EEB C219B (Ecological Modeling): Final Report

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Introduction

Vultures and mortality by poisoning

Eurasian griffon vultures (*Gyps fulvus,* hereafter "griffons" or "griffon vultures") are obligate scavengers (Ruxton and Houston 2004) and social foragers (Harel et al. 2017). This means that they feed exclusively on carcasses. They locate these food sources largely by following other individuals—using social information to locate food is essential in an environment where food sources are both ephemeral and spatio-temporally unpredictable.

However, vultures' tendency to aggregate at carcasses makes them particularly vulnerable to poisoning at carcasses laced with pesticides, which are often illegally deposited by farmers to target predators that threaten their livestock (BBC News 2019a). Another source of poisoning is non-steroidal anti-inflammatory drugs (NSAIDs), which are often used for veterinary treatment of livestock and can be toxic to vultures (Anglister 2022). Poisoning is a major threat to griffon vulture populations. It is the leading cause of death in the griffon population in Israel, where the species is locally endangered (Anglister 2022). It also threatens vulture species across the world (Ives et al. 2022). Crucially, because vultures gather to feed at carcasses, poisoned carcasses can kill many individuals within a very short time period. For example, on 2021-10-24 in the southern part of Israel, 13 vultures died in a single poisoning event (Anglister 2022). In 2019, eight vultures were poisoned in one day in the Golan Heights, in northern Israel, with two more transported to a wildlife hospital for treatment after they were found alive at the carcass site (BBC News 2019b).

Effects of mortality on social structure

Mortality events such as those caused by poisoning affect not just the raw number of individuals in a population but also the population's social structure—the frequency and patterns of relationships between particular individuals. Social structure can have important consequences for information transfer and resource acquisition (Gil et al. 2018), as well as the spread of disease [Griffin and Nunn (2012)](Silk et al. 2019), and population growth (Allee and Bowen 1932). The population of griffon vultures in Israel is small; the birds rely heavily on social information to find food; and the population is threatened by infection with mycoplasma, which may spread through shared feeding events (Anglister 2022). Therefore, the impact of multiple mortality on griffon vulture social networks is of both theoretical and practical interest.

One way of understanding population social structure is by modeling it as a social network. Node

Figure 1: A Eurasian Griffon Vulture (*Gyps fulvus*) and an Egyptian Vulture (*Neophron percnopterus,* at left) feed at a carcass provided at a feeding site in Israel. Photo by Noa Pinter-Wollman, 2022.

removal has been a topic of interest in the social network literature for some time, with a particular focus on understanding how the characteristics of the removed node mediate the effect of its removal on the network. In behavioral ecology, this question has been explored both through simulations and experimental removals (Shizuka and Johnson 2020a). Theoretical literature has also explored how networks react to sequential removals of multiple nodes; for instance, while scale-free networks are surprisingly robust to individual node failures, they are vulnerable to targeted sequential removals of the most connected nodes (Albert, Jeong, and Barabási 2000). Literature on sequential removals in ecology has largely focused on the sequential extinction of species or habitats in ecological networks (e.g. (Biella et al., n.d.)); I could not find an example of sequential removal in social interaction networks. Similarly, while some theory exists on the response of networks to the removal of multiple nodes simultaneously (Schwarze, n.d.), the effect of simultaneous multiple node loss on animal social networks remains unknown.

Global network measures

Here, I use a modeling approach to simulate a vulture population in which several individuals are lost simultaneously. I examine the effect of the removals, and the subsequent rewiring of the network, on several global measures of social network structure.

Network **density** describes the number of edges present in the network, divided by the total number of possible edges. In a co-feeding network of vultures, density could be directly related to the transmission of mycoplasma during feeding events. Since vultures detect carcasses through social information transmission in flight, the density of a co-flight network also has the potential to affect how quickly and/or reliably vultures can find food.

Mean distance, or average path length, describes the average minimum distance between each pair

of nodes in the network, following existing edges. A larger mean distance between nodes indicates that the network is more spread out, with individuals interacting with fewer other individuals on average.

Finally, **modularity** measures whether a given division of the network into clusters is good, i.e. the extent to which there are more within-cluster edges than between-cluster edges (Clauset, Newman, and Moore 2004). Networks with intermediate levels of modularity transmit social information most efficiently (Romano et al. 2018), and

Characterizing the lost nodes

The effect of multiple-node loss on these network measures should depend not only on **how many** nodes are lost, but also on **the characteristics** of those nodes, relative both to the network at large and to each other. Understanding how the characteristics of the removed nodes affects the consequences of the removal will help us predict the consequences of real-world removals. We might measure the characteristics of the removed nodes either individually or in aggregate, and each of these levels might be important to understanding the effect of the removal on the network structure.

First, we might ask how **central** the removed nodes were. We know that removing a single more central individual has a greater effect on the network than removing a node selected at random (Albert, Jeong, and Barabási 2000). By extension, I predict that when the multiple removed nodes are more central on average, there will be a greater effect on network structure as a result of their removal. This type of measure will be important if, for example, more central individuals tend to arrive at a poisoned carcass first (e.g. because they have more access to social information about food resources) and/or get better access to the carcass (and therefore a higher dose of the poison) than less central individuals.

Second, we can ask to what extent the removed nodes are **clustered** on the network, as opposed to evenly spread across it. This is a relevant question if, for example, social transmission of information about the carcass location results in poisoned individuals being more closely clustered on the network than would be expected by chance.

Question 1: How is the effect of multiple-node loss on global network measures mediated by the centrality and clusteredness of the removed nodes?

Predictions:

Removed node characteristic	(delta) network density	(delta) mean distance	(delta) modularity
Mean centrality	Negative relationship: more central removed individuals –> greater decline in density.	Positive relationship: more central removed individuals –> greater increase in mean distance.	Positive relationship: more central removed individuals –> greater increase in modularity.

Removed node characteristic	(delta) network density	(delta) mean distance	(delta) modularity
Clustering	No effect: the change in network density should be independent of the extent to which the removed individuals form their own cluster.	Negative relationship: more clustering of lost individuals -> greater decline in mean distance.	Negative relationship: more clustering of lost individuals -> greater decline in modularity.

Recovery and rewiring of the network following losses

Network "rewiring" is the process of individuals establishing new social connections (or, in a weighted network, strengthening existing ones) following the loss of some individuals from the population. New connections may form at random, or they may follow a pattern based on how individuals behave in response to the loss(es). For example, in a songbird social network, rewiring after flockmate loss follows a pattern of "second-degree rewiring," whereby individuals with ties to the lost individual are more likely to form new connections with each other than with other individuals (Farine 2021).

Since I am interested in determining how the simultaneous loss of multiple individuals affects the structure of the griffon vulture social network, I wanted to be able to test hypotheses about how rewiring proceeds in this system. In other words, how does having been connected to removed individuals affect an individual's tendency to make new connections or retain existing ones? Does second-degree rewiring operate in the griffon vulture system, or do we observe a different pattern?

In behavioral ecology, (Shizuka and Johnson 2020b) has distinguished between different types of mortality or node removals, arguing that the response of the social network should be different in cases where mortality can be reasonably anticipated by individuals in the population (such as mortality due to sickness or old age) than in cases of unanticipated mortality (e.g. predation or anthropogenic causes like shooting or poisoning). When vultures die from poisoning, mortality is sudden and unanticipated; especially given the magnitude of the losses in relation to the population size, it is of particular importance to understand how other individuals in the population will react.

Question 2: How do the effects of multiple-node loss differ under different assumptions about how individuals are affected by the deaths of their connections (i.e. rewiring rules)?

Methods

Study System: A Vulture Co-Feeding Network

The system that inspired this model is a GPS-tagged population of griffon vultures (*Gyps fulvus*) in Israel. The species is locally critically endangered (Efrat et al. 2020), and its conservation is managed by the Israel Nature and Parks Authority (INPA), which runs supplemental feeding stations throughout the country (Spiegel et al. 2013). Israel's griffon vultures live mainly in the Negev and Judean deserts in the south. There is a small population in northeastern Israel and a declining population in the northwest.

