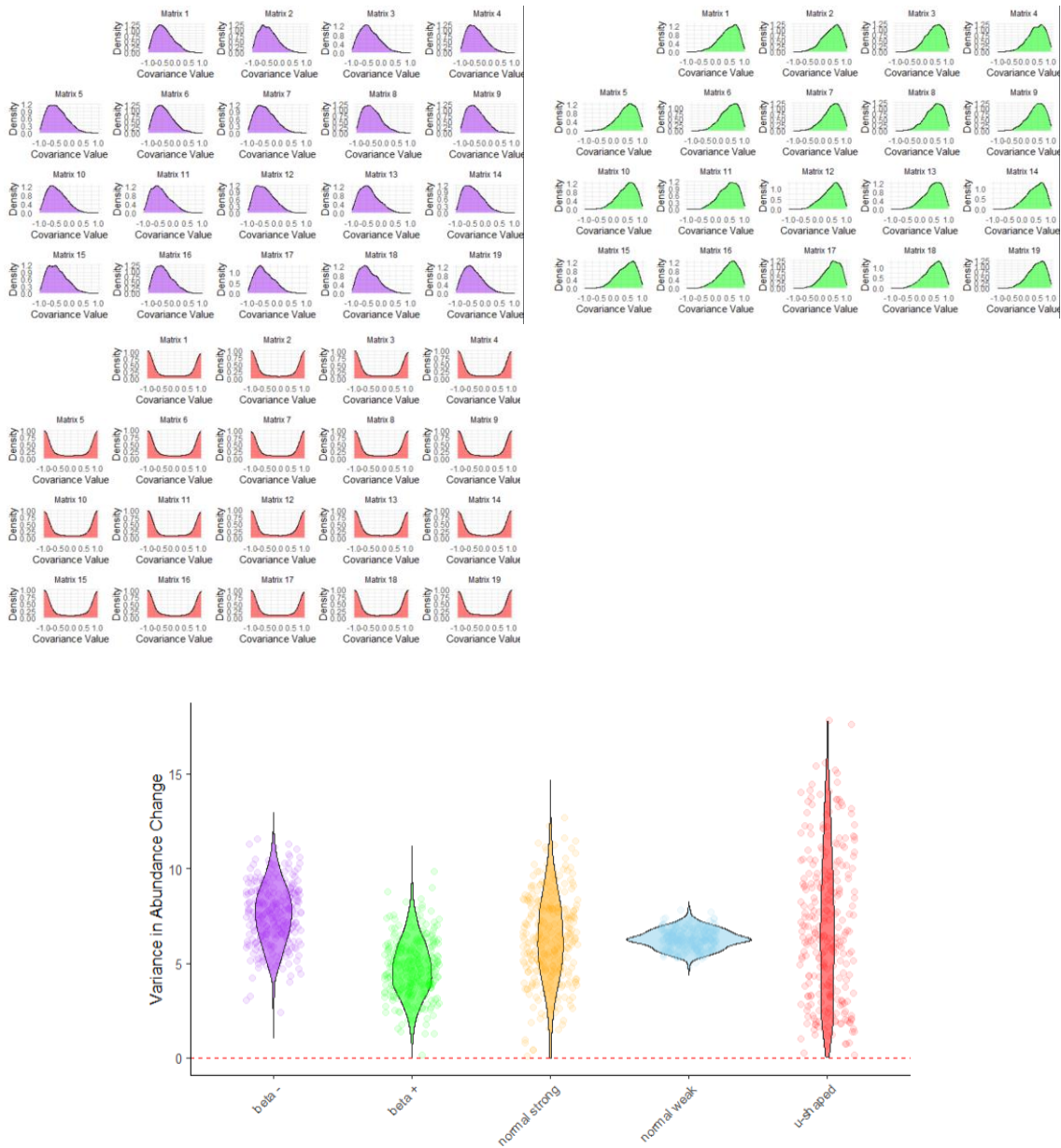
- Distributions with stronger positive or negative correlations (normal strong and u-shapped) can lead to more unpredictable dynamics for some species. As predicted, these distributions lead to either a strong offset of interaction and covariance effects leading to very low variance, or strong interaction effects combining with strong covariances leading to extremely high variances.