ENC definition

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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 (refs) and theoretical advancements (refs) 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 (refs). This integrated approach underscores the interconnectedness of species dynamics and their collective impact on ecosystem stability (ref). 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.

### 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).

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| fig1 |
| **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,, 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).

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| fig2 |
| **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 can be filtered out (multiplied) by the adjacency matrix of interactions , 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 given location in space and time, which we define as Ecological Network Coherence.

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| fig3 |
| **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 as 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, promoting collaboration and enhancing our ability to understand and predict changes in ecosystem structure and function.

# Linking ENC to ecosystem functioning

Let be the abundance of species in a Lotka-Volterra system, with intrinsic growth rate and interaction coefficient with species given by . We can write the dynamics of species as:

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| --- | --- | --- |
|  |  | (1) |

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

|  |  |  |
| --- | --- | --- |
|  |  | (2) |

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

|  |  |  |
| --- | --- | --- |
|  |  | (3) |

If a push perturbation is applied to the system over a sufficiently long time, we thus expect the equilibrium to shift away from by a quantity , given by:

|  |  |  |
| --- | --- | --- |
|  |  | (4) |

Now assuming that 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 the mean push perturbation and the variance of push perturbation among species. For commodity, we note the vector comprising as many 1’s as the number of species in the system, and is used as the symbol for transposition.

|  |  |  |
| --- | --- | --- |
|  |  | (5) |

|  |  |  |
| --- | --- | --- |
|  |  | (6) |

In the same way, we can define the mean abundance change due to the perturbation and the variance of these abundance changes among species.

|  |  |  |
| --- | --- | --- |
|  |  | (7) |

|  |  |  |
| --- | --- | --- |
|  |  | (8) |

Hereafter, we use the notation in order to look at the effect of on changes in abundances at equilibrium. Getting back to equation and developing the sums, we get:

|  |  |  |
| --- | --- | --- |
|  |  | (9) |

In this final expression, we recognize the average (*sensu* “among all species”) of the product of the and the column sums of . Hence, if we further decompose this using the abusive and notations (expectations are to be understood as averages over columns):

|  |  |  |
| --- | --- | --- |
|  |  | (10) |

Adopting the perspective where the vector 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:

|  |  |  |
| --- | --- | --- |
|  |  | (11) |

|  |  |  |
| --- | --- | --- |
|  |  | (12) |

with (as above) the inverse of the LV interaction matrix.

### 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 changes in abundance 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 . The equation sums up the contributions of all pairs of species ( and ) to the variance of the abundance change of species . This means that the variance in abundance changes for a focal species is influenced by how all other species in the network respond to perturbations (as captured by the covariances and how these responses propagate through the network (as captured by the elements of the matrix ).

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

|  |  |  |
| --- | --- | --- |
|  |  | (12) |

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. and have the same sign

* is positive.
* If **positive covariance** ( > 0), the term will be positive.
* If **negative covariance** ( < 0), the term will be negative.

Positive covariance increases the overall variance , potentially making the system less predictable, whereas negative covariance has the contrary effect.

#### 2. and have opposite signs

* is negative.
* If **positive covariance** ( > 0), the term will be negative.
* If **negative covariance** ( < 0), the term will be positive.

Positive covariance decreases the overall variance , potentially making the system more predictable, whereas negative covariance has the contrary effect.

#### 3. Heterogeneity of interaction effects

The scenarios discussed 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:

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| C:\Users\alexf\AppData\Local\Microsoft\Windows\INetCache\Content.Word\fig4.png |
| **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.

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| **\*** seems that this is not the case for mutualistic networks, whose B matrix does not contain positive values:  # 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 and compute the abundance change and variance in abundance change according to formulas and . We test different covariance structures: strong negative, weak negative, null (zero covariance), weak positive, strong positive, weak mixed (positive and negative), and strong mixed. Based on our mathematical intuition, we expect to find that the variance in abundance change is higher for the scenarios with strong positive, strong negative, and strong mixed covariances, and lower for weak positive, weak negative, and null covariances.

S <- 25  
set.seed(120)  
  
# Function to generate mixed covariance matrices  
generate\_mixed\_cov\_matrix <- function(S, range\_neg, range\_pos) {  
 mat <- matrix(runif(S^2, range\_neg[1], range\_pos[2]), nrow = S)  
 diag(mat) <- runif(S, range\_neg[1], range\_pos[2])  
 return(mat)  
}  
  
cov\_matrices <- list(  
 "Strong Positive" = matrix(runif(S^2, 0.6, 1), nrow = S),  
 "Weak Positive" = matrix(runif(S^2, 0.1, 0.4), nrow = S),  
 "Strong Negative" = matrix(runif(S^2, -1, -0.6), nrow = S),  
 "Weak Negative" = matrix(runif(S^2, -0.4, -0.1), nrow = S),  
 "Mixed Weak" = generate\_mixed\_cov\_matrix(S, c(-0.4, 0), c(0, 0.4)),  
 "Mixed Strong" = generate\_mixed\_cov\_matrix(S, c(-1, 0), c(0, 1)),  
 "Null" = matrix(0, nrow = S, ncol = S)  
)  
  