As part of a collaborative NSF-BSF project between Orr Spiegel and Noa Pinter-Wollman, nearly 100 vultures have been fitted with GPS transmitters over the past two years. These tags provide location information at 10-minute intervals, with data automatically transmitted to Movebank. As of 2022, approximately 70% of the griffon population in Israel is tagged. This high coverage of the population means that the majority of a tagged individual's social interactions are with other tagged individuals, allowing us to study social interactions with greater certainty than is possible in many studies of free-ranging animals.

Despite the extent of this dataset, it is not sufficient to directly address questions about the impact of multiple mortality on the vulture social network. While poisoning events pose a severe threat to the vulture population, mass poisonings have occurred only a handful of times during the current study, and in several instances they occurred in regions where relatively smaller proportions of the population were tagged. Therefore, I sought to create a model that I could perturb to test hypotheses about the effect of multiple mortality on the griffon vulture social network.

Model structure and parameterization

I set out to create an individual-based model that would plausibly capture the day-to-day dynamics of the griffon vulture social network. In the past, the NSF-BSF vulture team has created interaction networks specific to different social situations, defining the network edges in different, biologically meaningful ways for each situation (Sharma et al. 2022). For example, an interaction in the "co-feeding" network is defined as two individuals coming within 50 meters of each other during at least two consecutive 10-minute intervals. My model is intended to represent a co-feeding network in an abstract way.

Baseline

The initial network consists of `N` nodes, each of which is assigned an inherent interaction probability, which I will refer to as `sociability`. `sociability` values are drawn from an exponential distribution with mean `mnSocExp`; the default is an exponential distribution with mean 0.3. Multiplying all combinations of individual `sociability` values generates an undirected probability matrix, which is then used to perform a series of weighted coin flips to select whether an edge does or does not exist between the two individuals in question. Two adjacency matrices are generated in this way for the first two time steps of the model.

Subsequent time steps take into account the presence or absence of edges in the previous two time steps. For each edge, the baseline edge probability (`sociabilityA * sociabilityB`) is modified by one of four modifier coefficients (`mod00`, `mod01`, `mod10`, and `mod11`) according to its history. For example, an edge with history "00" (i.e. the edge did not exist in either of the previous two time steps) will have the new probability $p_{A,B}$ = `sociabilityA * sociabilityB` *(1+`mod00`). (By analogy, `mod01` is used for edges that existed in the most recent time step but not in the one before, `mod10` for edges that did not exist in the most recent time step but *did* exist in the one before, and `mod11` for edges that have existed in both previous time steps.) By default, the modifier values are set as follows:

`mod00` = -0.4 (i.e. an edge with history "00" is 40% *less* likely to exist in the next time step than would be predicted by the baseline sociability values of its two nodes. The individuals are unfamiliar with each other and disinclined to make connections with strangers).

`mod10 = 0.1` (an edge with history "10" is 10% more likely to exist in the next time step: the individuals have some familiarity with each other and therefore might be more inclined to interact).

`mod01 = 0.2` (an edge with history "01" is 20% more likely to exist in the next time step: the individuals have just previously interacted and might be inclined to maintain the connection).

`mod11 = 0.3` (i.e. an edge with history "11" is 30% *more* likely to exist in the next time step than would be predicted by the baseline sociability values of its two nodes. The two individuals are familiar with each other and are likely to continue to interact).

These values are intended to introduce social preference into the model. Previous associations are more likely to persist into the next time step, but once an edge has been lost, it is likelier to stay lost.

In some cases, these adjustments will produce probability values greater than 1 or less than 0. After computing the probabilities, they are truncated, with any values > 1 set to 1 and any values < 0 set to 0.

This process is repeated in each time step for the length of the `baseline.in` period, producing steady-state dynamics, with individuals' degrees being relatively stable over time. The network in the time slice following the `baseline.in`th network is the one from which nodes will be removed (see Removal).

Here is an example series of graphs demonstrating the baseline network dynamics over five time steps. Nodes are colored by their sociability values, with lighter colors indicating higher inherent sociability.
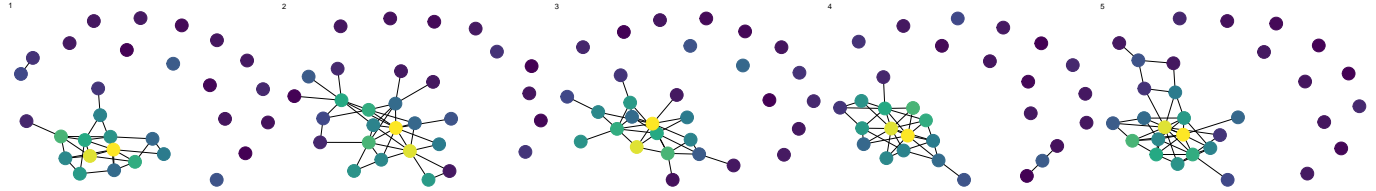
Removal

In the removal phase, `n.removed` nodes are removed from the network, along with all of their edges. This simulates a multiple mortality event (e.g. a poisoning). By default, the removed nodes are chosen randomly, though the model contains an `id` parameter that can be used to optionally specify the identities of `n.removed` particular nodes. Thus, the network at time step `baseline.in + 1` contains `N - n.removed` individuals, as will the networks at all subsequent time steps.

Rewiring

For each individual remaining in the network after the removal time step, a `bereavement` proportion is calculated as the (number of its associates in the time step immediately before removal that were subsequently removed)/(degree in the time step immediately before removal). In other words, what proportion of the individuals it was connected to died in the mortality event? This is a coarse measure of how directly affected the focal individual is by the multiple mortality event.

For example, if individual A had interacted with B, D, and E, and individuals B and D subsequently died in the mortality event, then individual A would have a value of $2/3 = 0.66$ for its `bereavement`.

Meanwhile, individual E, which had interacted only with A and C, would not be affected at all (`bereavement` = 0).

The degree to which an individual's `bereavement` proportion affects its interaction probability is controlled by `coefBereavement`. By default, `coefBereavement` is 1, which means that for every percentage point that `bereavement` increases, an individual's `sociability` increases by that same amount. Using the example shown above, if individual A had a `sociability` value of 0.5 and individual E had a `sociability` value of 0.3, their new sociability values would be as follows:

`sociabilitynew` = `sociabilityold` * (1+(`bereavement` * `coefBereavement`))

`sociabilityAnew` = 0.5*(1+0.66*1) = 0.83

`sociabilityEnew` = 0.3*(1+0*1) = 0.3

Next, a new probability matrix is computed using these modified sociability values.

Finally, the modified probability matrix is adjusted using the `mod` values, according to the same process described above, and the probabilities are truncated to ensure that they fall between 0 and 1. The final probability matrix is used, once again, for a series of weighted coin flips that assign edges to exist or not in the first time step following removal.

Finally, the model is allowed to return to its baseline dynamics for a number of time steps specified as `baseline.out`.

Results

Proportion of nodes removed

To investigate how the number of individuals lost affects the global social network measures, I ran the model with a network of 50 individuals, removing different numbers of individuals, up to 40 (80% of the population). I set the edge history `mod` parameters to their defaults, and I set `coefBereavement` to its default of 1 (meaning that an individual losing a proportion X of its connections makes it X times more likely to interact in the next time step).

