Directional NK Paper Supplement

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Introduction

This document (created using Rmarkdown) contains: 1) all analysis code used to generate figures for this paper, 2) supplemental figures that did not fit in the main body of the paper.

First, lets setup our R environment

```
library(ggplot2)
library(reshape)
library(dplyr)
library(tidyr)
library(readr)
library(ggraph)
library(tidygraph)
```

Next, we'll load in all our data, which are expected to be in the directory above the one where this script is.

```
base <- "../"

# Read in the file that contains the names of the output documents
files <- read.table(paste(base, "files.txt", sep = ""), stringsAsFactors = F)
nval <- 15
ntimes = nrow(files)

# Compile the summary statistics, populations, and (reproductive) landscapes into individual data frame
#row <- 1
filename <- files[1,]
subfolder <- strsplit(filename, "/")[[1]][1]
subfile <- strsplit(filename, "/")[[1]][2]

# read in the statistics
trace <- read.table(paste(base, subfolder, "/stats-", subfile, sep = ""), header = T, stringsAsFactors =

# Read in the population output
pops <- read.table(paste(base, subfolder, "/popt-", subfile, sep = ""), header = T, stringsAsFactors = 

# get N, K, mu, replicate (seed), and regime arguments
subpieces <- strsplit(subfile, "-")
kval <- as.numeric(substring(subpieces[[1]][2], 2))

# seed <- as.numeric(substring(subpieces[[1]][3], 2)) # if seed is followed by another argument
seed <- as.numeric(substring(strsplit(subpieces[[1]][3], "[.]")[[1]][1], 2)) # if seed ends argument li
muval <- ifelse(length(subpieces[[1]]) == 5, as.numeric(substring(subpieces[[1]][4], 2)), as.numeric(pa
regparam <- subpieces[[1]][length(subpieces[[1]])]
regval <- ifelse(length(regmatches(regparam, gregexpr("S", regparam))[[1]]) > 0, "Sudden", "Gradual")
```

```r
# read in the reproductive landscape (requires the N value and the K value).
# For the shock landscape, use "/sland-" instead of "/land-".
peaks <- read.table(paste(base, subfolder, "/land-", subfile, sep = ""), skip = (6+nval+2^(kval+1)), col
shock_peaks <- read.table(paste(base, subfolder, "/sland-", subfile, sep = ""), skip = (6+nval+2^(kval+

# Assign treatment parameters to each data frame
trace$k <- kval
pops$k <- kval
peaks$k <- kval
shock_peaks$k <- kval
trace$n <- nval
pops$n <- nval
peaks$n <- nval
shock_peaks$n <- nval
trace$seed <- seed
pops$seed <- seed
peaks$seed <- seed
shock_peaks$seed <- seed
trace$regime <- regval
pops$regime <- regval
peaks$regime <- regval
shock_peaks$regime <- regval
trace$mu <- muval
pops$mu <- muval
peaks$mu <- muval
shock_peaks$mu <- muval
for (f in 2:nrow(files)){
  filename <- files[f,]
  subfolder <- strsplit(filename, "/")[[1]][1]
  subfile <- strsplit(filename, "/")[[1]][2]
  thistrace <- read.table(paste(base, subfolder, "/stats-", subfile, sep = ""), header = T, stringsAsFac
  thispop <- read.table(paste(base, subfolder, "/popt-", subfile, sep = ""), header = T, stringsAsFacto
  subpieces <- strsplit(subfile, "-")
  kval <- as.numeric(substring(subpieces[[1]][2], 2))
  #seed <- as.numeric(substring(subpieces[[1]][3], 2))
  seed <- as.numeric(substring(strsplit(subpieces[[1]][3], "[.]")[[1]][1], 2))
  regparam <- subpieces[[1]][length(subpieces[[1]])]
  regval <- ifelse(length(regmatches(regparam, gregexpr("S", regparam))[[1]]) > 0, "Sudden", "Gradual")
  print(paste(seed, regval))
  muval <- ifelse(length(subpieces[[1]]) == 5, as.numeric(substring(subpieces[[1]][4], 2)), as.numeric(
  thispeak <- read.table(paste(base, subfolder, "/land-", subfile, sep = ""), skip = (6+nval+2^(kval+1)
  thisshockpeak <- read.table(paste(base, subfolder, "/sland-", subfile, sep = ""), skip = (6+nval+2^(k
  thistrace$k <- kval
  thispop$k <- kval
  thispeak$k <- kval
  thisshockpeak$k <- kval
  thistrace$n <- nval
  thispop$n <- nval
  thispeak$n <- nval
  thisshockpeak$n <- nval
  thistrace$seed <- seed
  thispop$seed <- seed
  thispeak$seed <- seed
  thisshockpeak$seed <- seed
  thistrace$regime <- regval
  thispop$regime <- regval
  thispeak$regime <- regval
  thisshockpeak$regime <- regval
  thistrace$mu <- muval
  thispop$mu <- muval
  thispeak$mu <- muval
  thisshockpeak$mu <- muval
  trace <- rbind(trace, thistrace)
  pops <- rbind(pops, thispop)
  peaks <- rbind(peaks, thispeak)
  shock_peaks <- rbind(shock_peaks, thisshockpeak)
}

# Create regime label for future plotting
shock_peaks$Landscape <- "shock"
peaks$Landscape <- "reproduction"
```

Next, we do some additional post-processing:

```
# Check number of persisting generations
ntimes <- length(unique(trace$seed))
survivals <- data.frame(n = rep(NA, ntimes), k = rep(NA, ntimes), seed = rep(NA, ntimes), regime = rep(
for(s in 1:ntimes){
  sd <- unique(trace$seed)[s]
  sub <- subset(trace, seed == sd)
  survivals[s, ] <- subset(sub, gen == max(sub$gen), select = c(n, k, seed, regime, cutoff, gen, unique
}
```

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## Warning in `[<-.data.frame`(`*tmp*`, s, , value = structure(list(n = c(15, :
## replacement element 18 has 2 rows to replace 1 rows
```