  
  
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)  
  
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(title = "Covariance Matrices",  
 x = NULL,  
 y = NULL,  
 fill = "Covariance") +  
 theme\_minimal() +  
 theme(plot.title = element\_text(hjust = 0.5)) +  
 facet\_wrap(~ Scenario, ncol = 3, scales = "free")+  
 my\_theme  
  
p

|  |
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| fig4 |
| **Fig 5.** Covariance matrices tested in the simulation to analyze their impact on the mean and variance of population change. |

Simulations (similar results for mutualistic, competition, and predator-prey interactions):

num\_simulations <- 100  
set.seed(120)  
  
# Function to simulate quantitative networks  
sim\_quantitative\_network <- function(Net\_type, S, C, aij\_params, rho = 0) {  
 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")  
 }  
 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)  
}  
  
  
  
calculate\_metrics <- 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  
  
 }  
   
 # Mean of the sum of each row of B  
 mean\_sum\_B <- colMeans(B)  
   
 # Mean of delta\_r (assuming it is an average of a random distribution)  
 mean\_delta\_r <- mean(cov\_delta\_r)  
   
 # Covariance between sum of each row of B and delta\_r  
 cov\_sum\_B\_delta\_r <- cov(rowSums(B), cov\_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))  
}  
  
  
################# Simulation  
  
run\_simulations\_with\_metrics <- function(cov\_matrix, num\_simulations, Net\_type, S, C, aij\_params) {  
 results <- replicate(num\_simulations, {  
 interaction\_matrix <- sim\_quantitative\_network(Net\_type, S, C, aij\_params)  
 inverse\_matrix <- solve(interaction\_matrix)  
 if (is.null(inverse\_matrix)) {  
 return(list(Variance = rep(NA, S), Abundance\_Change = NA))  
 }  
 calculate\_metrics(inverse\_matrix, cov\_matrix)  
 }, simplify = FALSE)  
 return(results)  
}  
  
# Generate results for each scenario  
Net\_type <- "predator-prey" # Example network type  
S <- 25 # Number of species  
C <- 0.2 # Connectance  
aij\_params <- c(0, 0.1) # Parameters for interaction strengths  
num\_simulations <- 100 # Number of simulations  
  
simulation\_results\_with\_metrics <- lapply(cov\_matrices, function(cov\_matrix) {  
 run\_simulations\_with\_metrics(cov\_matrix, num\_simulations, Net\_type, S, C, aij\_params)  
})

############### Plot results  
  
  
# 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]]  
 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)  
}  
  
# Prepare the data  
combined\_plot\_data <- prepare\_combined\_plot\_data(simulation\_results\_with\_metrics)  
  
scenario\_order <- c(  
 "Strong Negative",  
 "Weak Negative",  
 "Null",  
 "Weak Positive",  
 "Strong Positive",  
 "Mixed Weak",  
 "Mixed Strong"  
)  
  
combined\_plot\_data$Scenario <- factor(combined\_plot\_data$Scenario, levels = scenario\_order)  
  
  
color\_palette <- scales::brewer\_pal(palette = "RdBu", direction = -1)(5)  
mixed\_color <- "violet"  
  
scenario\_colors <- setNames(c(color\_palette, mixed\_color, mixed\_color), scenario\_order)  
  
# Plot variance in abundance change  
p1 <- 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") +  
 my\_theme  
  
# Plot abundance change  
p2 <- 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") +  
 my\_theme  
  
# Display plots  
ggarrange(p1, p2, nrow = 2, ncol = 1, labels = LETTERS[1:2])

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| **Fig 6.** Effects of community covariance on the change in abundance of species in foodwebs (A) and the predictability of these changes (B). Each dot represents a species within one of the 100 simulated foodwebs. |

The simulations reveal that:

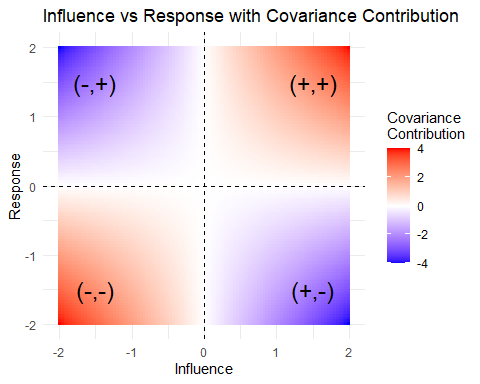
* Increasing coherence increases the number of abrupt changes and makes the system less predictable.
* The maximumhen coherence is strong in both positive and negative signs.