First, I examined whether the proportion of nodes removed from the network affects the magnitude of the immediate change in global network (direct effects of removal). The y axis in these graphs, "Change due to removal," is defined as the difference between the global measure values in the time slice immediately after removal (but before rewiring) and in the time slice immediately before removal.

```
## `summarise()` has grouped output by 'propRemoved'. You can override using the
## `.groups` argument.
```
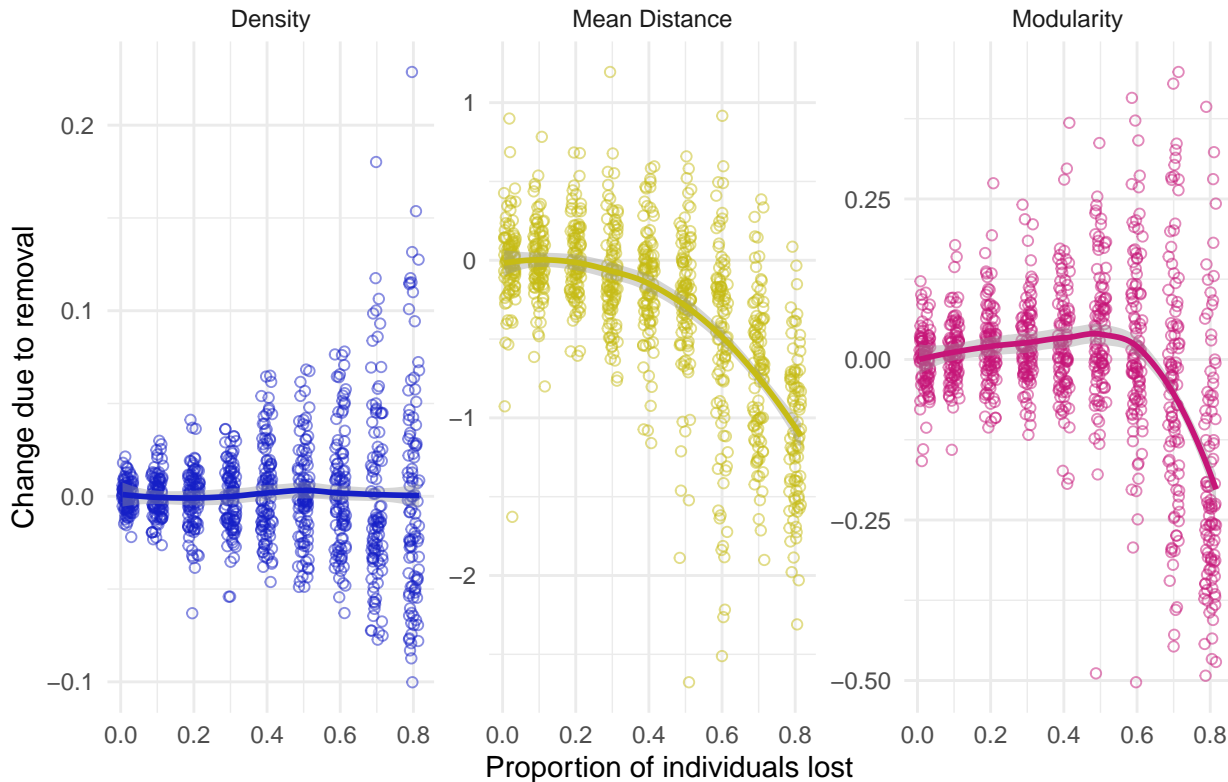
```
## `geom_smooth()` using method = 'loess' and formula 'y ~ x'
```

```
## Warning: Removed 14 rows containing non-finite values (stat_smooth).
```

```
## Warning: Removed 14 rows containing missing values (geom_point).
```

Removal

Density   Mean Distance   Modularity

Change due to removal

Proportion of individuals lost

The proportion of nodes removed has no consistent effect on the density of the network. There is little effect on mean distance until the proportion of nodes removed reaches about 0.4, at which point mean distance declines sharply. At high proportions of individuals lost, mean distance is almost 1 edge less than it was in the network before the removal. Modularity increases slightly when smaller proportions of nodes are removed, up to around 0.5, after which point it declines.

Next, I examined the ultimate, indirect effects of these removals (i.e. the overall effect on the network after rewiring has occurred). I examined two ratios: values after rewiring compared to pre-removal; and values after rewiring compared to post-removal, pre-rewiring. The latter directly measures the amount of "recovery" provided by the rewiring process, while the former measures the net change in the network after allowing for individuals' indirect response to the node removals.

`geom_smooth()` using method = 'loess' and formula 'y ~ x'

Warning: Removed 22 rows containing non-finite values (stat_smooth).

Warning: Removed 22 rows containing missing values (geom_point).
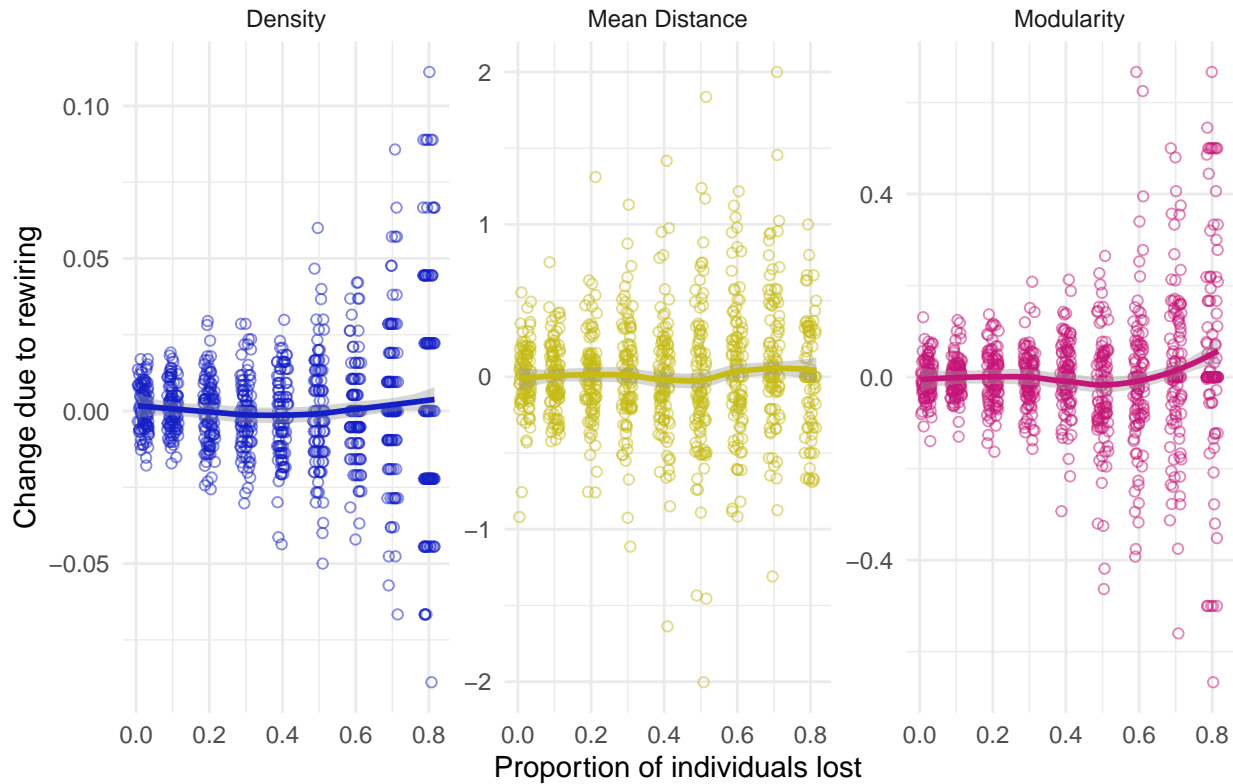
Rewiring