```r
# Adjust significant digits on mutation rate for plotting
survivals$mu <- format(survivals$mu, digits=3, drop0trailing = TRUE, format="g")
survivals <- survivals %>% mutate(mu = case_when(
  mu=="0.066667" ~ "0.0667",
  TRUE ~ mu
  )
)
```

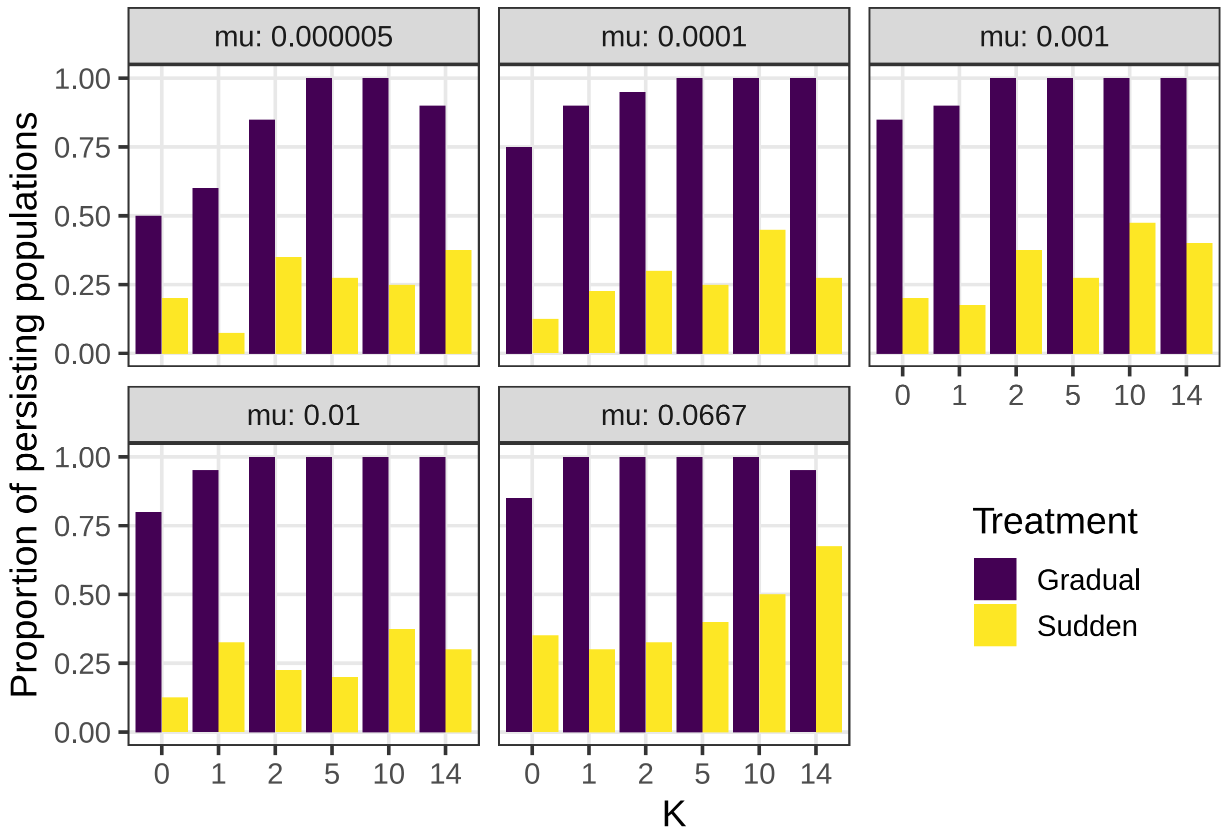
Analysis

Survival probability

First, we assess the effect of different evolutionary regimes on the probability of a population surviving until the end of the experiment:

```
pd <- position_dodge(.5)
ggplot(data = survivals %>%  # Do some additional processing of the data
                filter(gen == 51) %>%  # Only grab data points from the final generation (eliminates po
                group_by(k, regime, mu) %>%   # Calculate percentages per condition (combo of k, regime
                summarise(
                  percent_survive = ifelse(  # The sudden regime had 40 replicates while the gradual re
                                            regime == "Sudden",
                                            n()/40,
                                            n()/20
                                          )
                ),
      aes(x = as.factor(k), fill = regime)) +  # Plot each regime as a different color with k as x axis
      scale_x_discrete() +
      geom_bar(  # Plot data as bars indicating proportion of population that survived
        aes(y=percent_survive),
        position = position_dodge(.92),  # Put bars for each regime side by side
        stat = "identity"
      ) +
      theme_bw(base_size = 14) +
      theme(panel.grid.minor = element_blank(),
        panel.grid.major = element_line(color = "grey91"),
        strip.text.y = element_text(face = "italic"), legend.position = c(.85, .25)) +
      facet_wrap(~mu, labeller = labeller(mu=label_both)) +  # Make a panel for each mutation rate
      scale_fill_viridis_d(name = "Treatment") +
      ylab("Proportion of persisting populations") +
      xlab("K")
```

```
## `summarise()` has grouped output by 'k', 'regime', 'mu'. You can override using
## the `.groups` argument.
```

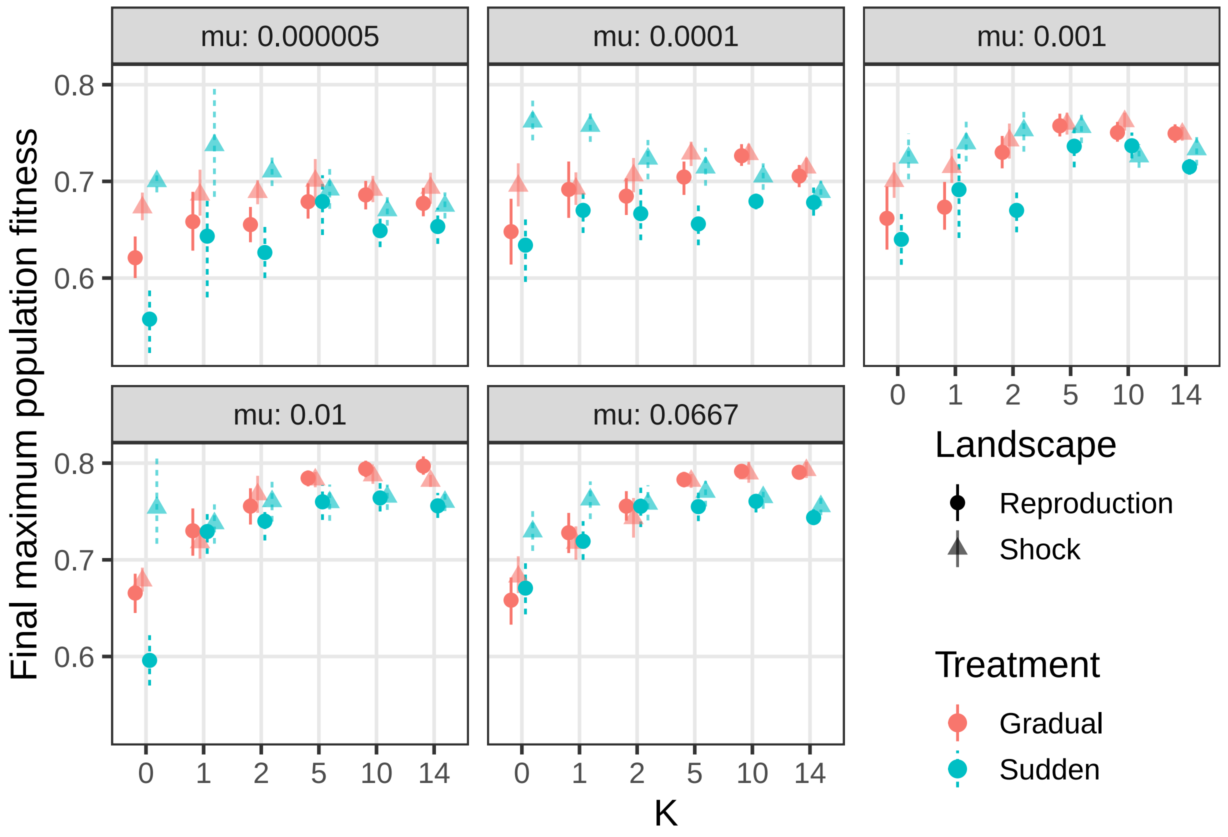


Final fitness

Next, we compare the maximum fitness at the end of the run (in both landscapes) across conditions (for runs that did not go extinct):