**Doubts**

* While mathematically, the variance cannot be negative, Equation (11) can yield negative values due to the summation of positive and negative terms, especially in systems with highly heterogeneous interactions

The covariance contribution in Formula 10, , suggests that species with higher centrality or influence within the interaction network (as captured by the matrix) and their corresponding responses () significantly impact the overall change in abundance. If species that are central in the network exhibit major responses to perturbations, this will likely lead to substantial changes in community abundance.

# Define a grid for influence and response  
influence <- seq(-2, 2, length.out = 100)  
response <- seq(-2, 2, length.out = 100)  
  
# Create a dataframe with all combinations of influence and response  
grid <- expand.grid(influence = influence, response = response)  
  
# Compute the covariance contribution for each combination  
grid$covariance <- grid$influence \* grid$response  
  
# Create the plot  
ggplot(grid, aes(x = influence, y = response, fill = covariance)) +  
 geom\_tile() +  
 scale\_fill\_gradient2(low = "blue", high = "red", mid = "white", midpoint = 0,   
 limit = c(-4, 4), space = "Lab",   
 name = "Covariance\nContribution") +  
 geom\_vline(xintercept = 0, linetype = "dashed", color = "black") +  
 geom\_hline(yintercept = 0, linetype = "dashed", color = "black") +  
 annotate("text", x = 1.5, y = 1.5, label = "(+,+)", size = 6, color = "black") +  
 annotate("text", x = -1.5, y = 1.5, label = "(-,+)", size = 6, color = "black") +  
 annotate("text", x = -1.5, y = -1.5, label = "(-,-)", size = 6, color = "black") +  
 annotate("text", x = 1.5, y = -1.5, label = "(+,-)", size = 6, color = "black") +  
 labs(x = "Influence", y = "Response", title = "Influence vs Response with Covariance Contribution") +  
 theme\_minimal()



# Parameters  
S <- 20 # Number of species  
C <- 0.3 # Connectivity  
aij\_params <- c(0, 1) # Mean and SD for interaction strengths  
net\_type <- "random" # Type of network  
  
# Simulate the interaction matrix A  
A <- sim\_quantitative\_network(net\_type, S, C, aij\_params)  
  
# Compute the inverse matrix B  
B <- solve(A)  
  
# Generate a random response vector Delta\_r  
Delta\_r <- rnorm(S, 0, 1)  
  
# Compute the influence and response for plotting  
influence <- rowSums(B) # Sum of rows in B  
response <- Delta\_r # Response vector  
  
# Scale the influence and response to fall within [-2, 2]  
scale\_to\_range <- function(x, new\_min = -2, new\_max = 2) {  
 old\_min <- min(x)  
 old\_max <- max(x)  
 (x - old\_min) / (old\_max - old\_min) \* (new\_max - new\_min) + new\_min  
}  
  
influence <- scale\_to\_range(influence)  
response <- scale\_to\_range(response)  
  
# Generate a grid for the underlying color field  
x <- seq(-2, 2, length.out = 100)  
y <- seq(-2, 2, length.out = 100)  
grid <- expand.grid(influence = x, response = y)  
grid$covariance <- grid$influence \* grid$response # Covariance contribution  
  
# Convert real network data to a data frame  
real\_data <- data.frame(influence = influence, response = response)  
  
# Create the plot  
ggplot(grid, aes(x = influence, y = response, fill = covariance)) +  
 geom\_tile() +  
 scale\_fill\_gradient2(low = "blue", high = "red", midpoint = 0,   
 limit = c(-4, 4), space = "Lab",   
 name = expression(paste("Covariance\nContribution\nto", bar(Delta), "X"))) +  
 geom\_vline(xintercept = 0, linetype = "dashed", color = "black") +  
 geom\_hline(yintercept = 0, linetype = "dashed", color = "black") +  
 annotate("text", x = 1.5, y = 1.5, label = "(+,+)", size = 6, color = "black") +  
 annotate("text", x = -1.5, y = 1.5, label = "(-,+)", size = 6, color = "black") +  
 annotate("text", x = -1.5, y = -1.5, label = "(-,-)", size = 6, color = "black") +  
 geom\_point(data = real\_data, aes(x = influence, y = response), color = "black", size = 2, inherit.aes = FALSE) +  
 annotate("text", x = 1.5, y = -1.5, label = "(+,-)", size = 6, color = "black") +  
 labs(x = "Influence", y = "Response", title = "Influence vs Response with Covariance Contribution") +  
 theme\_minimal() +  
 theme(plot.title = element\_text(hjust = 0.5))