XXX FILL THIS IN

```
## `geom_smooth()` using method = 'loess' and formula 'y ~ x'

## Warning: Removed 11 rows containing non-finite values (stat_smooth).

## Warning: Removed 11 rows containing missing values (geom_point).
```
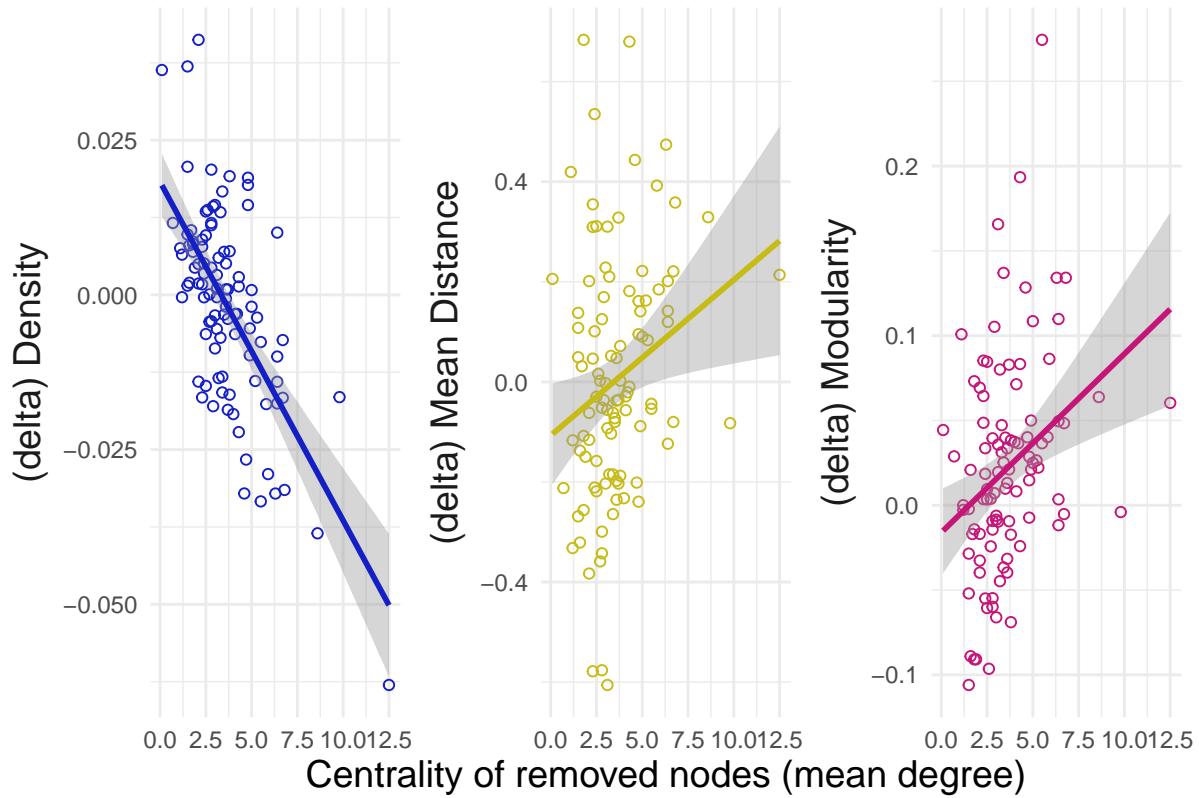
Rewiring
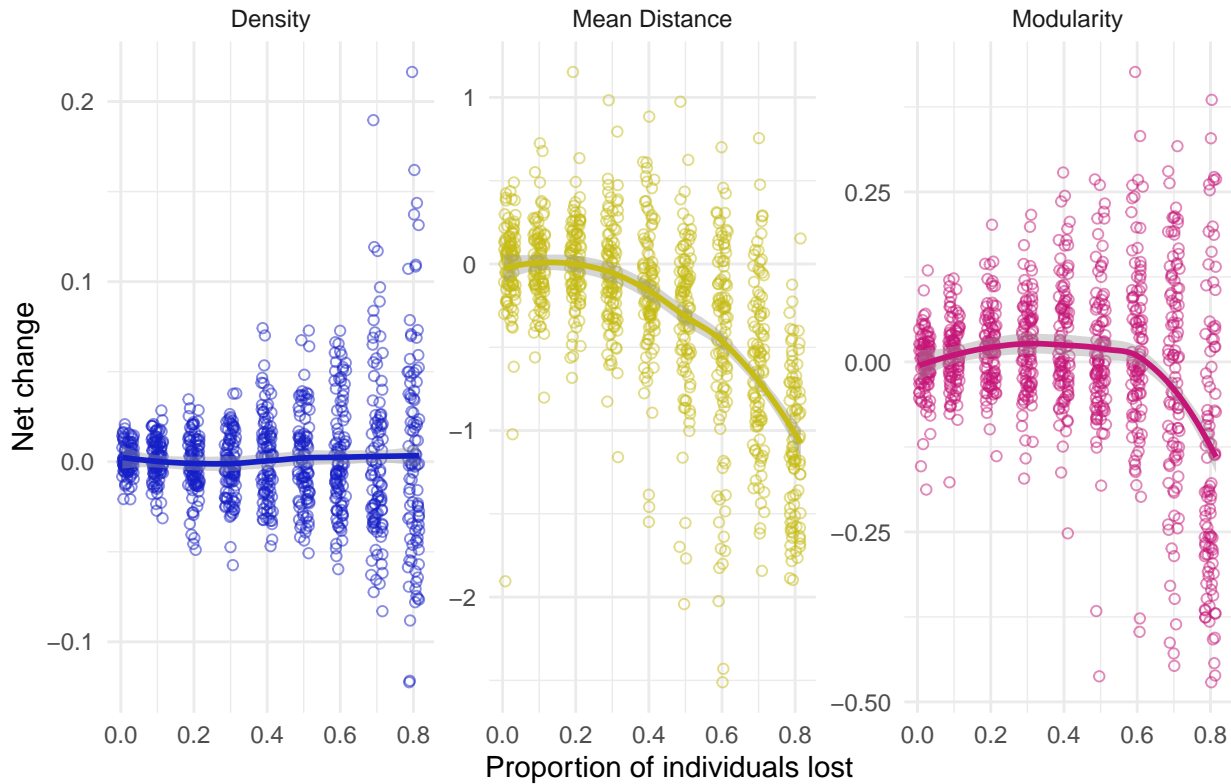
XXX FILL THIS IN TOO

Characteristics of nodes removed

To illustrate the impact of the characteristics of the removed nodes on the changes in network structure, I chose a network of 50 individuals in which 20% of the nodes (10 individuals) are removed.

Centrality

```
## `geom_smooth()` using formula 'y ~ x'
```
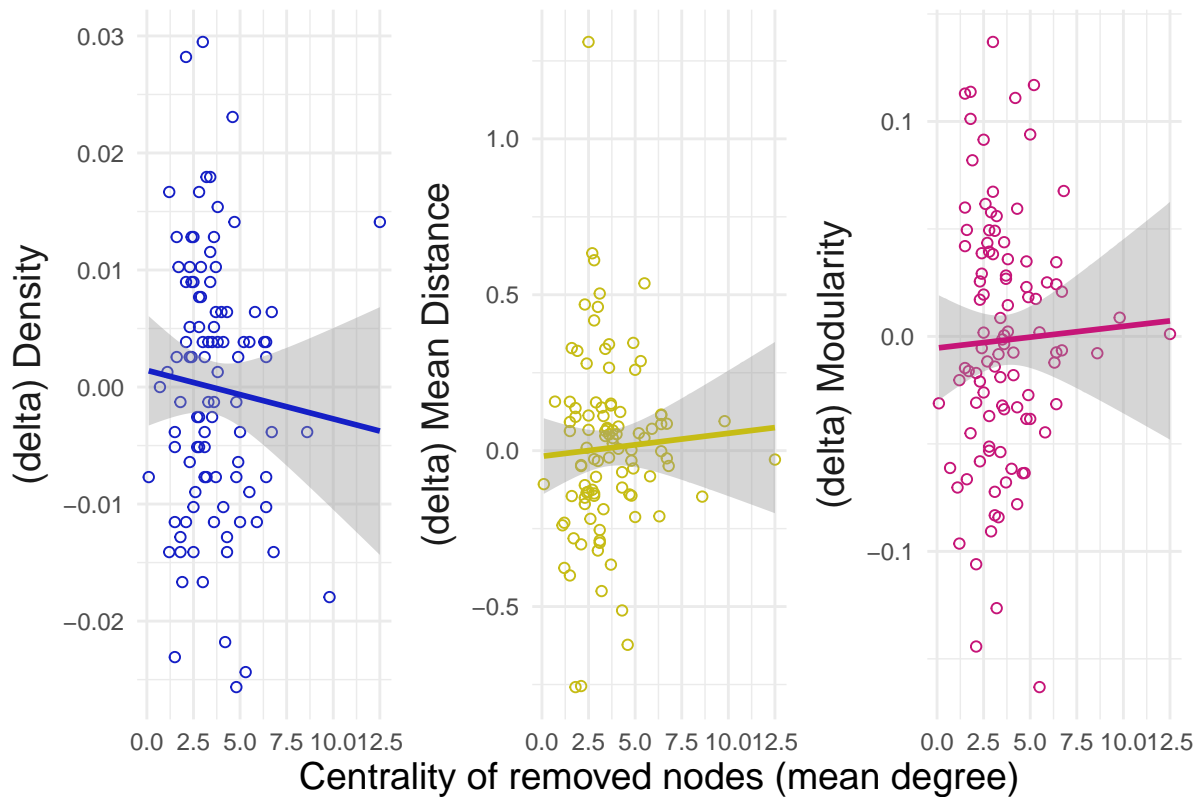
Removal