```
ggplot(data = survivals %>%  # Pivot shock and reproductive fitness into a single column so we can easi
                filter(gen==51) %>%  # Grab only final generation, to exclude populations that went ext
                pivot_longer(c(max, shockMax), names_to="Landscape", values_to="max_fitness") %>%
                mutate(Landscape = case_when(
                                      Landscape == "max" ~ "Reproduction",
                                      Landscape=="shockMax" ~ "Shock")
                       ),
       aes(x = as.factor(k),
           y = max_fitness,
           color = regime,
           shape=Landscape,
           linetype=regime, # Give regimes different linetype for greyscale readability
           alpha=Landscape  # Plot different landscapes at slightly different alpha levels for greyscal
          )
  ) +
  stat_summary(fun.data = "mean_cl_boot", geom = "pointrange", position = pd) +  # Plot a bootstrapped
  theme_bw(base_size = 14) +
  theme(panel.grid.minor = element_blank(),
        panel.grid.major = element_line(color = "grey91"),
        strip.text.y = element_text(face = "italic"), legend.position = c(.85, .20)) +
  scale_color_hue(name = "Treatment") +
  scale_alpha_discrete(range = c(1,.6)) +  # Set alpha levels for the two landscapes
  facet_wrap(~mu, labeller = labeller(mu = label_both)) +
  ylab("Final maximum population fitness") +
  scale_linetype("Treatment") +
  xlab("K")
```

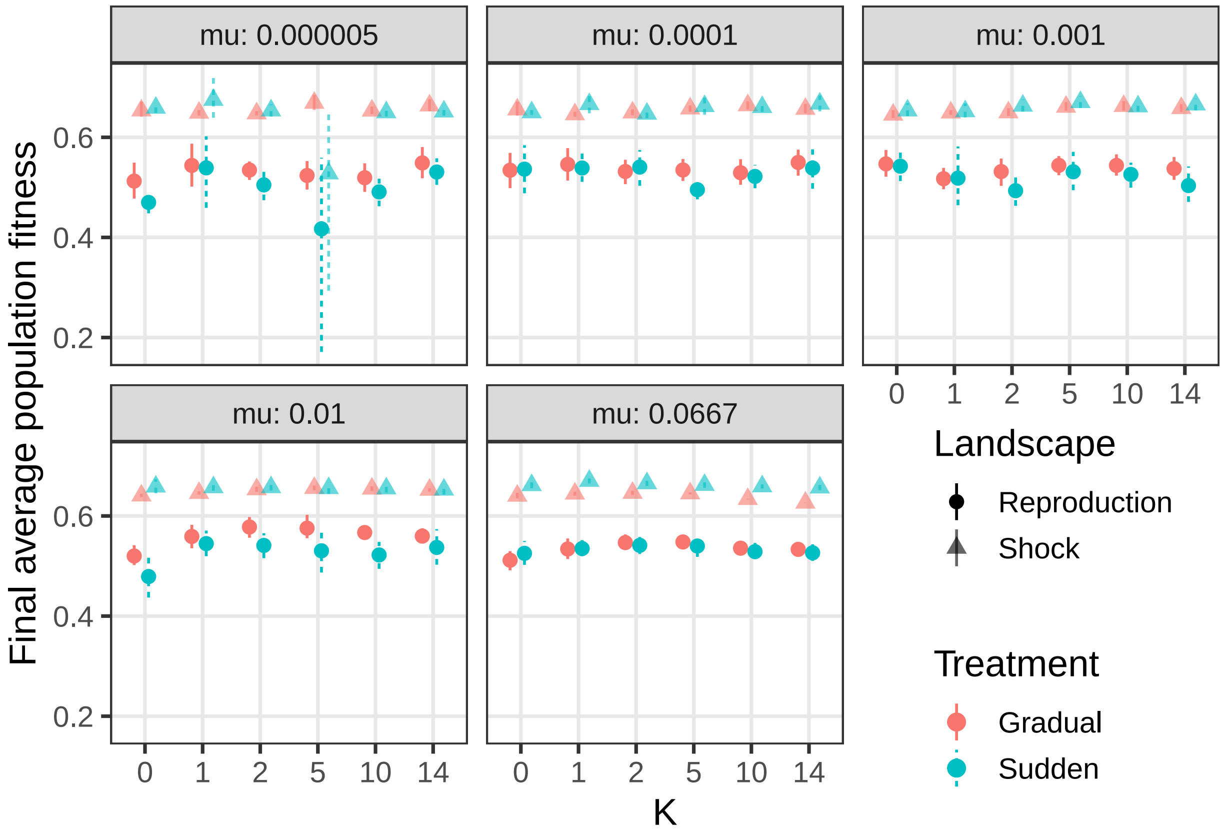
```
## Warning: Using alpha for a discrete variable is not advised.
```



We make the same plot for average fitness (recall that there the shock landscape is the only source of death, so there are many low fitness individuals in the population at any point in time):