`geom_smooth()` using formula 'y ~ x'

Rewiring

`geom_smooth()` using formula 'y ~ x'

Net

Clustering

`geom_smooth()` using formula 'y ~ x'

Removal

`geom_smooth()` using formula 'y ~ x'

Rewiring
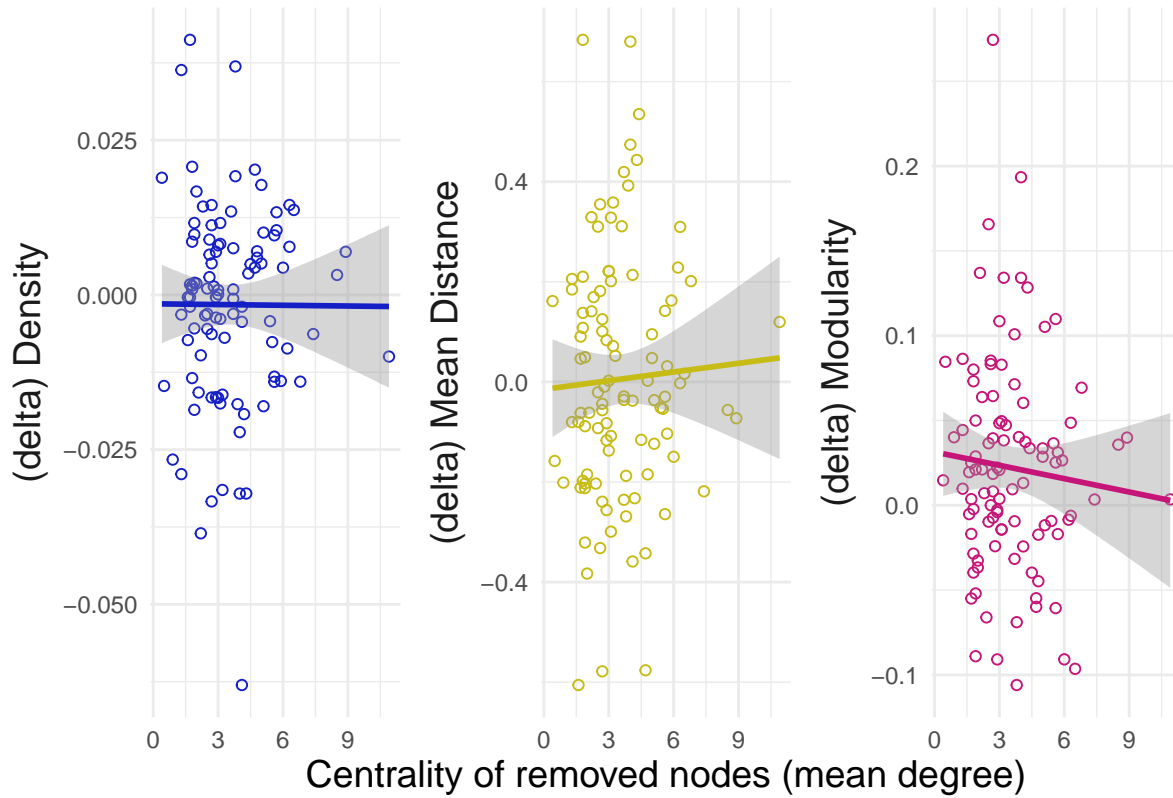