```
ggplot(data = survivals %>%
                filter(gen==51) %>%
                pivot_longer(c(average, shockAvg), names_to="Landscape", values_to="max_fitness") %>%
                mutate(Landscape = case_when(
                                        Landscape == "average" ~ "Reproduction",
                                        Landscape=="shockAvg" ~ "Shock")
                ),
       aes(x = as.factor(k),
           y = max_fitness,
           color = regime,
           shape=Landscape,
           linetype=regime, alpha=Landscape)
       ) +
  stat_summary(fun.data = "mean_cl_boot", geom = "pointrange", position = pd) +
  theme_bw(base_size = 14) +
  theme(panel.grid.minor = element_blank(),
        panel.grid.major = element_line(color = "grey91"),
        strip.text.y = element_text(face = "italic"), legend.position = c(.85, .2)) +
  scale_color_hue(name = "Treatment") +
  facet_wrap(~mu, labeller = labeller(mu = label_both)) +
  ylab("Final average population fitness") +
  scale_alpha_discrete(range = c(1,.6)) +
  scale_linetype("Treatment") +
  xlab("K")
```

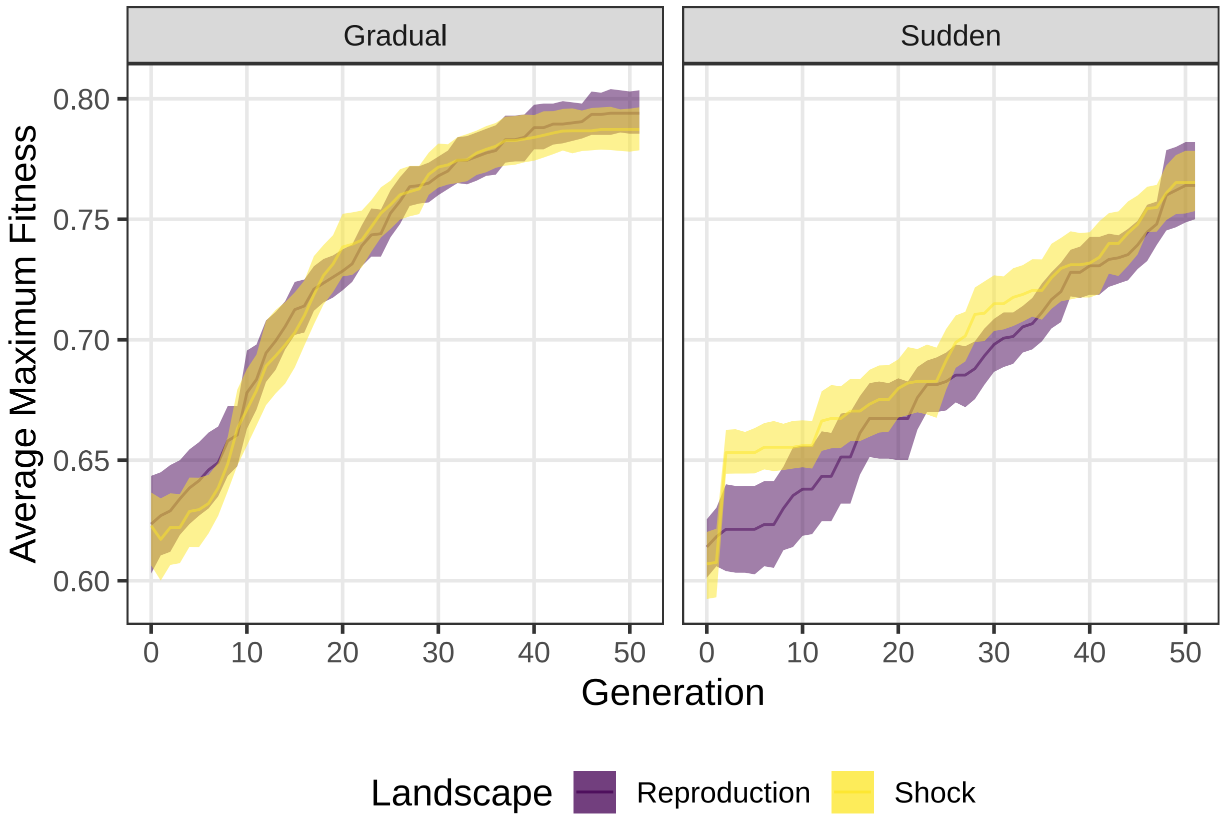
```
## Warning: Using alpha for a discrete variable is not advised.
```



Fitness timeseries analysis

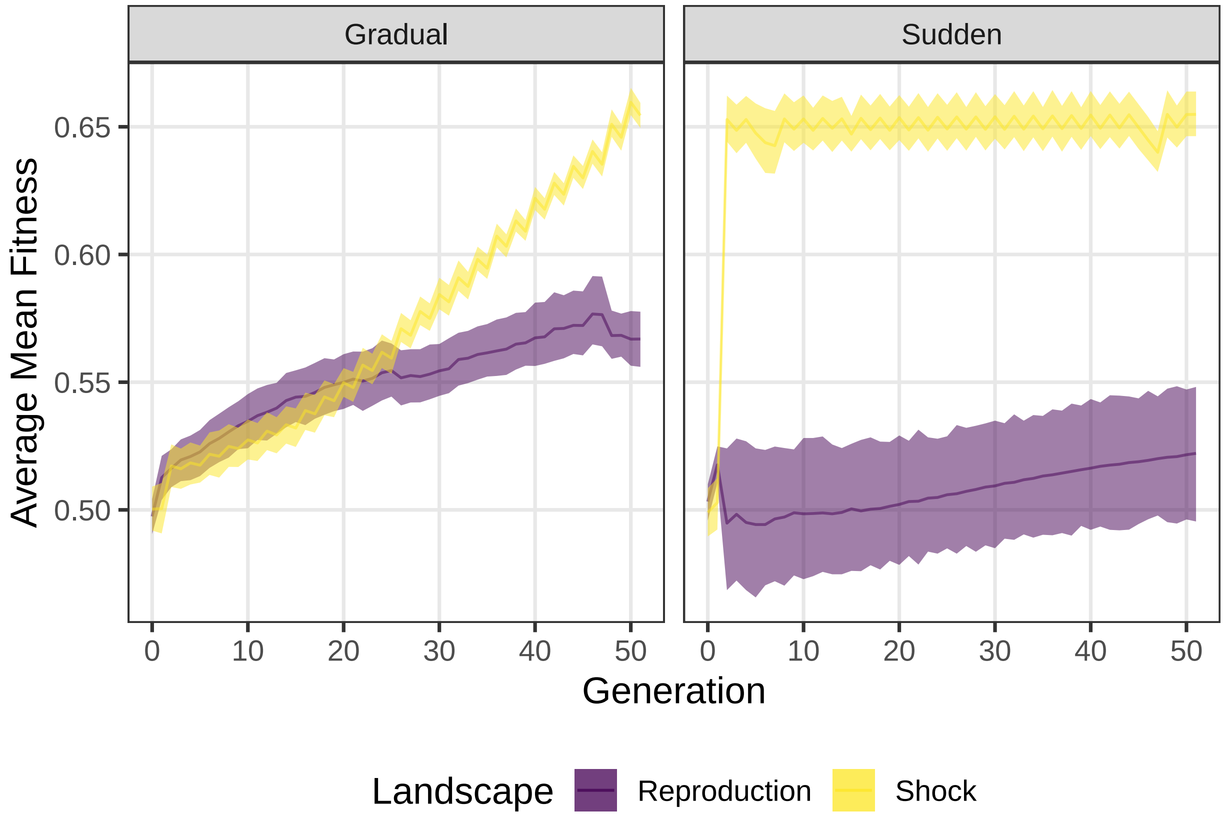
Next, we analyze the behavior of maximum fitness (within each individual population) over time:

```
ggplot(data = trace %>%
         filter(mu==.01, k==10),  # Plot a single representative combination of mu and k
       aes(x = gen, y = max)
  ) +
  facet_wrap(~regime) +  # A panel for each shock regime
  stat_summary(fun.data="mean_cl_boot", geom="ribbon", alpha=.5, aes(fill="Reproduction")) +  # Bootstr
  stat_summary(fun.data="mean_cl_boot", geom="line", alpha=.5, aes(color="Reproduction")) +  # Avg max
  stat_summary(aes(y=shockMax, fill="Shock"), fun.data="mean_cl_boot", geom="ribbon", alpha=.5) +  # Bo
  stat_summary(aes(y=shockMax, color="Shock"), fun.data="mean_cl_boot", geom="line", alpha=.5) +  # Avg
  theme_bw(base_size = 14) +
  theme(panel.grid.minor = element_blank(),
        panel.grid.major = element_line(color = "grey91"),
        strip.text.y = element_text(face = "italic"),
        legend.position = "bottom")  +
  scale_color_manual("Landscape", values = c("Reproduction"="#440154", "Shock"="#fde725")) +  # Clean u
  scale_fill_manual("Landscape", values = c("Reproduction"="#440154", "Shock"="#fde725")) +
  ylab("Average Maximum Fitness") +
  xlab("Generation")
```



And we do the same for average fitness:

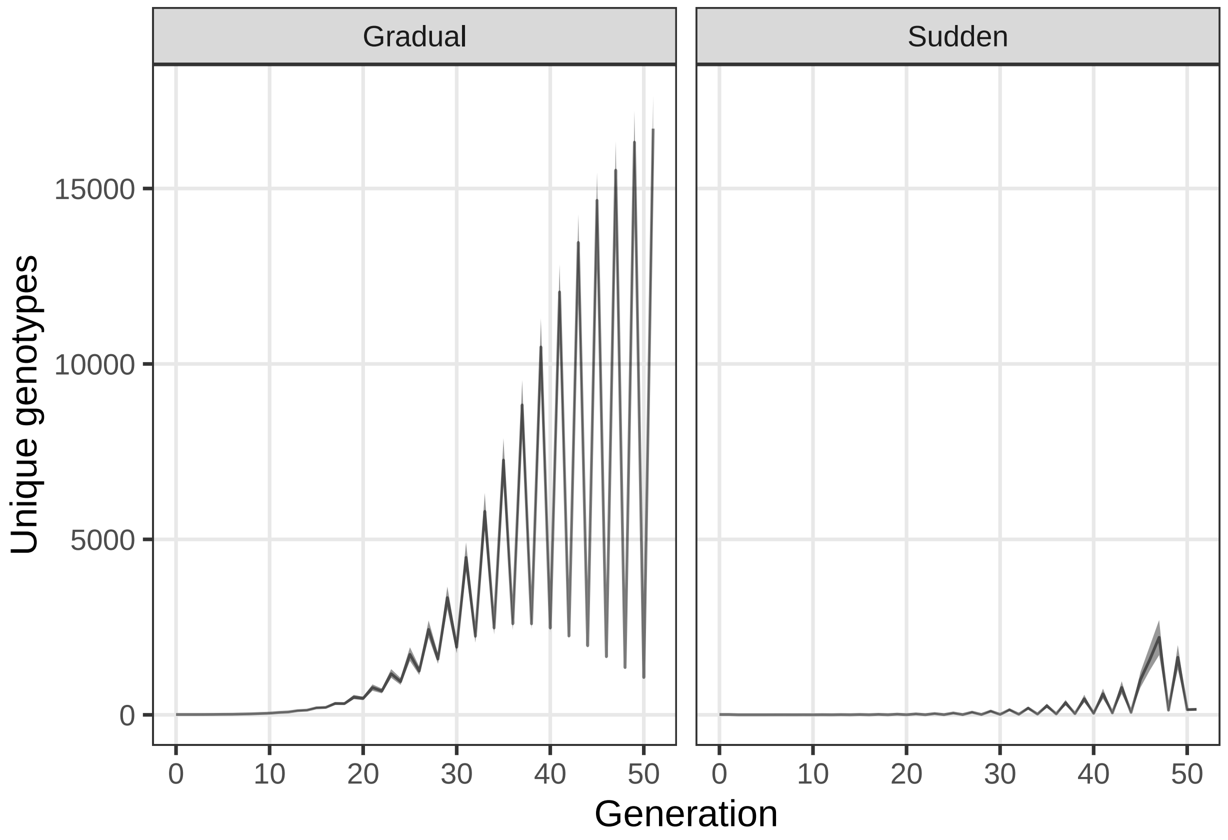
```
ggplot(data = trace %>%
         filter(mu==.01, k==10),
       aes(x = gen, y = average)) +
  facet_wrap(~regime) +
  stat_summary(fun.data="mean_cl_boot", geom="ribbon", alpha=.5, aes(fill="Reproduction")) +
  stat_summary(fun.data="mean_cl_boot", geom="line", alpha=.5, aes(color="Reproduction")) +
  stat_summary(aes(y=shockAvg, fill="Shock"), fun.data="mean_cl_boot", geom="ribbon", alpha=.5) +
  stat_summary(aes(y=shockAvg, color="Shock"), fun.data="mean_cl_boot", geom="line", alpha=.5) +
  theme_bw(base_size = 14) +
  theme(panel.grid.minor = element_blank(),
        panel.grid.major = element_line(color = "grey91"),
        strip.text.y = element_text(face = "italic"),
        legend.position = "bottom")  +
  scale_color_manual("Landscape", values = c("Reproduction"="#440154", "Shock"="#fde725")) +
  scale_fill_manual("Landscape", values = c("Reproduction"="#440154", "Shock"="#fde725")) +
  ylab("Average Mean Fitness") +
  xlab("Generation")
```



Diversity

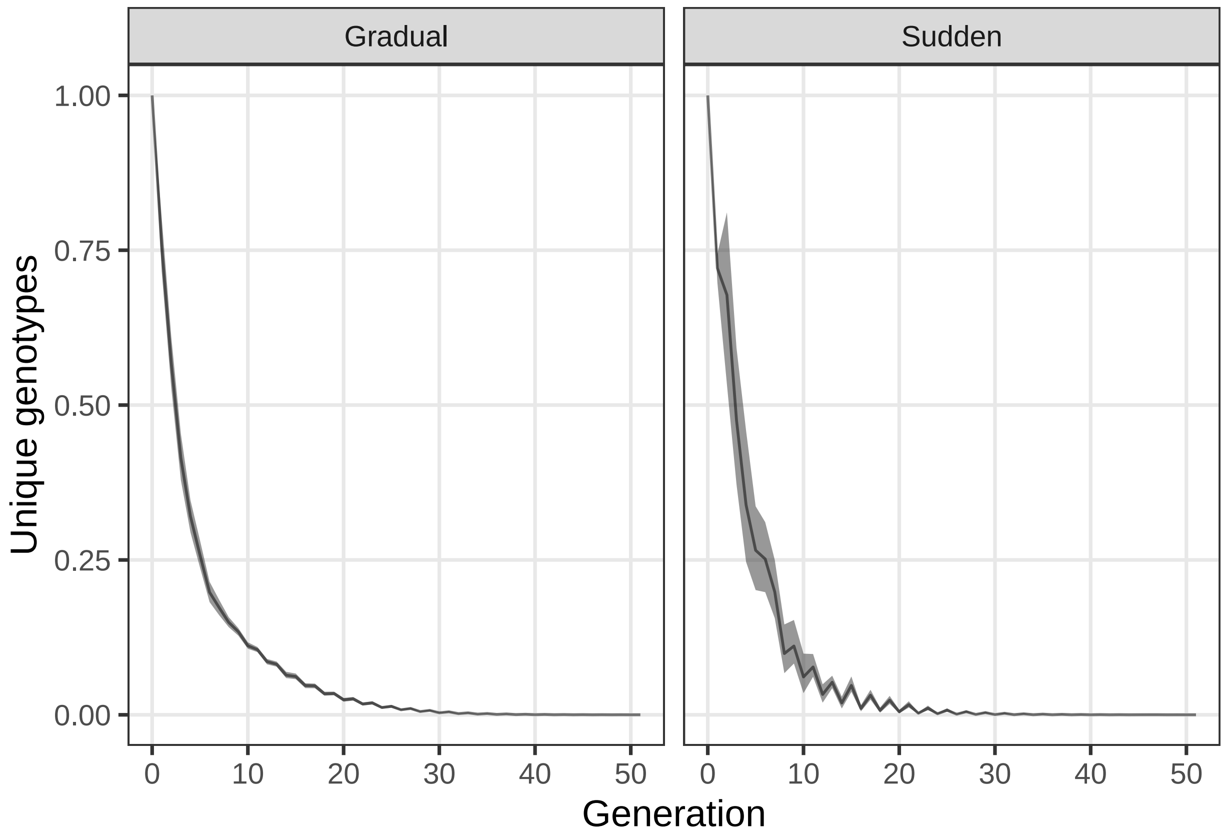
Diversity clearly plays an important role in the dynamics we observe. Here, we plot the number of unique genotypes over time in each condition:

```
ggplot(data = trace %>%
         filter(mu==.01, k==10),
       aes(x = gen, y = uniques)) +
  facet_wrap(~regime) +  # One panel for each regime
  stat_summary(fun.data="mean_cl_boot", geom="ribbon", alpha=.5) +  # Bootstrapped 95% CI around mean c
  stat_summary(fun.data="mean_cl_boot", geom="line", alpha=.5) +  # Mean count of unique genotypes
  theme_bw(base_size = 14) +
  theme(panel.grid.minor = element_blank(),
        panel.grid.major = element_line(color = "grey91"),
        strip.text.y = element_text(face = "italic"),
        legend.position = "none")  +
  ylab("Unique genotypes") +
  xlab("Generation")
```



A lot of this trend is likely being driven by population size, so it may also be worth looking at the same plot normalized by population:

```
ggplot(data = trace %>%
         filter(mu==.01, k==10),
       aes(x = gen, y = uniques/population)) +
  facet_wrap(~regime) +  # One panel for each regime
  stat_summary(fun.data="mean_cl_boot", geom="ribbon", alpha=.5) +  # Bootstrapped 95% CI around mean c
  stat_summary(fun.data="mean_cl_boot", geom="line", alpha=.5) +  # Mean count of unique genotypes
  theme_bw(base_size = 14) +
  theme(panel.grid.minor = element_blank(),
        panel.grid.major = element_line(color = "grey91"),
        strip.text.y = element_text(face = "italic"),
        legend.position = "none")  +
  ylab("Unique genotypes") +
  xlab("Generation")
```



Landscape analysis

We see relatively high fitnesses in both landscapes. The next obvious set of questions to ask concern the way the population is traversing the two landscapes.

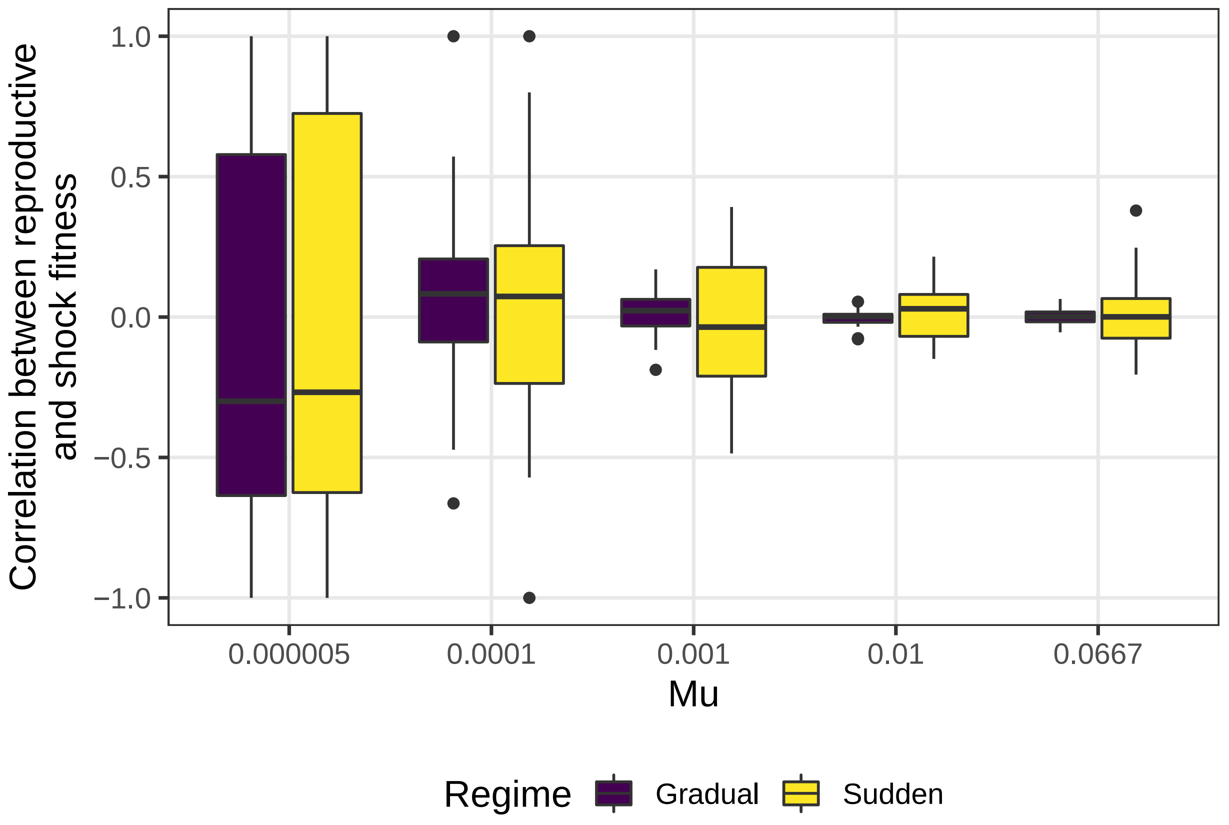
One possibility is that successful populations are finding regions of the fitness landscape that are highly fit in both landscapes. To assess this possibility, we measure the correlation between reproductive fitness and shock fitness among evolved genotypes in the population. We measure this correlation for each population:

```r
# Make new dataframe with all the correlations
df <- pops %>%
        group_by(seed, Genome) %>%  # Group by run (as indicated by random seed used for each run) and
        arrange(Gen) %>%  # Sort by generation so time series are in order
        filter(last(Gen)==50, first(Gen) < 48, row_number() == 1) %>%  # Grab the first appearance of a
        summarise(Gen = first(Gen),   # Condense each genome into a single row - these values should al
                  Fitness= first(Fitness),
                  ShockFitness=first(ShockFitness),
                  regime=first(regime),
                  k=first(k),
                  mu=first(mu),
                  .groups = "drop_last"  # Keep data frame grouped by run
                  ) %>%
        summarise(r=cor(Fitness, ShockFitness, method="spearman"),  # Calculate correlation between fit
                  regime=first(regime),
                  k=first(k),
                  mu=first(mu)
                  )
```