```
## `geom_smooth()` using formula 'y ~ x'
```
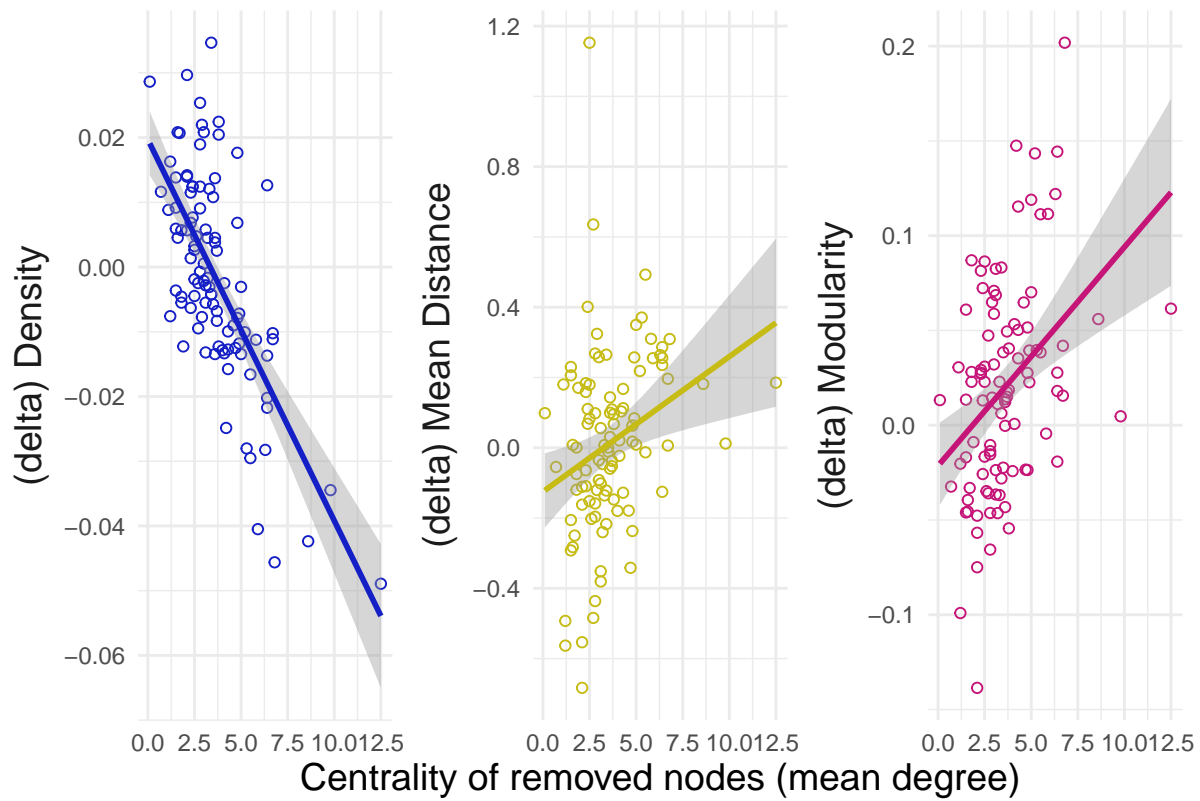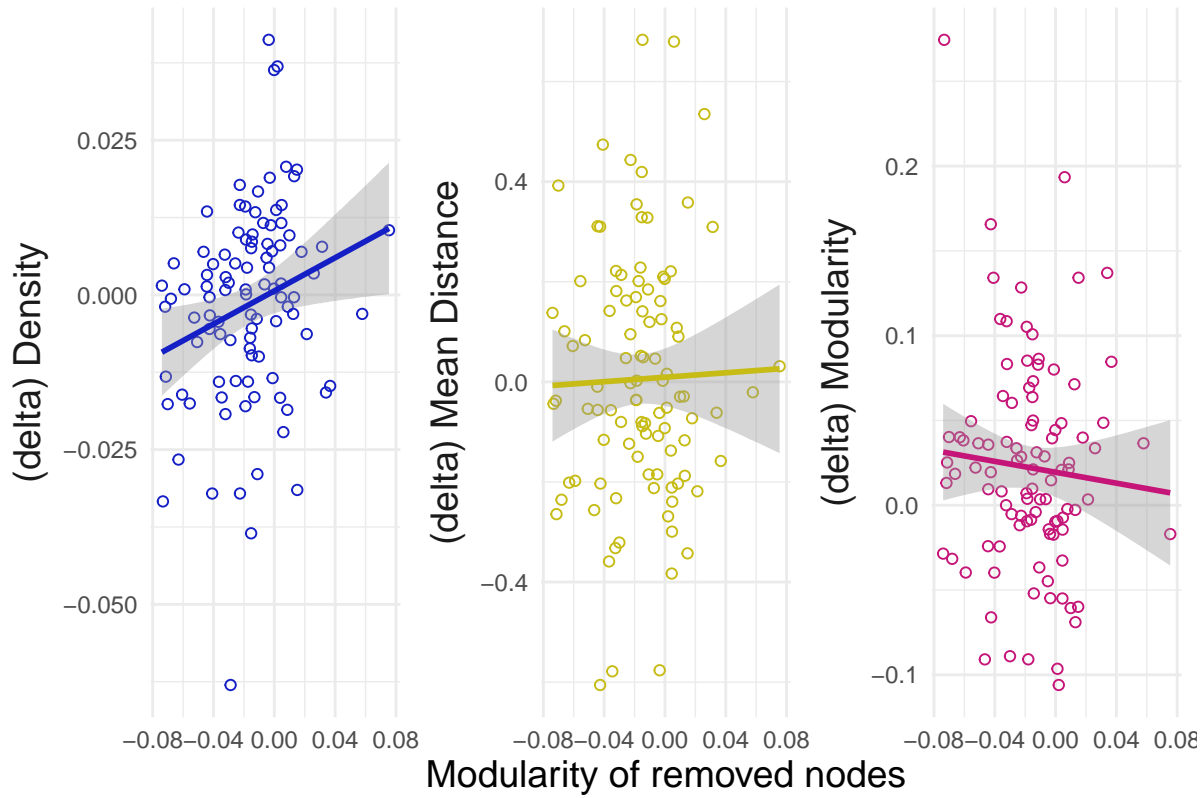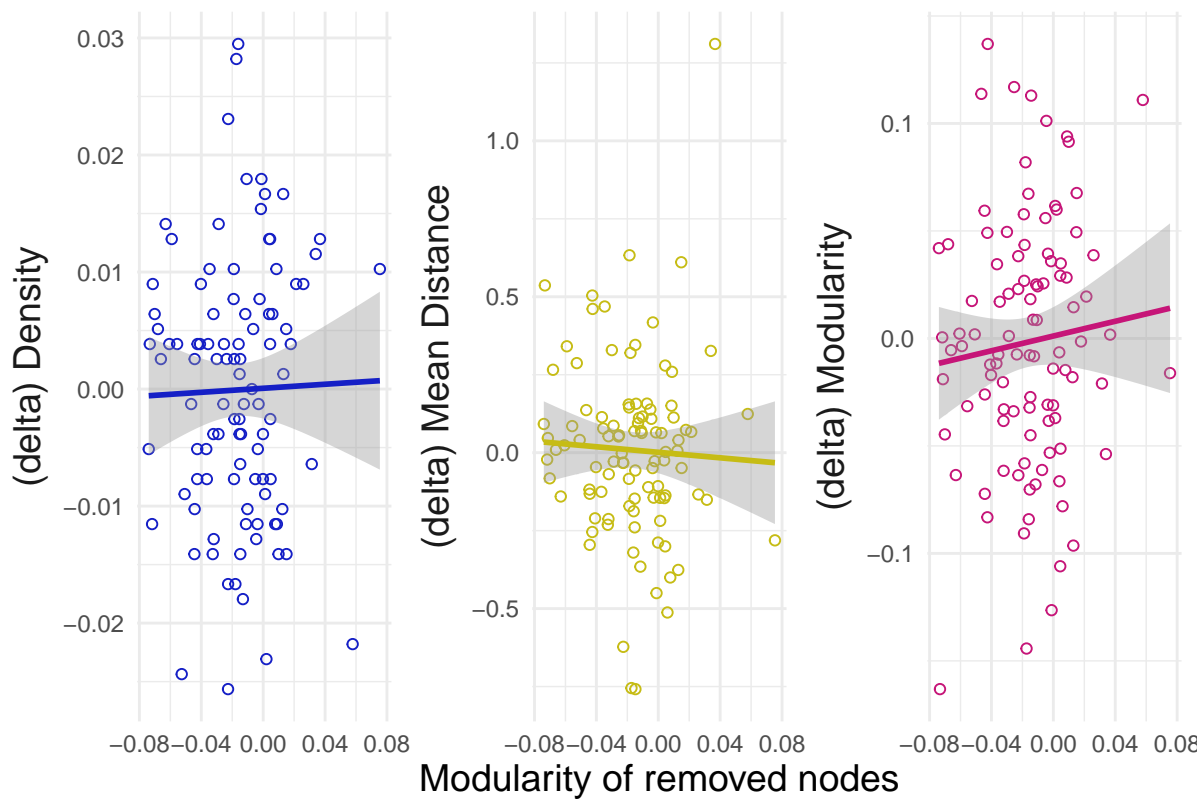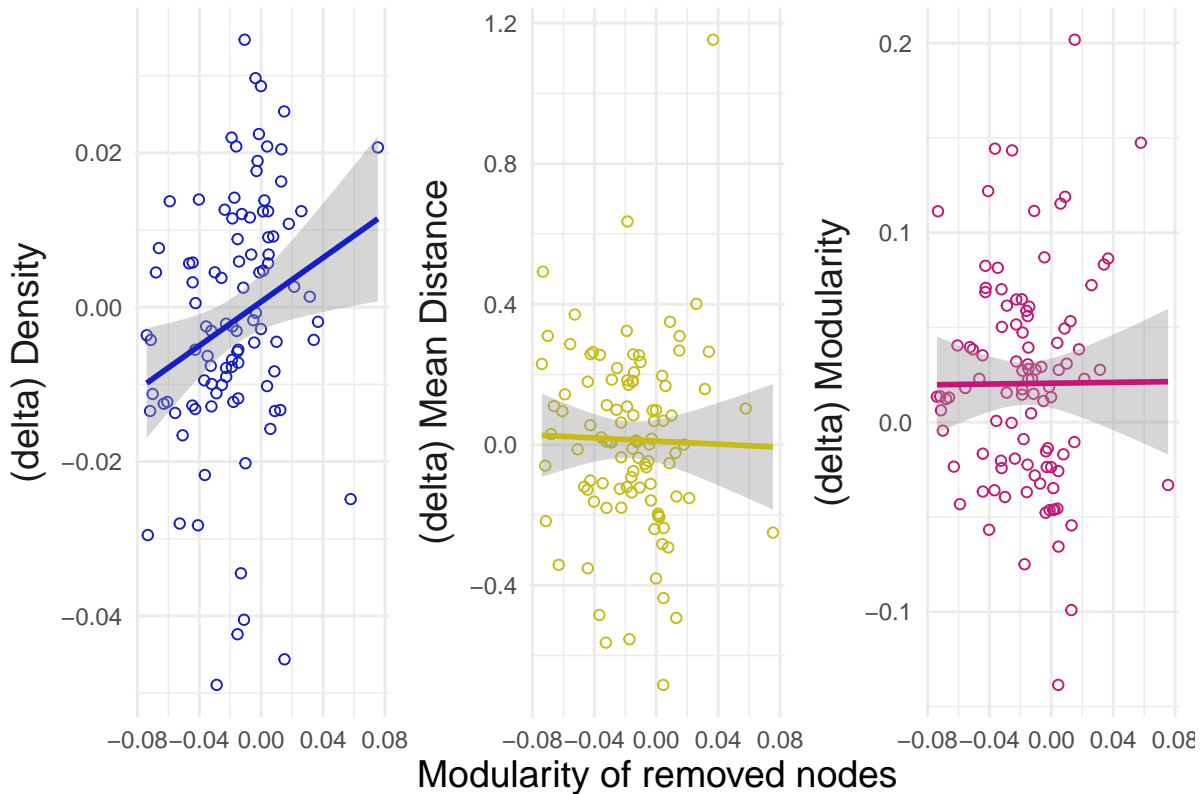

Rewiring rules

Run the model again, both times with 50 individuals, remove 10. In the "sociable" case, losing friends makes individuals **more** inclined to interact (`coefBereavement = 1`). In the "unsociable" case, losing friends makes individuals **less** inclined to interact (`coefBereavement = -2`).
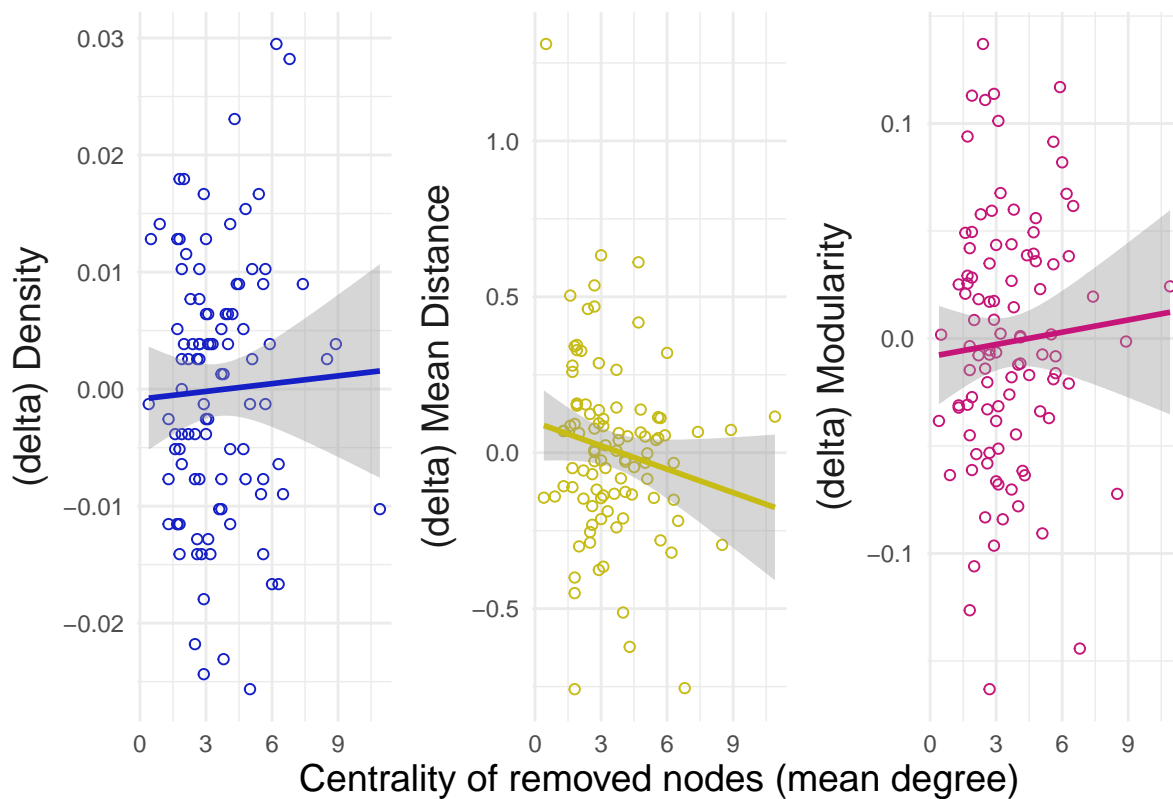
Centrality

```
## `geom_smooth()` using formula 'y ~ x'
```
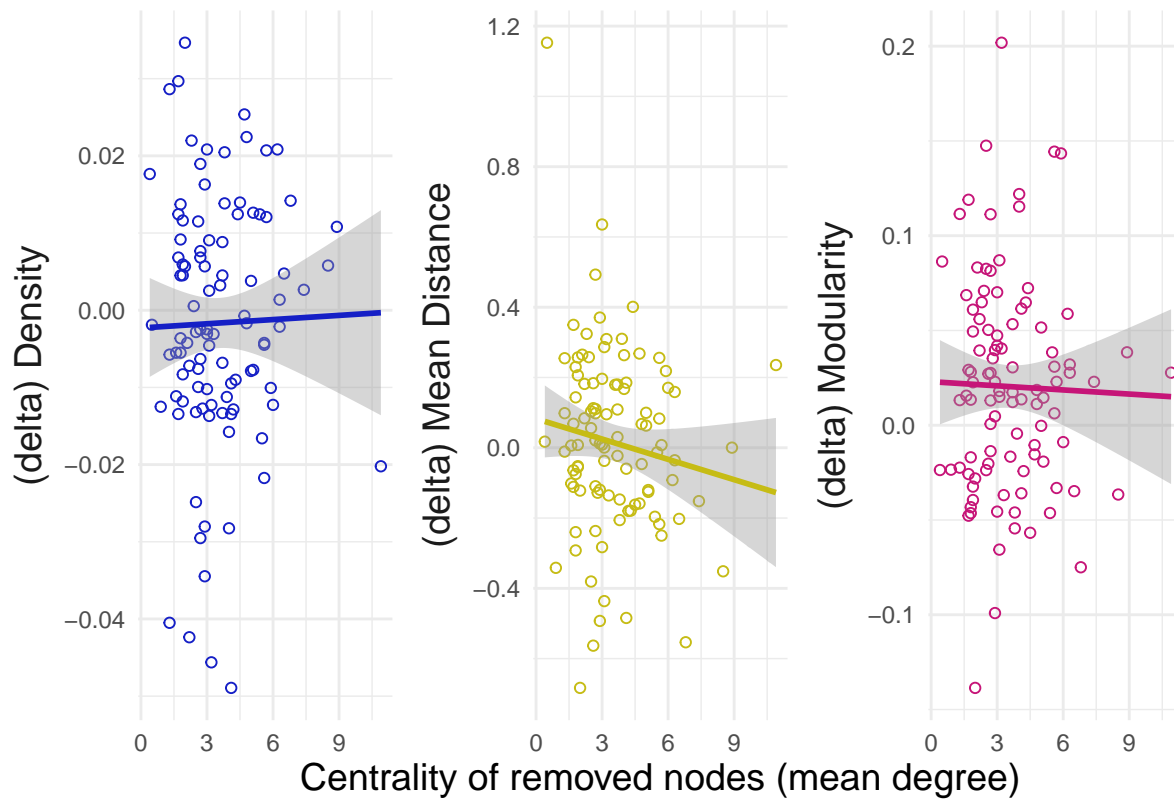
Removal

`geom_smooth()` using formula 'y ~ x'