```r
# Clean up significant digits on mutation rate for label
df$mu <- format(df$mu, digits=3, drop0trailing = TRUE, format="g")
df <- df %>% mutate(mu = case_when(
  mu=="0.066667" ~ "0.0667",
  TRUE ~ mu
  )
)

# Actually plot the data
ggplot(df %>% filter(k== 10)) +
  geom_boxplot(aes(x=as.factor(mu), y=r, fill=regime)) +
  xlab("Mu") +
  scale_fill_viridis_d("Regime") +
  ylab("Correlation between reproductive\nand shock fitness") +
  theme_bw(base_size = 14) +
  theme(panel.grid.minor = element_blank(),
        panel.grid.major = element_line(color = "grey91"),
        strip.text.y = element_text(face = "italic"),
        legend.position = "bottom")
```

```
## Warning: Removed 3 rows containing non-finite values (stat_boxplot).
```



This implies that different genotypes have high fitness in each landscape rather than a single genotype being good at both. To understand better what is happening, it would be helpful to more directly examine the traversal of these landscapes. Unfortunately, doing so is very challenging with an N=15 landscape due to the high dimensionality. To build intuition, we undertake a case study in a lower-dimensional landscape.

Lower dimensional case study

Here, we use a pair of N=6, K=1 fitness landscapes. We plot these landscapes as graphs in which noddes represent genotypes and edges represent single-mutation adjaceny between genotypes.

First, we set up the data:

```r
# Read in a file containing all the edges for this fitness landscape graph
edges <- read_csv("edges_6.csv")
```

```
## Rows: 384 Columns: 2
## -- Column specification --------------------------------------------------------
## Delimiter: ","
## dbl (2): from, to
##
## i Use `spec()` to retrieve the full column specification for this data.
## i Specify the column types or set `show_col_types = FALSE` to quiet this message.
```

```r
# Read in fitnesses from reproduction fitness landscape
repro_fits <- read_csv("repro_fits_1963.csv")
```

```
## Rows: 64 Columns: 4
## -- Column specification --------------------------------------------------------
## Delimiter: ","
## dbl (4): genotype, ones, fitness, prop_max
##
## i Use `spec()` to retrieve the full column specification for this data.
## i Specify the column types or set `show_col_types = FALSE` to quiet this message.
```

```r
# Read in fitnesses from shock landscape
shock_fits <- read_csv("shock_fits_1963.csv")
```

```
## Rows: 64 Columns: 4
## -- Column specification --------------------------------------------------------
## Delimiter: ","
## dbl (4): genotype, ones, fitness, prop_max
##
## i Use `spec()` to retrieve the full column specification for this data.
## i Specify the column types or set `show_col_types = FALSE` to quiet this message.
```

```r
# Clean up dataframes
colnames(repro_fits)[1] <- "name"
colnames(shock_fits)[1] <- "name"
colnames(shock_fits)[3] <- "shock_fitness"

# Make sure name is the same type in all data frames for easy joining
repro_fits$name <- as.character(repro_fits$name)
shock_fits$name <- as.character(shock_fits$name)
edges$from <- as.character(edges$from)
edges$to <- as.character(edges$to)

# Read in population time series data from run of evolutioon
pop <- read_table("../outs/popt-N6-k1-s1963-r0.001-Gradual.txt",skip = 3)
```

```
##
## -- Column specification --------------------------------------------------------
## cols(
##   `0` = col_double(),
##   `29` = col_double(),
##   `1` = col_double(),
##   `0.320976` = col_double(),
##   `0.416563` = col_double()
## )
```

```r
# Clean up data frame
colnames(pop) <- c("gen", "genome", "count","fitness", "shockfitness", "placeholder")
pop$placeholder <- NULL
pop$genome <- as.character(pop$genome)

# For now we're only worrying about the last generation
pop <- pop %>%filter(gen == max(gen))

# Build tidygraph data frame containing all the data we need
graph <- as_tbl_graph(edges)  # Make graph object
graph <- graph %>% full_join(repro_fits) %N>%  # Join in reproductive landscape data
                   group_by(ones) %>%   # Set up data for positioning nodes in an intelligble way
                   arrange(as.numeric(name)) %>%
                   mutate(pos = row_number(), total = n()) %>%
                   ungroup()
```

```
## Joining, by = "name"
```

```r
graph <- graph %>% full_join(shock_fits, by = c("name", "ones"))  # Join in shock landscape data
graph <- graph %>%  # Join in population data frame
            full_join(pop %>%  # We can only have one row for each genome so we have to summarize
                        group_by(genome) %>%
                        arrange(gen) %>%
                        summarise(count=max(count), gen=first(gen)), by = c("name" = "genome")) %N>%
                        mutate(count=ifelse(is.na(count), -1, count),
                              gen=ifelse(is.na(gen), -1, gen)) %>%
                        mutate(count=ifelse(count > 1000, 1000, count))

# Set up edge data
graph <- graph %E>%
            mutate(
              fitness = if_else(.N()$fitness[to] > .N()$fitness[from],
                                .N()$fitness[to],
                                .N()$fitness[from]),
              shock_fitness = if_else(.N()$shock_fitness[to] > .N()$shock_fitness[from],
                                      .N()$shock_fitness[to],
                                      .N()$shock_fitness[from]),
              followed = if_else(is.na(.N()$count[to]) | is.na(.N()$count[from]),
                                 0,
                                if_else(.N()$count[to] > .N()$count[from],
                                        .N()$count[to],
                                        .N()$count[from]))
              )
```

Next, we visualize the data for the reproductive landscape:

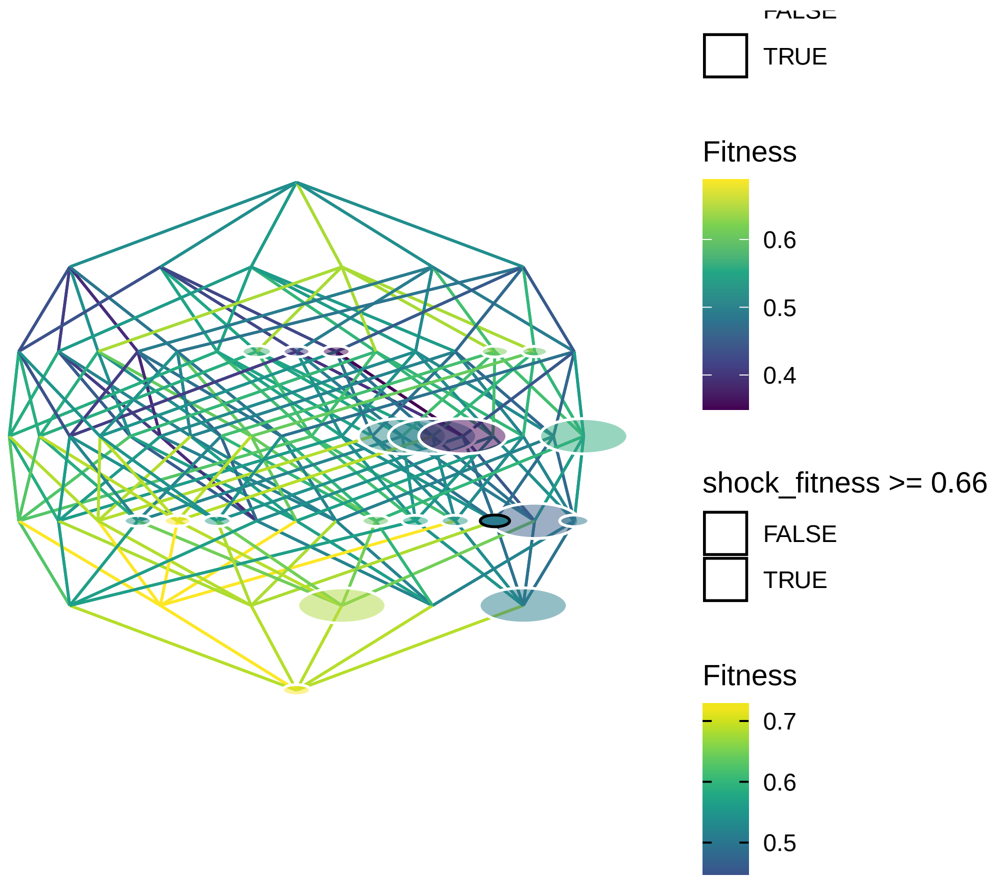
```r
ggraph(graph, layout = 'manual', x=max(ones)/2 * (pos)/(total+1), y=ones) +
  geom_edge_link(aes(color=fitness)) +
  geom_node_circle(aes(fill=fitness,
                       r = (.05*(count>0)) + sqrt(count)/200,
                             alpha=shock_fitness>=.66,
                             color=shock_fitness>=.66)) +
  theme(legend.position = "none") +
  theme_graph(base_family = 'Helvetica') +
  scale_fill_viridis_c("Fitness") +
  coord_fixed(ratio = .4) +
  scale_edge_color_viridis("Fitness") +
  scale_alpha_discrete(range = c(.5,1)) +
  scale_color_manual("Can survive highest shock", values=c("FALSE"="white", "TRUE"="black"))
```

```
## Warning: Using alpha for a discrete variable is not advised.

## Warning in sqrt(count): NaNs produced

## Warning in sqrt(count): NaNs produced

## Warning: Removed 43 rows containing non-finite values (stat_node_circle).
```



And the shock landscape:

```
ggraph(graph, layout = 'manual', x=max(ones)/2 * (pos)/(total+1), y=ones) +
  geom_edge_link(aes(color=shock_fitness)) +
  geom_node_circle(aes(fill=shock_fitness,
                       r = (.05*(count>0)) + sqrt(count)/200,
                       alpha=shock_fitness>=.66,
                       color=shock_fitness>=.66)) +
  theme(legend.position = "none") +
  theme_graph(base_family = 'Helvetica') +
```

```r
  scale_fill_viridis_c("Fitness") +
  coord_fixed(ratio = .4) +
  scale_edge_color_viridis("Fitness") +
  scale_alpha_discrete(range = c(.5,1)) +
  scale_color_manual("Can survive highest shock", values=c("FALSE"="white", "TRUE"="black"))
```

```
## Warning: Using alpha for a discrete variable is not advised.

## Warning in sqrt(count): NaNs produced

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## Warning: Removed 43 rows containing non-finite values (stat_node_circle).
```

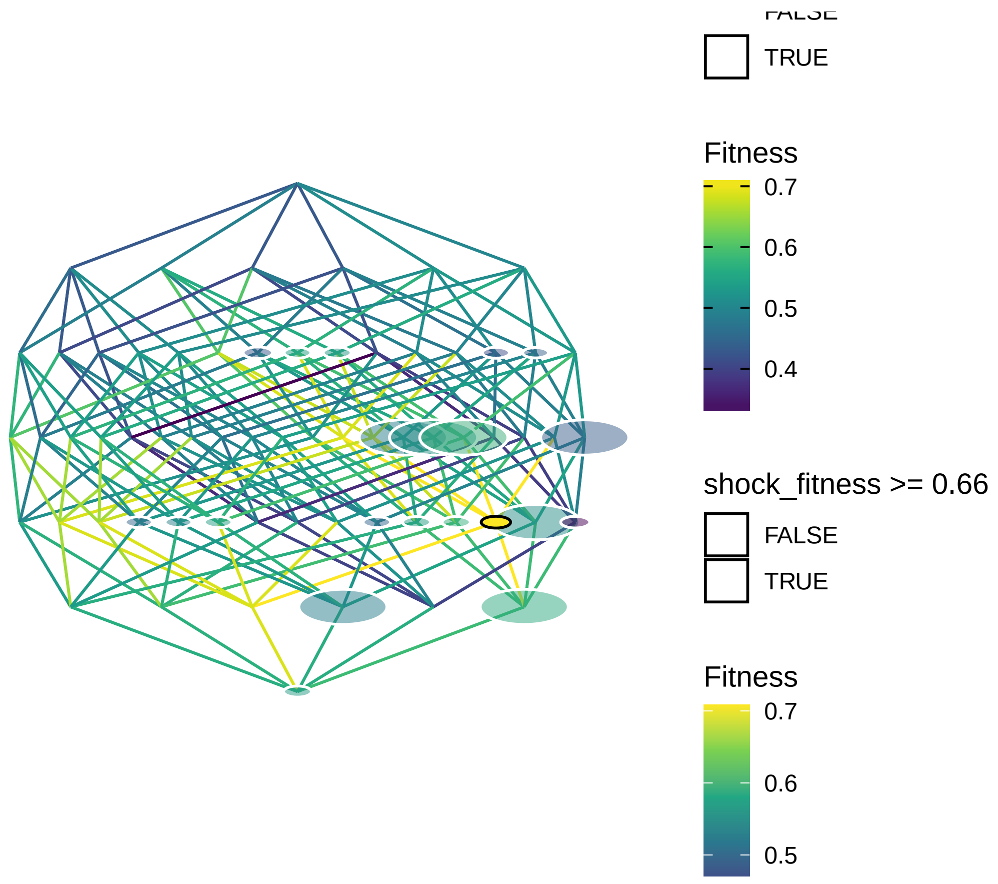

Note that in these graphs: node color indicates fitness in the reproductive and shock fitness landscapes respectively, edge color also indicates fitness in the landscape being visualized (specifically, the fitness of the fitter of the two genotypes being connected by the edge), and node size indicates final population size of that genotype. Node opacity indicates whether that genotype is capable of surviving the maximum shock in the shock landscape, as does node outline color.

From this data visualization, it appears that (in this run at least) the genotypes that are successful in each landscape are indeed very different. The population of genotypes that are fit in the reproductive landscape grows quickly but is wiped out at each shock event and most then be repopulated by mutations from the genotypes that can survive the shocks. This phenomenon explains the pattern of oscillations with increasing amplitude observed in the graphs of unique genotypes and population size.