Rewiring

```
## `geom_smooth()` using formula 'y ~ x'
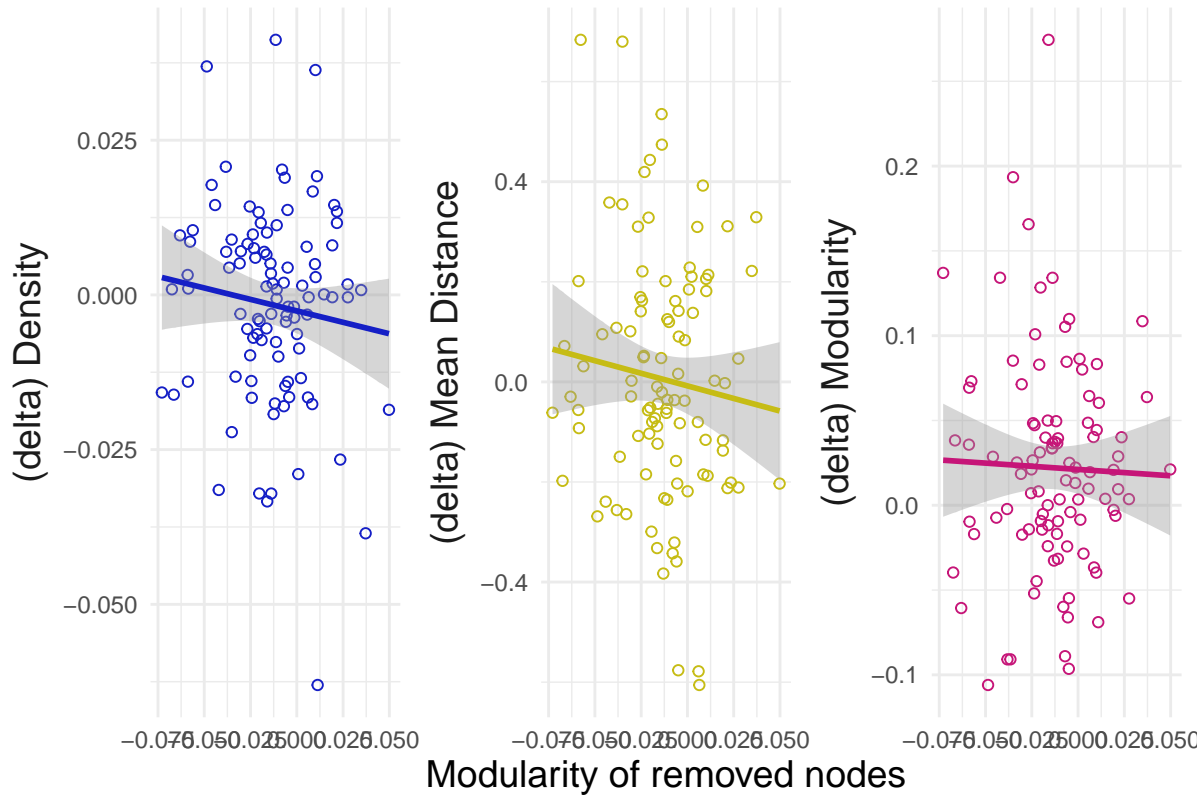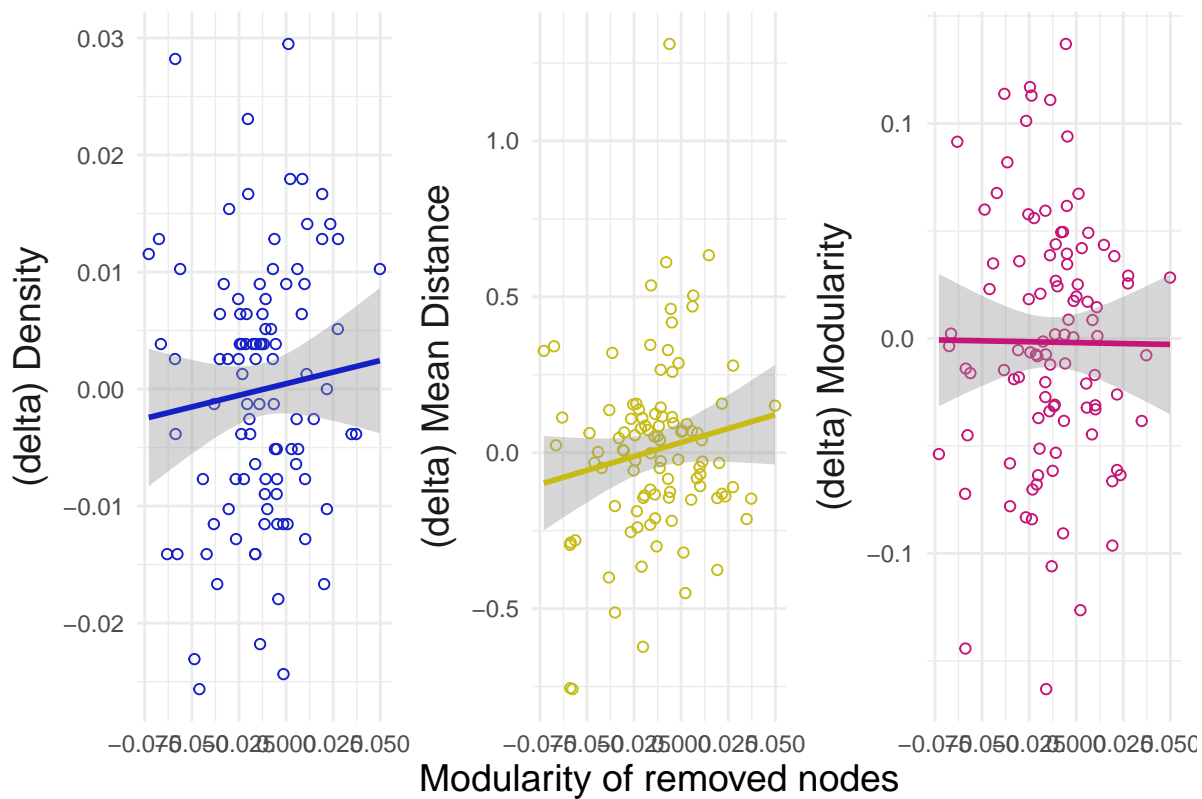```

Net



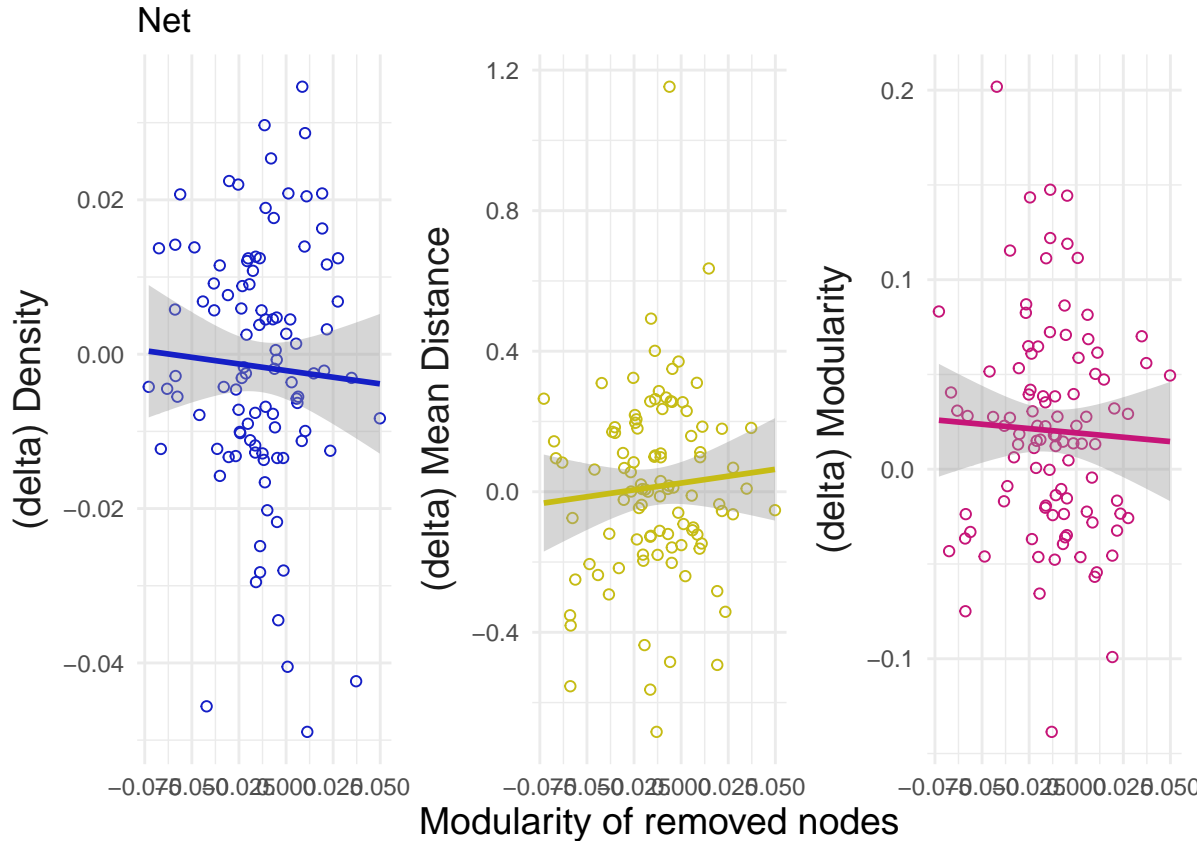Clustering

```
## `geom_smooth()` using formula 'y ~ x'
```

Removal

`geom_smooth()` using formula 'y ~ x'

Rewiring

`geom_smooth()` using formula 'y ~ x'

Discussion and future directions

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